INTEGRATIVE PHYSIOLOGY:
TEMPERATURE REGULATION[1]

I. TEMPERATURE AND METABOLISM

A. **GENERAL**: In this section we shall examine the effects of temperature on metabolism. We will start with a simple but very important question:

What are the effects of temperature on an animal (or plant)?

There are several answers to this question, some have to do with direct effects on rates of reaction, others with avoidance of physical damage to membranes and proteins, others with points that make optimal use of energy available for certain processes.

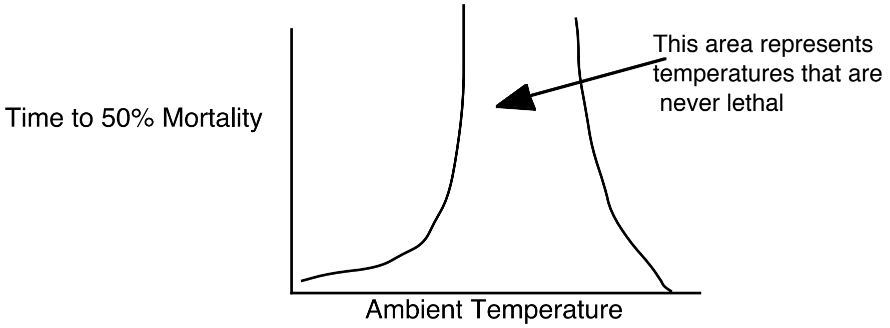
Three terms relating to the temperature range an organism tolerates should be learned:

1. **Stenothermic**: tolerates only a **narrow range** of temperatures: ex. many tropical and deep-sea organisms.
2. **Eurythermal**: tolerates a **wide range** of temperatures.

The two terms above may be applied to both daily swings in temperature and also to seasonal changes.

3. **Eccritic temperature**: the **preferred** temperature.

B. **LETHAL LIMITS**: these are temperatures that are incompatible with life. We generally talk about an upper and lower lethal limit. For those who are interested in such things, lethal limits are established by determining LD_{50}s (Lethal dose: 50%): points of exposure where 50% of a population dies. Obviously this implies both the temperature and duration of exposure to that temperature.



C. Why do different temperatures kill organisms? -- The effects of extreme temperatures

1. **Cold** -- the effects of freezing
   a. **physical damage** to structures caused by the formation of ice: the membrane bound structures are destroyed or damaged.
   b. **chemical damage** due to the effects of high solute concentrations. When freezing occurs, solute concentrations increase in non-frozen areas. These high concentrations may denature enzymes, etc.
2. **Heat**:

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a. **inadequate O_2 supply for metabolic demands** (especially in areas where O_2 is low, such as water and burrows)

b. rapid depletion of substrate stores

3. **Heat and Cold**

a. **reduced activity or denaturation of proteins** -- **the inactivation of certain proteins** with the result that <u>metabolic pathways are distorted</u>.

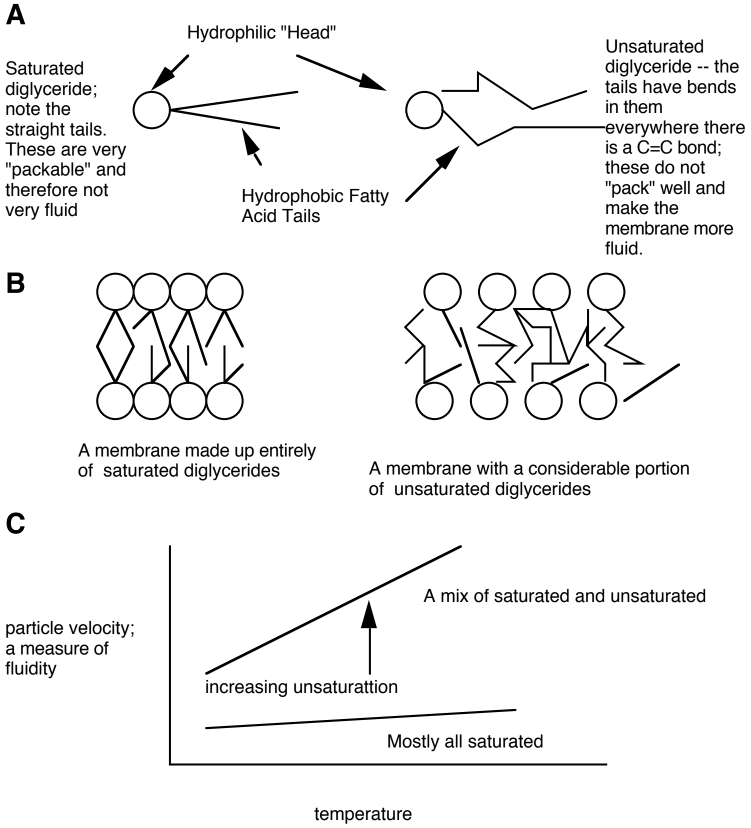
b. **disruption of enzyme pathways by differential temp effects on different enzymes** (like b, except what happens here is that temperature affects different reactions in different pathways differently.

c. **effects on membrane fluidity**:. These lead to problems with any membrane dependent function; <u>the nervous system is especially prone to disruption from fluidity changes</u>. the types of fatty acids in a membrane determine the motility of substances in the membrane and therefore their ability to interact with each other and allow substances that require protein mediated transport to pass through the membrane.

a. This effect is due to the inter-relationship between temperature (which causes a certain mean velocity for membrane molecules) and the structure of the fatty acids making up the lipid bi-layer.

b. At a given temperature, the more **saturated** fatty acids that are present, the less fluid the membrane will be. This is because saturated fatty acids are relatively straight chains and can easily be packed into a membrane, producing a stable and not very fluid result. (Think of fats such as butter that are primarily saturated).

c. By contrast, **unsaturated** fatty acids have bends at the location of every double bond; as a result, they cannot pack as effectively into a membrane and the membrane tends to be more fluid. (Think of oils, which are very unsaturated):



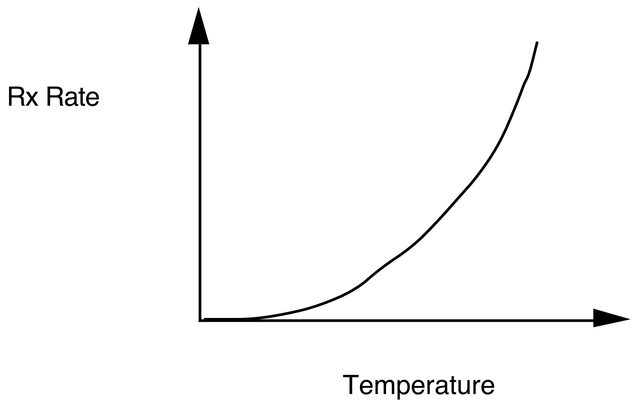
? Describe a way whereby membrane fluidity could be kept constant when temperature changes; i.e., describe a homeostatic mechanism to maintain constant membrane fluidity.

THIS NEXT SECTION (D) SHOULD BE REVIEW FROM OTHER CLASSES

D. GENERAL EFFECTS OF TEMPERATURE ON CHEMICAL AND PHYSICAL PROCESSES

1. **CHEMICAL REACTION MEDIATED PROCESSES**: all chemical reactions leading to such macro phenomena as: muscle contractions, nerve transmission (both of these relate to sensation and movement), digestion, growth, etc.

a. **UNCATALYZED REACTIONS** (rate vs. T_a). We know that many chemical reactions commonly double their rate with a 10^oC increase in temperature (next page):



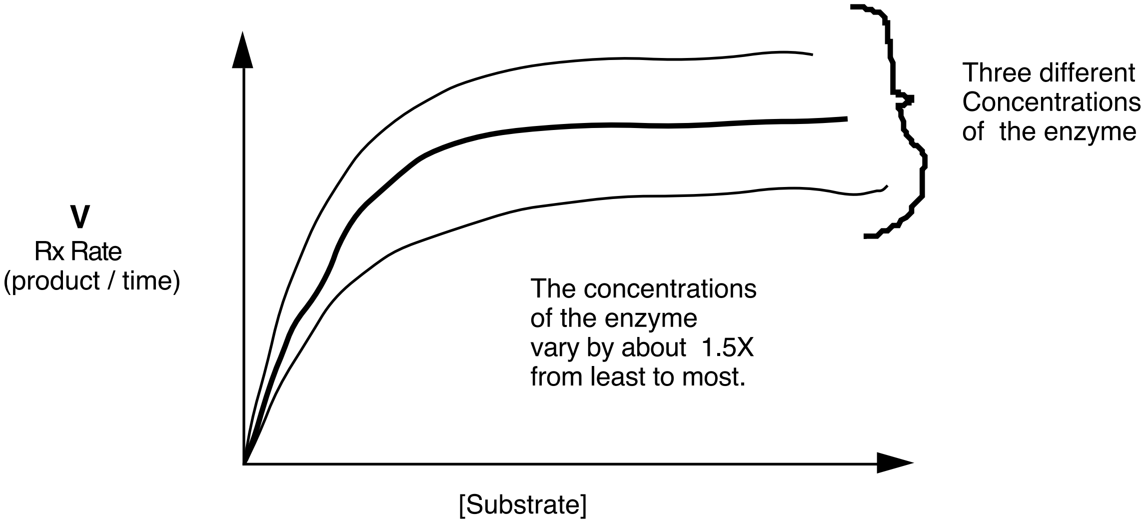
In chemistry, the effect of temperature on reaction rate is usually described using the Arrhenius relationship -- it calculates **reaction rate constants based on temperature and activation energy**.

b. However, the Arrhenius function is not a very meaningful way to examine reactions that occur in an organism since nearly all are **CATALYZED REACTIONS**:
Here is a quick review of the kinetics of catalyzed reactions followed by a graphical interpretation.

$$A \overset{\text{enzyme}}{\longleftrightarrow} B$$

Given a reaction: A <--------------> B (enzyme)

We know that nearly every reaction in an organism is catalyzed by an enzyme, and therefore, to a large extent, understanding metabolic processes is really understanding how enzymes work. If for our reaction **we keep the concentration of e constant** and vary the concentration of its **substrate A**, we can measure the **rate of reaction (V)** as a function of the [A]. Here are **the results of three such experiments**; for each case the enzyme is set at a concentration and then the substrate concentration is altered.:

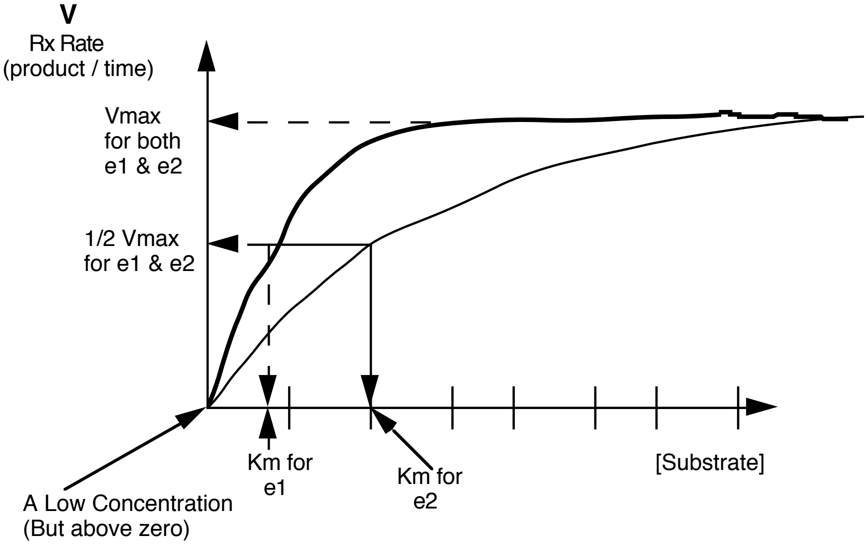


Notice that the reaction rate is a function of the enzyme concentration (the more, the higher the rate) and the concentration of the substrate. The maximum reaction rate ($V_{\max}$) corresponds to a condition when the enzymes are **saturated** (they gain new substrate as fast as they release products). Notice that:

1. $V_{\text{Max}} \propto$ [enzyme]

The next graph reviews the concept of affinity. Recall that with enzymes affinity is a measure of how likely it is that a substrate molecule will bind to the enzyme long enough for a reaction to occur. Affinity is measured by the **Michaelis Constant**, **K_m,. The larger the value of K_m (i.e., the greater the [A] at $1/2V_{\max}$), the lower the affinity of e for A**.

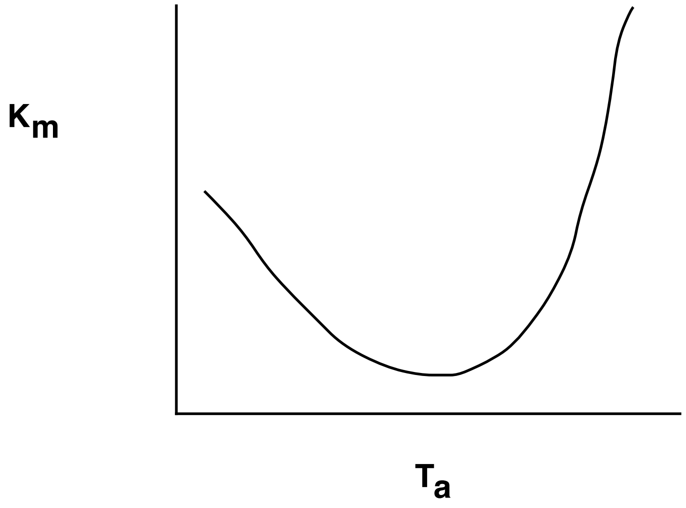
Below are illustrated two **allozymes** (different forms of the same enzyme) of e: e1 and e2. Remember that they both catalyze the same reaction but note how these have two different K_ms:



? What does the graph above mean functionally?
For one enzyme type, say e1; what is the effect of different [e1] on V_{max}? On 1/2 V_{max}? On K_m? Explain your reasoning.
On the molecular level, what causes the differences in K_m in different allo- and isozymes?
Besides [substrate], list two other things that a cell has control over in which it can use to control reaction (and eventually metabolic) rate (hint -- the answer is what you've just been working on.
At saturating concentrations of substrate, is affinity an important determinant of reaction rate?

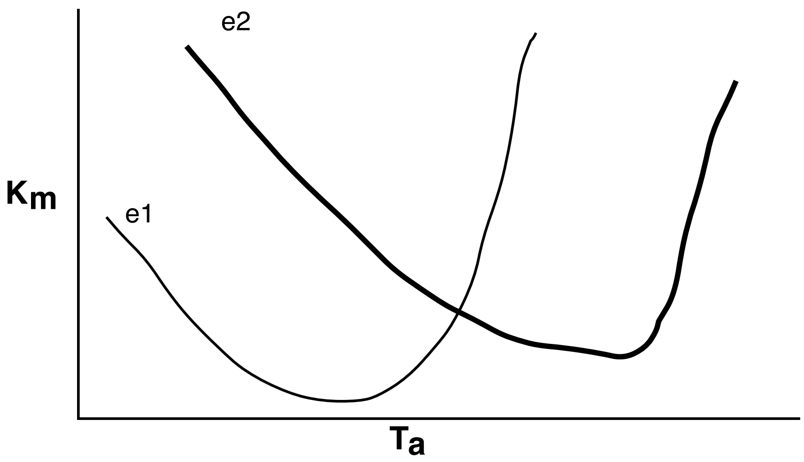
PROBABLY NEW MATERIAL, BUT HOPEFULLY NOT VERY DIFFICULT:

Temperature affects the value of K_m for an enzyme. Suppose that we determined the curves for rate for substrate concentrations for an enzyme at several different temperatures. We would have a series of curves as shown above except in this case they would correspond to different temperatures instead of different allozymes. Now suppose that we **plotted the K_m we find for each temperature as a function of the temperature at which the K_m was determined**. The result would look like this:



? What is the best temperature (show on the graph) for this enzyme in terms of maximizing reaction rate at non-saturating conditions?
How does temperature cause differences in K_m?
In the plot below: at a common temperature why are the K_m values of the two enzymes different? What does this imply about their primary structures? Tertiary structures?

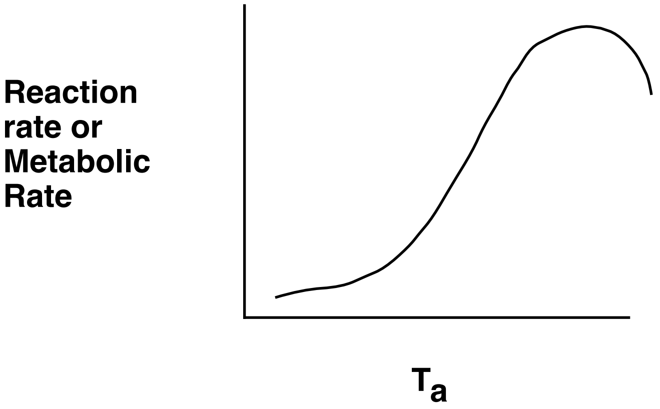
We could now do the same experiment as above in cases where the enzyme occurred as two allozymes:



? What does this graph imply? What might this organism do in response to different temperatures?

PROBABLY NEW MATERIAL, BUT HOPEFULLY NOT VERY DIFFICULT:

3. **Temperature and Reaction Rate -- Temperature and Metabolism:** The consequence of the effects of temperature on enzyme conformation and on the rate of favorable collisions between the enzyme and its substrate is the following curve:



4. The same general type of a curve can be drawn for single reactions, pathway rates, or the metabolism of a whole organism ($\dot{Q}$) whenever the single reaction, pathway or organism is heated or cooled.

(a) recall from the two earlier plots that the number of favorable collisions per second increases with temperature but that the conformation of the enzyme is such that it is best able to bind the substrate and catalyze the reaction at an intermediate temperature.

(b) thus, the early exponential increase in rate is due to the fact that an increase in temperature both causes more sterically favorable collisions and also puts the enzyme in a better conformation.

(c) at higher temperatures the number of favorable collisions continues to increase but the conformation gets worse and eventually the enzyme can be thought of as being severely damaged, perhaps even denatured.

5. **Is there a way to describe the relationship between temperature and reaction rate (or metabolic rate) mathematically**? As mentioned above, the rigorous mathematical treatment given by the Arrhenius function (you probably only learned this if you have taken physical chemistry) is not appropriate for enzyme-catalyzed reactions. It does not take into account the complexities of the behaviors of enzyme with respect to temperature that we have just briefly explored.

1. Making precise models of metabolism is very difficult. So, instead we'll drop back and punt and develop a simple descriptive mathematics for the catalyzed reactions. This description will be only roughly correct but it will be useful. We call this description **Q_{10}**. It is **defined as the factor by which a single reaction or organisms' entire metabolism will change over a 10^{o} C range**. Thus,

2. $$Q_{10} = \frac{R_2}{R_1}$$ --- for a 10^{o}C (or k) difference in temperature

where **R_1 and R_2** refer to the reaction rates at two different temperatures.
For any temperature range, the equation becomes:

3. $$Q_{10} = \{\frac{R_2}{R_1}\}^{(\frac{10}{T_2 - T_1})}$$

where T_2 and T_1 refer to the temperatures at which reaction rates R_2 and R_1 were observed.
A restated version of eq. #3 is:

4. $$R_2 = R_1 * Q_{10}^{(\frac{T_2 - T_1}{10})}$$

What do different values of Q_{10} mean?:

(i) When $Q_{10} = 1.0$ it means that the reaction rate is independent of temperature (often called a **flat Q_{10}**);

(ii) if $Q_{10} < 1$ the rate drops with an increase in T;

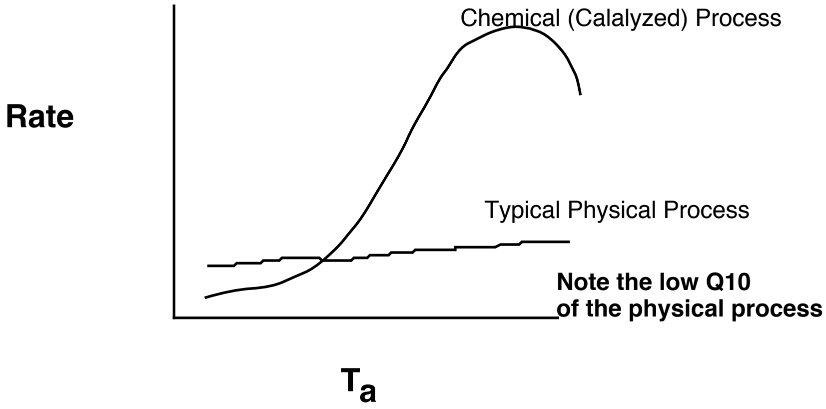
(iii) if $Q_{10} > 1$ then the rx rate increases with temperature.

? On the preceding graph, identify regions of the curve that correspond to each of the three conditions just outlined.

Notice, however, that Q_{10} is not an accurate predictor of rx rate over the entire range of temperatures. *It is merely a description of a portion of the range*. The only theoretical value it has is that much of the curve is an exponential increase. The mathematics of Q_{10} are simply those of an exponential increase. To summarize, the only reason that Q_{10} is preferable to the Arrhenius description is that it makes no pretense to actually explaining what is going on -- it merely describes a complicated process. However, we will find it a useful one over the next few weeks so be sure that you understand it.

d. Q_{10} can be applied as a description of many biological phenomena, especially if they are based on rx rates.

2. **PHYSICAL PROCESSES**: these often dependent on temperature to a lesser degree than chemical processes.



a. For example, the properties of certain elastic proteins, such as the material a flea uses to store the energy for its jump (resilin) show remarkably flat Q_{10}s. However, it is equally important to realize that other materials may undergo sudden phase transitions at certain temperatures and thus discontinuities occur in the curve.

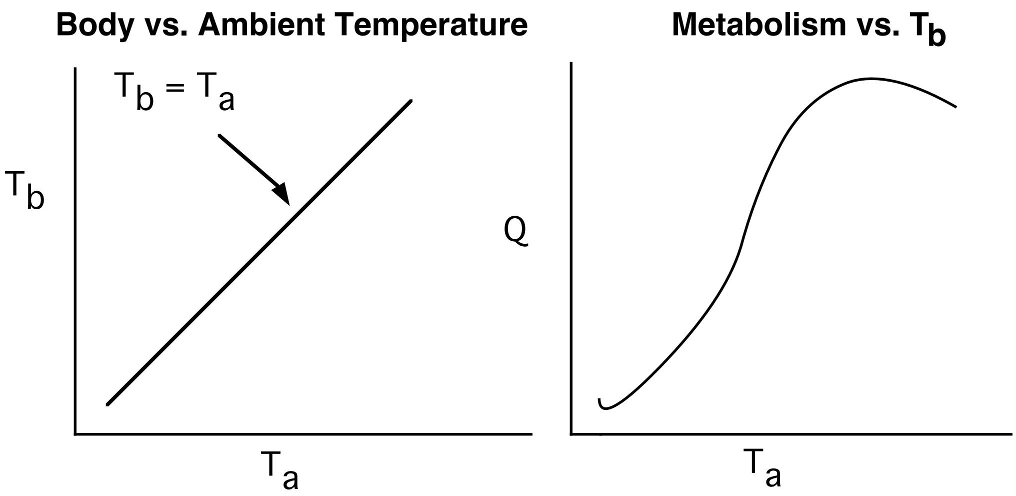
b. Diffusive processes where absolute temperature is the relevant temperature (such as gas and ion diffusion) also have relatively flat Q_{10}s since they depend of absolute, not Celsius temperature.

? What would be the effect of a decrease in temperature on the number of jumps a flea could make per minute? The height per jump? Hint: fleas jump by using their muscles to compress a block of resilin; they jump by releasing the mechanism that keeps the resilin compressed -- much of the energy stored in the resilin is transferred to the legs to produce the jump

THIS NEXT SECTION (II) SHOULD BE MOSTLY A REVIEW FROM BIOLOGY 162

II. POIKILOTHERMY -- TEMPERATURE CONFORMITY

Many animals are totally incapable of temperature regulation. Their only significant source of heat is the environment and their body temperature is directly determined by the ambient temperature. We call these temperature-conforming animals **poikilotherms**. If we choose to look at a single process or at a whole organism, we know that METABOLISM TENDS TO INCREASE WITH BODY TEMPERATURE. (For the next few lectures, we will deal with whole organisms for the most part.). Thus;



Poikilothermy is the condition of many organisms and all isolated tissues or cells. For instance, we will see that although many animals can regulate their overall body temperature, their individual organs and tissues do not have this property and act poikilothermically. Heart surgeons take advantage of this by perfusing the heart (and sometimes other tissues also) with cool blood. This lowers the metabolism of the organ(s). Likewise, we will see that under the proper conditions any organism can be turned into a conformer -- when its ability to regulate is exceeded.

III. TEMPERATURE REGULATION

A. In the sections above we have examined the effects of temperature on metabolism (page 1 of this class, last few pages of previous classes) and we have seen how animals that are forced to endure cold body temperatures do so without suffering extensive damage. We will now consider how animals actually regulate their body temperatures (thereby avoiding the high and low T_bs discussed above).

B. **A TAXONOMY OF TEMPERATURE REGULATION**

1. we just described **POIKILOTHERMY** (many temperatures); these are organisms whose T_b can fluctuate considerably. Tb is controlled by agents in the environment. DO NOT USE "COLD BLOODED" as a synonym for a poikilotherm. Many of these animals maintain body temperatures that are like those of mammals and birds. The key to understanding this term is to realize that Tb fluctuates and that the heat source is external to the animal.

2. **ECTOTHERMY**: a term preferred to poikilotherm; it signifies simply that the main determinant of the organisms' Tb is environmental. Here are two of the SUBHEADINGS of ectothermy, they are (obviously) divided as to the identity of the major source of heat,

a. **HELIOTHERM**: the sun is the direct source of heat. So these are ectotherms that use the sun as their most significant direct heat source.

b. **THIGMIOTHERM**: warm substratum or medium (and not the sun directly) is the main heat source.

3. **HOMEOTHERMY**: this simply refers to a constant body temperature, presumably maintained by some sort of regulatory mechanism. However, many also apply this term to animals that live in very constant thermal environments that therefore have very little in the way of changes in body temperature.

4. **ENDOTHERMY**: the primary source of heat is internal chemical reactions.

5. **HETEROTHERMY**: An animal that acts like an endothermic homeotherm part of the time and like a poikilothermic ectotherm the rest of the time.

C. Important questions about temperature regulation:

1. **Why regulate T_b?**

2. **What are the costs associated with regulation?**

Answers(?)

3. Within limits, the speed and power of most animal's movements (thus, their ability to move about and find food, mates, and avoid predators) are determined largely by Tb.

4. The costs involved in temperature regulation fall primarily under two categories: **TIME and ENERGY**

a. **Time is most important for ectotherms**, to regulate temperature they must go in and out of the sun or hide when cold.

b. **Energy is the big cost for endotherms** since the costs associated with a high rate of metabolism are so large. It also involves a large time cost for many species due to the time they must spend looking for and eating large amounts of food. Both of these factors may result in great limitations on how small an animal can be and still be an endotherm.
They also relate to the particular ecological niche that is possible for an animal.

Why?

Notice that time and energy are not really independent of each other. Animals that need to eat to eat a lot to support endothermy also spend a lot of time eating and therefore they indirectly spend lots of time on temperature regulation.

THIS SECTION (IV) IS MORE DETAILED THAN YOU NEED BUT IS GIVE FOR REFERENCE. THE IMPORTANT THING IS TO UNDERSTAND EQ. 5 AND KNOW THE GENERAL AVENUES OF HEAT GAIN AND LOSS

IV. Understanding Temperature Regulation: How does an organism gain or loose heat?

A. Avenues of heat gain and loss include internal heat production (**METABOLISM; for heat gain only**) and
external avenues of heat gain and loss including **CONDUCTION, CONVECTION, and RADIATIVE EXCHANGE**, and what is usually an avenue of heat loss, **EVAPORATION**.

B. Heat balance (total heat) for an organism is thus the algebraic sum of all of these processes:

5. $$\dot{Q}_{tot} = \dot{Q}_{met} + \dot{Q}_{cond} + \dot{Q}_{conv} + \dot{Q}_{rad} + \dot{Q}_{evap}$$

where a positive sign in all of these represents heat gain

? Which of the terms above would tend to have negative values? Positive? Which would tend to be relatively large in ectotherms? In endotherms?

C. What are the specific equations for each of these processes?

1. **Metabolism** can be dealt with by knowing $\dot{V}_{O2}$ and assuming or knowing RQ; alternatively by some other measure.

2. **Conduction** is nothing more that the diffusion of random thermal motion.

6. $$\dot{Q}_{cond} = k\,A\,\frac{(T_2 - T_1)}{L}$$

Where **k** is the THERMAL CONDUCTIVITY, **A** is the area through which the conduction is occurring, and $\mathbf{\frac{(T_2 - T_1)}{L}}$ is the temperature gradient over distance **L**. Thermal conductivities are material-specific; for biological materials they tend to be close to that of water since tissues are largely water.

NOTICE THAT EQ. 6 IS NOTHING BUT A DIFFUSION EQUATION – THE MAIN DIFFERENCE IS THAT THE CONSTANT DESCRIBES HEAT CONDUCTANCE (DIFFUSION) AND DEPENDS ON MATERIALS

Some examples of values of k:

water:	**0.0014**	$\mathbf{\frac{cal}{(sec.* cm * ^oC)}}$
air :	**0.000057**	**""**
non-bone tissue:	**0.0011**	**""**

3. **Convection or BULK FLOW**: The mathematics of convection is rather complex and specific to each situation. As such the relevant factors include:

7. $$\dot{Q}_{conv.} \propto \text{(INCURRENT – EXCURRENT HEAT CONTENT)/VOL * FLOW RATE (VOL/t)}$$

EQUATION 7 SHOULD ALSO BE FAMILIAR – IT IS JUST LIKE THE CONVECTION EQUATIONS WE SAW EARLIER FOR GAS TRANSPORT, ETC. (INCURRENT AND EXCURRENT ARE ANALOGOUS TO A-V DIFFERENCE)

One important thing to remember about convection of heat is that ultimately, the actual transfer of heat is linked to conduction (or radiation – see below) – these processes are what cause the incurrent-excurrent differences.

RADIATION IS PROBABLY THE ONE YOU ARE LEAST FAMILIAR WITH – WE WILL TALK ABOUT IT BRIEFLY BUT SINCE WE ARE CENTERING THE CLASS ON MAMMALS, IT IS NOT NORMALLY THE MAIN HEAT GAIN OR LOSS AVENUE. DON'T GET TOO HUNG UP ON IT , THERE WILL BE NO CALCULATIONS BASED ON IT, ETC.

4. **Radiation**: This term can be extremely important for certain types of animals including insects, lizards and college students and professors from northern liberal arts schools at spring break. Radiation is described by **Stefan-Boltzmann's law:**

8. $\dot{Q}_{rad} = s * e_1 * e_2 * A * (T_2^4 - T_1^4)$

Note that like convection, radiation is independent of distance. The terms here require some explanation: A is the surface across which radiative exchange is occurring; the **T**s' are in kelvins; **s** is the **Stefan-Boltzmann constant,** and $\mathbf{e_1}$ and $\mathbf{e_2}$ are the **EMISSIVITIES** of the two objects exchanging heat by radiation.

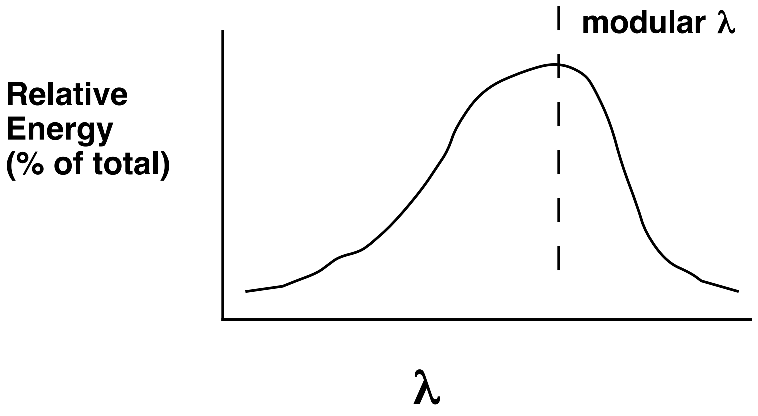
i. $\dot{Q}_{rad}$ is directly proportional to the **4th power of absolute T and that as the difference between the two Ts increases, the heat transferred rapidly increases**.

ii . **Radiation by Black Bodies** -- objects that are hotter than 0^o K emit energy at a wavelengths that are proportional to their absolute T. For an **IDEAL BLACK BODY**, that is, one that emits energy equally well at any wavelength, the wavelength where most energy is radiated is referred to as the **MODULAR WAVELENGTH** and is given by **Wein's Law**:

9. λ = Modular Wavelength (in nm) = 2,990,000 / T

where T is in kelvins. It is worthwhile to realize that radiation occurs at other wavelengths that are above and below the modular wavelength:

(please go to the next page)



Realize that most objects are not ideal black bodies and that they will emit (and absorb) radiation at certain wavelengths better than others (see below).

? Calculate the modular wavelength of your personal radiations. For that of the sidewalk when ice has just started to melt. For the sun (surface temperature = 8000 ^{O}C).

ANS.: 9465 nm; 10,952 nm; 361 nm

Both people and the earth emit in the infrared and the sun is at the boarder between the violet and ultraviolet (Why isn't the sun deep violet?)

iii. **ABSORPTIVITY**. No, this doesn't have to do with "Pampers". Absorptivity refers to the **proportion of the light at some given wavelength that is absorbed by an object**. It is very **frequency dependent**.

a. All radiation is either reflected or absorbed. The behavior of an object with respect to absorbing light at a certain wavelength can be given a number between 1 (all absorbed) and 0 (all reflected).

b. This is important because it determines the amount of energy that an organism can absorb from a radiant source at a given wavelength.

c. Any body that emits energy will also **EMIT** radiation well at the same frequencies. Thus, we can define a similar term called **EMISSIVITY**[2] that defines how well a body will emit radiation at a given wavelength. It, like absorptivity is a fudge factor that runs between 0 (no emission) and 1.0 (perfect emitter). In fact, for our purposes the terms are the same. To discuss radiative heat exchange it is therefore necessary to know the emissivities of both the radiator and target since e determines how well heat is transferred and absorbed.

iv. Dealing with absorption and emissivity in biological systems undergoing radiative heat exchange.

a. We will assume that we are interested in how an animal can heat or cool using radiation. The hottest environmental object is the sun and the coldest will either be some earth-bound ice or a cold section of the sky (away from the sun).

b. Heating: This occurs as described by the Boltzmann relationship above. The organism never manages to come into equilibrium with the heating object (such as the sun!). The rate of heat gain is largely determined by the wavelengths of the incident radiation and the emissivity of the organism. While all organisms are black in the i.r. region, little exchange occurs there because very little of the i.r. radiation from the sun is able to get through the atmosphere. However, much visible light does enter the atmosphere and this energy can be absorbed by the animal. And, color and shade are good guides to the ability to absorb energy from visible light.

c. **Cooling: all organisms on earth are radiating black bodies**. All that heating or cooling an organism over a biologically important range does is change the modular wavelength of radiation slightly. Skin, hair and feathers of all colors all absorb strongly and therefore emit **strongly between 5,000 and 10,000 nm** -- all organisms are essentially black

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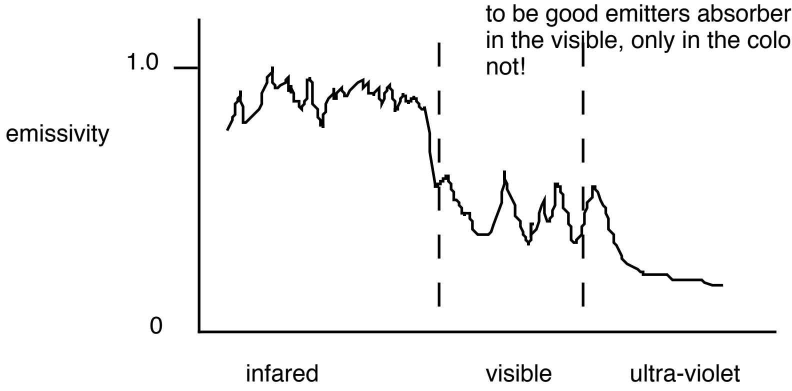
[2] For a more detailed and excellent discussion of emissivity and radiation in general, please go to Schmidt-Nielsen's *Animal Physiology* text.

bodies with an e of 1.0 in this range. Thus, **the color of an organism in the visible range has nothing to do with it is ability to loose heat by radiation**.



An example of the wavelength dependence of emissivity. Animals tend to be good emitters absorbers in the IR; in the visible, only in the colors they are not!

EVAPORATION IS IMPORTANT – AND EASY TO UNDERSTAND.

5. **EVAPORATION:** usually an avenue of heat loss: ex; panting, gular flutter (the way birds pant), sweating, and more common types of evaporation from the skin.

10. $$\dot{Q}_{evap} = L * E$$

where **L** is the latent heat of evaporation (its value is partially temperature-dependent) and **E** refers to the amount of water evaporated.

THE NEXT SECTION – ALL IN BLUE, WILL NOT BE COVERED AND YOU ARE NOT RESPONSBILE FOR IT – IT IS INCLUDED FOR INTERSEST AND ALSO BECAUSE YOU MAY FIND THAT IT HELPS YOU UNDERSTAND SOME OF THE THINGS EUTHERMIC ANIMALS LIKE OURSELVES DO!

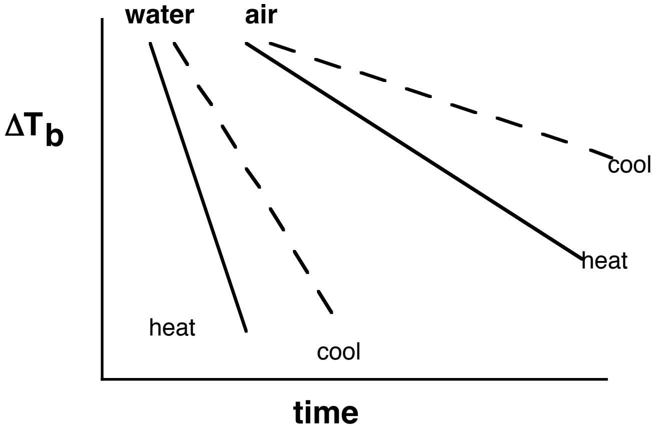
D. How is THERMAL INDEPENDENCE ACHIEVED?

1. Temperature regulation is not something that all animals are capable of doing; the ability and need to temperature regulate is determined by such factors as:

a. the **ENVIRONMENT** that the animal lives in:

1. **WATER VS AIR**: thermal conductivity of water is 25X that of air. All else being equal, heat is transferred 25 times faster in water than air and therefore **organisms in water will reach thermal equilibrium much more rapidly**. Thus, it is more difficult to be independent of Ta in the water.

Heating and Cooling in Marine Iguanas both in and out of the water



This figure shows that the rate of heat loss in a diving lizard, the marine iguana of the Galapagos Islands is much greater when it is in the water than in the air. Notice that in both air and water, the animal will heat more rapidly than it cools. What does this argue about its heating and cooling? Are these passive processes or does the animal have some control over them? (Incidentally, this is a rather interesting curve called a cooling curve -- we will further investigate these and what they mean in lab)

2. AVAILABILITY OF LIGHT OR A SOURCE OF HEAT.
3. AVAILABILITY OF FOOD sufficient for internal generation of heat.

b. the DESIGN of the organism itself

1. its SIZE and specific heat

a. **SPECIFIC HEAT** = # of calories required to raise the temperature of one gram of a material one degree C:

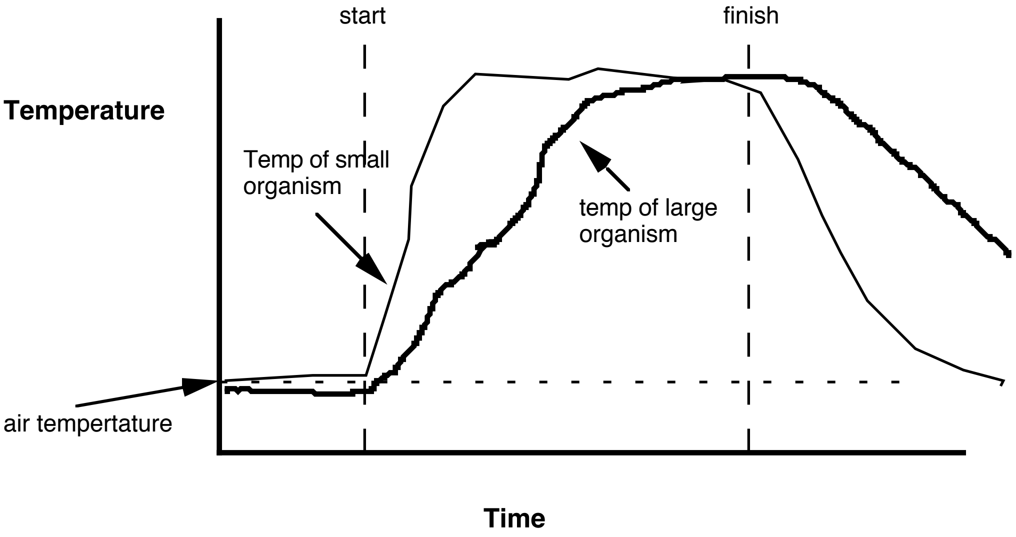
WATER, the specific heat is about 1.0 $\frac{\mathbf{cal}}{\mathbf{g\ ^{o}C}}$ **at 15C**

TISSUE, """" "" "" 0.8 "
AIR 0.24

What is important about specific heat is the difference between the specific heats of the organism and its environment. If they are near the same (such as if the organism is in water), heat transfer will readily occur. If they are different, transfer is much more difficult. Thus, they are related to the thermal conductivity terms treated earlier.

b. **MASS** is important since it and specific heat determine the amount of heat that can be stored in an animal. Thus to heat a 10 kg animal 1 C requires 0.8 X 10,000 = 8 kcal. Likewise, it means that this organism must loose 8 kcal to drop 1C. So, mass is also a measure of **THERMAL INERTIA** -- the ability of a body to resist changes in temperature since so heat must be transferred before the T will change significantly:

A large and small organism are exposed to a heat source
(for example, the sun) for some period of time. The large body
will remain warm in the absense of the heat sorce for a relatively long period of time.



2. MOBILITY; GENERAL ACTIVITY LEVEL. Obviously, the more active an organism is, the more metabolic heat that it will produce. On the other hand, its conductive and convective heat losses will also be greater. WHY?

E. DO ECTOTHERMS REGULATE THEIR BODY TEMPERATURES AND IF SO, HOW DO THEY DO IT?

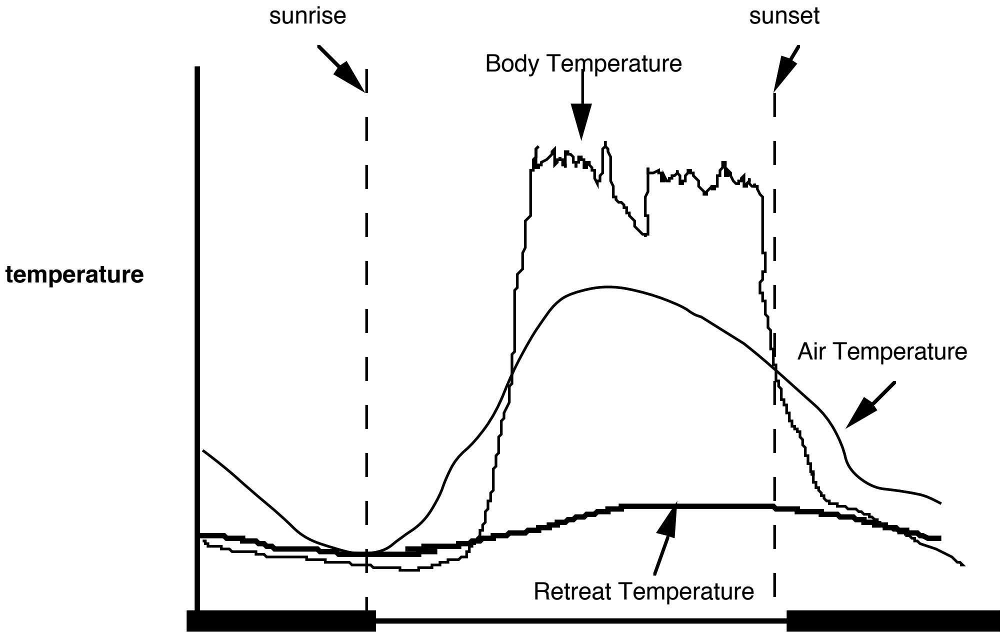
1. The earliest data suggesting that poikilotherms might regulate their T_b came from observations that animals in the sun had higher T_bs than their environment (they were said to have a large **ΔT**). So much for "cold blooded"

2. Is a difference between T_b and T_{air} enough to posit Temp regulation?

a. Of course not. In a classic study done in the 60's that has come to be known as "Thermoregulation in beer cans" James Heath was able to show (not surprisingly) that beer cans full of water in the hot sun were hotter than the air (i.e., $T_{b(eer)} > T_{(air)}$. However, he then pointed out that regulation implies more than passively heating to a temperature greater than that of the environment.

b. True behavioral and physiological temp. regulation in ectotherms:

HELIOTHERMY:



Time of the Day
(Dark underline indicates night)

? What differences would you expect between this lizard and some of its larger cousins that may weigh 100X more?

In large heliotherms, Tb changes very little. The animal can go in and out of the sun. However, it takes a while to heat up and so they are slow starters in the morning. Small heliotherms heat quickly and they also cool quickly, therefore they can afford to spend less time in the shade if they wish a large ΔT.

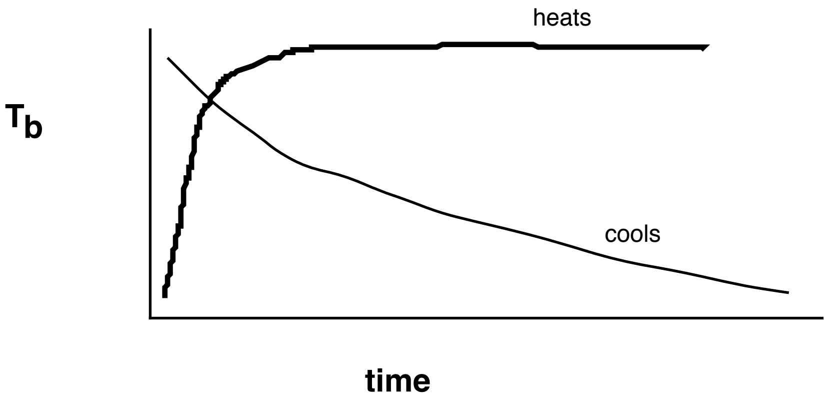
1. Behavioral mechanisms in HELIOTHERMY
   a. Movement in and out of the sun.

b. Posture changes:

1. orientation control: change direction towards the sun (i.e., vary your SHADOW SIZE)
2. body shape: variation in the animal's surface area (flatten out in order to heat)

? To which heat exchange equations does this apply?

2. Physiological mechanisms. Here is a curve for the heating and cooling rates of our *Anolis*. The animal has been tethered in one environment where it will tend to heat (in the sun) and in another where it tends to cool (in the shade). You will notice that it is able to heat much faster than it cools -- an inanimate object (or for that matter an animate object that cannot in any way regulate temperature will heat and cool at about the same rate given constant environmental conditions. Incidentally, this is the sort of data that was used to obtain the marine iguana curves given on page 9 of these notes. We will investigate heating and cooling curves further in lab.



One more point: even if we restrict the animal's movement and postures, we still see a difference between heating and cooling rates.

a. **Chromatophores**: by varying color, emissivity varies and heat transfer (gain) by radiation varies.

b. **Circulation** -- In a heating animal, blood is circulated to the part of the skin that is exposed to the sun and this warm blood is then moved to the organs and tissues that need to be heated. When the animal is cooling but it doesn't want to cool, circulation to the skin is reduced greatly.

The thing to realize is that the animal has very fine control over the path of blood flow and what is being heated and cooled (nervous system, organs of digestion (turtle), muscles or entire core). Do these same mechanisms apply to cooling?

? What are the relationships between thermal independence, size, and time?

THE REMAINING MATERIALS WILL BE THE CENTER OF THE CLASS:

V. Endothermic Temperature Regulation

A. Animals that more or less constantly regulate their body temperatures endothermically are often referred to as being **EUTHERMIC**.

1. Eutherms include most all mammals and birds during most of their lives (and for many species, all of their lives).

2. By contrast, another group of endotherms includes animals that only regulate their Tb endothermically for a small portion of the time. These are referred to as **HETEROTHERMS** or **INTERMITTENT ENDOTHERMS**. Many mammals and birds fall into these groups for at least part of their lives. In addition, there are many species of insects and some fish and reptiles that also are intermittent endotherms.

3. Thus, we should view types of endothermic temperature regulation as being on a **continuum** from eutherm to intermittent endotherm with many types of animals fitting into more than one category at different times. We will see each of the different patterns as adaptive to the animal that possesses them and not simply being the condition of trying to become a eutherm, but not quite making it.

4. **However**, before we go any further we need to be aware of the fact that <u>even in eutherms **not all parts of the body are regulated at the same temperature**</u>. Some definitions:

a. The <u>**core**</u>: the portions of the body, usually deep in the animal and most containing important organs whose function is most dependent (highest Q_{10}) on a constant high body temperature. In most vertebrates the core includes the brain and perhaps the heart and digestive system or the entire viscera.

b. The remainder of the animal is termed the <u>**periphery**</u> and is regulated to various degrees. For instance, the temperature of the skin and to a lesser degree much of the limbs is less regulated than the core. These areas may get relatively warm or even approach freezing with long-term harm or without totally knocking out function.

c. In our discussion about euthermy we will largely dwell on the condition of the core, but we will also make reference to the periphery, both in terms of regional temperature regulation and also in regards to its role in core regulation.

B. **General model for euthermy**

1. In attempting to mathematically model endothermy, the simplest considerations are:

a. we assume a constant body temperature; therefore the following situation must be true:

1. Heat gain = Heat loss

b. Since in endothermy, we assume that heat gain is entirely the result of metabolism, then we can restate eq. 1 as:

2. Metabolism = Heat Loss

2. Thus, all we need is an equation that will explain heat loss. Such an equation exists and is called **Newton's Law of Cooling**:

3. $\dfrac{\Delta H}{\Delta t} = M * C * (T_2 - T_1)$

where $\dfrac{\Delta H}{\Delta t}$ is the heat flux from the cooling body in watts, **$(T_2 - T_1)$** is the difference in temperature between the cooling body and the environment usually in ^{o}C, ***M*** is the mass of the animal, and ***C*** is the ***coefficient of thermal conductivity*** in $\dfrac{\text{watts}}{\text{mass} * {}^{o}\text{C}}$. The value of *C* is specific for a certain set of circumstances in terms of environment and cooling object.

a. This model is generally valid for any animal that is acting as a true endothermic homeotherm at any moment.

b. **THE DERIVATION OF THIS LAW IS FROM THE EQUATI0NS FOR CONDUCTION, CONVECTION AND RADIATION AND IS GIVEN AS AN APPENDIX TO THIS CLASS'S NOTES**. Learn the derivation in general terms, but **do not memorize** it. NOTE THAT UNLIKE THE CONSIDERATIONS FOR HELIOTHERMY, FOR ENDOTHERMY, WE ARE MOST CONCERNED WITH CONVECTION, CONDUCTANCE, AND RADIATION AWAY FROM THE ANIMAL.

? Can the cooling equation (#3) be applied to organisms that are not eutherms? If so, which ones?

4. We need to make one final modification to Newton's Law to make it useful in considering organisms. **We need to add a term for evaporative water loss.** This can obviously be very important in many types of animals:

4. $\dfrac{\Delta H}{\Delta t} = M * C * (T_2 - T_1) + L * E$

where ***L*** is the *latent heat of evaporation for water* and ***E*** is the *mass of water that evaporates per unit time* (i.e., ***E*** is a RATE).

a. Latent heat of evaporation is dependent on temperature, therefore to be strictly accurate you must know the actual temperature at which the animal is operating to use a given latent heat.

b. **FOR OUR PURPOSES, SIMPLY BE AWARE OF THE FACT THAT LATENT HEAT IS TEMPERATURE-DEPENDENT NEVERTHELESS, ASSUME A CONSTANT VALUE OF:**

$$\mathbf{2443\ \frac{J}{g}\ \text{at}\ 20\ {}^{o}C\ (584\ \frac{cal}{g})}$$

5. Now, we will substitute this expression for heat loss into equation #1 (first page), substitute rate of metabolism ($\dot{Q}$) for the rate of heat production, and change the notation for temperatures into something more biologically relevant:

5. $\dot{Q} = C * (T_b - T_a) + L * E$

where $\dot{Q}$ is the rate of metabolism, ***C*** is the coefficient of thermal conductance, ***T_b*** is the body temp. and ***T_a*** is the ambient temperature.

a. The units of *C* will depend on how we are measuring $\dot{Q}$. See section c below.

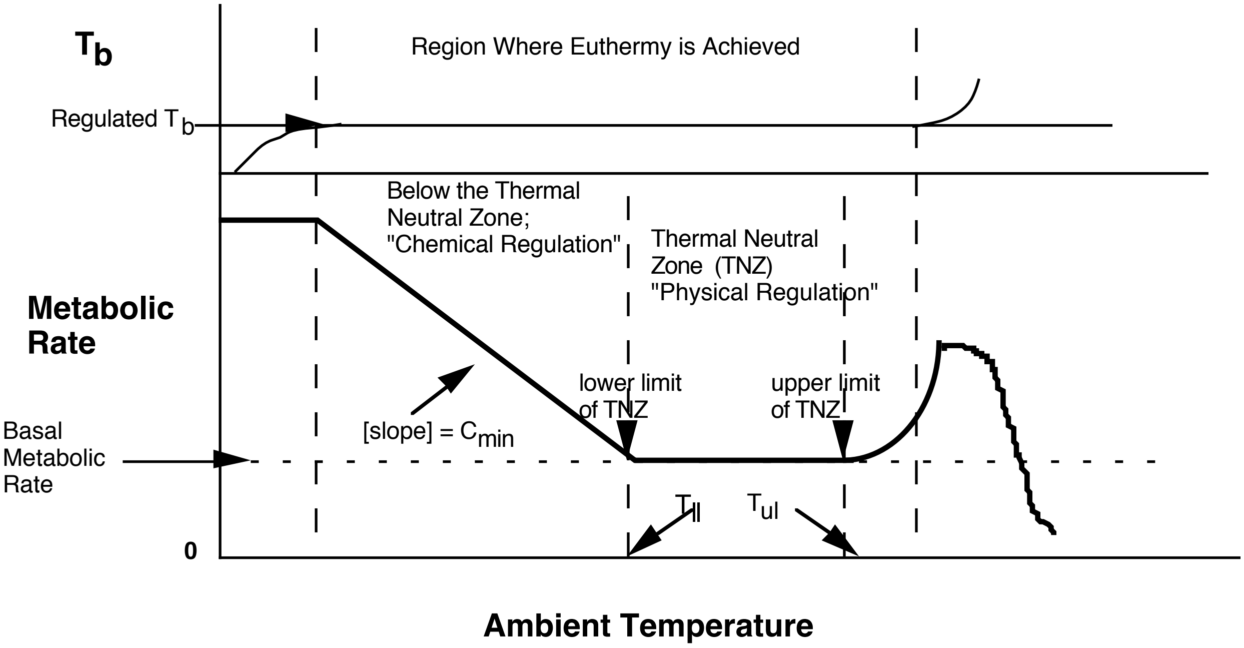
b. Note that we ignore the mass term. Biologists are often simply interested in whole organism metabolism (i.e., the metabolism is X watts in a 20 kg animal).

c. **Examples of units of C**:

units of Q	units of C
watts	$\frac{\text{watts}}{^{\circ}\text{C}}$
$\frac{\text{watts}}{\text{kg}}$	$\frac{\text{watts}}{(^{\circ}\text{C} * \text{kg})}$
$\frac{\text{Liters } O_2}{(\text{h} * \text{kg})}$	$\frac{\text{Liters } O_2}{(^{\circ}\text{C} * \text{kg} * \text{h})}$

ETC.

6. Now, we are ready to graph the relationship between metabolism and temperature. Unlike the poikilotherm (ectotherm) graph presented in an earlier class' notes, we will plot T_a on the abscissa since we know that for an endotherm, T_b is constant (i.e., T_a does not equal T_b). The graph for a typical endotherm is shown on the next page:



7. The graph is obviously not like that shown for the first plot of Newton's Law of Cooling. Here are the explanations of the graph:

a. The central region of the graph where there is no change in metabolism with body temperature is called the **THERMAL NEUTRAL ZONE** or **TNZ**.

1. The metabolic rate at the TNZ represents the **BASAL METABOLIC RATE**. This was the rate used, for example, by Hemmingsen.

2. The lowest temperature that is still in the TNZ is called the **LOWER LIMIT OF THERMAL NEUTRALITY, T_{ll}**.

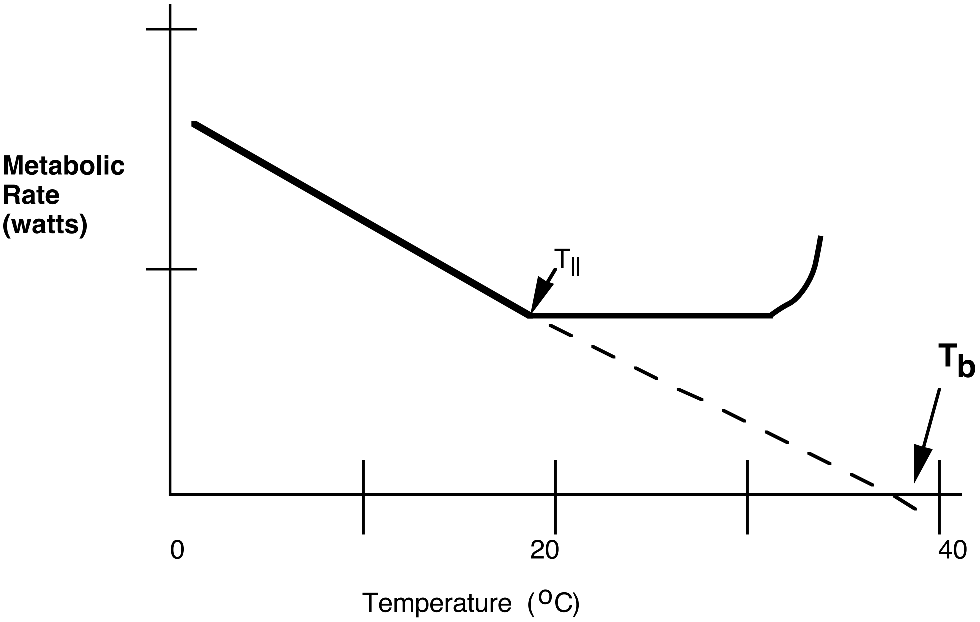
3. The Highest temperature that is still in the TNZ is called the **UPPER LIMIT OF THERMAL NEUTRALITY, T_{ul}**.

4. The TNZ is also called the **ZONE OF PHYSICAL REGULATION** for reasons that will be discussed below.

b. The slope of the metabolism vs. temperature line below the TNZ gives the value of the **MINIMAL THERMAL CONDUCTANCE (C_{min})**.

c. This line (the one below the T_{ll}) may be extrapolated to the X-axis to give the T_b (dotted line); the argument being that where $T_b = T_a$, metabolism must be zero. As crazy as this seems, it in fact works pretty well!

(please go to the next page)



d. The metabolism curve for below the T_{ll} is also called the **ZONE OF CHEMICAL REGULATION**.

1. While this is not a great name, it nevertheless indicates that the animal is regulating T_b by changing the rate of its chemical reactions, that is, by changing its rate of metabolism.

2. Thus, in this zone, we see that there is an inverse relationship between metabolism and T_a; as T_a decreases Q increases. This is obviously the complete opposite from

what happens in poikilotherms or for that matter in endotherms whose ability to thermoregulate has been lost (such as a surgery patient being perfused with cold blood).

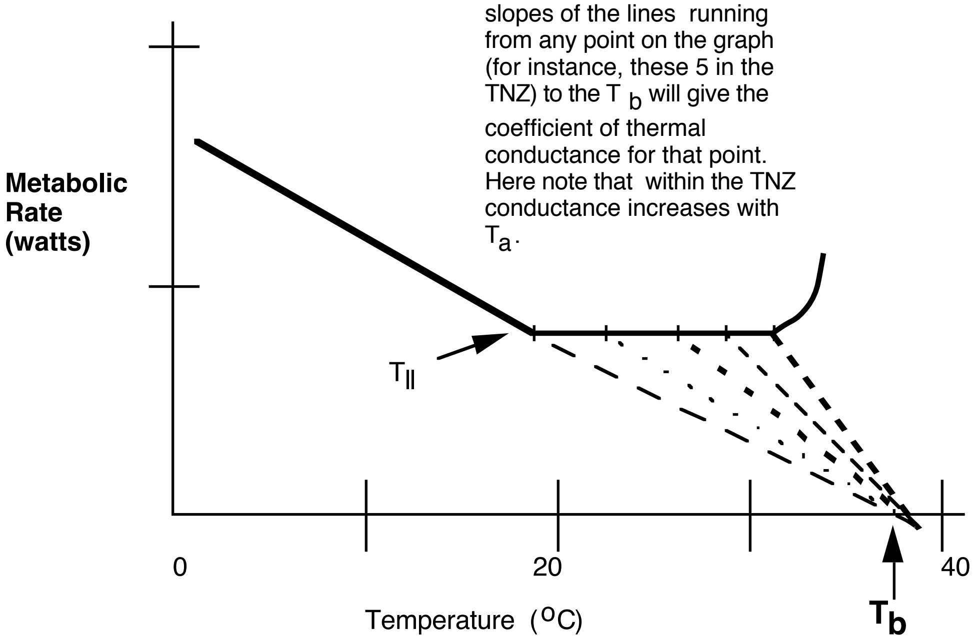
e. Now let's get more complicated: What is the value for C at any point in the TNZ?

1. This can be found graphically by drawing a line from the metabolism curve in the TNZ to the T_b (exactly analogous to the procedure that we used to find C_{min}.).

2. Notice that **as we move up the TNZ the value of C INCREASES**, just as we said it would and as common sense dictates (what do you do when a room gets hotter if you can't change the room temperature -- one thing you may well do is increase your C both by "flushing" (changing your circulation) and by removing coats or sweaters.)

(a) Notice that the actual rate of heat loss does not increase -- since the heat gain (metabolism) is constant, the rate of heat loss must be the same.

(b) But to achieve a constant rate of heat loss, mechanisms that make it easier to lose heat in the face of a smaller ΔT must be evoked as the temperature increases within the TNZ.



Note that we can also easily find these values mathematically simply by re-arranging and solving Newton's Law of Cooling as written for eutherms.

a. Thus, we can now see the mechanism for the TNZ: here the conductance (heat loss constant) increases as T_a goes up while the metabolism stays constant. Presumably the metabolism cannot drop anymore since lower rates would not be compatible with life. By contrast, below the T_{ll}, C (instead of Q) has reached a minimum value and therefore to hold T_b constant Q must increase.

b. We call the TNZ the zone of physical regulation because constant T_b is achieved by varying C not Q. Let's quickly list the factors that are responsible for varying C:

1. Internal circulation
2. Insulation

3. Surface to Volume ratio -- size and shape -- obviously the larger animal, for the amount of the heat produced, the less area for it to loose heat. Additionally, animals can change their shapes. How do animals act in the cold as compared to warm?

4. Ventilation outside the animal (air and water currents).

In fact, we can lump all of these terms into one and simply refer to them as things that affect the animal's **INSULATION**. That is essentially what was done in the derivation of Newton's Law in the appendix. The relationship between insulation and conductance is very simple as is given as:

6. $I = \frac{1}{C}$

That is, insulation is the inverse of thermal conductance.
Thus, we refer to the TNZ as the zone of physical regulation since it is C (and **I**) that is changed and as we have seen from the list of things that control C and I, these are largely physical (vs. chemical) phenomena.

f. In addition, as we move up the TNZ, evaporation becomes more and more important in at least some animals (such as ourselves) in increasing heat loss. However, evaporative heat loss obviously has nothing to do with C.

g. Finally, **the area <u>above</u> the T_{ul} is caused by two factors:**

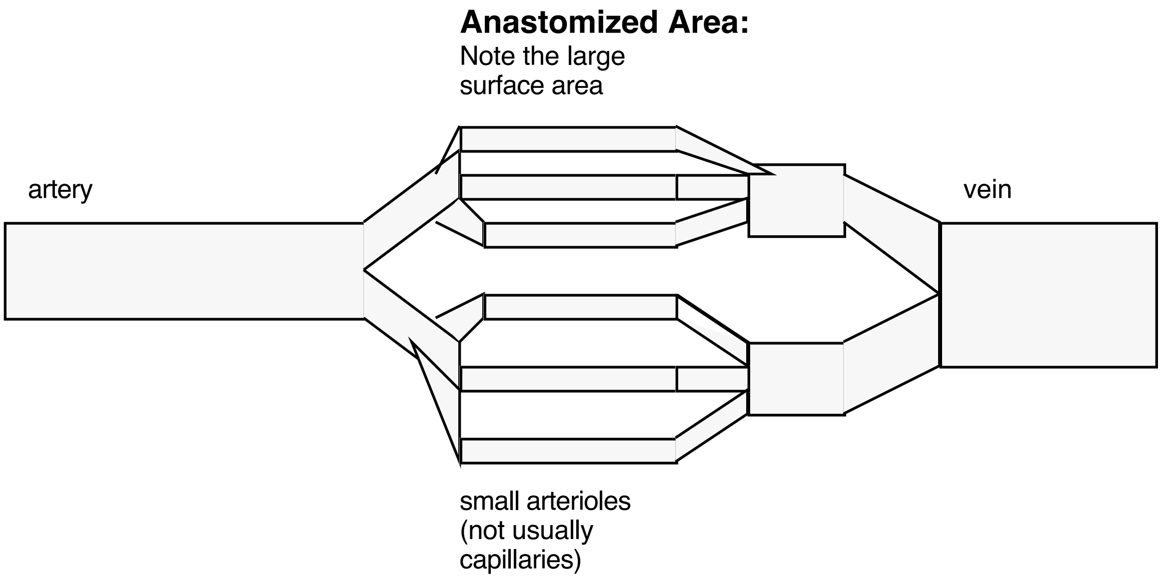
1. at temperatures close to the T_{ul} the increased metabolism with temperature is due to the costs associated with using muscles to try to increase heat loss. In all animals there will be **additional increases in circulation** to the periphery and this costs energy since the heart must still meet the metabolic demands of other tissues in addition to pumping blood for heat dissipation. More externally obvious maneuvers include **panting** (many mammals), **gular flutter** (the avian analog to panting), and **fanning** all require muscular activity and will increase Q.

2. As we move further and further above the T_{ul} these mechanisms no longer remove more heat than they generate and the animal is now in serious trouble. **Thermoregulation breaks down and T_b begins to rise**, this increases Q causing a further increase in T_b. Unless this (+) feedback loop is quickly broken this **MALIGNANT HYPERTHERMIA** results in death.

VI COUNTER –CURRENT HEAT EXCHANGERS:

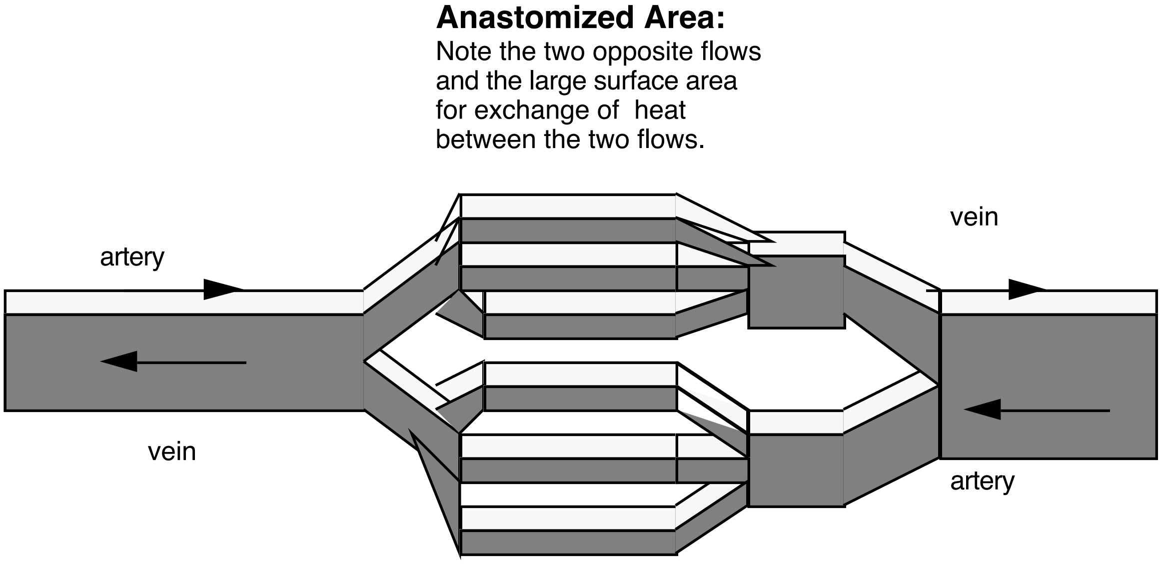
A. There are often situations where you want to separate the flow of water (blood) and heat. Good examples are in limbs, especially in endothermic animals that might spend time standing in water. We have learned about counter-current exchange before (with the kidney) – what follows is a description of how it used in heat exchange

B. We start with anastomatized vessels – what is called a *rete mirabile*:



Generally, these anastomoses are always found in pairs, such that one "blood vessel net" is closely associated with another that is carrying blood in the opposite direction:

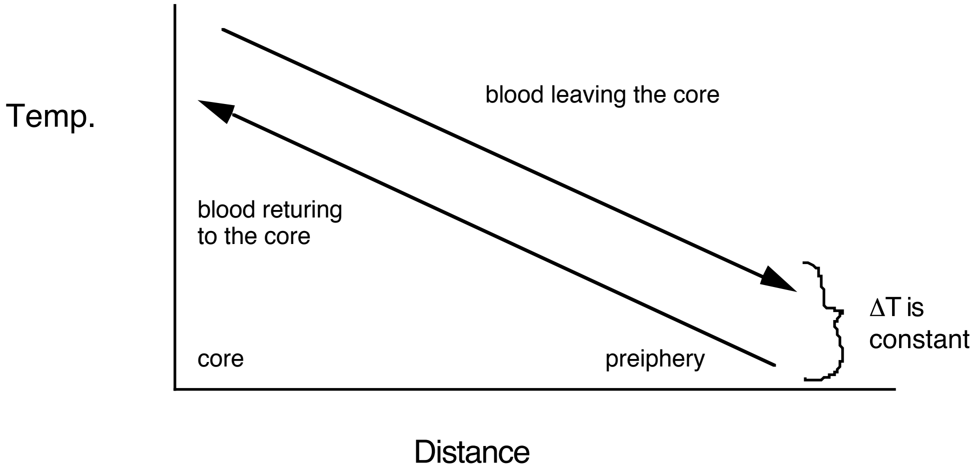
Counter-Current Exchange of Heat:
the *rete mirabile*



Thus, we have a counter current system. We call this network of blood vessels as "***RETE MIRABILE***" **or "marvelous network"**. For our purposes, they serve to increase surface area to which the blood is exposed and to maximize the transfer of something (such as heat) from one vessel to another.

If the blood in the two vessel networks that makes up the *rete* is of different temperatures, heat exchange will occur. Thus, warm core blood transfers heat to cool blood from the periphery. As a result, the heat tends to stay in the core and little heat is lost through the surface.

The operation of the counter-current heat exchanger can be visualized according to the graph below:



IV. ACCLIMATION IN EUTHERMIC ENDOTHERMS

A. The figures shown above show how a eutherm would respond to changes in temperature on the short term, that is, within any season.

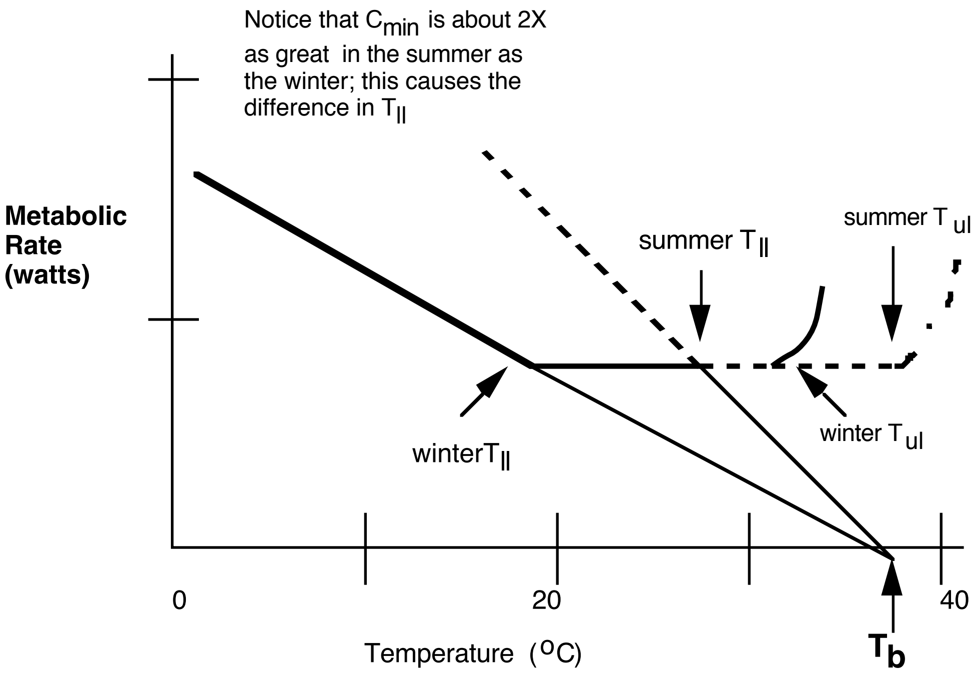
1. Obviously, if an animal finds that most summer temperatures are in its TNZ and if it makes no changes, then, when the winter arrives, it will need to raise its metabolism quite a bit just to maintain T_b. This during the season when food is least available.

2. Conversely, if the animal spent the winter in its TNZ and then made no adjustments going to the summer, it would be heat-stressed or perhaps killed by the heat.

B. Given this, we can ask the question, what do animals do to adjust to different seasons of the year?

1. **Change the bmr**. In going from one season to another, one mechanism of compensation is to increase or decrease the bmr. This is not, however, the major method of acclimation. Reflect on the reasons for this.

2. The biggest single change is to **alter the value of insulation**. Since we know that $C = \frac{1}{I}$, then if we double the insulation, we half the conductance. This will have effects not only on the change in Q as we go below the TNZ but also on the actual T_{ll}. This can best be seen graphically. In the figure below we show the same animal with two different values of C, one that is twice the other (1/2 the insulation). Note that to help clarify the issue, we have ignored any changes in bmr.



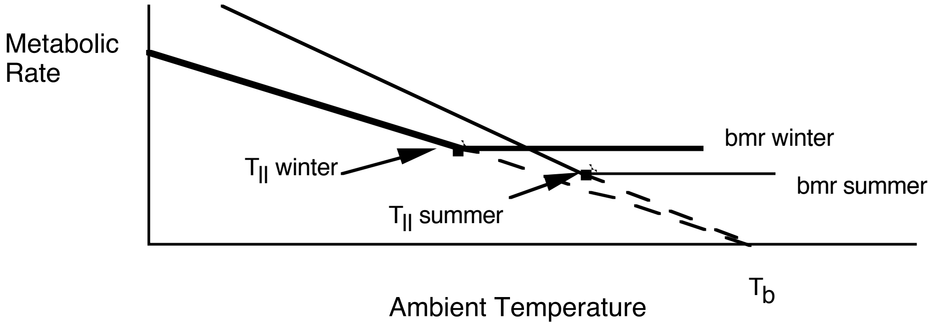
a. Here are the results of this type of acclimation. We will talk about the things from the reference point of going to thicker insulation (lower conductance); in other words, "winter acclimation".

1. The **T_{ll} is effectively moved to a lower temperature**, thus the animal can be "on idle" (i.e., at bmr) at a lower temp (or higher temp in the summer)

2. **Below the TNZ, the increase in metabolism with decreasing T_a is less in a better-insulated animal. This, like the change in the T_{ll} also lowers food requirements**.

b. **In going from winter to summer, an animal that decreases its insulation generally experiences an upward shift in its T_{ul}.**

3. In the case where both the bmr and C change, the effects noted in #1 and b just above) are magnified even further:

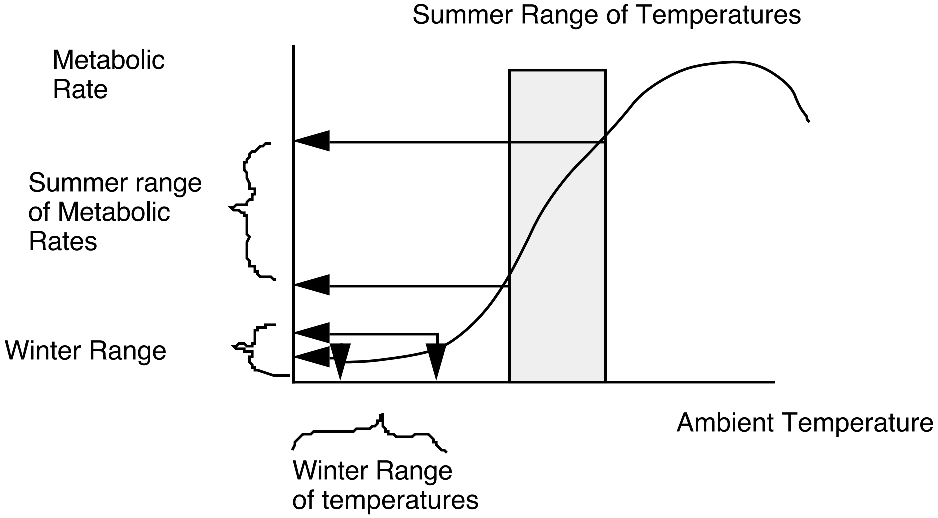


IV. THERMAL COMPENSATION AND METABOLISM IN POIKILOTHERMS

A. THE PROBLEM:

1. Ectothermic animals that don't hide from extreme temperatures (for instance, those that are active over most of the year in temperate regions) are known to have similar activity patterns regardless of the temperature.

2. This is not predicted by their metabolic rates vs. T_a when these measures are taken in one season:



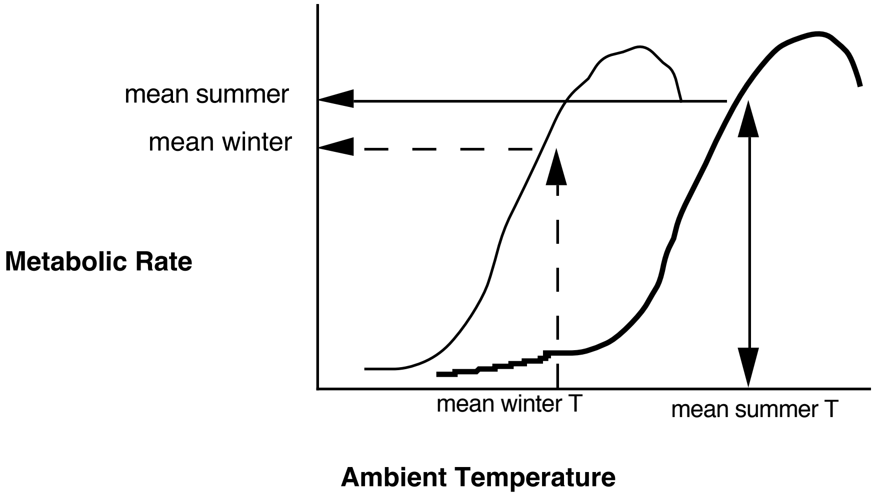
Since aerobic activity level is to some degree proportional to aerobic resting metabolism, then from this graph we would predict a very sluggish animal in the winter and an active one in the spring.

3. Examples of the above pattern are most species of animals that are not birds or mammals.

B. In fact many ectothermic animals have ways of changing their metabolism in response to shifts in the average daily temperature. This allows them to remain much more active than would be possible without such a mechanism.

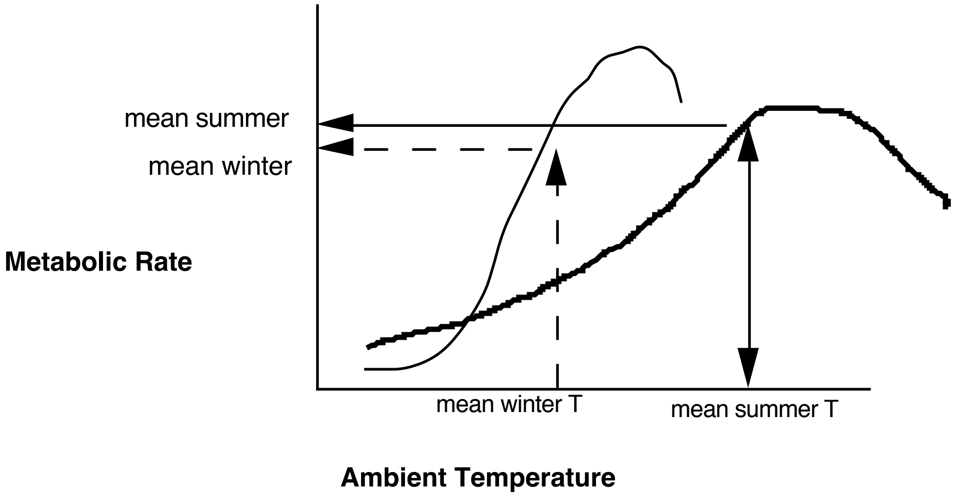
1. The graph above showed that if no shifts were made, the mean daily metabolism would be very high in the summer and low in the cold seasons.

2. However, what we really find in ectotherms that are active in several seasons is this:



a. Notice that for the **eccritic temperature of the animal in the two different seasons the metabolic rates are much more alike than if there had been no adjustments**. However, note that as is usually the case, the adjustments are not perfect.

b. Besides showing a shift in the position of the curve, it is also possible for the curves to have two different slopes, i.e. to affect the Q_{10}.



Note that either season might have the flatter (smaller Q_{10}).

? Why not just go for the highest possible metabolic rate in both seasons?
Why should activity be linked to resting metabolic rate? (This is an important question we have not discussed previously -- think about it!)
Which conditions would tend to go with having a relative flat Q_{10} as compared to those that would tend to encourage the evolution of a steeper Q_{10}?

C. Terms:

1. **ACCLIMATIZATION**: the long-term (chronic) adjustments that are made to seasonal changes in temperature.

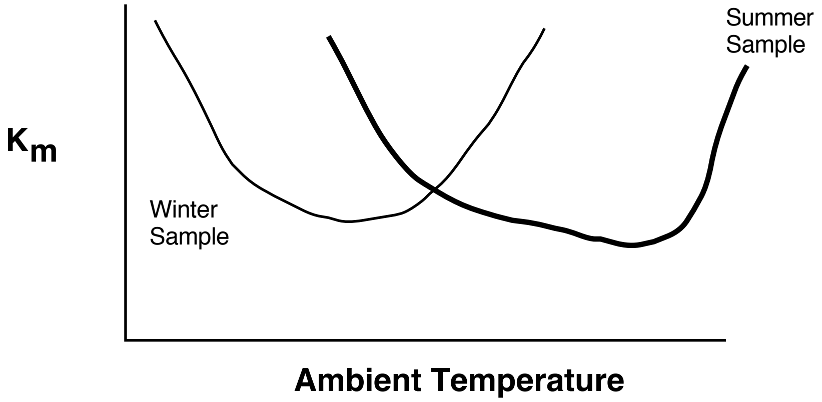
2. **ACCLIMATION**: short-term changes quickly made to a changing set of conditions. This term is very often applied to adjustments that are made by an animal to some specific set of laboratory conditions. Thus, it is fair to say that they differ from acclimatization in being acute rather than chronic changes.

3. **COMPENSATION**: A process whose end result is to maintain a constant state regardless of the conditions, i.e. a constant average daily metabolic rate regardless of the season through thermal acclimatization.

D. The Molecular Basis of Thermal Acclimation in Ectotherms:

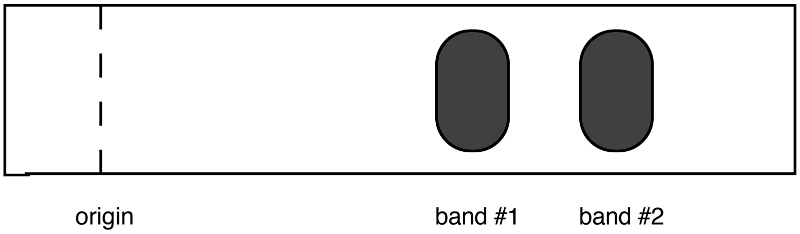
1. If summer and winter acclimatized ectotherms of the same species are sampled and the activities of different enzymes are measured, it is found that their catalytic abilities with respect to temperature have been shifted:

If we measure the K_ms for this enzyme in summer and winter we may get:



? Explain how this shows thermal acclimatization.

Notice that this graph is essentially identical to the one presented in lecture 4, page #7. It would therefore be reasonable to hypothesize that the acclimation in these animals is at least in part achieved by producing different versions of the same enzyme (versions with different temperature tolerances) at different seasons. It is possible to answer this question by isolating a particular enzyme from "summer" and "winter" animals and then running them together electrophoretically. Any differences in charge, mass, or shape will result in separate "bands". In fact the results show two or more separate bands for the protein thus confirming that more than one form is being produced:



This is an example of an organism's use of **ALLOZYMES**: different forms of the same enzyme (a related and similar term is **ISOZYME** -- this refers to alternate forms of the same enzyme which can be identified by electrophoresis. For our purposes, consider both terms as equivalent and feel free to use either one). They catalyze the same reaction but they have (in this case) different properties with respect to temperature. True allozymes have slightly different 3-D structures due to the interaction of slightly different amino acid sequences with roughly constant environments. Allozyme production is generally controlled through the regulation of gene expression. We might assume that in the summer all of enzyme **e** would be the hot weather form and in the winter only the cold weather form would be found.

? Explain what would be seen in the spring and fall. How would the K_m and metabolism curves look during these seasons relative to the summer and winter curves? What would the electrophoretic banding patterns look like in each of the four seasons?
Would you expect all enzymes to show multiple forms in ectotherms that attempt to compensate for seasonal temperature differences? Explain. If not, for the enzymes that did not

show compensation, what attributes would they have in common in terms of Q_{10} and position on a rate vs. T_a plot.
How would different shaped K_m vs. T_a plots be translated into differences in rate vs. temp plots? Make a couple of drawings where you change the position and/or steepness of the Km plots and then try to approximate rate vs. temp plots for these.

Finally, realize that differences in temperature response in enzymes can also be the result of processes that directly modify the enzyme such as (a) removing amino acids, (b) attachment or removal of ligands, (c) changes in pH etc.

2. Changes in the Fluidity of Membranes:

a. Membrane fluidity is a key component of determining how easily substances can enter or leave the cell and further how easily certain membrane-bound reactions can occur. This is because changes in fluidity will cause differences in how membrane proteins function, in particular those that must interact with other proteins in order to perform some task.

b. The enzyme systems of the cell are obviously adapted for one set of conditions of fluidity.

c. As mentioned in class #4, fluidity is determined primarily by the relative amounts of unsaturated to saturated fatty acids: the proportionately greater amounts of unsaturated f. acids result in, at a given temperature, a more fluid membrane.

d. In many ectothermic species, acclimatization results in the fluidity being maintained at a constant value even though T_b has shifted. This is done by changing the types of f.a. that are in the membrane.

? How would f.a. composition change when an animal went from summer to fall?

e. These changes are especially important in the nervous system and allow the animal to continue to respond rapidly to stimuli even at colder temperatures.

THE REMAINING IS PURELY FOR INTEREST (IF INTERESTED AND IF YOU HAVE THE TIME OR FOR SOME FUTURE TIME!) – ALL IN BLUE

V. Endothermy in Fish, Snakes, Turtles, And Lizards.

A. Fish

1. The difficulties that a potentially endothermic fish must face when compared to an endothermic terrestrial animal:

a. The **heat capacity of water is much higher than that of air and slightly higher than tissue** (which is mostly water). **The same is true of the coefficient of thermal conductance of water compared to air and tissue.**

Thus, compared to a terrestrial animal, an aquatic animal experiences rapid loss of any heat the animal generates.

b. **O_2 concentrations of water are much lower than in the air** -- therefore to get a given amount of O_2, **a fish must breathe a greater volume of water than must an air breather** must breathe air:

EXAMPLE : Assume 1 L of seawater at 20^o C has an O_2 concentration of $\frac{5.3\ mLO_2}{L\ water}$.

In air the concentration is about $\frac{209\ mLO_2}{L}$.

If an animal has a metabolic rate of 1 $\frac{LO_2}{min}$ how much air must it breathe?

How much water?

ans.: **If breathing air:** $\frac{1}{0.209} = 4.78\ \frac{L}{min}$ (if all O_2 is removed from inspired air)

If breathing water: $\frac{1}{0.0053} = 188.7\ \frac{L\ water}{min}$

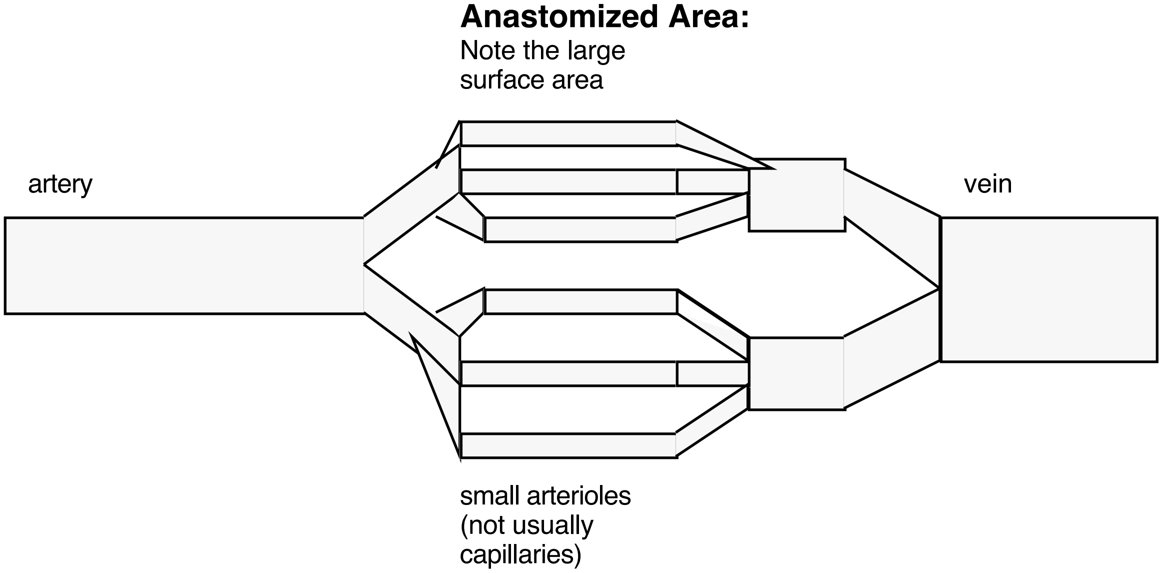
Thus, the water breather must breathe about 40X as much water as does the air breather to obtain the same amount of O_2.

c. **One final corollary: the area of respiratory exchangers in most animals is much larger then the general body surface.** ***Thus, in a water-breathing aquatic animal, any heat that is produced via metabolism potentially will be lost via the gills since a large amount of water must be exchanged to get the oxygen the animal would need to be endothermic.***

d. There is a solution to this constraint. As with the intermittent counter-current exchanger above, if the fish can successfully separate the circulation of oxygen and heat, the problem is potentially solvable:

1. In the few fish that are endothermic, there are areas where the blood vessels anastomatize into smaller and smaller vessels (the smallest usually being arterioles which are not gas and nutrient exchange vessels but nevertheless are small and the flow through them can be easily regulated since there are muscles at their entrances which can constrict and reduce flow or relax and increase it). In any case, the anastomatized area

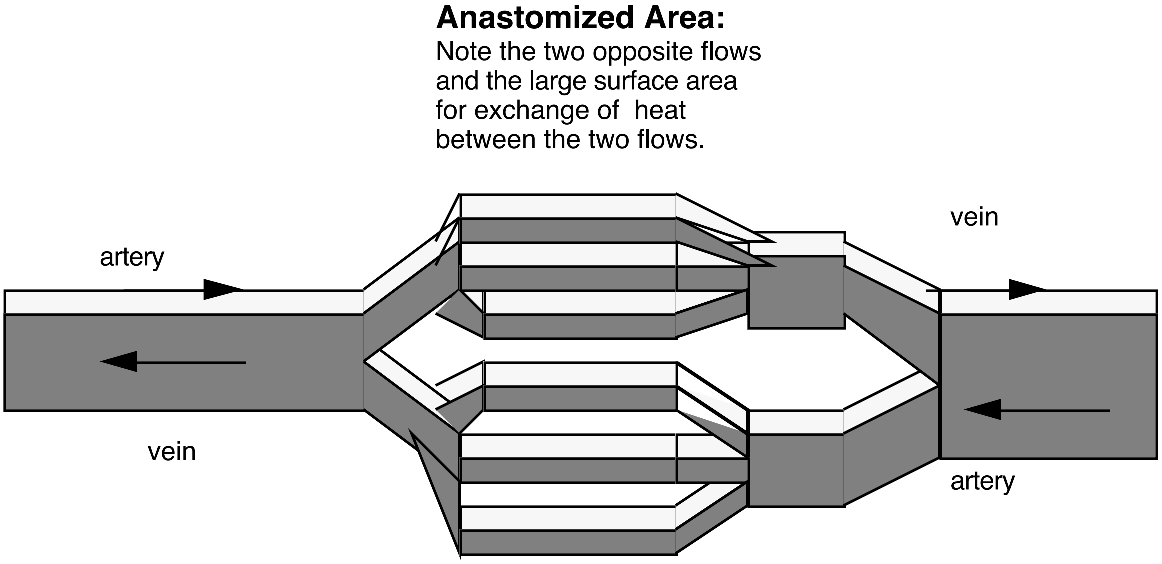
greatly increases the surface area the blood is exposed to:



The blood eventually is re-collected into larger vessels.

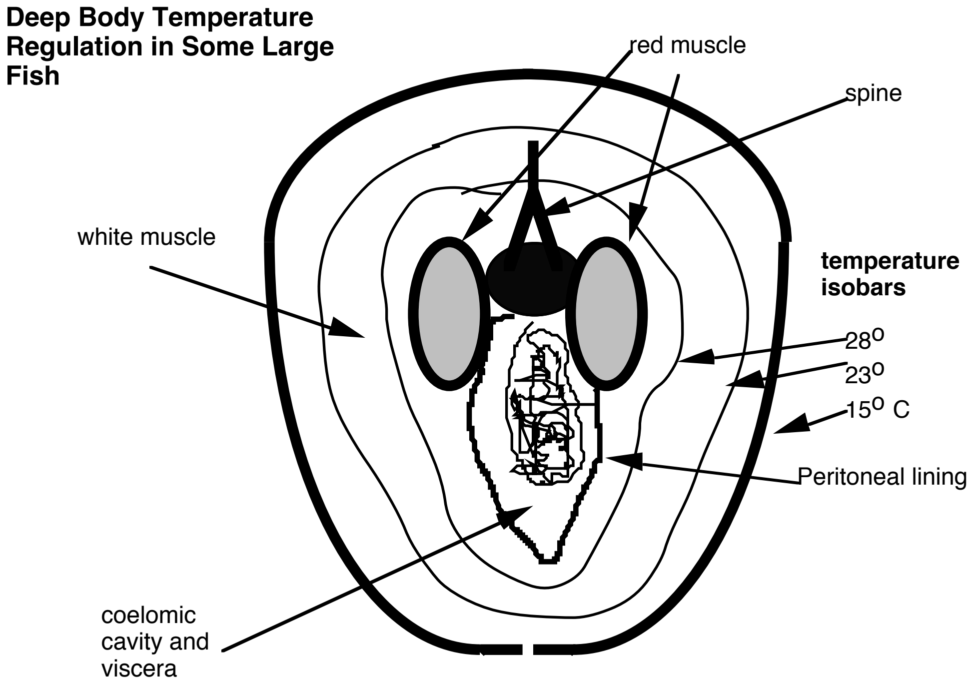
2. Generally, these anastomoses are always found in pairs, such that one "blood vessel net" is closely associated with another that is carrying blood in the opposite direction:

Counter-Current Exchange of Heat:
the *rete mirabile*

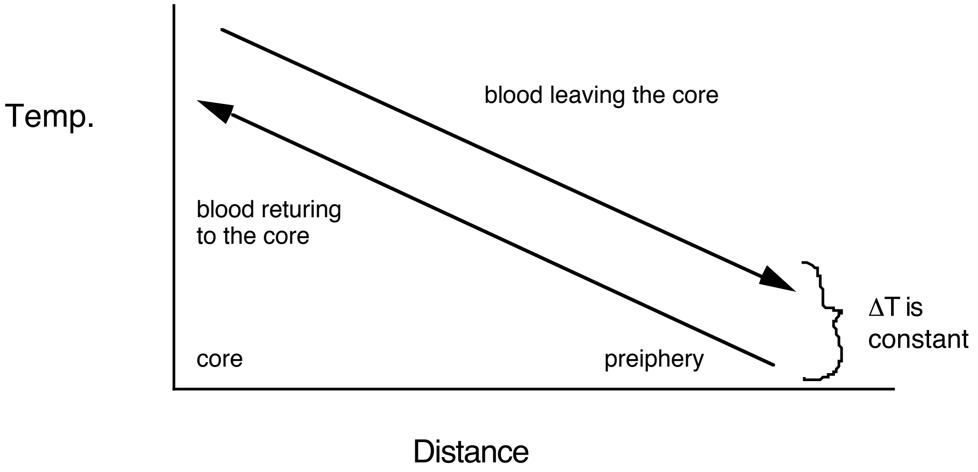


Thus, we have a counter current system. We call this network of blood vessels as "***RETE MIRABILE*" or "marvelous network"**. For our purposes, they serve to increase surface area to which the blood is exposed and to maximize the transfer of something (such as heat) from one vessel to another.

If the blood in the two vessel networks that makes up the *rete* is of different temperatures, heat exchange will occur. In the endothermic fishes, the *retes* occur where blood leaving the core meets blood from the surface, including the gills. Thus, warm core blood transfers heat to cool blood from the periphery and gills. As a result, the heat tends to stay in the core and little heat is lost through the surface. A profile of an endothermic fishes body would look like this in terms of temperature:


Deep Body Temperature Regulation in Some Large Fish

The operation of the counter-current heat exchanger can be visualized according to the graph below:



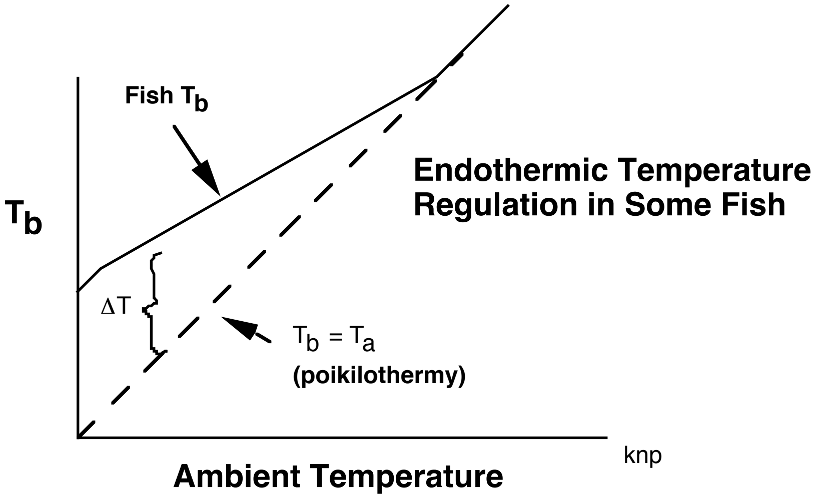
5. Next, we need a heat source. In many fish there are two distinct groups of muscles: the largest mass is made up of white muscle and is used for sprinting and the smaller mass is red muscle. The red muscle(see diagram above) is located surrounding the spine and the coelomic cavity (containing the gut and other organs). It is used for "cruising"; in other words, it is continuously active as the fish makes its way around. The red muscle is the heat source:

a. it is continuously active.
b. it is at the core whereas white muscle is nearer to the periphery

c. it surrounds the organs -- warming them will increase rates of digestion etc.

6. One final requirement for an endothermic fish -- What about body size? Would it be easier for a small or large fish to be endothermic? Or does it even matter? To help you answer this, realize that the only endothermic fish are adult pelagic beasts such as bluefin tunas (Charlie), great white, tiger, and mako sharks.

7. Finally, if we ask the question "How good are these fish at being thermoregulators?" we see that they are pretty good considering all of the constraints that operate on them:



? Why is it so easy for dolphins and whales and penguins to be endothermic (compared to fish?)?

What other types of aquatic animals would you think could be endothermic?

C. Other unusual examples of endothermy in vertebrates.

1. What body shape found in a terrestrial vertebrate would seem least conducive to endothermy? Ans.: snake, due to high S/V and large area of contact with the ground (much more thermally conductive than the air).

2. At least one snake is an endotherm during part of its life: the **Burmese Python**, a common python sold in many pet stores, it grows up to about 20 feet. The females wrap around their eggs and contract their muscles to generate heat and incubate the eggs. During this time, the females maintain an appreciably elevated body temperature. The T_b vs. T_a curve has the same general shape as the generalized one shown above for endothermic fish.

? What is the role of this type of endothermic temperature regulation? Pythons are the most morphologically primitive snakes. What does this say about endothermy as a supposedly "advanced" trait?

VI. Endothermy in Insects:

A. Flight is the most energetically demanding activity that any animal performs; there are many situations where a high body temperature will aid in achieving flight.

1. This is most true in insects that have relatively great mass and small wings: i.e., high wing loading. Examples are the highly maneuverable insect such as bees, dragonflies, some large flies, moths, and beetles, and certain other insects such as some cicadas, crickets and grasshoppers (the latter are not particularly maneuverable).

2. The smaller flying insects simply have too great of a S/V for endothermic flight to be possible (ex.: fruit flies).

3. Large insects with lightly loaded wings (e.g. butterflies, many moths) do not flap their wings often enough to generate enough heat to be endothermic.

4. Many other insects are Behavioral Thermoregulators: this is especially true of butterflies.

B. As an example of endothermy, we will consider **Bumblebees**.

1. Endothermy must be considered in these animals both in terms of what happens in the animal and also how the colony thermoregulates.

2. Endothermy in a bumblebee:

a. Basic anatomy: three **TAGMATA**: **head** (contains most of the ***nervous system)***, **thorax** (contains ***flight and walking muscles*** **)** and **abdomen** (***heart, digestive and reproductive structures***). The thorax and the top of the abdomen are heavily insulated with a kind of **"fur"**.

b. **Hemolymph flow** can be regulated between the different tagmata. *Since O_2 is delivered via a tracheal system, it is possible to completely shut off flow to a certain tagma for many minutes and no ill effects result.* In addition, some vessels between tagmata have counter-current heat exchangers (and thus tend to keep heat where it is) while others lack this arrangement. The animal can select which path its hemolymph will take according to what it needs to do with the heat it is generating.

c. Warm-up and take off: temperature is regulated in the thorax and head, the abdomen serves as a heat sink to dump out extra heat.

1. On a cold day before she takes off, the bumblebee will **"whir" her wings to raise the T_{thorax} (T_{th}). This is nothing more than shivering. Metabolism may raise 20 to 50 times that of resting.**

2. When T_{th} approaches flight temperatures, she sends some hemolymph to her head.

3. **As she takes off, she will generate even more heat. At this point her metabolism may be several hundred times her resting rate.** However, her thermal conductance will be much higher. WHY?

4. **On relatively warm days, her T_{th} and T_{head} (T_{hd}) will begin to get too high.**

a. **hemolymph will be shunted to the abdomen** through a vessel that lacks counter-current exchange, in the abdomen heat will be radiated off from the less insulated under-potion.

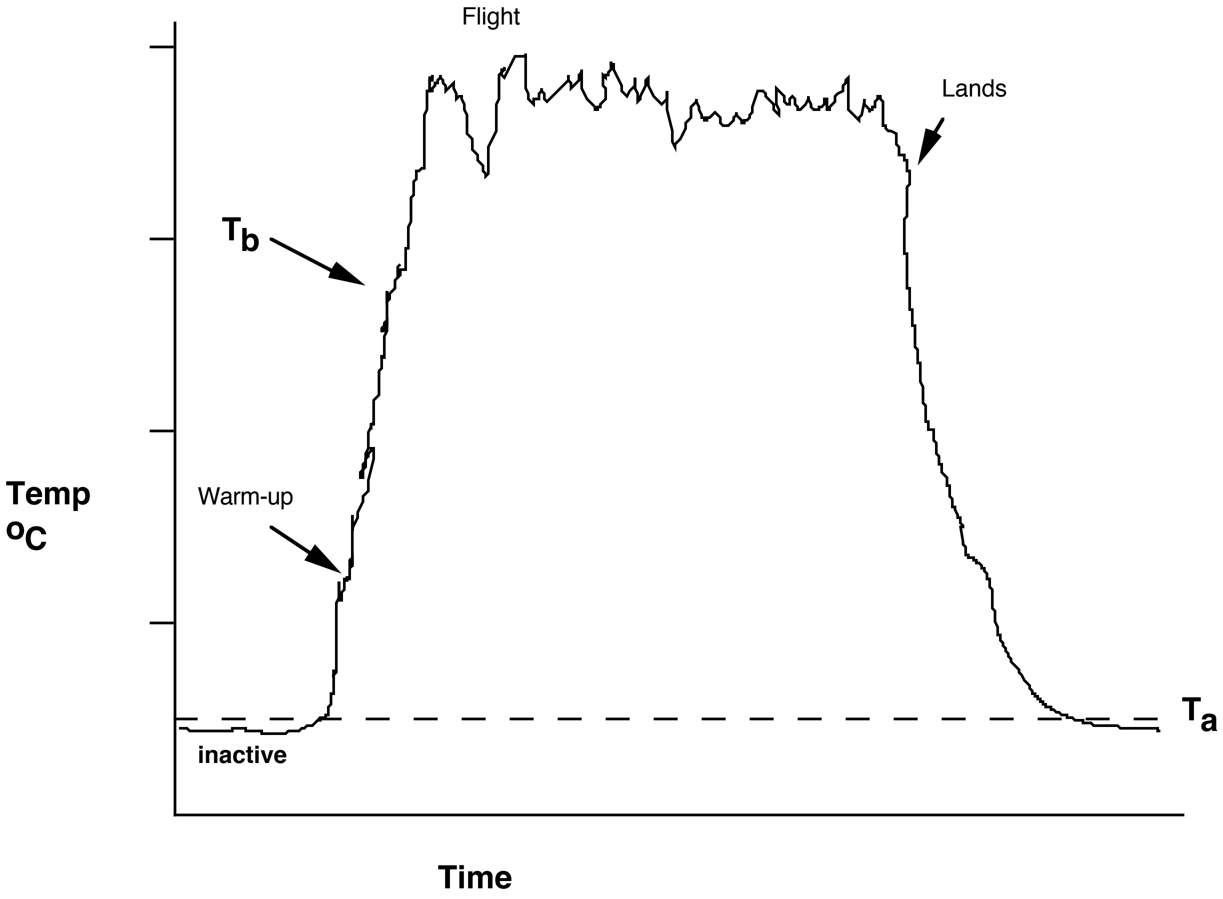
b. If she continues to heat up, **she will exude a drop of water or nectar onto her tongue**. This will **evaporate** and cool her, especially her head.

5. If she gets too cool, hemolymph circulation is restricted to the thorax and head, what goes to the abdomen passes through a vessel system with a counter-current heat exchanger and thus heat does not flow out of the thorax and head.

6. **Her color (black) helps by allowing her to absorb solar radiation.**

7. The pattern of thermoregulation:

(please see next page)



Notice the swings in T_{th}, this is in large part due to the small size of the bumblebee and also the relatively poor control of circulation present in these animals when compared to those possessing a closed circulation.

3. **Colony thermoregulation:** Bumblebees live in colonies that are founded by a single queen in the spring. After several months there may be 100-200 bees in a colony (by contrast there are as many as 50,000 honeybees in a colony). The bees in the nest regulate the temperature of the entire nest. Thus, the bees take on the characteristics of a "super-organism".

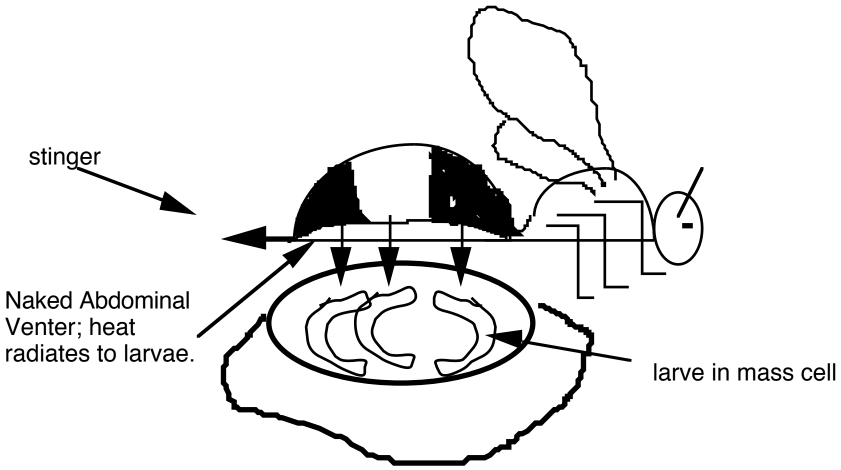
a. when conditions are cold, the bees huddle together into a cluster with the queen and brood (larvae) in the center. This cluster reduces heat loss. Bees whir their wings to generate additional heat. This is fueled from honey stores.

b. In warm conditions, the cluster disperses and the bees may even evaporate water on the warmest days to cool the colony.

4. Behavior of the queen. Queen bumblebees (unlike honeybees) found colonies on their own after hibernating throughout the winter. They are the very large, scary looking bumblebees that you see in early spring and late fall.

a. they incubate their eggs and larvae to speed their development.

b. This is done by generating heat through wing whirring and then pumping the warm hemolymph to a patch of un-insulated abdomen that is on the venter. Heat is then radiated and conducted to the brood:



? Why is thermoregulation especially important to bumble bees. Hint: they are found primarily in the non-tropical parts of the world and at high elevations.

What are the 3 or 4 factors that you think are most important if an animal is to be an endotherm?