Lecture: Physiological Ecology

Goals: learn basic principles of animal physiological ecology; apply them to the physiology of response to temperature

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The Lecture:

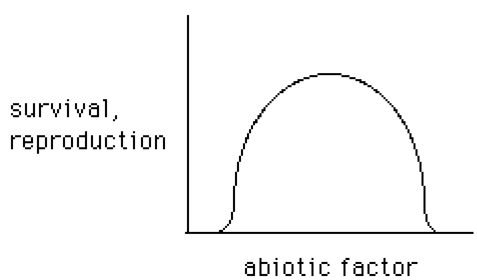
We are going to start looking at what determines the abundance of organisms; questions related to abundance will take up much of the semester. So we'll be looking at how large populations grow.

One basic starting point for studying abundance is:

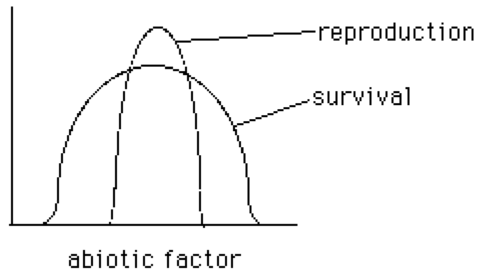
Liebig's Law of the Minimum: population growth will be limited by the required factor that is in shortest supply.

For example, if there's enough water in an area to support 1000 antelope, enough shelter from predators to support 500, and enough food to support 20, how many antelope will be in the area? (answer: 20)

We can refer to a **limiting factor:** the factor in shortest supply. This can refer to biotic or abiotic factor. When we talk about abiotic factors, we often need to consider the factor not just in short supply but how growth and reproduction are limited by tolerance to a range of conditions for the factor. This is addressed by evaluating **tolerance curves:** plots of some measure of survival and reproduction versus level of the abiotic factor such as the following:

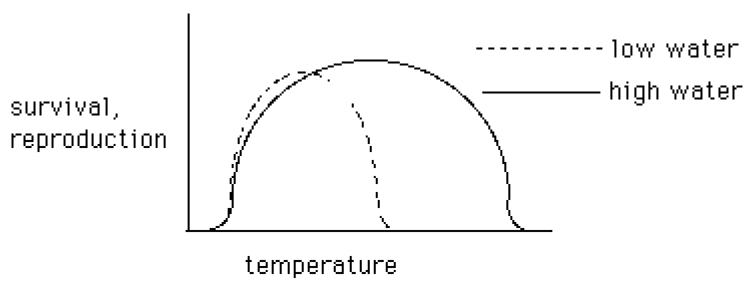


It is easiest, in laboratory conditions, to measure survival over a range of conditions of some factor. However, curves for reproduction are better indicators of conditions within which populations could actually occur. As shown here, curves for reproduction are often narrower than those for survival:



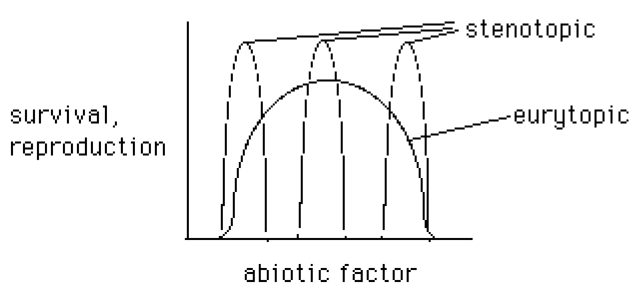
Unfortunately, it is difficult to measure reproduction, so often we have to make do with curves for survival.

Another important consideration about tolerance curves is that tolerances to different factors can interact. For example, consider the following curves for tolerance to temperature in high water conditions versus low water conditions:



Different animals clearly have different levels of factors that they can tolerate -- a marine fish, for example, survives in a different range of salinities from a freshwater fish. In addition, different species can differ in the width of the range for some factor that they can tolerate.

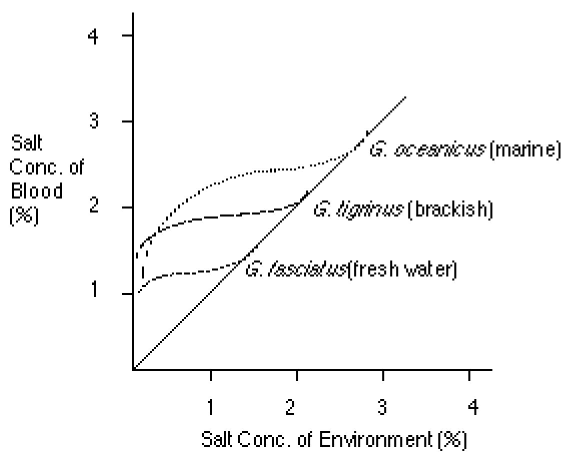
Eurytopic animals have a broad range of tolerance; **stenotopic** animals have a narrow range of tolerance. Note the **eury-** and **steno-** can be used as prefixes, meaning broad or narrow, with various suffixes that refer to particular factors. For example "eurythermal" would mean having a broad range of tolerance for temperatures. The following graph shows a eurytopic animal and three stenotopic animals that tolerate different narrow ranges of some abiotic factor:



Now let's consider different ways in which animals deal physiologically with abiotic factors. One important distinction is between **conformers**, which allow their body conditions to change with environmental conditions, and **regulators**, which maintain constant body conditions over different environmental conditions.

Consider costs and benefits to these two strategies. **Conformers** benefit because they save energy -- it would take energy to maintain body conditions different from environmental conditions. They suffer a cost with regard to enzyme function, however; the enzymes that catalyze the biochemical reactions in cells upon which all life activities depend typically have specific conditions in which they perform best. If body conditions are allowed to change, under some conditions enzymes will not be functioning optimally. **Regulators** maintain constant conditions, which maintain high enzyme function. They suffer a cost in terms of energy; it takes energy to maintain body conditions different from environmental conditions.

The following graph shows regulation in three species of amphipod. Note that if they were conforming, values would fall along the straight line with slope 1 that runs through the graph. The amphipod body salinities do not fall on this line for the most part, so they are regulating. Note that when environmental salinity reaches the line, they do conform some. Many animals regulate over some range of conditions but may conform for extreme conditions.



Salt concentration in blood of three amphipodes (genus *Gammarus*) vs. salt concentration of their normal habitat. (re-drawn from Ricklefs 1979, from H. Werntz in Prosser and Brown 1961)

Species may conform for some factors and regulate for others. Also, there is no necessary relationship between conforming or regulating and being eury- or stenotopic.

For the rest of this lecture we will consider how animals deal physiologically with one abiotic factor: temperature. First, we need to consider the ways animals can gain and lose heat:

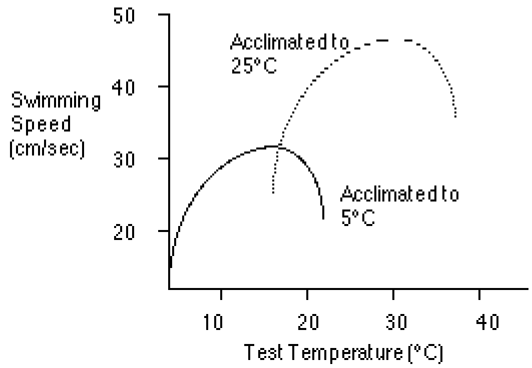
- **radiation** refers to light energy. Animals can gain heat from sunlight; they can lose heat as heat energy radiated away from their bodies.
- **conduction** refers to gain or loss of heat from one surface to another. Animals can receive heat from warm surfaces or lose it to cold surfaces.
- **convection** refers to gain or loss of heat to or from a fluid, such as air or water. Wind or water currents often carry heat away from animals; occasionally they can also bring heat to animals.
- **evaporative water loss** leads to heat loss when water evaporates off of the body surface of an animal because it takes energy to convert water from liquid form to gas form; this energy is lost from the animal as heat. Note that this only works if the water actually evaporates from the surface of the animal -- if it drips off, heat is not lost.

Several terms are used to describe whether and how animals conform/regulate to temperature.

- **poikilotherms** do not regulate body temperature -- their body temperatures change with environmental temperature. They are conformers for body temperature.
- **homeotherms** regulate body temperature
- **endotherms** regulate body temperature using the heat of their body metabolism
- **ectotherms** do not use metabolic heat to regulate. They may not regulate at all, in which case they are poikilotherms, or they may use **behavioral thermoregulation** -- behave in ways that modify heat input/output through radiation, conduction, convection, and evaporative water loss so that they maintain constant body temperatures. In that case, they are homeotherms.

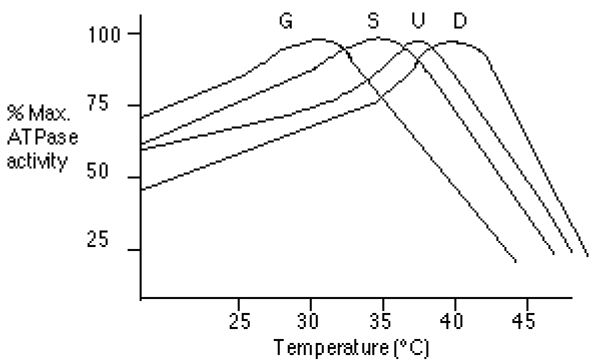
We will look at examples of how poikilotherms, homeothermic ectotherms, and homeothermic endotherms respond and are adapted to dealing with environmental temperatures.

Some poikilotherms can adjust the enzymes produced under different conditions to adjust to seasonal change in conditions. Physiological change in response to living in new conditions for some abiotic factor is called **acclimation.** The following graph illustrates acclimation in goldfish:



Swimming speed of goldfish (*Carassius arualus*)
(re-drawn from Ricklefs 1979 after Fry & Hart 1948)

Ectothermic homeotherms can modify their body temperature behaviorally. For example, orienting toward the sun can increase radiation and heat up the body. Allowing a wind or water current to pass over the body could increase heat loss through convection. Lying on a warm surface could increase heat gain through conduction. Experimental evidence indicates that homeothermic ectotherms do have a preference for a particular body temperature: given a choice they will select a particular temperature to be in. The following graph shows that lizards that naturally occur in different environments select body temperatures that are appropriate for their environment, and that their enzymes have maximum function at those selected temperatures.



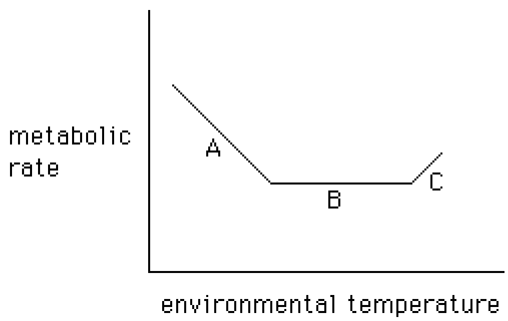
ATPase activity vs. temperature for lizard species: G= *Gerrhonotus mullicarinatus* (pref. temp. 30.0), S= *Scelopous undulatus* (pref. temp. 36.3), U= *Uma notata* (pref. temp. 37.5), D= *Dipsosaurus dorsalis* (pref. temp. 38.8) (re-drawn from Gordon 1977, from Licht 1964)

Gerrhonotus multicarinatus, the species with the lowest preferred body temperature, occurs on forest floors in cool environments. *Sceloporus undulatus*, which prefers intermediate temperatures, occurs in hotter areas but is active primarily at cooler times of the day. *Uma notata* and *Dipsosaurus dorsalis* are desert lizards, active during the heat of the day, and have the highest preferred temperatures. ATPase (a crucial enzyme for energy relations within cells) activity for each lizard is adapted to the temperature in which they occur, and which they prefer.

Note that the two desert lizards, *Dipsosaurus dorsalis* and *Uma notata*, differ somewhat in preferred body temperature. This may be related to the effect of body size. For geometric reasons, larger animals heat and cool more slowly than do smaller animals. To understand this, imagine that animals are spherical (they aren't, but the same logic applies to animal shapes.) Remember that the surface area of a sphere is proportional to the square of its radius, while the volume of a sphere is proportional to the cube of its radius. As a result, as we look at larger and larger spheres, we find that the volume increases faster than does the surface area.

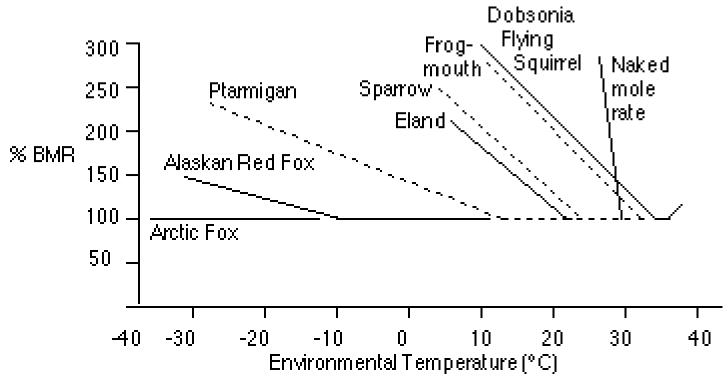
Heat gain and loss depend on the ratio of the surface area to the volume (the SA/V ratio) because heat is stored in the volume of an animal but gained or lost over the surface. The higher the SA/V, the faster an animal can heat or cool. Since as animals get larger, the SA/V gets smaller (because of the geometric argument made above -- V increases faster than SA as animals get larger), large animals heat or cool more slowly than do small animals.

Now let's consider how endotherms maintain a constant body temperature. The following graph shows the metabolic rate of an endotherm over a range of environmental temperatures (body temperature remains constant over this range):



In the area of the graph marked "B", endotherms can maintain their body temperature constant behaviorally, like ectotherms; they do not have to raise their metabolic rate to keep the temperature constant. Their metabolism provides enough heat to maintain the temperature without increasing the rate. In the area marked "A", it is cold, and animals increase metabolic rate through activities such as shivering. In the area marked "C", it is hot, and animals may be able to increase evaporative water loss by actively pumping sweat onto the body surface or by panting (running air rapidly over the moist lining of the respiratory tract); while the increase in metabolism produces a little heat, it is offset by the increased heat loss that occurs from evaporative water loss.

The following graph shows this curve for a variety of endotherms. Note that tropical species such as naked mole rats and *Dobsonia* flying squirrels can not tolerate very low temperatures and have only narrow (stenothermal) tolerance to temperatures. In contrast, species such as the arctic fox can tolerate extremely low temperatures without increasing metabolism.



Change in metabolic rate in response to environmental temperature in endotherms. Redrawn from Gordon 1977.

Endotherms can also acclimate to seasonal differences in temperature; by doing so they would decrease the temperature at which they have to increase their metabolism to thermoregulate in the winter, or increase the temperature at which they have to increase metabolism in the summer. Commonly, endotherms acclimate by changing the thickness of their insulation layer -- growing or shedding hair, or putting on or taking off fat.

Some endotherms do not regulate their bodies at a constant temperature all the time. They can avoid some of the energy cost of regulation by allowing their body temperatures to change to be closer to environmental temperatures. Two strategies observed in some endotherms in cold conditions are:

- going into **torpor**, which means letting the body temperature drop overnight as environmental temperature drops. They may still regulate at a lower temperature; if environmental temperature drops below freezing, they will regulate at above freezing (so their bodies do not freeze!)
- **hibernation** occurs when body temperature decrease, like torpor, occurs for a season rather than just overnight. Hibernating animals find a sheltered location (such as a cave, for bats, or an underground burrow, for ground squirrels) and allow their body temperatures to drop while they are inactive for the winter. They do not completely conform since they will regulate body temperature above freezing.

The following graph shows two mammals (endotherms) that occur in hot, desert conditions. The antelope ground squirrel is a small mammal (a ground squirrel); the dromedary (a kind of camel) is much larger. Note that both species allow their body temperatures to increase and decrease during the course of a day; they do not perfectly regulate. The dromedary, being large, heats and cools relatively slowly because of its low SA/V, so it heats gradually over the course of the day, then cools as the temperature cools. The antelope ground squirrel heats up much more rapidly. It will be active and let its body temperature increase until it approaches a temperature that would be lethal; then it quickly returns to its burrow, which is cool, and cools down. It repeats this a number of times during the day; that's why the graph has spikes of temperature increase.

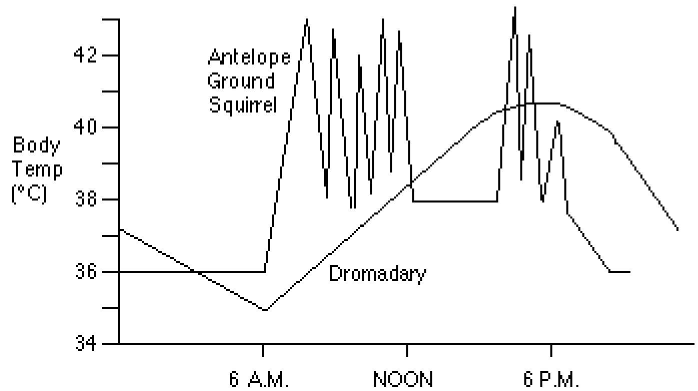


Diagram showing daily patterns of body temperature change in Antelope Ground Squirrel and Dromadary. (Redrawn from Bartholemew 1964 in Gordon 1977)