17 October 2005 **Temperature I – General Effects** ® R. B.Huey

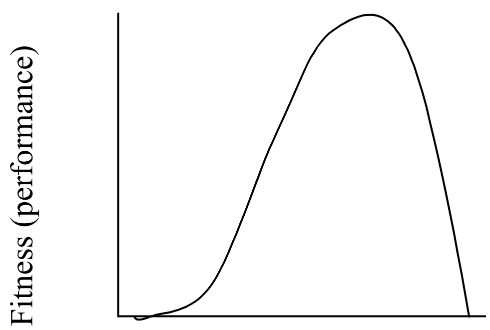
<u>Goals</u>:

- Appreciate how temperature (extreme high & low, intermediate) influences physiology and why temperature is an important physiological & ecological variable
- Know general evolutionary patterns for how in thermal sensitivity varies among ectotherms

I. Introduction

A. Why is temperature is a key <u>physiological</u> variable?

1. Temperature sets <u>limits</u> on organismal survival and reproduction. The limits for survivable $\underline{T}_b$ are narrow in endotherms (often, only ~ 2 or 3°C), but generally much broader for ectotherms (30 to 40°C). Range of temperatures occupied by life forms is **huge**, from freezing to almost boiling.
2. Within lethal limits, temperature affects performance of **all physiological activities**. As $\underline{T}_b$ increases, kinetic energy of molecules increases, resulting in an increase in physiological rates; but at high $\underline{T}_b$, rates decline.
3. "Thermal performance" (or rate) curve describes overall sensitivity of a trait to temperature. One can characterize the "optimum" temperature, degree of thermal specialization vs. generalization, etc.



B. Temperature is also a dominant <u>ecological</u> variable because of its effects on physiology, behavior, and survival. Examples

1. On sunny days, Galapagos land iguanas can bask, become warm, and readily evade hawks. But on overcast days, they are sluggish and often caught.
2. Western Gull chicks in exposed nests die if a heat wave hits during nesting
3. In US, human death rates increase a low and at high ambient temperatures

C. Reminder of basic thermoregulatory jargon (source heat vs. $\underline{T}_b$)

1. **Endotherms -** their major source of body heat is their own metabolism.
2. **Ectotherms** - virtually all body heat from <u>external</u> sources (e.g., solar radiation).
3. **Homeotherms** [1] –have a constant body temperature. Usually birds and mammals, but literally <u>any</u> animal with a constant $\underline{T}_b$ "is a homeotherm."

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[1] The terms poikilotherm and homeotherm are not always associated with ectotherms and endotherms, respectively. A deep-sea fish has a more constant $\underline{T}_b$ than does a human; and many mammals and birds have variable $\underline{T}_b$, at least under some conditions. "Warm-blooded" and

4. **Poikilotherms** - variable T_b (poikil = varied). Most animals.

D. Basic measurement scale. Official scale is Kelvin (0°C = 273K = 32°F). However, most physiologists in practice use Celsius scale.

II. Effects of Extreme Temperatures -- High T_b

A. How do physiologists measure tolerance to extreme high temperature?
   1. Lethal T_b -- not done very often in vertebrates.
   2. "Critical Thermal Maximum" -- T_b at which animal loses righting response -- hence ecologically dead). Animals survive these measurements.

B. Does heat tolerance vary much among species? Yes!
   1. Most animals (protozoa to vertebrates) die at T_b ~40°C. But Namib Desert beetle survives near 50°C and US desert iguana tolerates 47°C. Archaebacteria in deep sea hot vents grow at 110°C!
   2. In contrast, the Arctic ice fish dies from heat stress at only 6°C. Alpine insects go into heat shock at only 10 to 14°C! ⇒ So a temperature that is hot to one species, is cold to another. [Thus, "high" temperature is relative.]

C. What causes heat death? In general, death is probably from disruption of membrane integrity and function, but other factors may be involved

E. Evolutionary patterns: desert or low-latitude species typically tolerate higher temperatures than do non-desert or temperate-zone species.

F. Do other factors that influence heat tolerance? Yes, for example, age, acclimation state (e.g., in summer, are more heat tolerant).

III. Effects of Extreme Temperatures -- Low T_b

A. Very cold temperatures slow reaction rates, and membranes become viscous – not surprisingly, performance drops with temperature.

B. Do species also vary in low temperature tolerance? Yes.
   1. Vertebrate ectotherms generally tolerate T_b near 0° to 15°C. However, some frogs survive for 5 days at -6°C, even though most of their body water had been frozen. Arctic squirrel survives -2.9°C!
   2. Some insects are still active at around 0°C, and one tolerates *minus* 270°C.

C. Low temperature tolerance can be scored by determining lower lethal T_b or the "Critical Thermal Minimum," as above for high temperature tolerance.

E. Does cold tolerance vary? Yes, many factors can influence tolerance.
   1. Age -- embryos and young of vertebrates are generally less tolerant than adults. [but some insect eggs are highly resistant to extreme temperatures.]
   2. Exposure time -- tropical lizards (Anolis) survive acute exposure to 9°C, but die after a few days at only 16°C. So tolerance is 1/∝ to exposure time.
   3. Recent history - "**acclimation**" conditions influence tolerance. Acclimation to low T_b usually lowers CTMin. [Birds in Michigan die soon after exposure to T_a = 0°C in summer, but survive -40°C in winter!]
   4. Evolutionary changes. High altitude or latitude species are often cold tolerant.
   5. ➔ Many animals behaviorally avoid low (and high, for that matter) temperature stress. Some birds, monarch butterflies fly south. Various frogs, turtles, insects hibernate underwater or burrow below frost line.

"cold-blooded," though used commonly, are **not** used as synonyms of endotherm and ectotherm, respectively. Why? Some ectotherms have higher temperatures than some endotherms.

F. Why do animals die from cold? Intracellular ice formation is of course lethal – disrupts cellular microstructure and integrity (= a mechanical effect). "Normal" body fluids freeze at - 0.5°C (terrestrial animals) to - 1.7°C (marine animals).
➔ However, most species are already dead from cold before their cells freeze.

G. So if intracellular ice doesn't "get 'em," what does? [in other words, what are the "non-mechanical" but still lethal effects of cold]
1. Chemical reactions slowed. Ability of animal to respond drops.
2. If reactions are too slow, life can't be sustained. Fish may die of "anoxia" at low T_b: if increase O_2 levels in H_20, fish survive to lower T_b.
3. CNS (especially synaptic transmission) control and integration is reduced.

H. But some places are bitterly cold in winter. Can animals somehow avoid freezing? But first, what are the general ways of avoiding or reducing freezing of solutions?
1. Lower freezing point by having more solute particles in solution (a "colligative property"). Supercool -- the ability to remain unfrozen at T_b below the freezing point. Water (esp. with certain solutes) can supercool is cooled slowly and carefully.
2. Antifreezes -- macromolecules that inhibit ice formation and greatly lower the freezing point. Antifreezes have polar groups, bind to ice crystals, and prevent their growth.

I. Do animals use any of these alternatives ("freeze avoidance strategies")?
1. Animals aren't pure water, so their FP will be of course < 0°C. Moreover, many insects and some frogs accumulate glycerol in winter (30% of one wasp is glycerol!), thus lowering their freezing point.
2. Many insects supercool to -10 to 20°C, some to -40°C. Some lizards supercool to 8°C. However, supercooling is risky -- a supercooled insect or fish will "flash" freeze if seeded with ice crystals. Thus safe only for inactive animals!
3. Many animals (inverts, some polar fish) produce "antifreezes" in winter (e.g., peptides, glycopeptides), which lowers freezing point.

G. Can some animals actually survive freezing (= "freeze tolerance strategies")? Remarkably, some animals physiologically promote their own freezing. Occurs in animals (terrestrial insects, intertidal marine mollusks, barnacles, frogs) that are usually **inactive** during prolonged periods. [mussel can survive having 70% of total body water frozen at -20°C (all is extracellular). Wood frog survives (if not mistaken as a Popsicle) with 65% of body water being frozen.]

H. Cold temperature physiology is a "hot" area of research. Cryopreservation (human red blood cells, frozen bull spermatozoa) and cryosurgery.

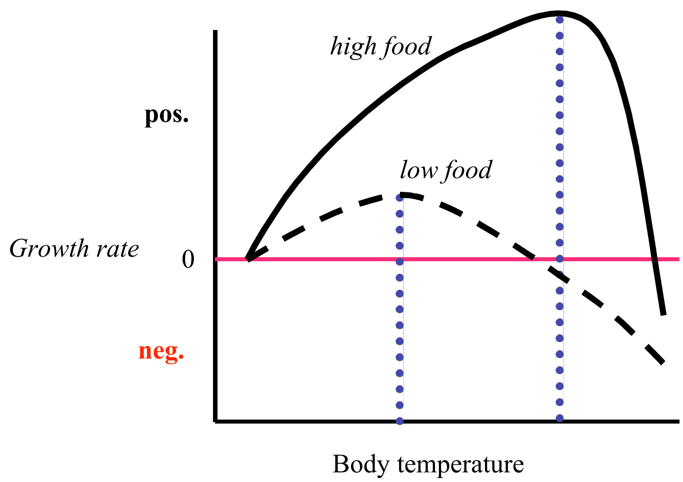
IV. Effects of intermediate temperatures

A. At temperatures below the optimum, physiological rates increase with T_b. In general, if T_b increases by 10°C, rates usually **double**, sometimes triple. Such a huge increase (~ 200% - 300%) is surprising when one recalls that a 10°C rise in T_b increases the average kinetic energy by only a 3%. So why are physiological reactions so temperature sensitive?

B. Sensitivity to temperature is often done by comparing rates at two temperatures differing by 10°C. Called "$\mathbf{Q_{10}}$" ("Q" for quotient, "10" for 10°C range). Q_{10} = rate at high T_b/rate at low T_b, where ΔT_b = 10°C

C. Examples of intermediate temperature effects on ECTOTHERMS
1. Physiological rates increase exponentially up to an optimum T_b then drop.

a. Food intake, swimming speed, growth of salmon are highly sensitive to temperature--optimum is about 15°C. But a low food ration results in lower growth at any T_b and the optimal growth temperature shifts to lower temperatures. Why?



b. Physiological processes may differ in thermal sensitivity. Digestion is often **more** sensitive to temperature (steeper Q_{10}) than is locomotion.

c. Fish learn faster (but forget faster) if at high T_b.

d. ⇒ Important take-home: body temperature affects ability to grow and reproduce, not just to survive.

2. Ectotherms often behaviorally select a characteristic "preferred" body temperature. They do this by seeking sites with favorable microclimates, or by shuttling between warm and cool spots, such that they "average" the thermal conditions of the two spots. Not surprisingly, physiological processes often peak near the preferred body temperature.

3. Some ectotherms such as the desert iguana (US deserts) have a high thermal preference (> 38°C) – so they are hardly cold blooded!

V. Temperature can have especially profound effects on developing organisms.

A. Embryos are usually more sensitive to extreme temperatures than are adults – thus often have a narrower "tolerance range." [N.B. Studies of environmental tolerances may therefore be less relevant than studies of tolerances of developing organisms.]

B. Development time (e.g., egg to adult) declines with temperature, and hatchling size also decreases with temperature. [If you want a superfly, raise it at a low temperature.] Faster generation times in warm seasons.

C. Developmental temperatures can permanently influence adult size, shape, vertebral number (e.g., in fish, snakes), color, reproductive output, etc. Extreme T_b during development can also induce morphological abnormalities, possibly increase mutation rates. [Obviously, be careful where you put your eggs!]

D. Sex of some reptiles (crocodiles, turtles, a few lizards) depends on egg T_b!

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[B. Molecules vary in their kinetic energy. To react a molecule must have at least a threshold energy level ["energy of activation" (E_a)]. At low temperature few molecules are above E_a, but at high temperature many do. The proportion of molecules with energies > E_a increases **exponentially** with temperature. Thus small changes in $\underline{T}_b$ lead to big changes in physiological reactivity.]

VII. Temperature not only has direct effects on animals, but it can have important <u>interactive</u> effects with other environmental variables

A. In nature, several environmental factors may change simultaneously. For example, O_2 availability and $\underline{T}_a$ (ambient temperature) decrease (and rate of dehydration increases) with altitude. Flooding of tide pool will influence temperature, pH, salinity, and O_2 concentration.

B. Environmental factors can have interactive effects of physiology (i.e., effect of one factor depends on another). For example, distance jumped by frog depends both on $\underline{T}_b$ and on level of dehydration. Optimal temperature for salmon growth is influenced by $\underline{T}_b$ and by food level. [Recall: interactive effects can be studied using "multivariate" experimental designs.]

VI. Evolution of thermal tolerance -- what kinds of evidence are relevant?

A. Standard approach -- use "comparative method." Compare heat or cold tolerances of different species (or populations of a single species) that are exposed to different temperatures (e.g., Arctic vs. tropical environments; hot springs or power-plant effluents vs. streams). This gives an <u>historical</u> perspective on evolution.

B. Use genetical techniques to demonstrate that thermal sensitivity shows genetic variation, such that <u>future</u> evolution is possible.

C. "Selection experiments" can be used to demonstrate genetic variation and to study physiological bases of differences in thermal sensitivity (or physiology in general).

1. Selection experiments involve selective breeding of certain phenotypes (e.g., cows with high milk production). Very successful in animal and plant breeding programs, and beginning to be used by physiologists.

2. Earliest study of artificial selection (on flagellates) by the Rev. W. H. Dallinger (1887). These flagellates normally flourish at 18°C but are apparently killed at 60°C. By gradually increasing the culture temperature over seven years, Dallinger could eventually maintain the population at 70°C Moreover, the selected lines could no longer tolerate the initial culture temperature

.2. What? But I just claimed (above) that freezing is lethal! The trick is that, in freeze-tolerant animals, the frozen water is <u>extracellular</u>, not intracellular.

3. Why do extracellular fluids (ECF) freeze first? ECF has lower protein concentration than in cells, so ECF will freeze first. As ECF water freezes (ice is pure water, no solutes), remaining ECF fluid becomes concentrated with remaining solutes, causing water to be withdrawn <u>osmotically</u> from cells. Thus, the concentrated cellular fluids can remain unfrozen

4. In fact, many beetles have special "ice nucleating agents" that actually promote ECF freezing. (p. 202)

3. More recent studies -- selection in <u>Drosophila</u> for increased heat or cold tolerance usually increases (genetic) resistance to high temperatures.

D. Selection studies being used to explore basic physiological issues in stress tolerance and in aging, and for manipulating biocontrol agents. Very useful.