4 Coping with Environmental Variation: Temperature and Water

4 Coping with Environmental Variation: Temperature and Water

- *Case Study: Frozen Frogs*
- CONCEPT 4.1 Each species has a range of environmental tolerances that determines its potential geographic distribution.
- CONCEPT 4.2 The temperature of an organism is determined by exchanges of energy with the external environment.
- CONCEPT 4.3 The water balance of an organism is determined by exchanges of water and solutes with the external environment.
- *Case Study Revisited*

Case Study: Frozen Frogs

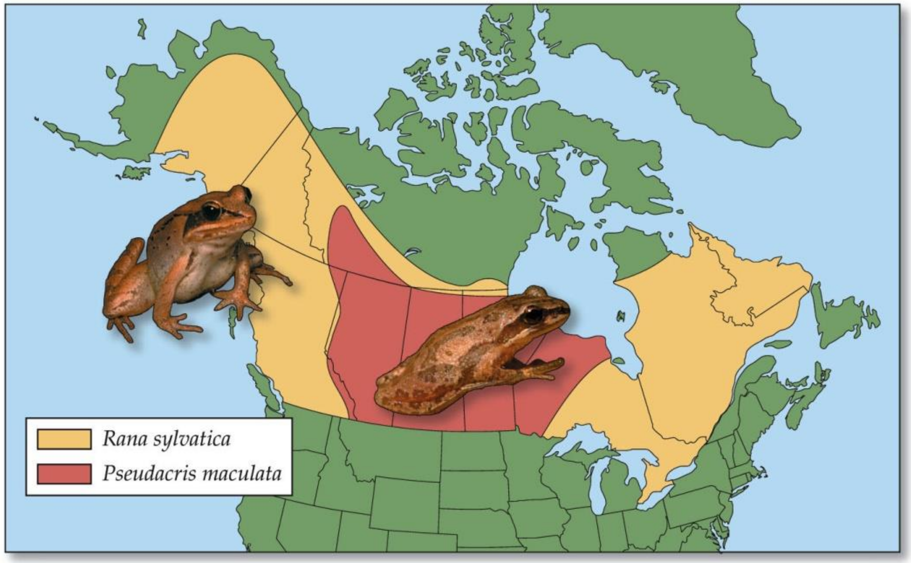
In the movie *Austin Powers: International Man of Mystery*,

- Austin Powers and Dr. Evil were frozen—put into a state of suspended animation— and unfrozen 30 years later.

Interest in this idea has resulted in ***cryonics*** — preservation of bodies by freezing, in hopes they can be brought back to life in the future

http://davidszondy.com/future/Living/cryonics01.jpg

Case Study: Frozen Frogs



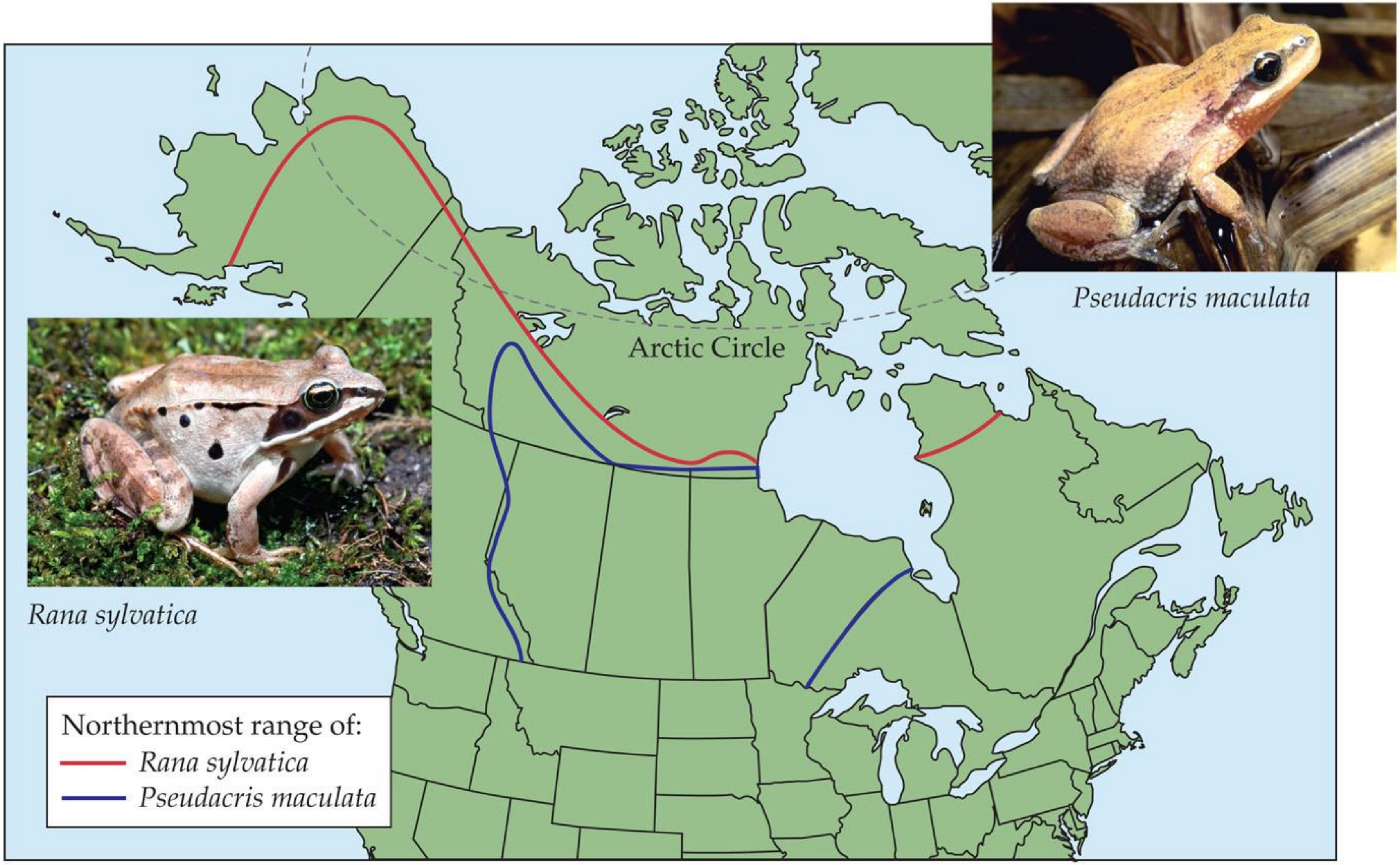
***ECOLOGY,* Figure 4.2**

***ECOLOGY,* Figure 4.1**

Organisms such as frogs can survive winter in a completely frozen state

- Although frogs first evolved in tropical biomes, two species live in the Arctic tundra
- They overwinter in shallow burrows, in a semi-frozen state, with no heartbeat, no blood circulation, and no breathing

Figure 4.2 Northern Exposure



ECOLOGY 3e, Figure 4.2

Case Study: Frozen Frogs

Few vertebrates can withstand freezing (**freeze tolerance**)

- In most organisms, freezing results in tissue damage as ice crystals perforate cell membranes and organelles

Examples of known "freezable" herps

Amphibians	**Reptiles**
Wood frog (*Rana sylvatica*)	Painted turtles (*Chrysemys picta*)
Gray tree frog (*Hyla versicolor*)	Box turtles (*Terrapene*)
Spring peeper (*Pseudacris crucifer*)	Garter snakes (*Thamnophis sirtalis*)
Chorus frog *(Pseudacris triseriata*)	European common lizard (*Lacerta vivipara*)

http://http-server.carleton.ca/~kbstorey/ftverts.htm

Introduction

Organisms have two options for coping with environmental variation:

- **Tolerance**
- **Avoidance**

Spruce trees (*Picea* sp.) in Alaska

- Spruce trees in the boreal forest can not avoid temperature extremes, and so must be able to tolerate air temperatures that drop below –50°C in winter, and reach 30°C in summer

http://www.denali.org/images/Spruce%20Trees%20and%20Sky.jpg

Physiological ecology…

- Study of interactions between organisms and their environment and
- How these interactions influence their survival and persistence.

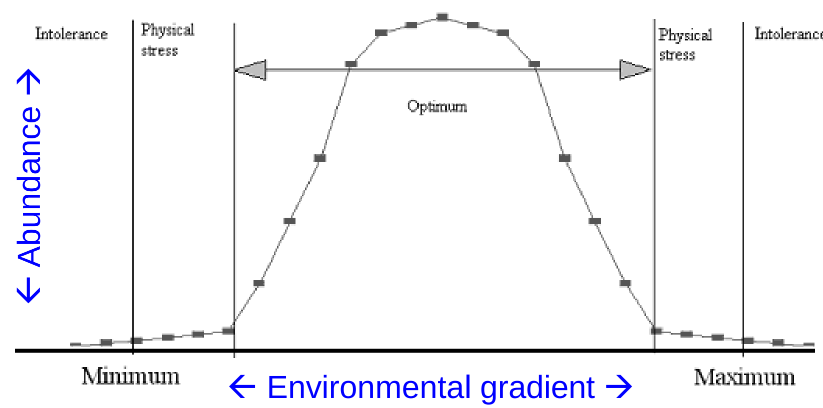
Pitcher plant near Okefenokee Swamp

Image by B. Tyler

Concept 4.1: Each species has a range of environmental tolerances that determines its potential geographic distribution.

A fundamental principle in ecology and biogeography is that *geographic ranges of species are related to* ***constraints imposed by the environment***

- Shelford's "**Law of tolerance**" – usually multiple environ-mental factors involved



Really important

http://www.elements.nb.ca/Theme/chemical/marc/fig1-e.gif

Response to Environmental Variation

The physical environment influences an organism’s success in two ways:

- Affects *availability of energy and resources* and the abiligy to maintain metabolic functions, grow and reproduce
- Extreme environmental conditions affect *survival*

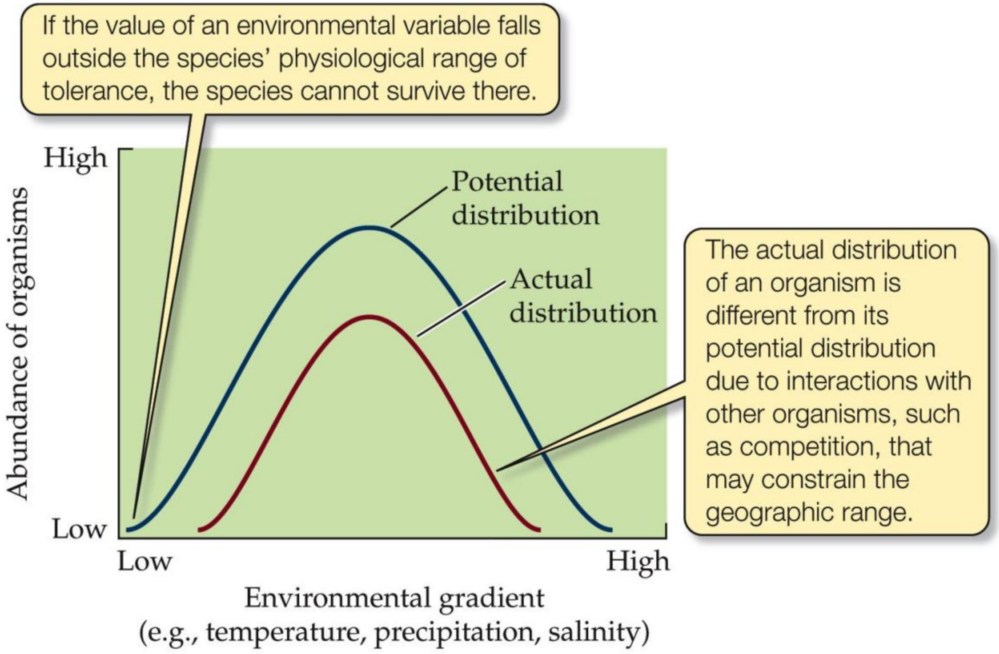
Pine growing Bryce Canyon National Park, Utah

Image by B. Tyler

Response to Environmental Variation

Energy acquisition and environmental tolerance limits are not mutually exclusive:

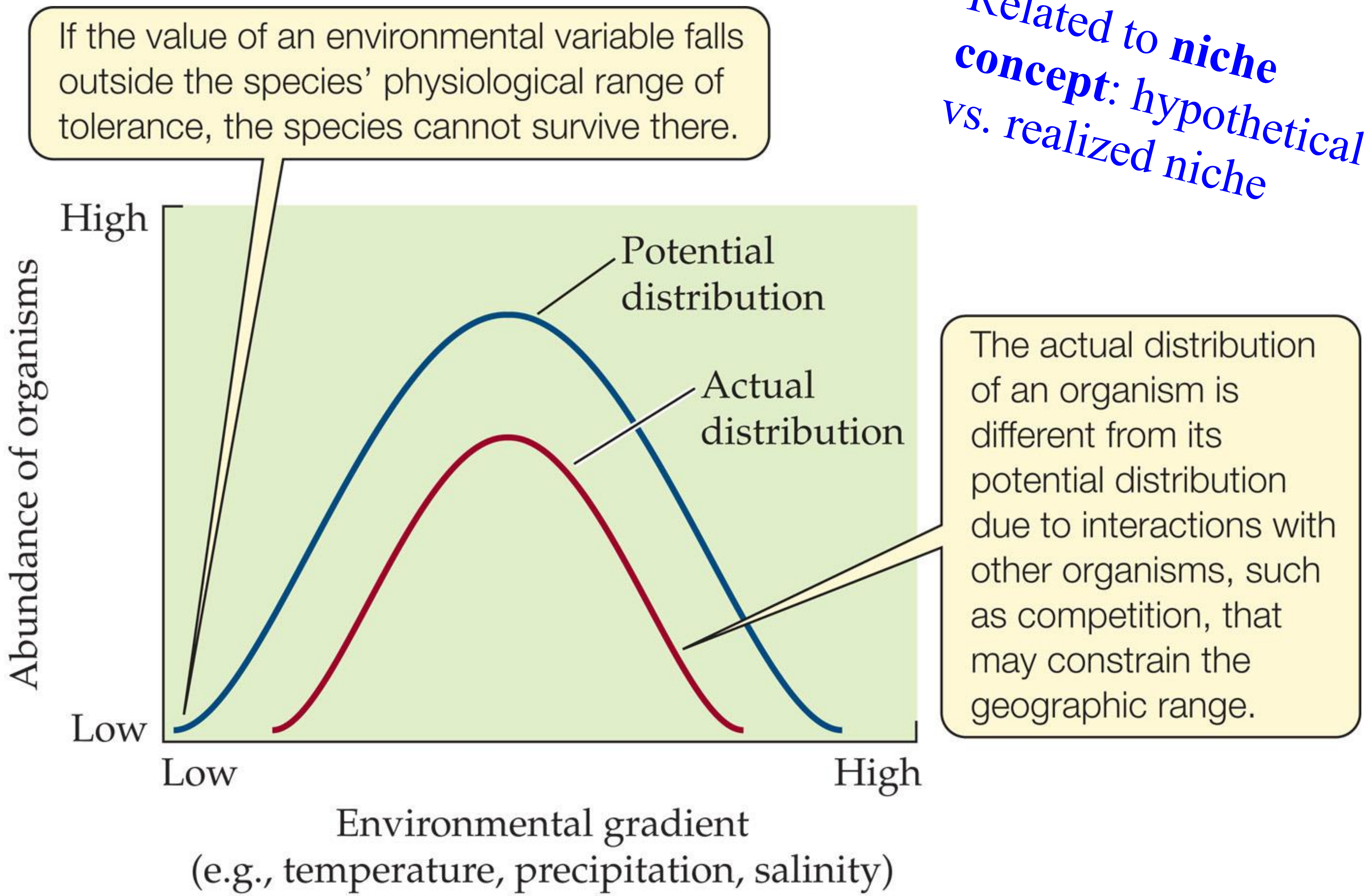
- Energy supply influences an organism's ability to tolerate environmental extremes
- Actual geographic distribution of a species also related to other factors, such as **disturbance** and **competition**



ECOLOGY, Figure 4.3

Figure 4.3 Abundance Varies across Environmental Gradients

Related to **niche concept**: hypothetical vs. realized niche



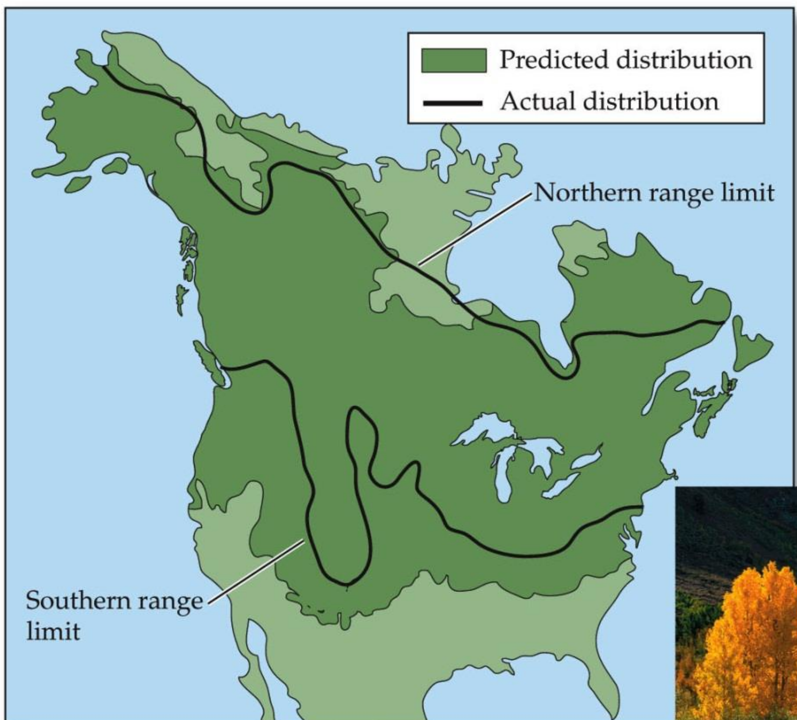
ECOLOGY 3e, Figure 4.3

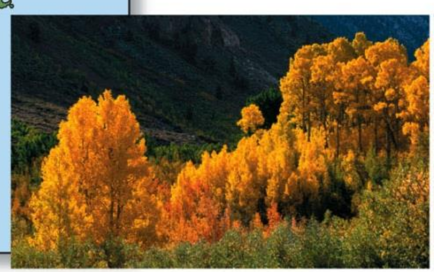
Response to Environmental Variation

Because plants do not move, they are good indicators of the physical environment

- Range of aspens is related to climatic tolerance
- Aspen distribution can be predicted based on climate – low temperatures and drought affect reproduction and survival

(A)

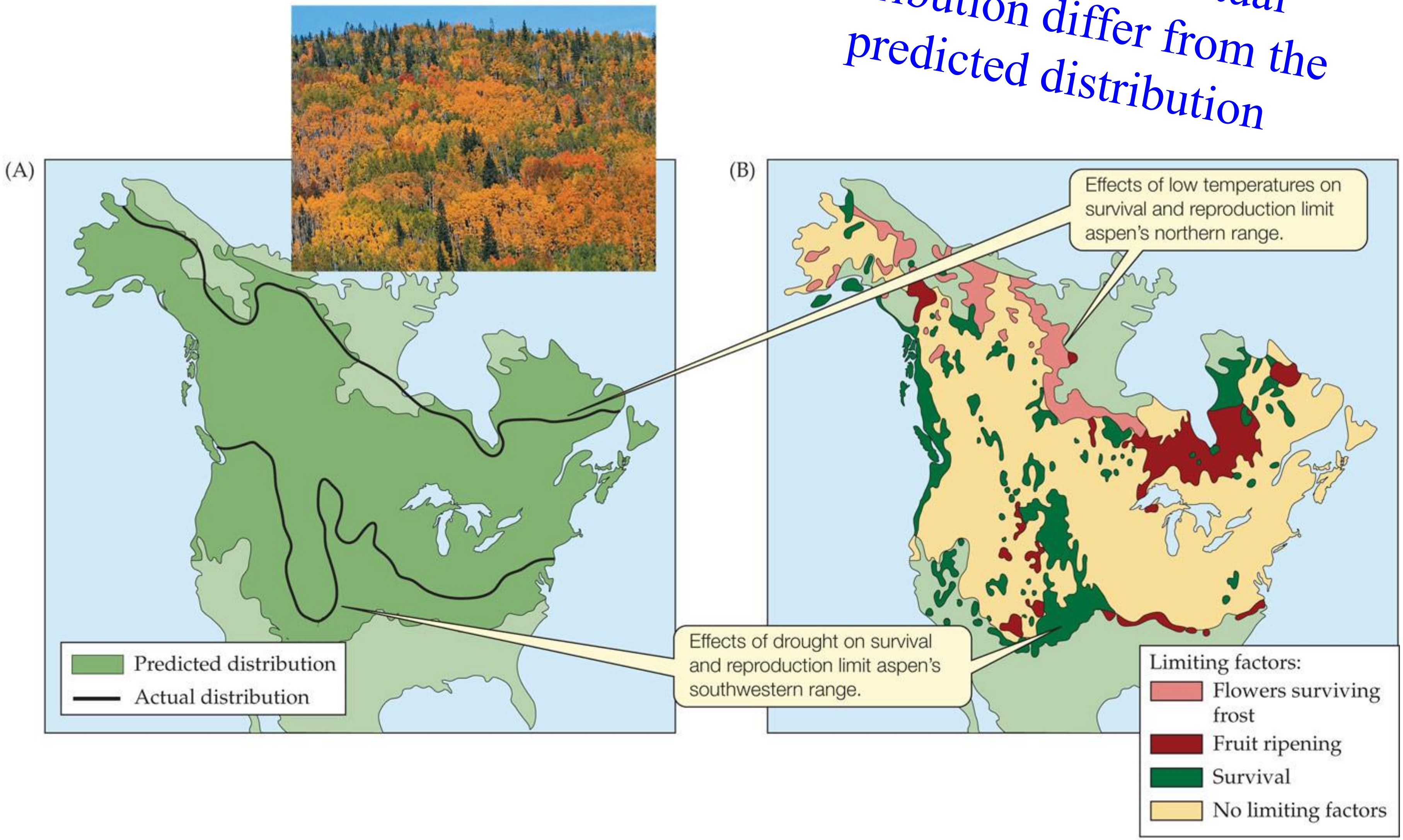




ECOLOGY, **Figure 4.4 (Part 1)**

Figure 4.4 Climate and Aspen Distribution

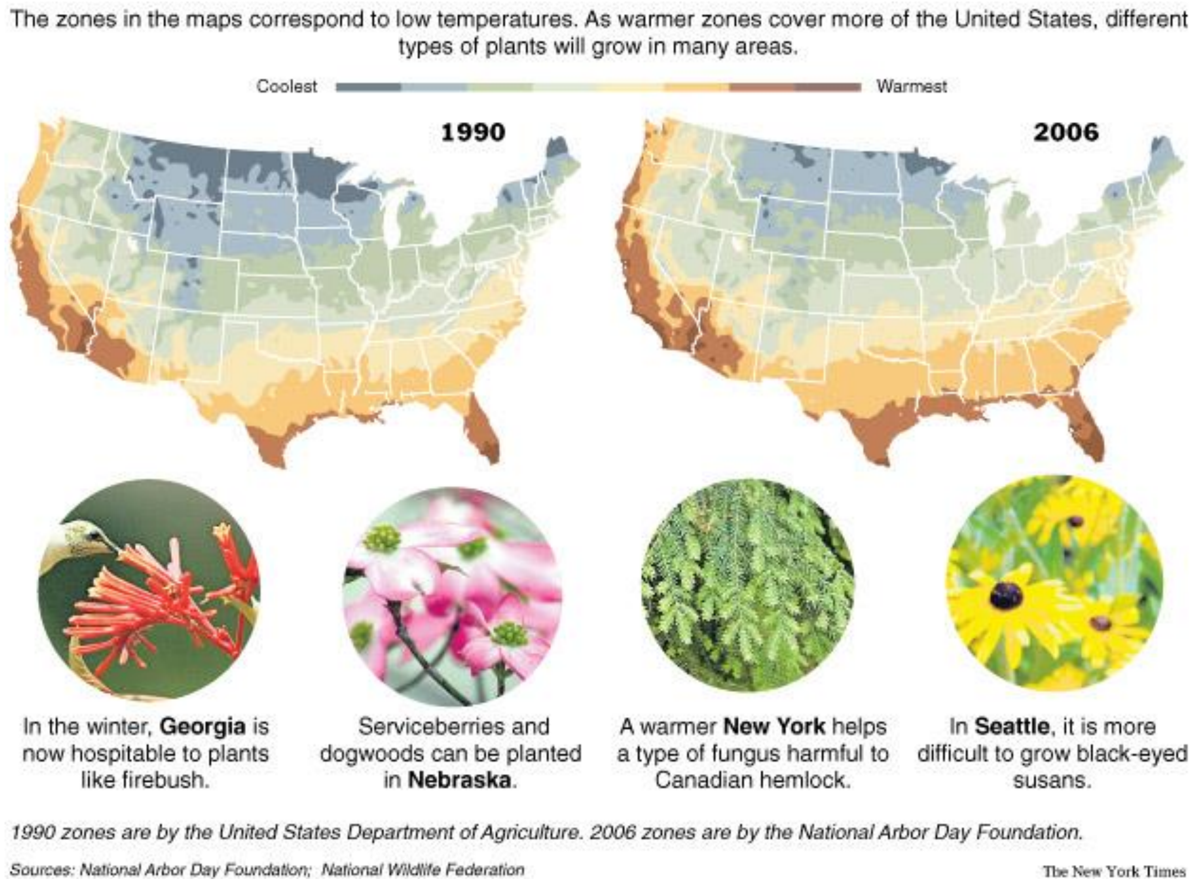
Why might the actual distribution differ from the predicted distribution



ECOLOGY 3e, Figure 4.4

A species' ***climate envelope*** is the range of conditions over which it occurs

- It is a useful tool for predicting its response to climate change

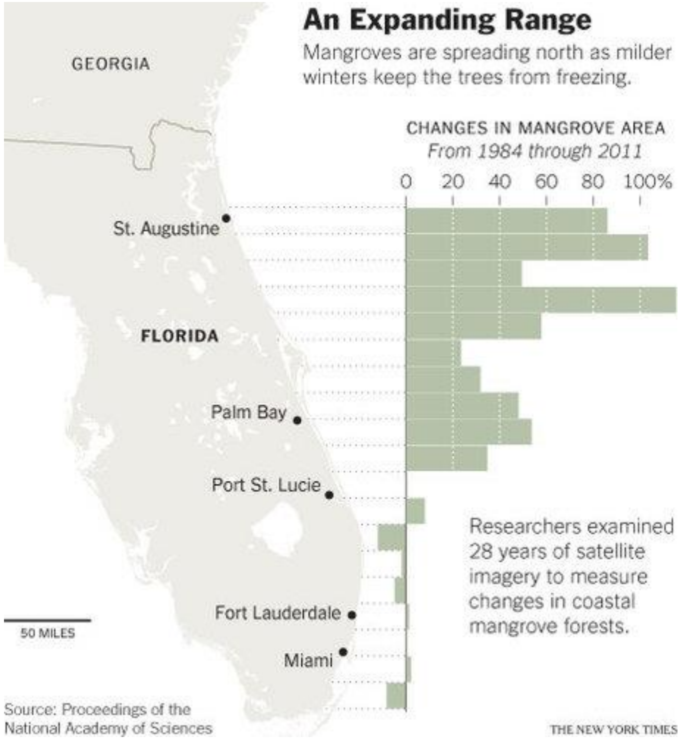


Note warmer temperatures "moving" north

http://media.artdiamondblog.com/images2/GlobalWarmingPlantsMoveNorth.jpg

Ranges are shifting as climate changes

- Range of mangroves is moving north
  - Originally dominated south of Cocoa Beach, and saltmarsh grasses dominated above St. Augustine.
  - With warmer extreme temps over last 28 years, lethal threshold of -4^{O}C has moved north allowing mangroves to spread

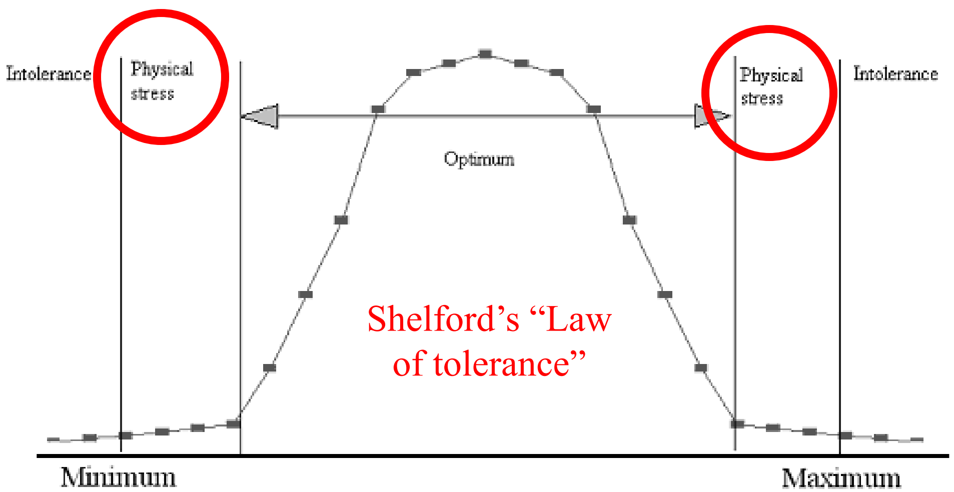


http://www.nytimes.com/2013/12/31/science/without-winter-freezes-mangroves-are-marching-north-scientists-say.html?pagewanted=2&_r=0&emc=eta1

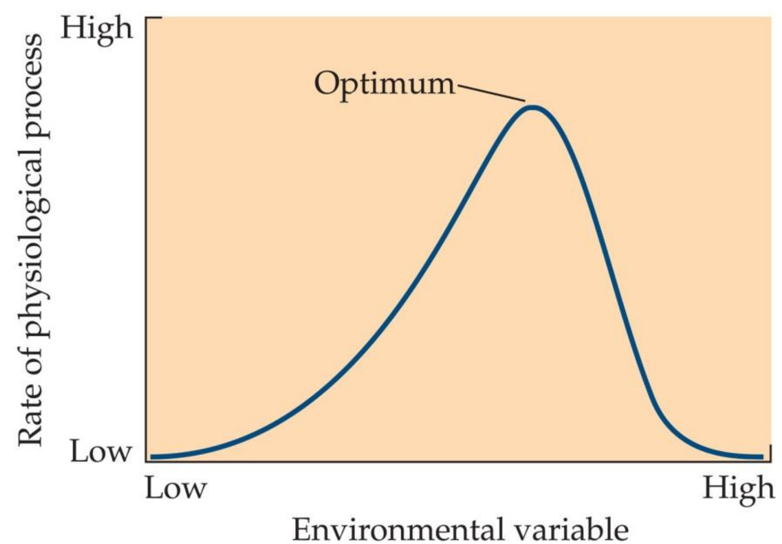
Response to Environmental Variation

Physiological processes have a set of optimal conditions for functioning

- Deviations from optimum reduce rate of the process
- **Stress** — environmental change results in decreased rates of important physiological processes, *<u>lowering</u> potential for survival, growth, or reproduction*



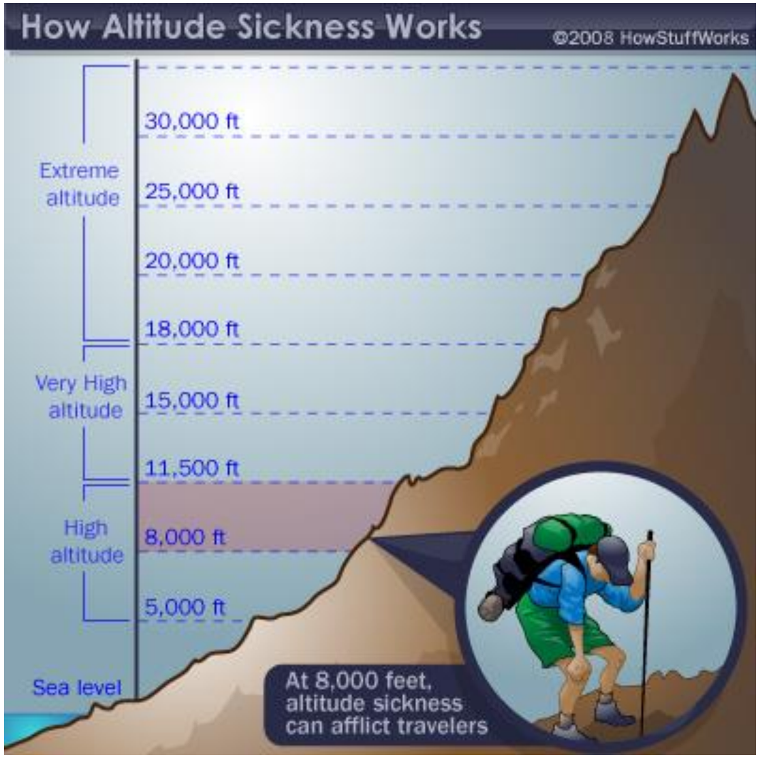
http://www.elements.nb.ca/Theme/chemical/marc/fig1-e.gif



ECOLOGY 3e, Figure 4.5

Example: High altitudes

- At high altitudes, lower partial pressure of oxygen in atmosphere results in ***hypoxia*** — not enough oxygen is delivered to your tissues
- Hypoxia causes "altitude sickness," which is physiological stress

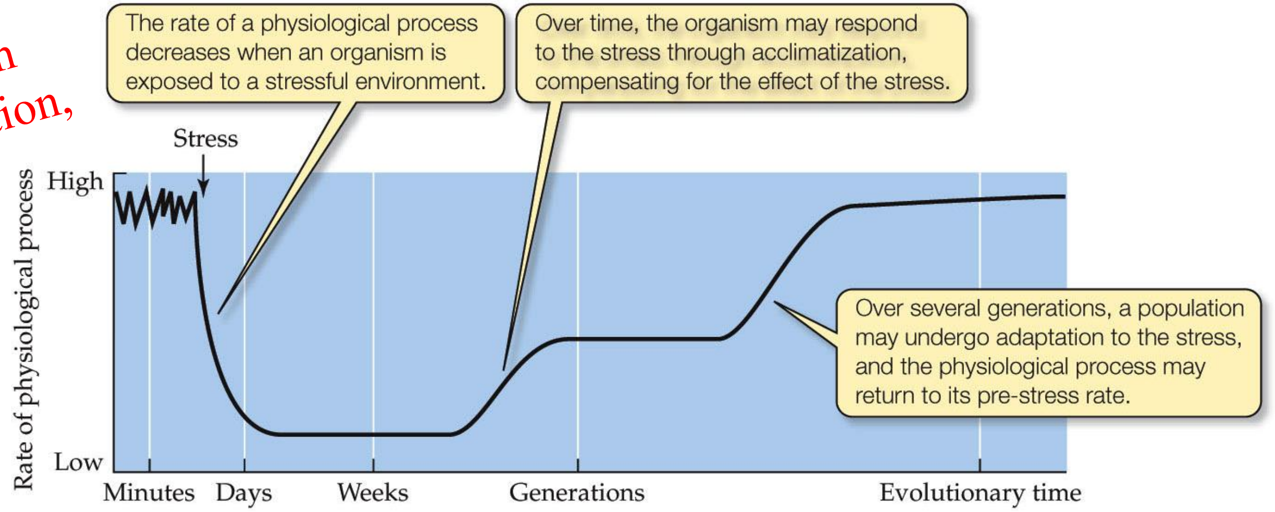


http://static.howstuffworks.com/gif/altitude-sickness-13.jpg

Acclimatization

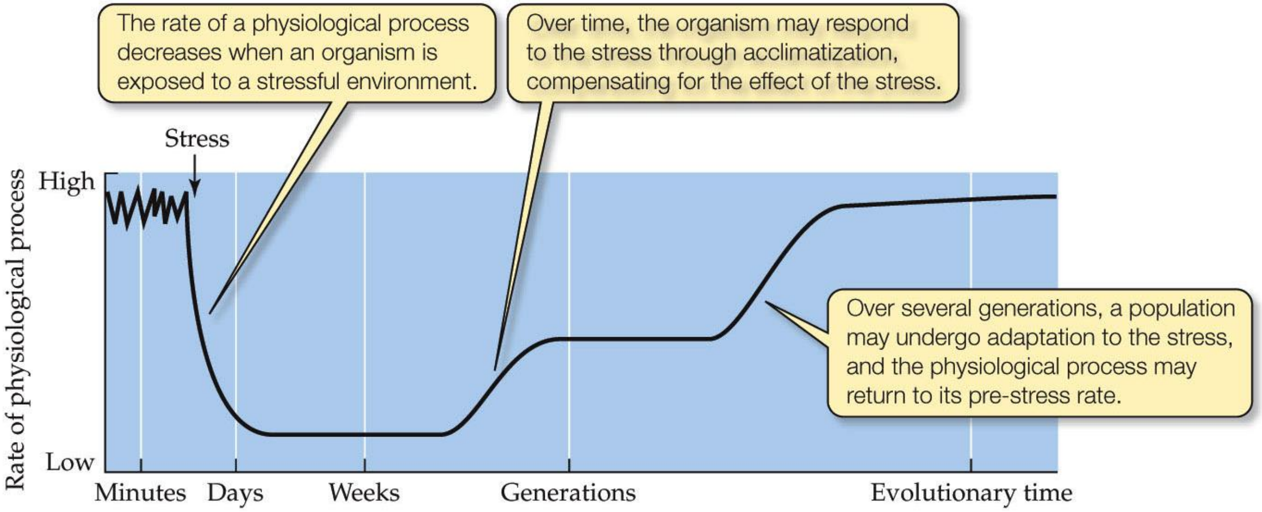
- Many organisms can adjust to stress through behavior or physiology over "*ecological time*"
- Short-term, *reversible* process within a single individual's lifetime (possibly seasonal) – an *individual phenomenon*
- Acclimatization to high elevations involves higher breathing rates, greater production of red blood cells, and higher pulmonary blood pressure

Know differences between acclimatization and adaptation, and examples



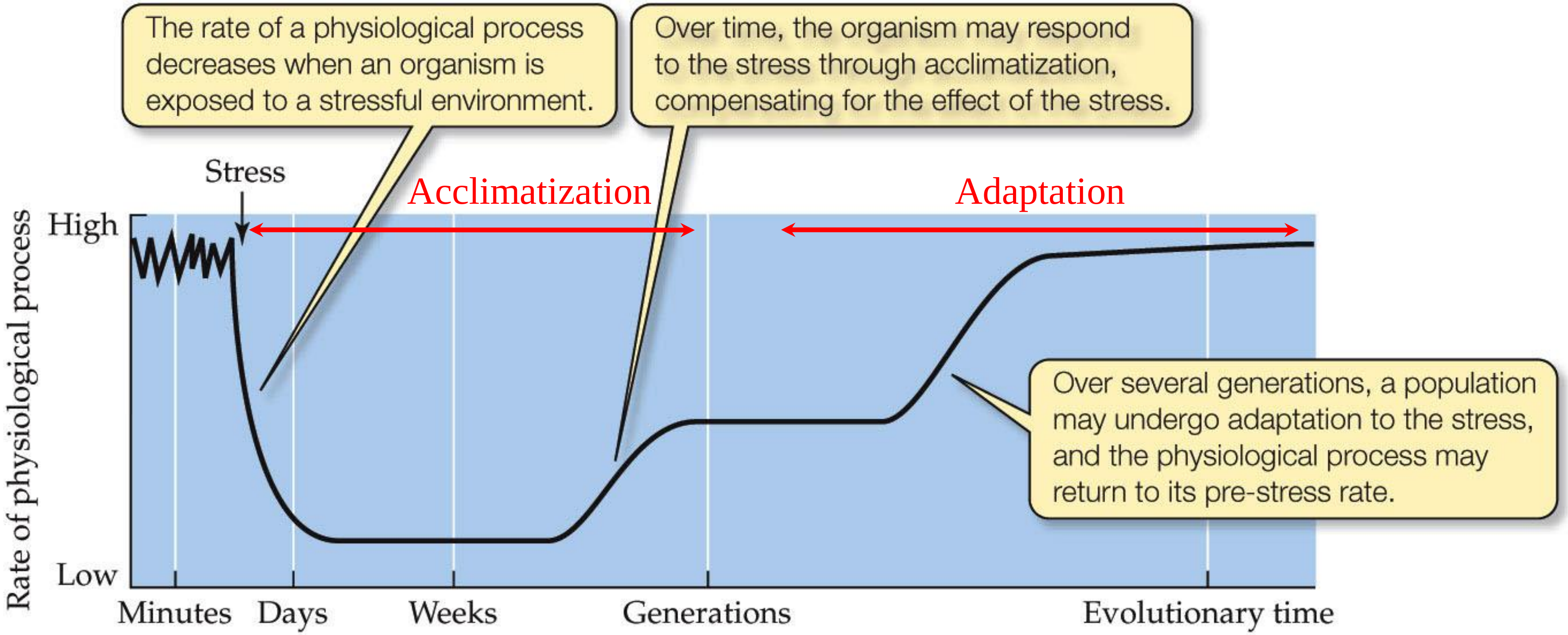
Adaptation (in contrast to acclimatization)

- Long-term, population-level change to environmental stress over time via natural selection
- Individuals with traits that make them best able to cope with stress are favored
- Over "*evolutionary time*", these unique, genetically-based solutions become more frequent in the population – a *population phenomenon*



- Adaptation is similar to acclimatization but adaptation is long-term, genetic response of a population to environmental stress that increases its survival and reproductive success
  - The *ability* of an organism to acclimatize is, in itself, an adaptation; genes controlling acclimatization would be advantageous

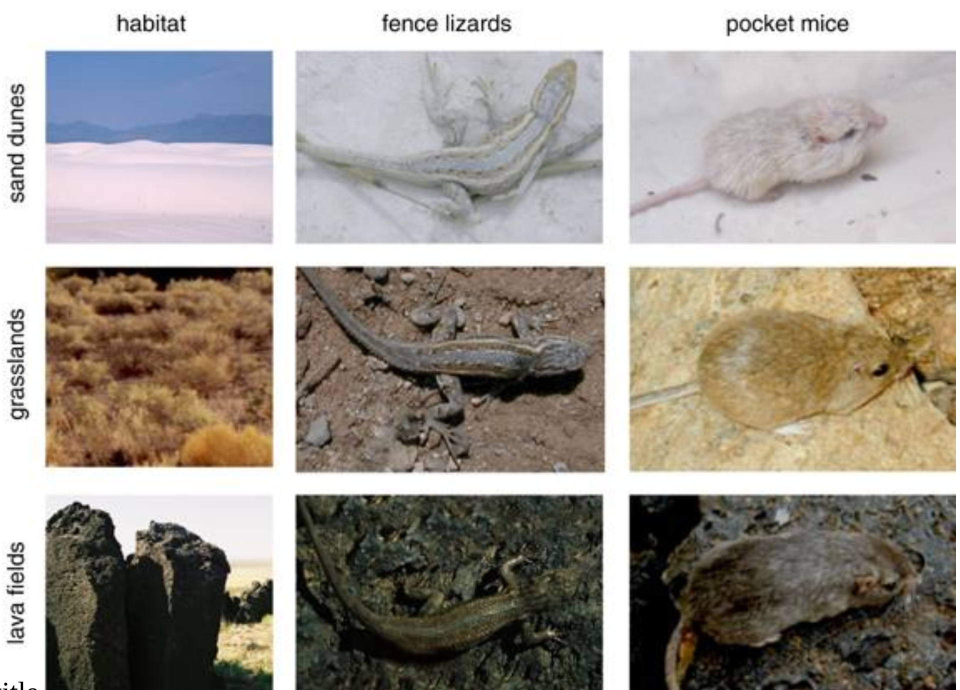
How would you differentiate these two responses in natural populations?



Ecotypes

- Populations with adaptations to unique environments
- Ecotypes may eventually become separate species as populations diverge and eventually become reproductively isolated

Convergent evolution of adaptive pigmentation in the Tularosa Basin of New Mexico. The Carrizozo lava field is separated from the gypsum sand dunes of White Sands by 25 km of desert grasslands. Western fence lizards, *Sceloporus undulatus*, rock pocket mice, *Chaetodipus intermedius* (melanic and wild-type morphs) and apache pocket mice, *Perognathus flavescens* (blanched morph) are pictured on the substrate where they were captured.



http://www.nature.com/hdy/journal/v97/n3/fig_tab/6800861f3.html#figure-title

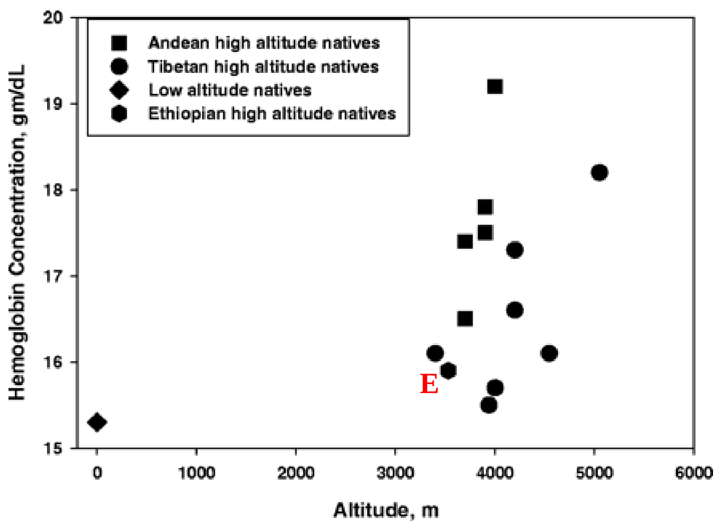
Response to Environmental Variation

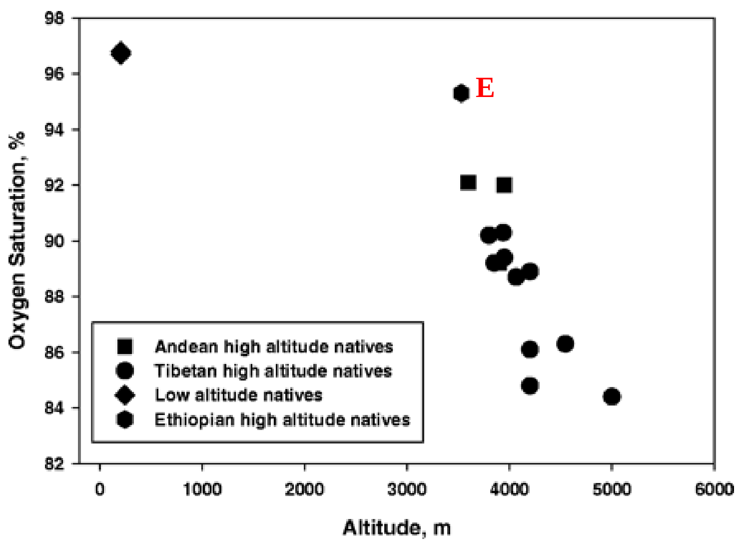
- Example of adaptation: Humans have lived in the Andes Mountains for 10,000 years
  - When Spanish first settled there in 16th and 17th centuries, their birth rates were low for 2–3 generations, probably due to poor oxygen supply to developing fetuses
  - In contrast, indigenous Andean populations were adapted to low-oxygen conditions by having *higher red blood cell production* and greater lung capacity

http://steinhardt.nyu.edu/photos/peru/pic2.jpg

Adaptations can vary among populations

- Populations at high elevations in Tibet and Ethiopia have different adaptations – *why might this be?*
- Tibetans don't have higher blood cell counts, but do have faster breathing rates
- Ethiopians don't have higher cell counts, but have *higher blood oxygen levels*





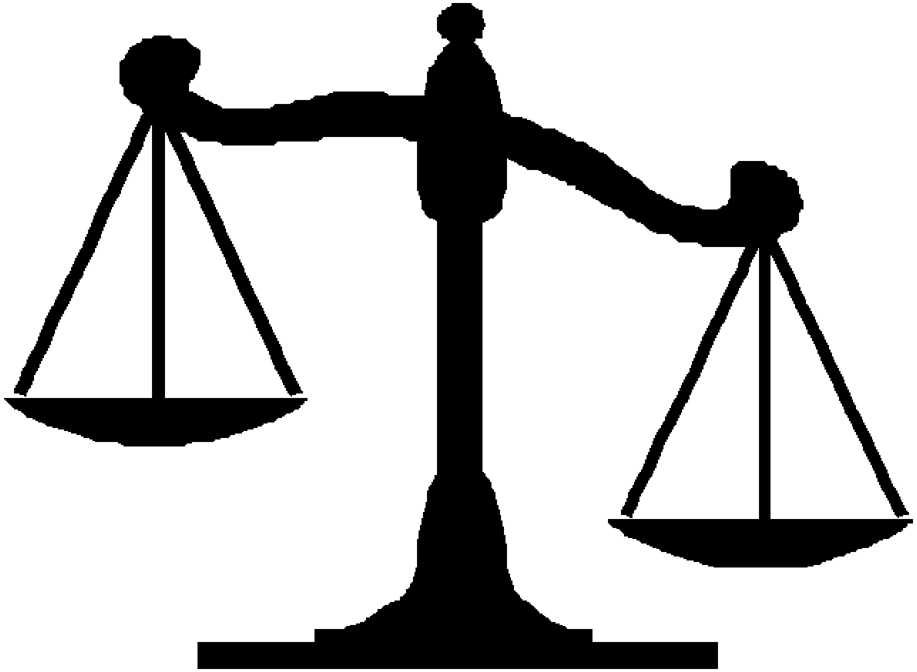
http://icb.oxfordjournals.org/cgi/content/full/46/1/18

Response to Environmental Variation

Acclimatization and adaptation require investments of energy and resources

- Represents possible **tradeoffs** with other functions that can also affect survival and reproduction
- Often constrained by other adaptations/acclimatization

Trade-offs are important to consider



http://www.tulanelink.com/legal/balance2.gif

Variation in Temperature

Concept 4.2: The temperature of organisms is determined by exchanges of energy with the external environment.

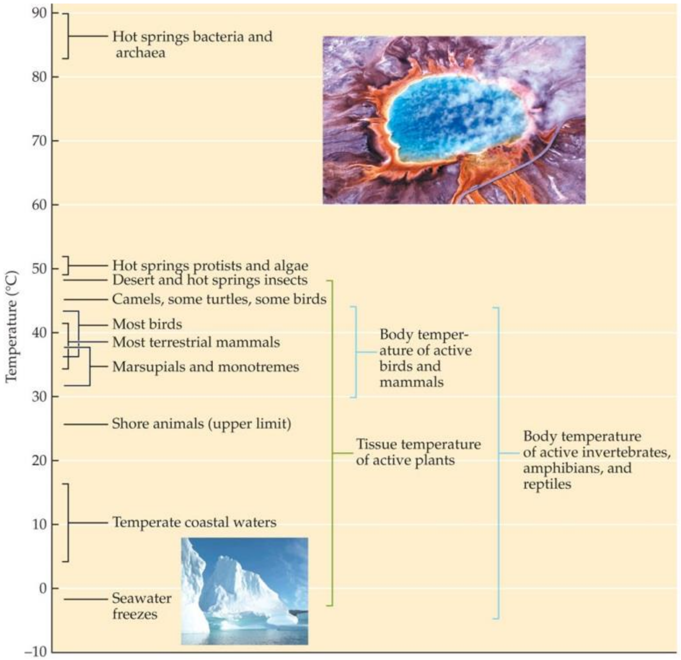
Environmental temperatures vary greatly throughout the biosphere

- Some habitats experience little variation, while others have large seasonal or daily variation
- i.e. "variability is variable"

Variation in Temperature

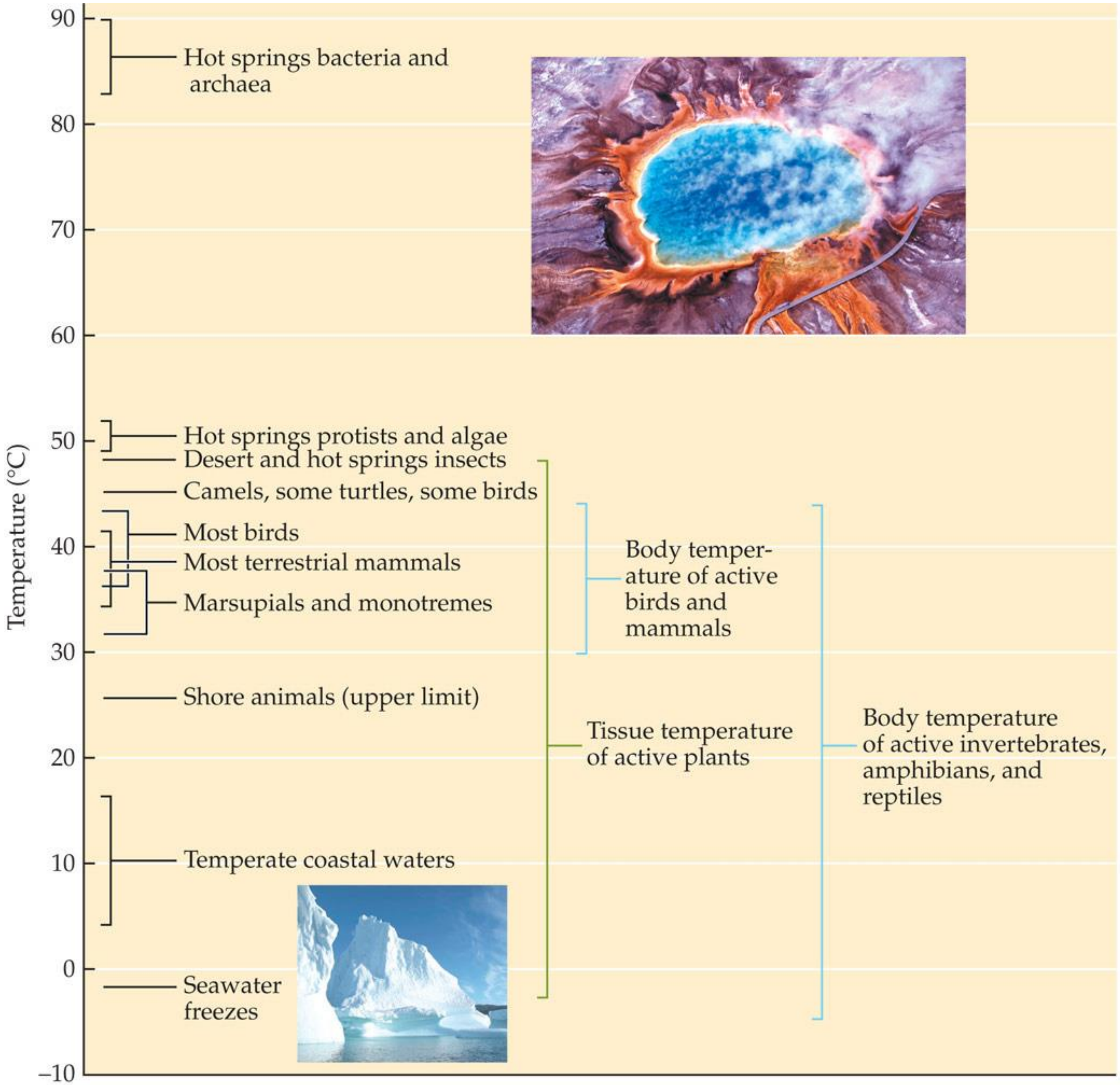
Survival and functioning of organisms strongly tied to their internal temperatures

- Some archaeans and bacteria in hot springs can function at 90°C
- Lower limits are determined by temperature at which water freezes in cells (–2 to –5°C)



ECOLOGY 3e, Figure 4.7

Figure 4.7 Temperature Ranges for Life on Earth



***ECOLOGY 3e*, Figure 4.7**

Variation in Temperature

Some organisms can survive periods of extreme heat or cold by entering a state of ***dormancy***, in which little or no metabolic activity occurs

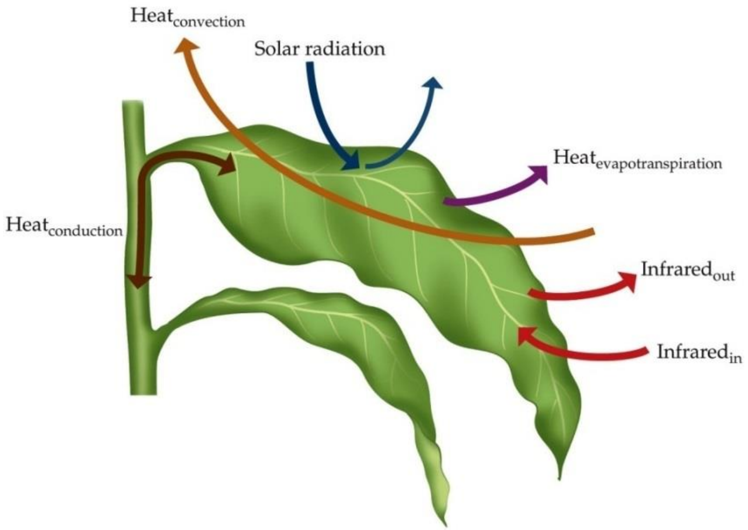
- **Hibernation**
- **Daily torpor**
- **Estivation**

http://staffwww.fullcoll.edu/tmorris/elements_of_ecology/images/chipmunk_hibernating.jpg

Variation in Temperature

Temperature controls physiological activity.

- An organism’s temperature is related to the balance between gains and losses of energy to the external environment
- Organisms must either tolerate internal temperature change or modify it by some physiological, morphological, or behavioral means (tolerance or acclimatization)

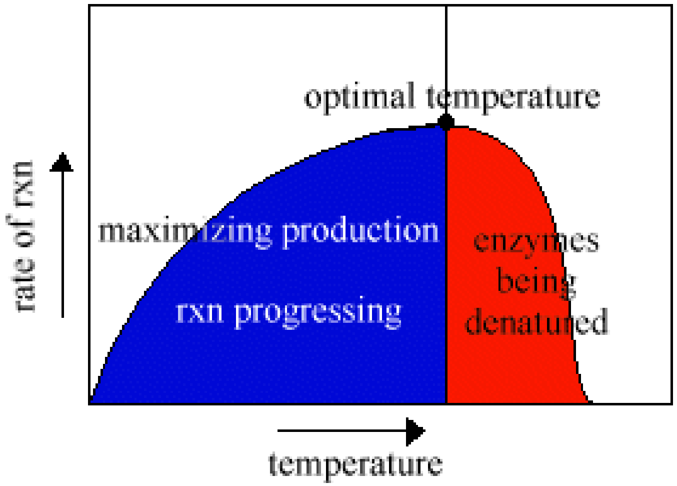


ECOLOGY, Figure 4.8

Variation in Temperature

Metabolic reactions are temperature-sensitive, due to the sensitivity of *enzymes*, which catalyze the reactions

- Enzymes are stable only within a narrow range of temperatures
- At high temperatures, enzymes become *denatured*, which destroys enzyme function
- **Q_{10} relationship** (from Bio II)



http://library.thinkquest.org/C006669/media/Biol/img/enzymes_optimal_temperature.gif

Variation in Temperature

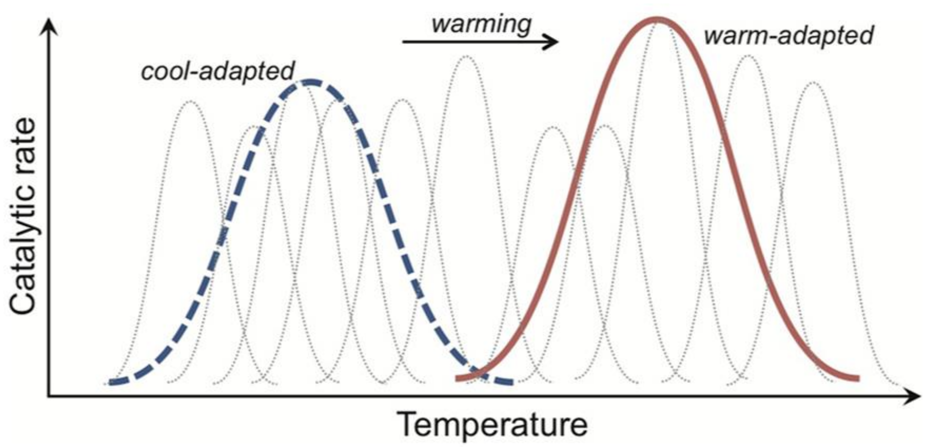
- Bacteria in hot springs have enzymes that are stable up to 100°C
- Antarctic fish and crustaceans must have enzymes that function at –2ºC
- Soil microbes are active at temperatures as low as –5ºC

The Antarctic ice fish has no red blood pigments (haemoglobine) and no red blood cells. This is an adaptation to the low temperature. The blood becomes more fluid; as a consequence, the animals save energy in pumping blood through their bodies.

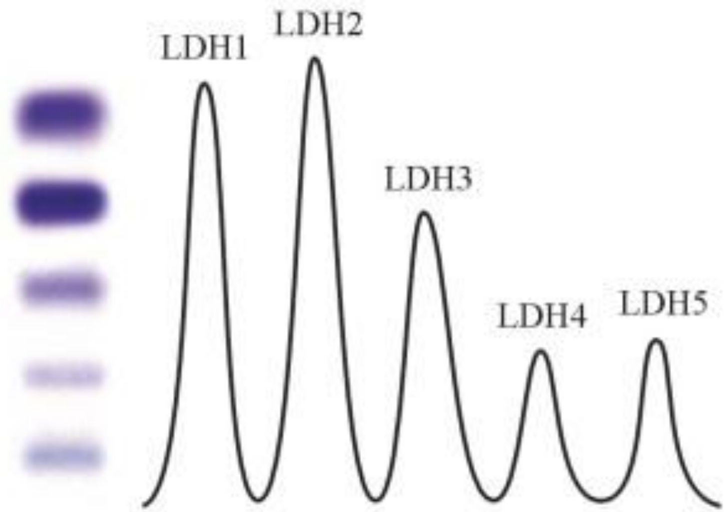
http://farm1.static.flickr.com/161/420033134_a1bf26c5b8.jpg?v=0

Some species produce different forms of enzymes (**isozymes; isoenzymes**) with different temperature optima.

- Isozymes allow acclimatization to changing conditions, such as seasonal temperature change.



http://journal.frontiersin.org/Journal/10.3389/fmicb.2013.00333/full

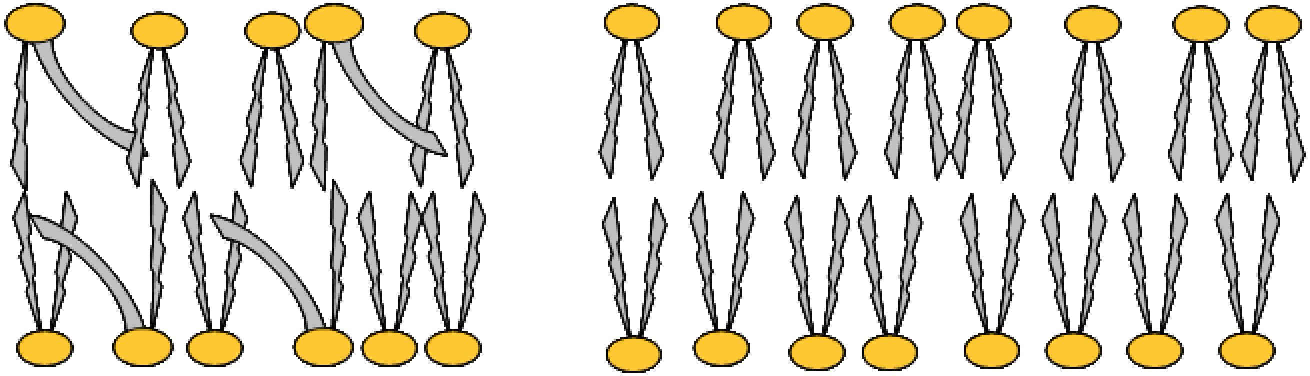


http://www.interlab-srl.com/en/test-menu/ldh-isoenzymes-electrophoresis-kit

Variation in Temperature

Temperature also affects the properties of cell and organelle membranes, which are composed of two layers of lipid molecules

- At low temperatures, these lipids can solidify, embedded proteins can't function, and the cells leak metabolites (remember from Bio I)

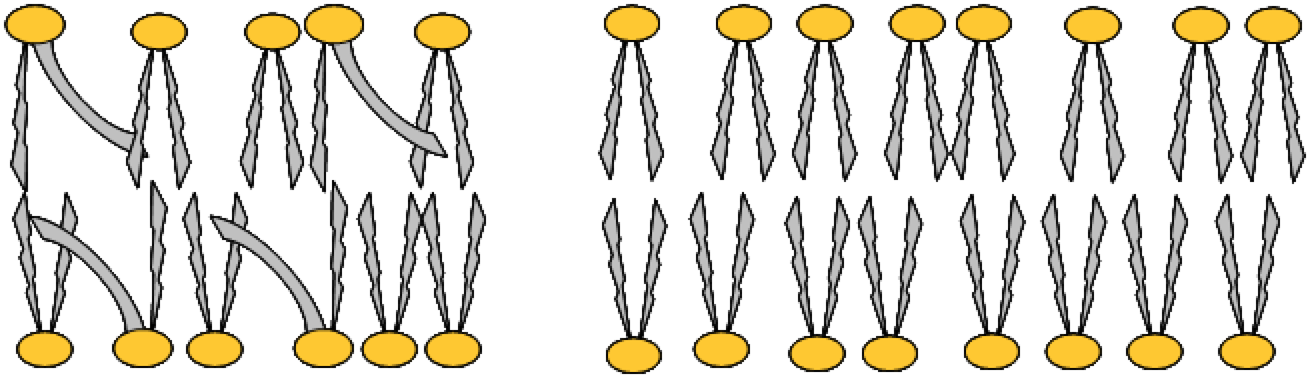


http://www.steve.gb.com/science/lipids_and_membranes.html

Variation in Temperature

The chemical composition of membrane lipid molecules affects temperature sensitivity

- Plants that thrive at low temperatures have higher proportions of unsaturated lipids (with double bonds) in their cell membranes
- Some plants can acclimatize by changing membrane fatty acid composition



http://www.steve.gb.com/science/lipids_and_membranes.html

Temperature also affects water availability

- The rate at which terrestrial organisms lose water from their bodies is related to air temperature

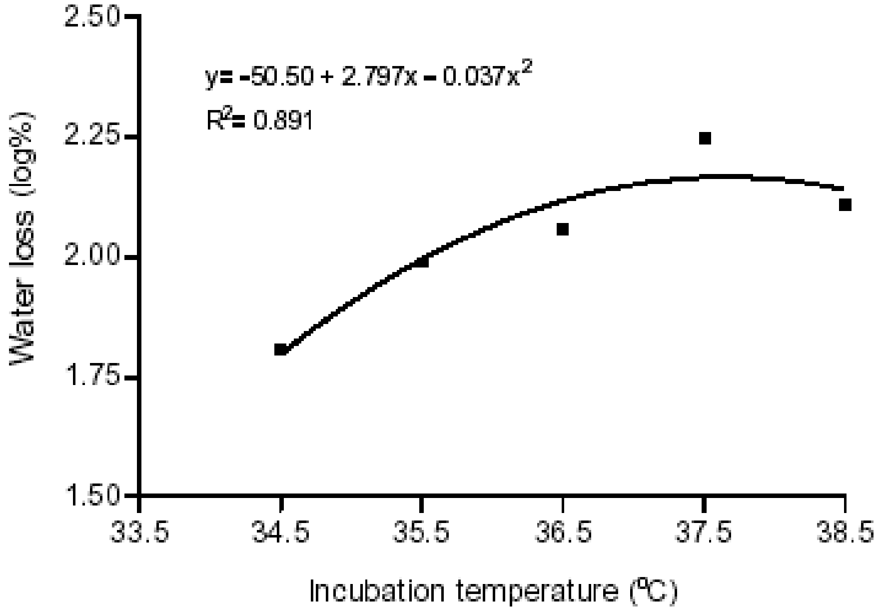


Figure 4 – Effect of different incubation temperatures on total water loss (log %) of partridge eggs, from day 1 to day 16 of incubation. N=20/temperature.

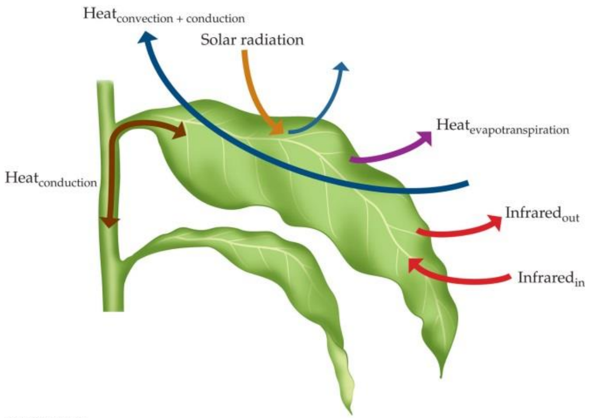
http://farm3.static.flickr.com/2063/2250488401_30ac751ef2.jpg?v=0

http://www.scielo.br/img/revistas/rbca/v5n2/a07fig04.gif

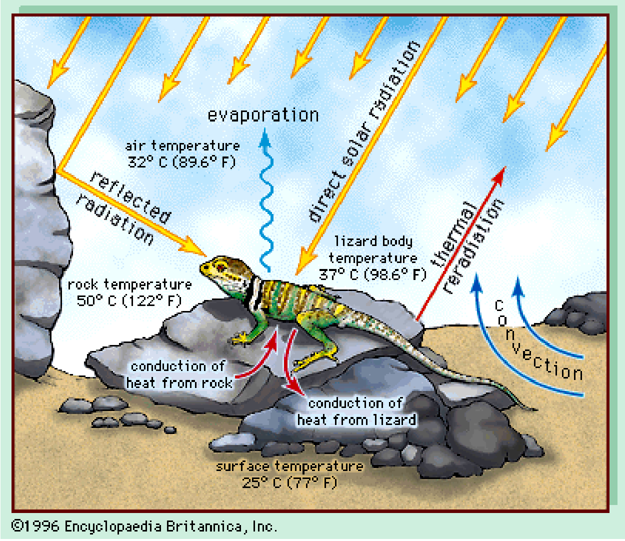
Variation in Temperature

Balance between inputs and outputs of energy determines whether temperature of any object will increase or decrease

- Organisms can adjust their exchange of energy with environment (e.g. move to shade)
- Many can change behaviors to avoid adverse temperatures
- many also have varying degrees of tolerance



ECOLOGY 3e, Figure 4.8



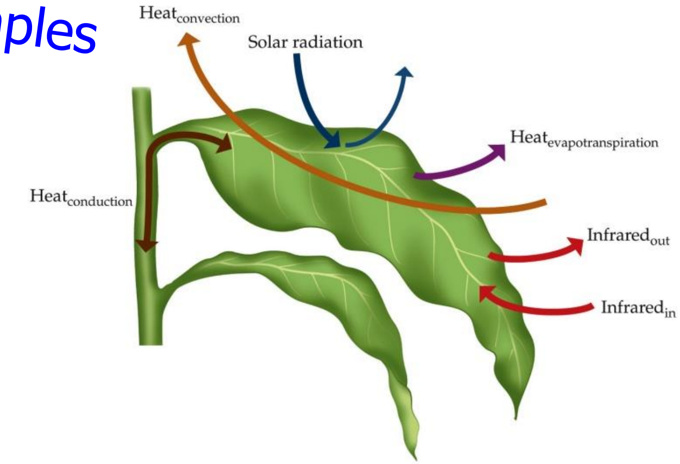
http://media-2.web.britannica.com/eb-media/40/6540-004-507B7D2B.gif

Variation in Temperature

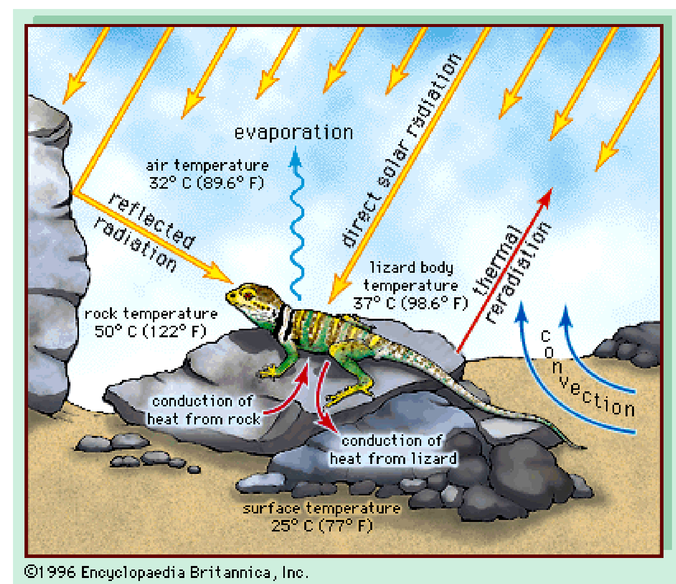
Know these four with examples

Energy exchange with environment can be by *four processes (recall from Ch 2)*:

- ***Conduction*** — transfer of energy from warmer to cooler molecules
- ***Convection*** — heat energy is carried by moving water or air
- ***Evaporation* (*latent heat transfer*)** — water absorbs heat as it changes state from liquid to gas
- ***Radiation*** — radiating heat (infrared radiation) from warmer to cooler



***ECOLOGY*, Figure 4.8**

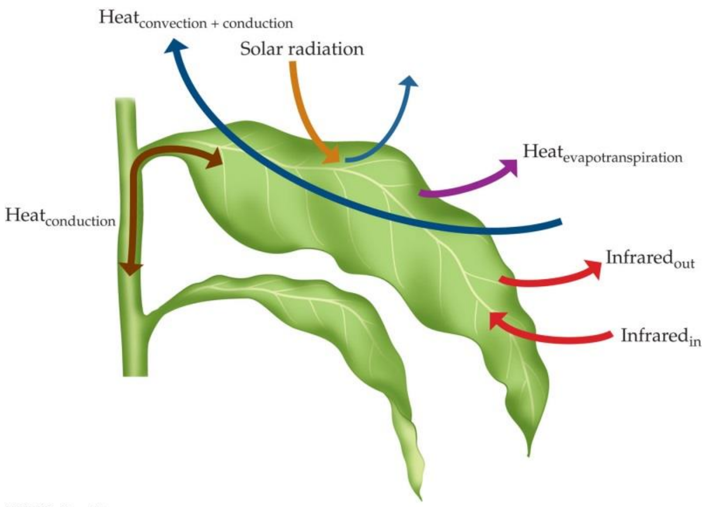


http://media-2.web.britannica.com/eb-media/40/6540-004-507B7D2B.gif

Variation in Temperature

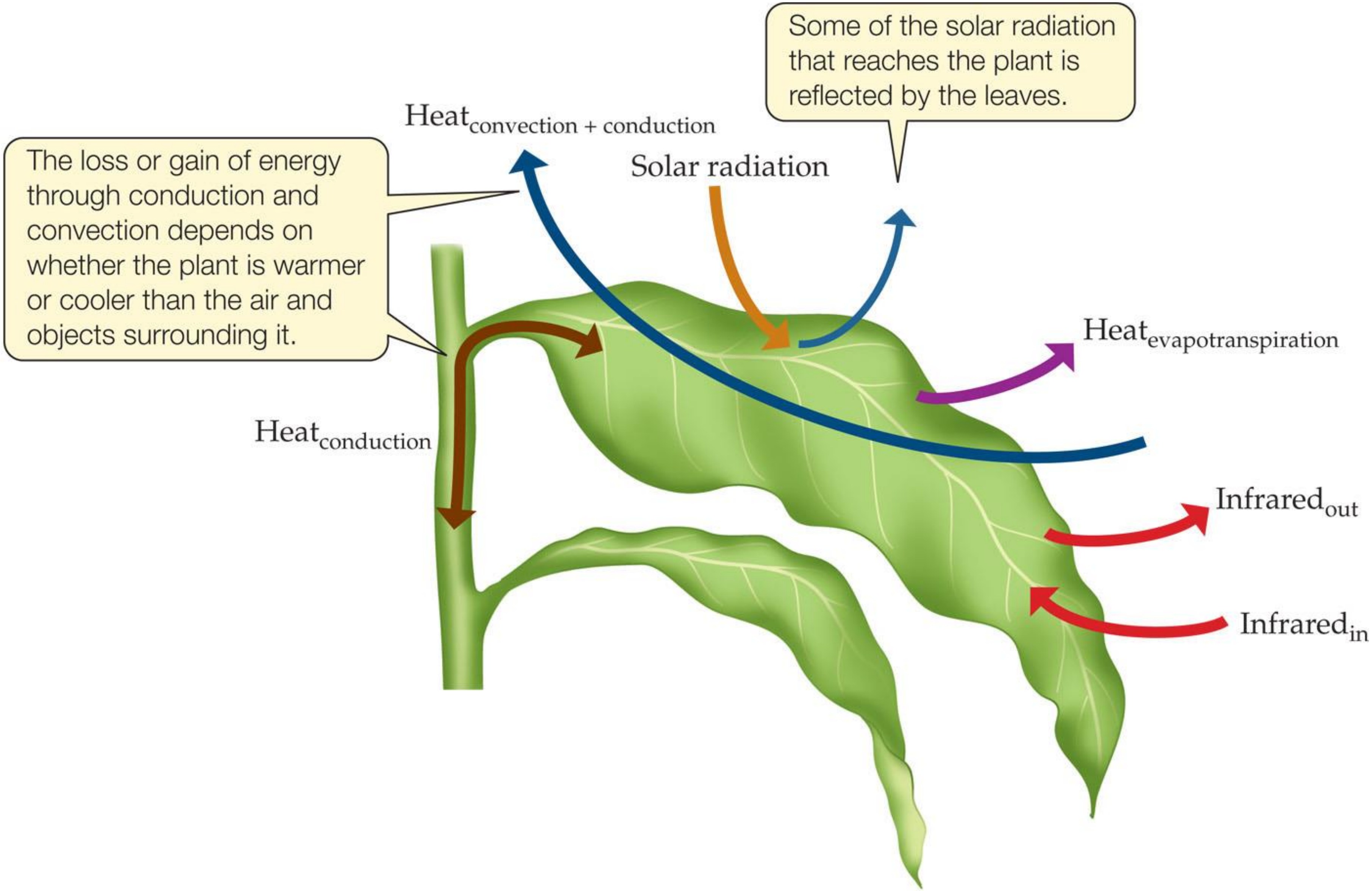
For terrestrial plants, energy inputs include sunlight and longwave (**infrared**) radiation from surrounding objects

- Losses of energy include emission of infrared radiation (heat) to environment, and through ***evapotranspiration***



ECOLOGY 3e, Figure 4.8

Figure 4.8 Energy Exchange in Terrestrial Plants



ECOLOGY 3e, Figure 4.8

Variation in Temperature

Temperature change in a plant can be expressed by the following equation

Don't memorize, but should know what factors effect energy transfer in plants

$$\Delta H_{plant} = SR + IR_{in} - IR_{out} \pm H_{conv} \pm H_{cond} - H_{et}$$

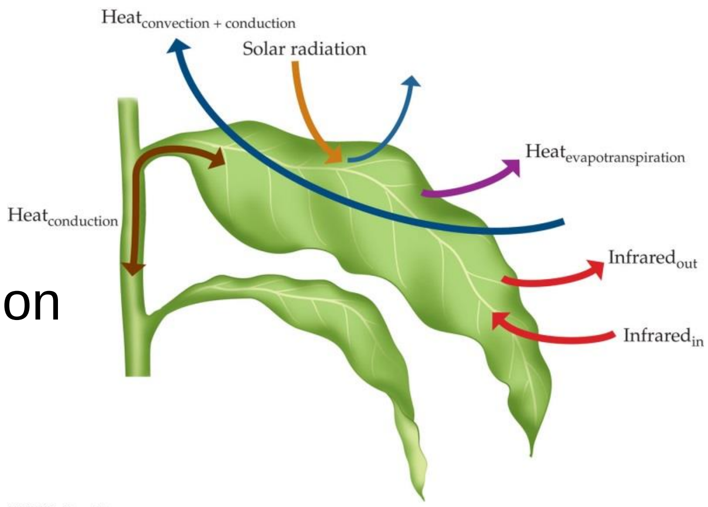
SR = Solar radiation

IR = Infrared radiation

H_{conv} = Convective heat transfer

H_{cond} = Conductive heat transfer

H_{et} = Heat transfer by evapotranspiration

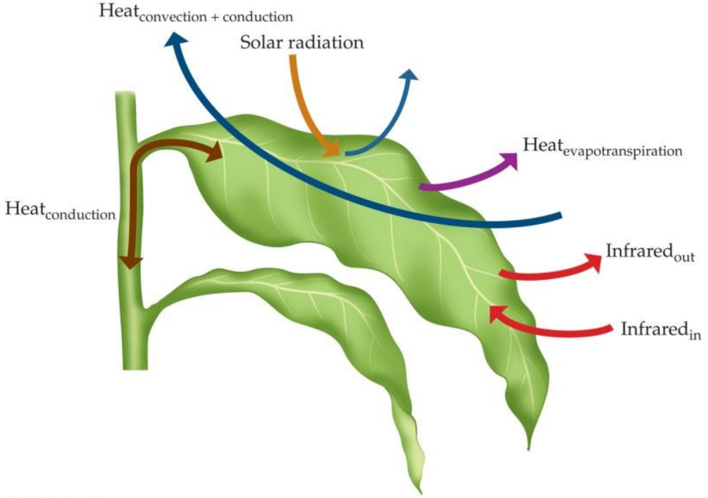


ECOLOGY 3e, Figure 4.8

Variation in Temperature

$$\Delta H_{plant} = SR + IR_{in} - IR_{out} \pm H_{conv} \pm H_{cond} - H_{et}$$

- If plant is warmer than the surrounding air, H_{conv} and H_{cond} are negative
- If total energy inputs exceed total outputs, then ΔH_{plant} is positive, and the plant's temperature is increasing
- If more heat is being lost than gained, then ΔH_{plant} is negative, and the plant's temperature is decreasing

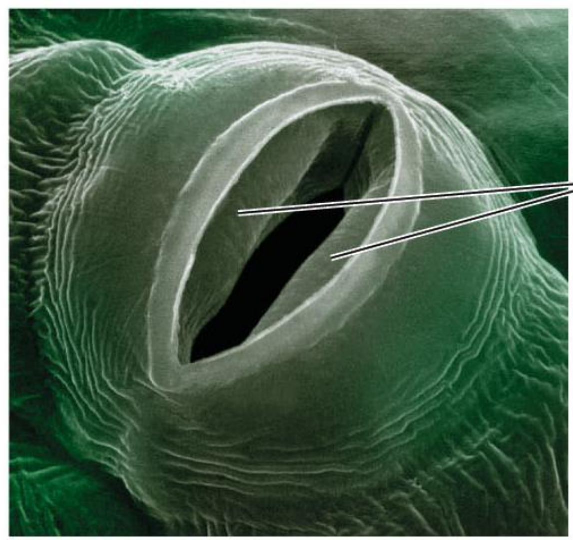


ECOLOGY 3e, Figure 4.8

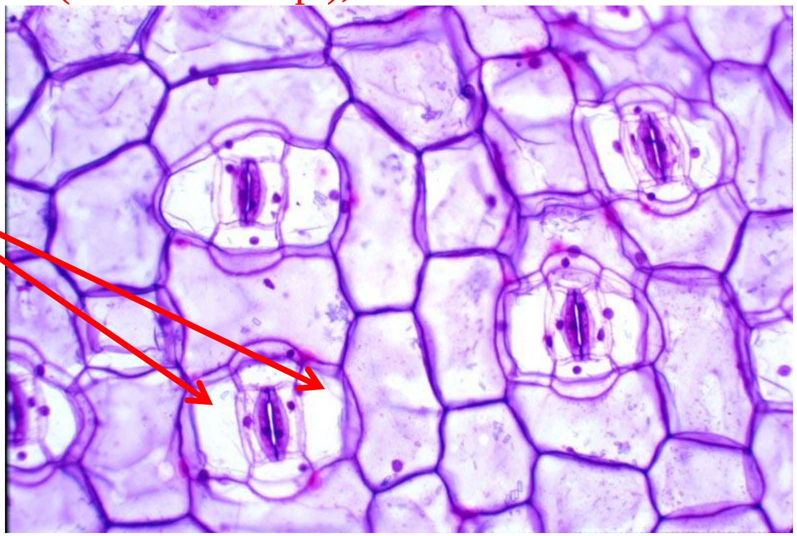
Plants can adjust energy inputs and outputs

- Transpiration rates can be controlled by specialized ***guard cells*** surrounding a pore, called a **stomate** (***stomata*** = pl.)
- Variation in degree of opening and number of stomata control rate of transpiration and thus control leaf temperature

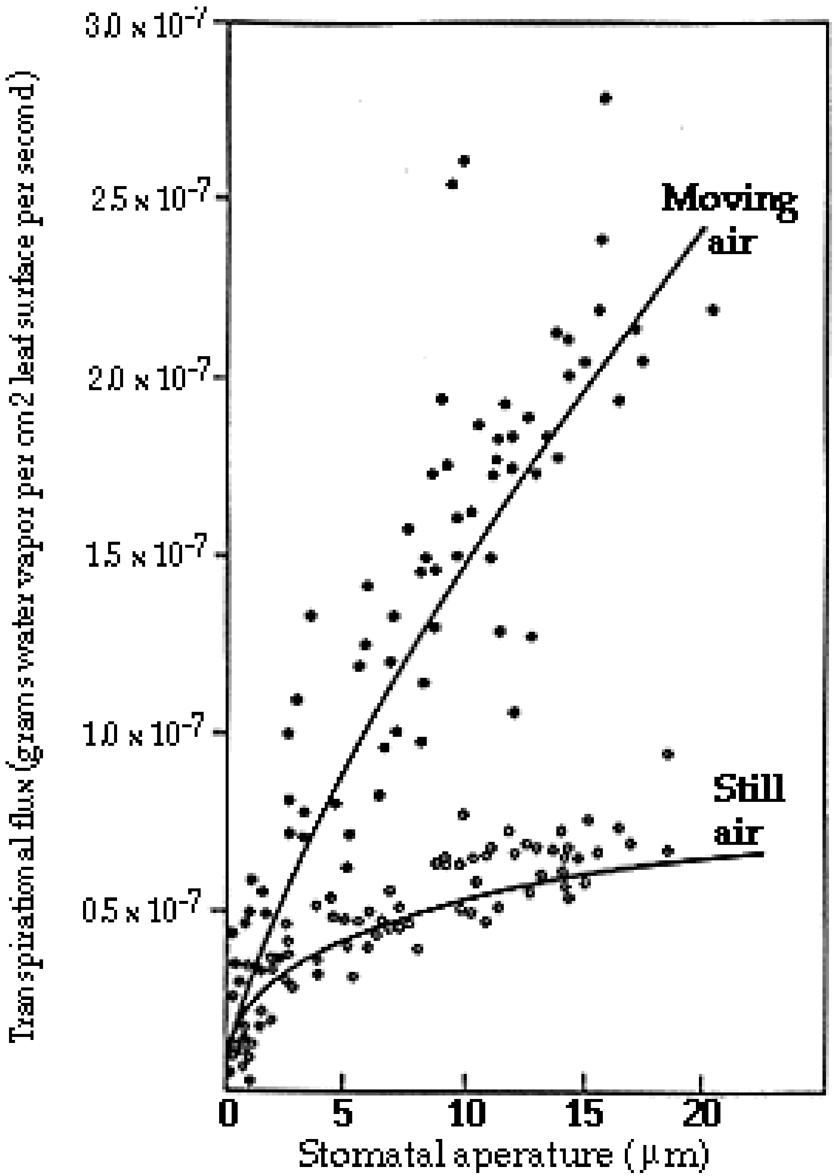
(A)



Leaf epiderm of dayflower (*Commelina* sp.), a monocot

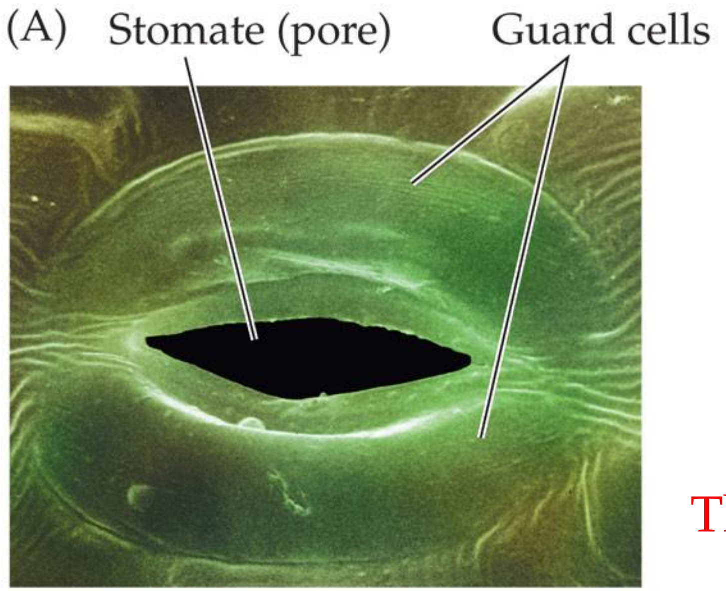


- Transpirational water loss increases with size of stomatal aperature *and* is greater in moving air



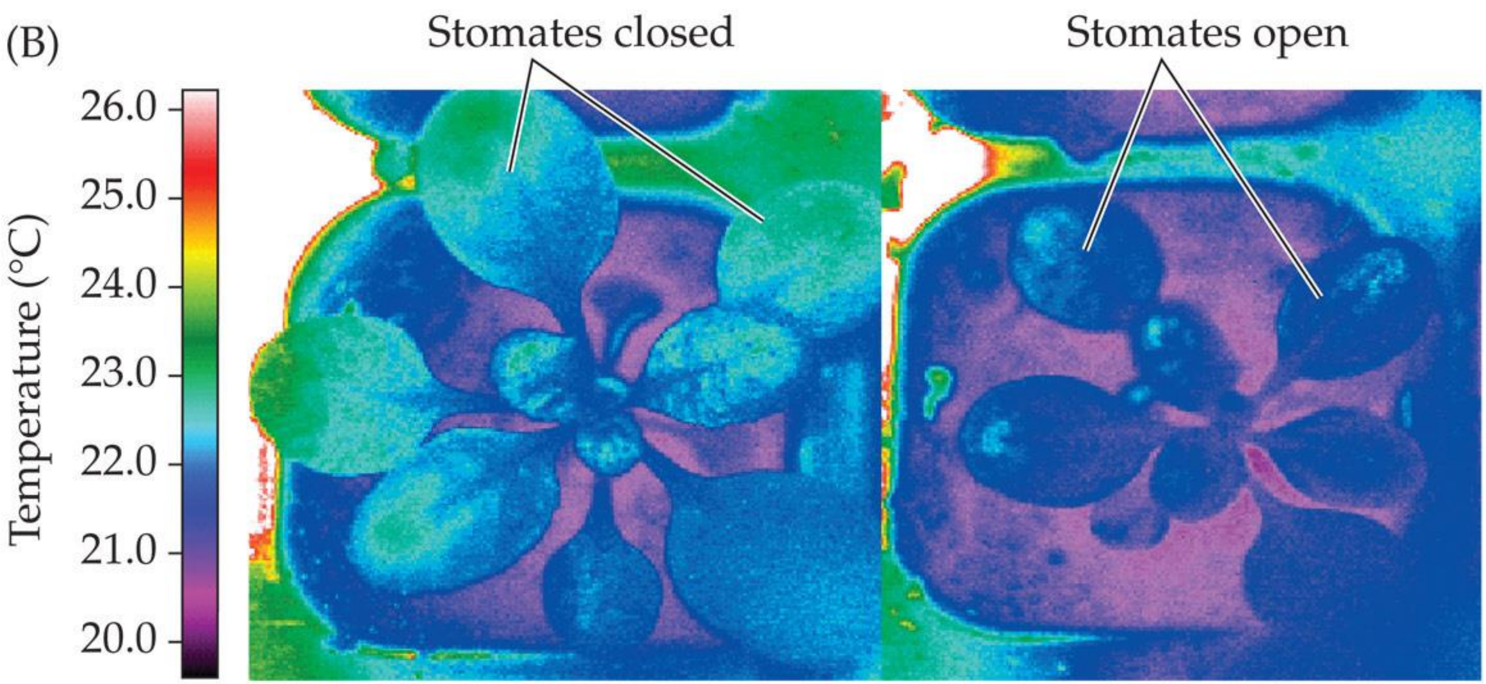
http://biology.uwsp.edu/faculty/ESingsaa/reference/lecture6/windspd.gif

Figure 4.9 Stomates Control Leaf Temperature by Controlling Transpiration



- Open stomata lower leaf temperature
  - But also looses water – ***<u>trade-off</u>***

Thermal infrared imagining of leaves with either open or closed stomata



***ECOLOGY 3e*, Figure 4.9**

Variation in Temperature

If soil water is limited, transpirational cooling is *not* a good mechanism

- Some plants shed their leaves during dry seasons
- Other mechanisms include **pubescence** — hairs on leaf surfaces that reflect solar energy;
  - But hairs also reduce conductive heat loss

Dry Deciduous Forest in Cambodia

http://ss.ffpri.affrc.go.jp/labs/sre/Homepage_CWCM_forLINK/CWCM/Image/Forest_Photo/KRC/KRC_03.jpg

Variation in Temperature

Pubescence has been studied in *Encelia* (in daisy family) (Ehleringer and Cook 1990).

- Desert species with high pubescence were compared with non-pubescent species in moister, cooler environments
- Plants of all species were grown in both locations – **reciprocal transplanting**

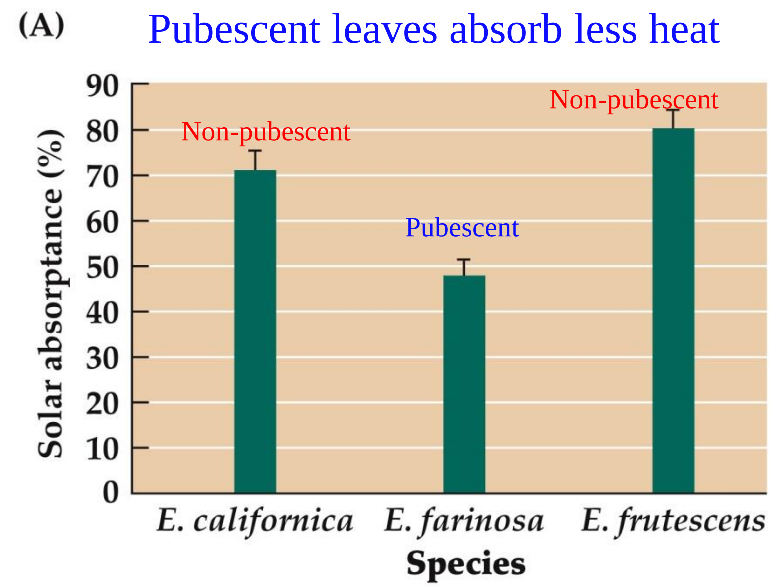
http://www.missouriplants.com/Bluealt/Ipomoea_hederacea_leaf_surface.jpg

Shrubby Encelia of southwestern desert evolved gray pubescent foliage to thwart heat and drought.

http://img.hgtv.com/HGTV/2005/05/24/SHNS_YardSmart05_23f_w190.jpg

Variation in Temperature

- In the cool, moist location, the three *Encelia* species showed few differences in leaf temperature and stomatal opening
- In the desert,…
  - Non-pubescent species maintained leaf temperature by transpiration (but this increases water loss)
  - Pubescent species reflected about twice as much solar radiation



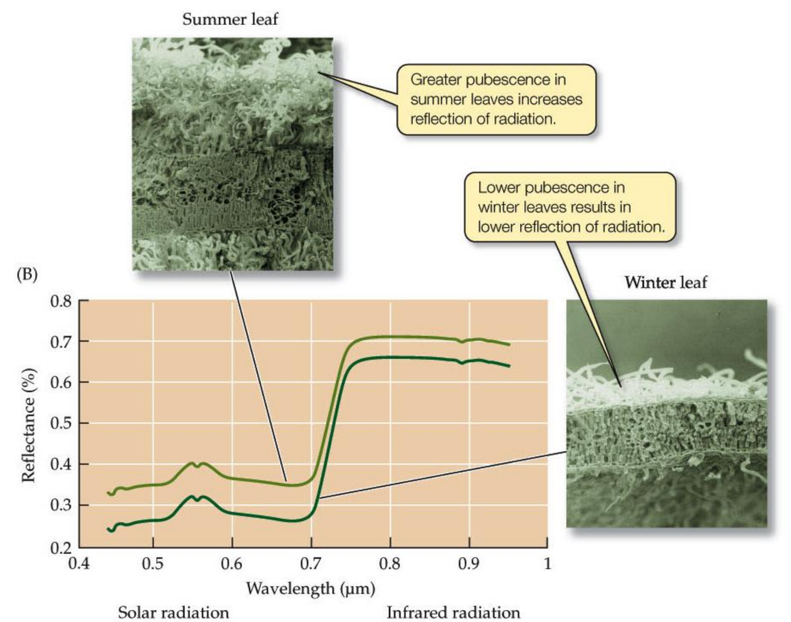
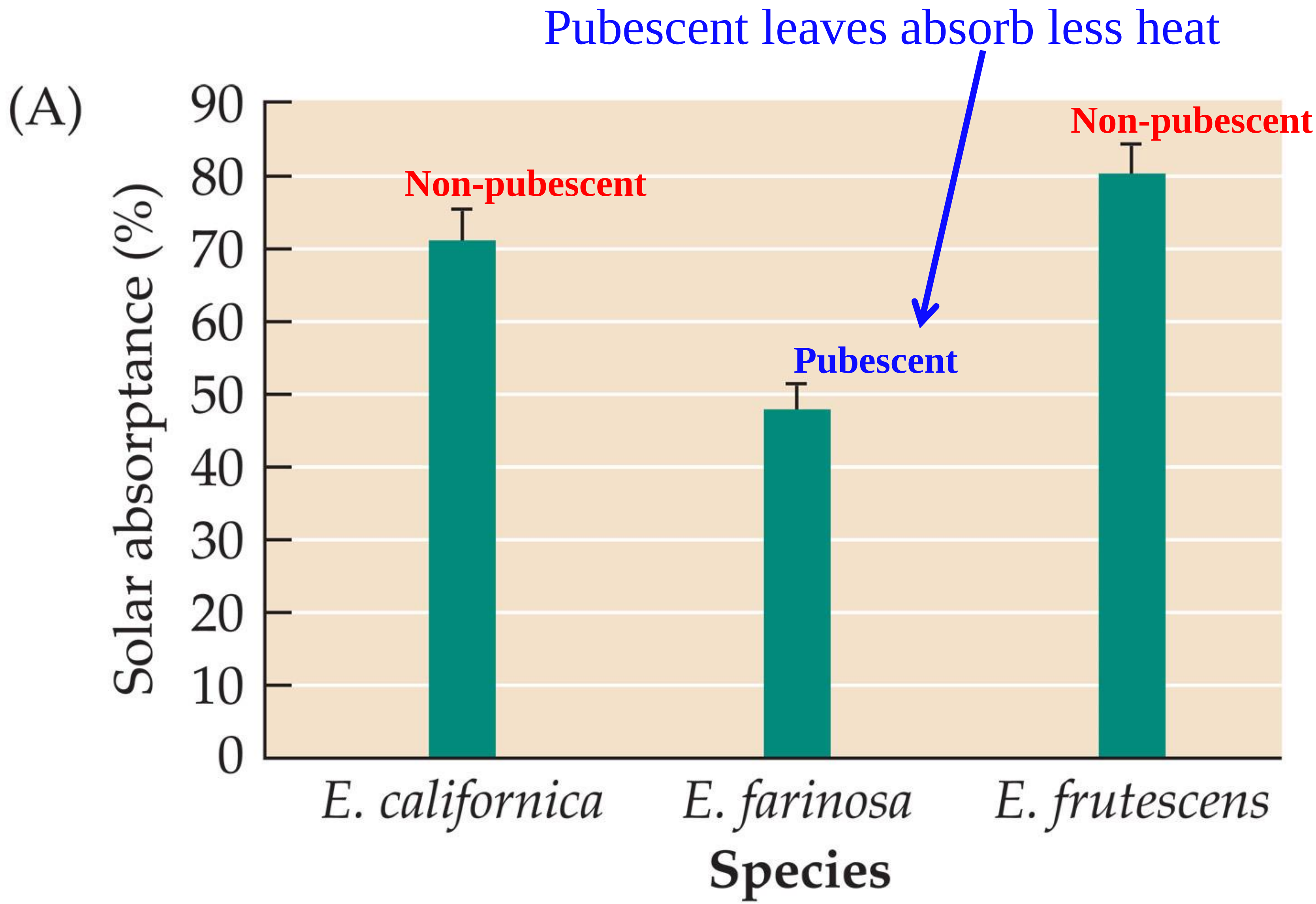
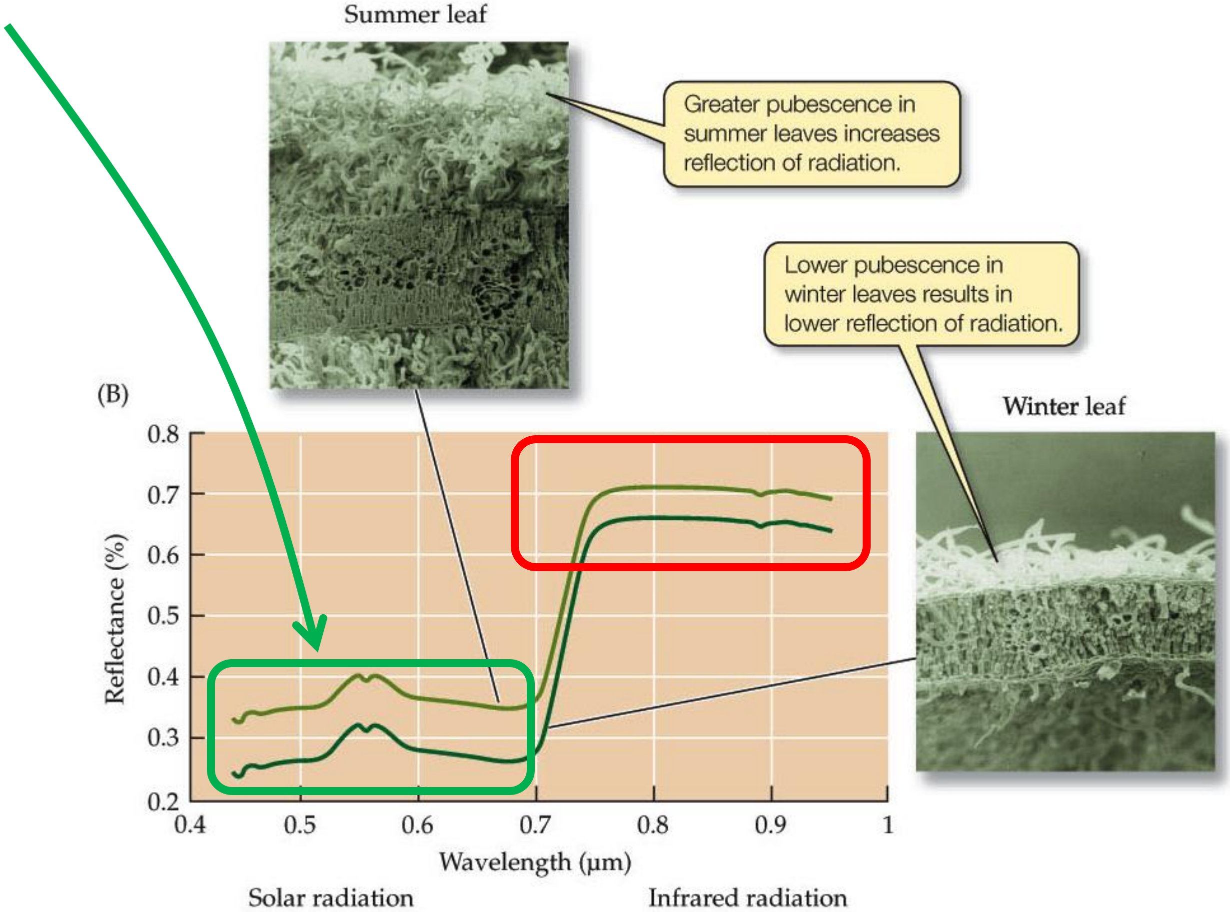


Figure 4.10 Sunlight, Seasonal Changes, and Leaf Pubescence (Part 1)



ECOLOGY 3e, Figure 4.10 (Part 1)

- *Encelia farinosa*, shows ***acclimatization*** by increasing pubescence in summer, compared to winter
    - Note that reflectance is higher for infrared (heat) compared to shorter wavelengths (more photosynthetically active radiation)



Variation in Temperature

Natural selection has acted on populations (**ecotypes**) of *E. farinosa* (brittlebush)

- In drier environments, leaves had more pubescence, and absorbed less solar radiation than populations from moister environments (Sandquist and Ehleringer 2003)

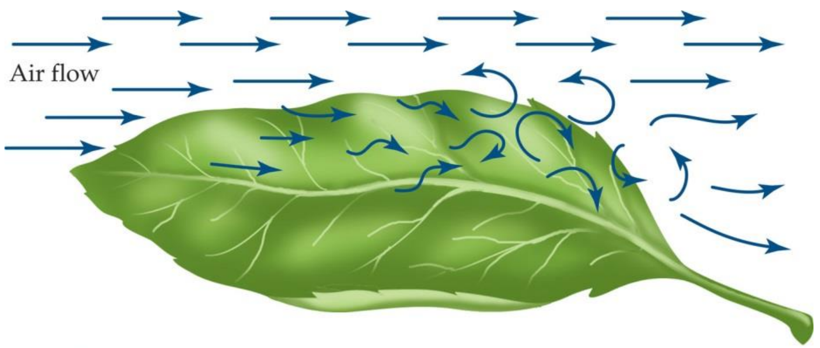
How can you test if pubescence differences between ecotypes are adaptations or acclimitazation?

Note pubescence on stem

Variation in Temperature

If air temperature is lower than leaf temperature, heat can be lost by convection, dependent on speed of air moving across leaf surface

- Moving air encounters more resistance close to object's surface → flow becomes more turbulent, forming eddies
- Zone of turbulent flow is the **boundary layer**



ECOLOGY 3e, Figure 4.11

Variation in Temperature

The boundary layer lowers convective heat loss

- The boundary layer thickness on a leaf is related to its size and its surface roughness
- Small, smooth leaves have thin boundary layers and lose heat more effectively than large or rough leaves
- Pubescence also increases roughness, thus decreasing heat loss

Sycamore leaves are especially noteworthy for the dense "down" they have on their undersides.

http://www.ipm.iastate.edu/ipm/hortnews/2007/3-21/sickplant.html

Variation in Temperature

In alpine environments, convection is main heat loss mechanism

- Most alpine plants hug ground surface to avoid the high wind velocities
  - → stay within boundary layer of ground that reduces wind speed and heat loss
  - Alpine ecotypes are often "stunted"
- Some have a layer of insulating "hair" to lower convective heat loss

Alpine habitat in Adirondack mountains of northeastern New York

http://www.adirondackjourney.com/MacIntyre_Range.htm

Figure 4.12 A Woolly Plant of the Himalayas

ECOLOGY 3e, Figure 4.12

- Animals, especially birds and mammals, can generate heat internally
  - Energy balance equation for animals is shown below…

$$\Delta H_{animal} = SR + IR_{in} - IR_{out} \pm H_{conv} \pm H_{cond} - H_{evap} + H_{met}$$

  - H_{evap} = Heat transfer by evaporation
  - H_{met} = Metabolic heat generation

Jump to slide #71

On your own – review from Bio II

Variation in Temperature

Evaporative heat loss is very effective at losing heat in dry environments

Evaporative heat loss in animals includes

- Sweating in humans
- Panting in dogs and other animals
- Licking of body parts by some marsupials

White-tailed deer (*Odocoileus virginianus*) panting

On your own – review from Bio II

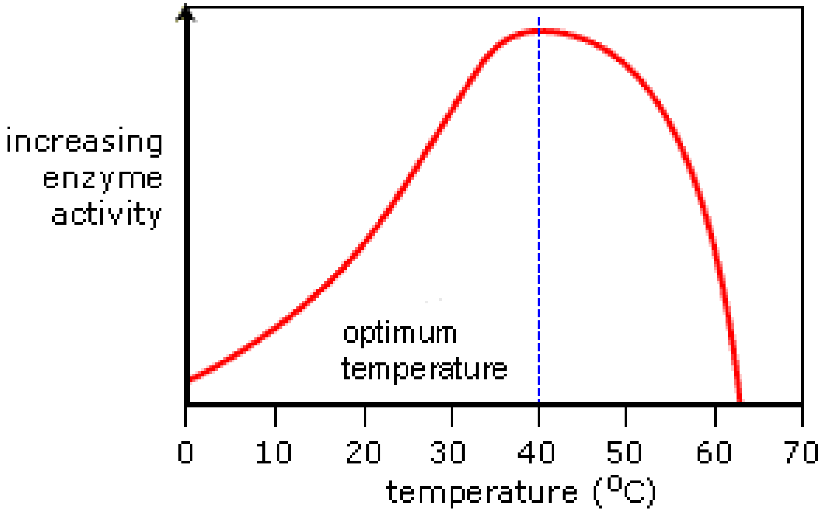
Eastern grey kangaroo (*Macropus giganteus*) licking forearms

http://lh3.ggpht.com/_AhmgTeQwr-w/SAhQXqtMXBI/AAAAAAAAJDk/hXyX04-F4mM/%5Ekangaroo14.jpg

Generating heat internally can be a selective advantage

- Animals can maintain relatively constant internal temperatures near optimum for metabolic functions under a wide range of external temperatures

On your own – review from Bio II



http://www.bbc.co.uk/schools/gcsebitesize/science/images/gcsechem_18part2.gif

Variation in Temperature

On your own – review from Bio II

Ectotherms:

- Primarily regulate body temperature through energy exchange with external environment
- Most organisms

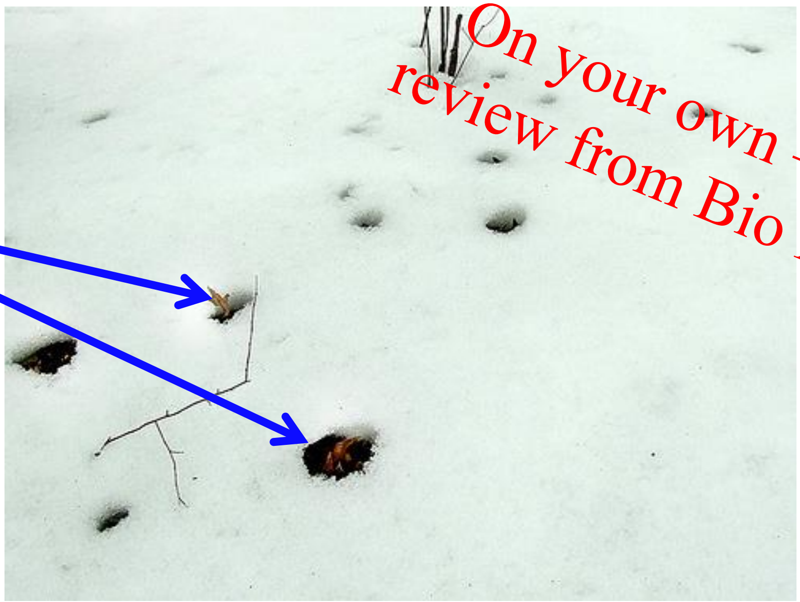
Endotherms:

- Rely primarily on internal heat generation
- mostly birds and mammals

http://www.pathcom.com/~wgbz/xv04014z.jpg

Variation in Temperature

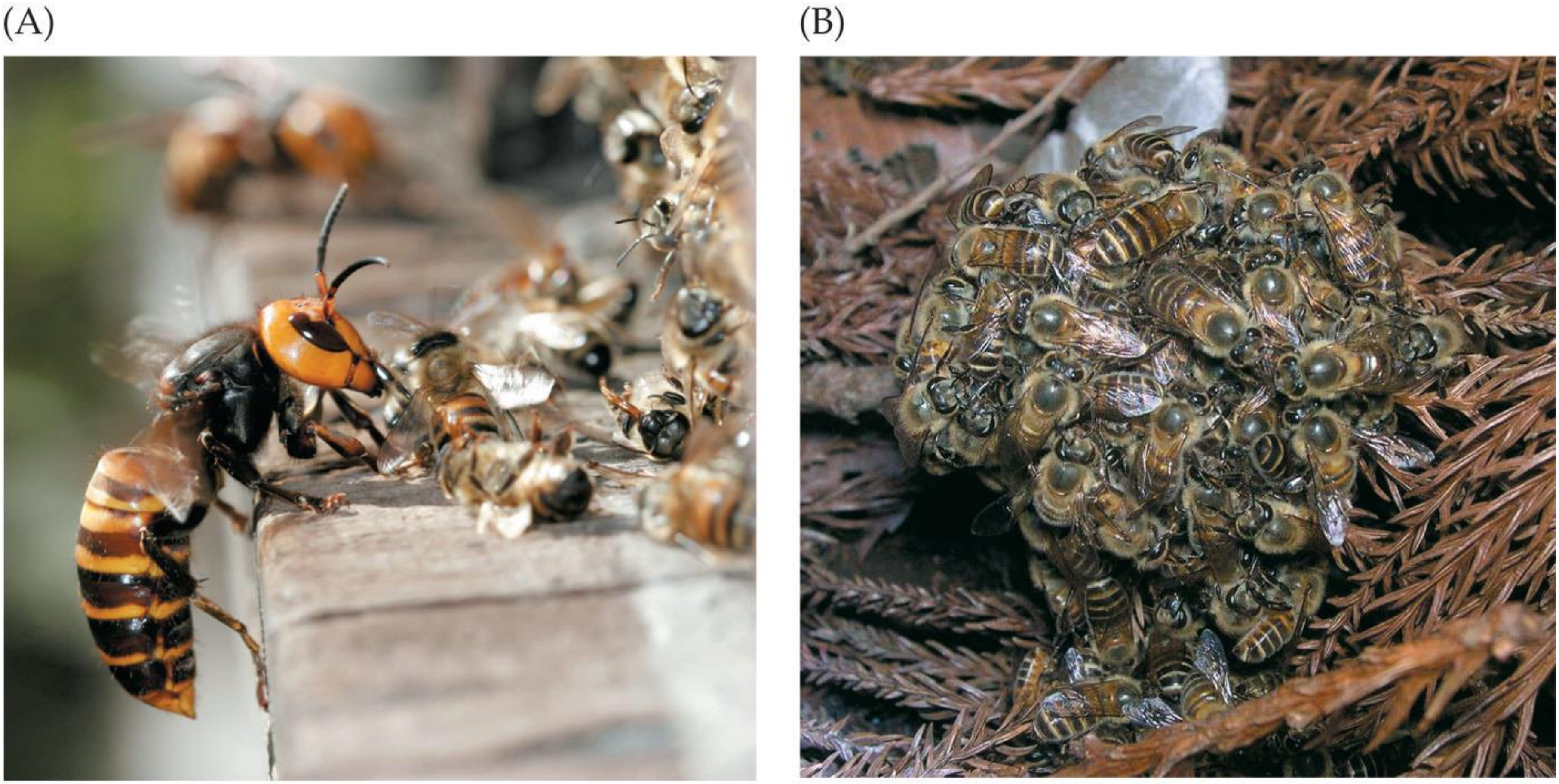
- Some other organisms that generate heat internally include bees, some fish, such as tuna, and even some plants
  - Skunk cabbage warms its flowers using metabolically generated heat during spring, melting surrounding snow



On your own – review from Bio II

Skunk cabbage flowers produce warmth over a period of 12-14 days, remaining on average 20° C (36° F) above outside air temperature, day or night, and can melt snow

http://farm3.static.flickr.com/2023/2366387160_e779117248.jpg?v=0



ECOLOGY 3e, Figure 4.13

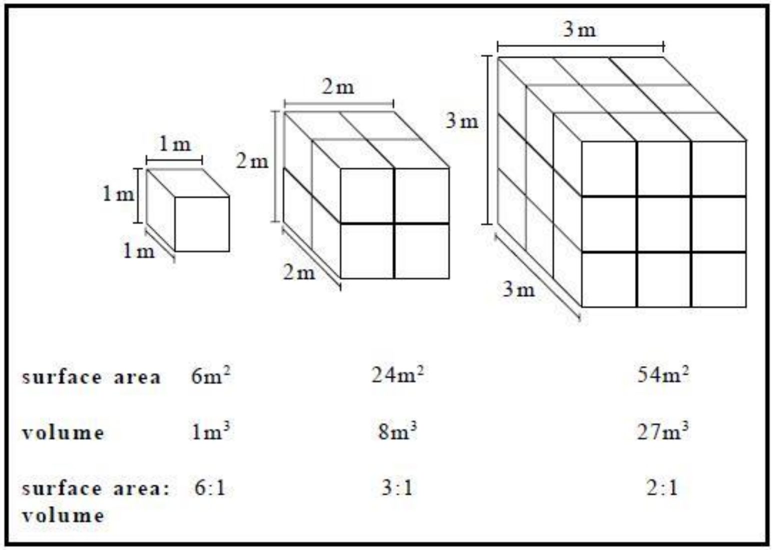
Variation in Temperature

Ectotherms generally have higher tolerance for internal temperature variation than do endotherms

- In exchanging heat with environment, the body's **surface area-to-volume ratio** is an important factor
- Compact body shape reduces SA/V ratio

Know this concept!! (from Bio I)

Fig 1. Surface area to volume ratios of differently sized cubes



http://1.bp.blogspot.com/_hhUdKwzDmA4/TIPFkG47OsI/AAAAAAAAArI/vsKBbBPi9us/s1600/TSA+over+V.jpg http://www.awf.org/files/3902_file_Bat_eared_fox_sholley.jpg

Variation in Temperature

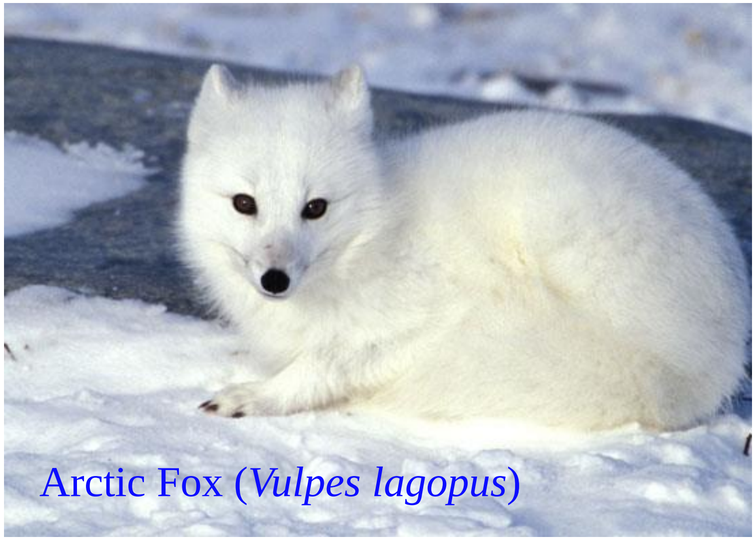
On your own – review from Bio II

Know this concept!!

- Larger surface area allows greater heat exchange/loss…
  - Adaptive in warm environments to dump excess heat
  - Longer appendages
  - but makes it harder to maintain internal temperature
- Smaller surface area relative to volume decreases animal's ability to gain or lose heat
  - Shorter appendages
  - Adaptive in cold environments to decrease heat loss

Note difference in surface area to volume ratio in the ears of the African bat-eared fox compared to the Arctic fox

Bat-eared Fox (*Otocyon megalotis*)



Arctic Fox (*Vulpes lagopus*)

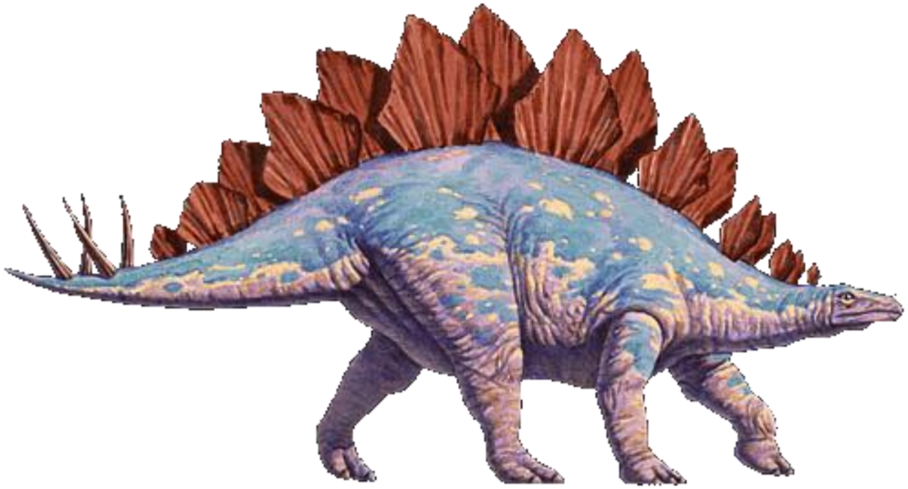
http://www.ri.net/schools/Glocester/WGES/Ulman/ppts06/Arctic%20Fox.ppt_files/slide0005_image004.png

Variation in Temperature

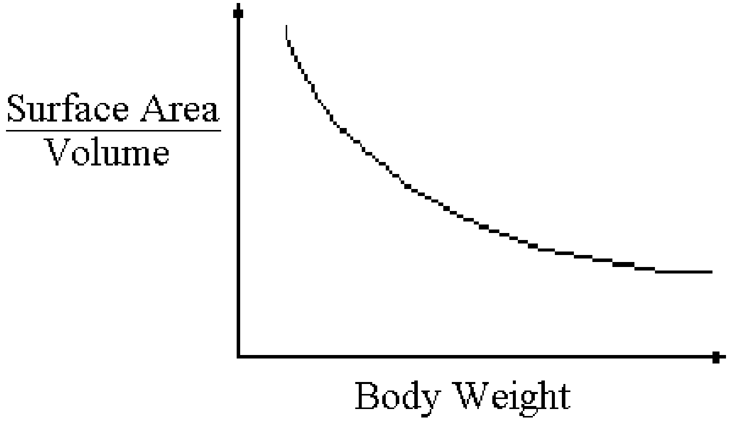
As body size increases, surface area-to-volume ratio decreases, thus large ectotherms are improbable

On your own – review from Bio II

- This had led to speculation that large dinosaurs may have had some degree of endothermy
  - E.g. Vascularized dorsal plates of *Stegasaurus* may have aided in temperature regulation



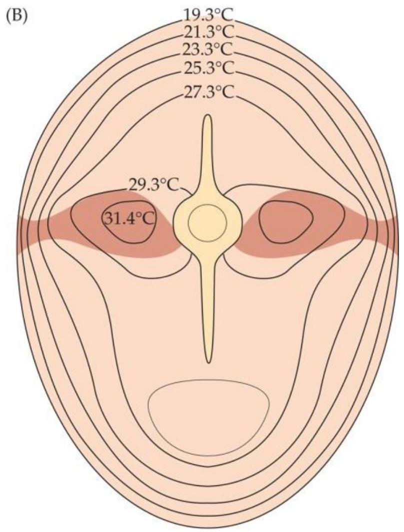
http://www.paleo.cc/ce/stegosaurus.gif



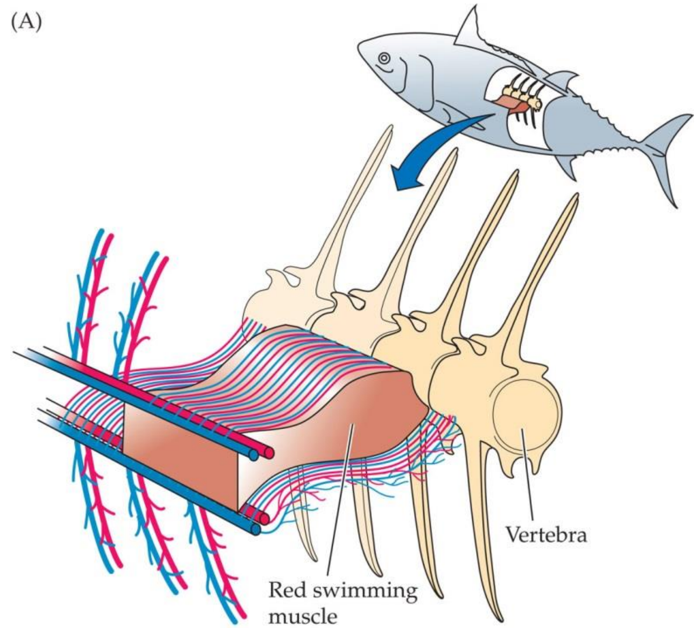
http://mark.asci.ncsu.edu/HealthyHogs/book1997/image11.gif

- Some large ectotherms can maintain body temperature above environmental temperature
  - Skipjack tuna use muscle activity in conjunction with **counter-current heat exchange** between blood vessels to maintain a body temperature as much as 14°C warmer than the surrounding seawater

On your own – review from Bio II

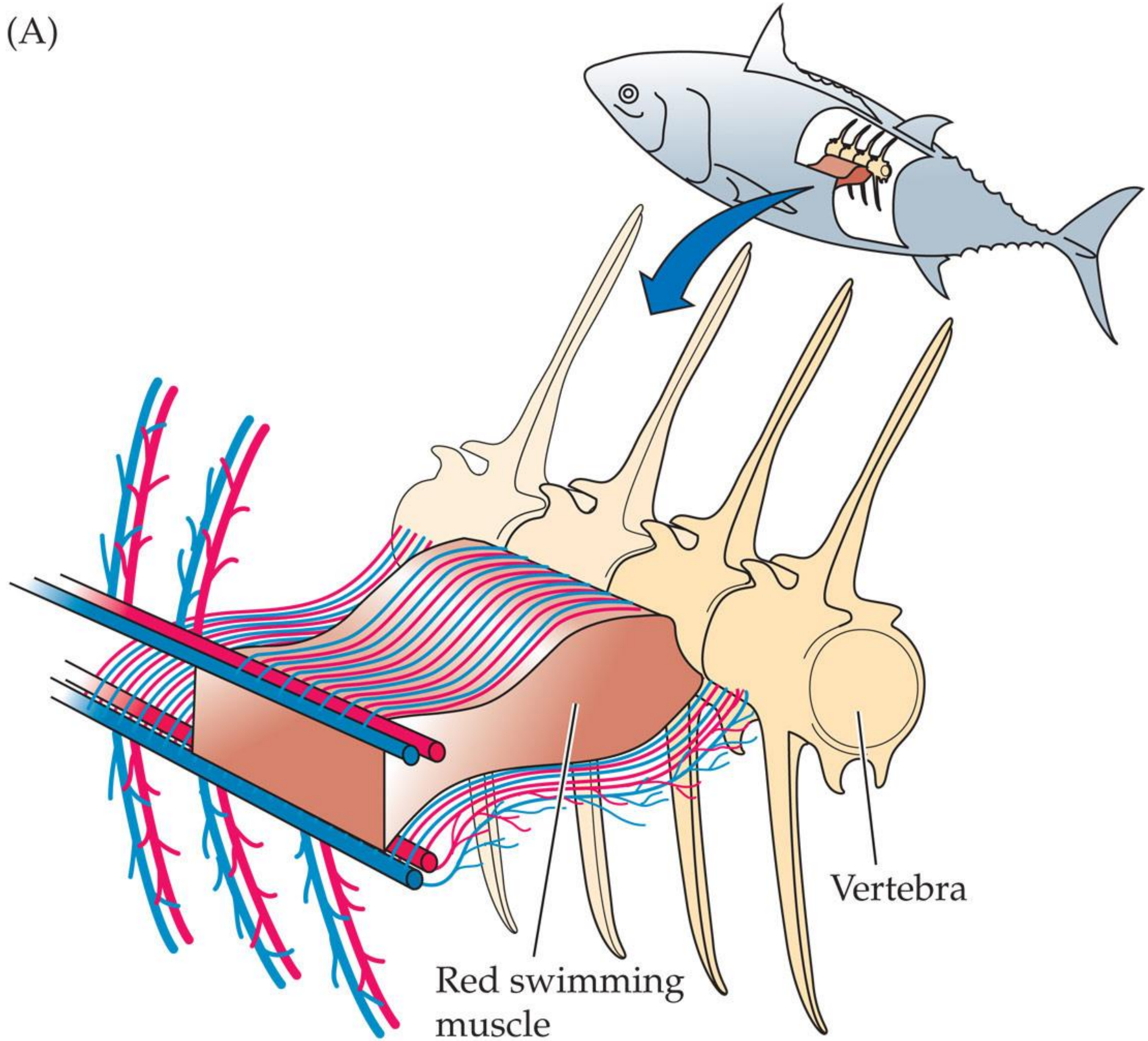


ECOLOGY 3e, Figure 4.14 (Part 2)



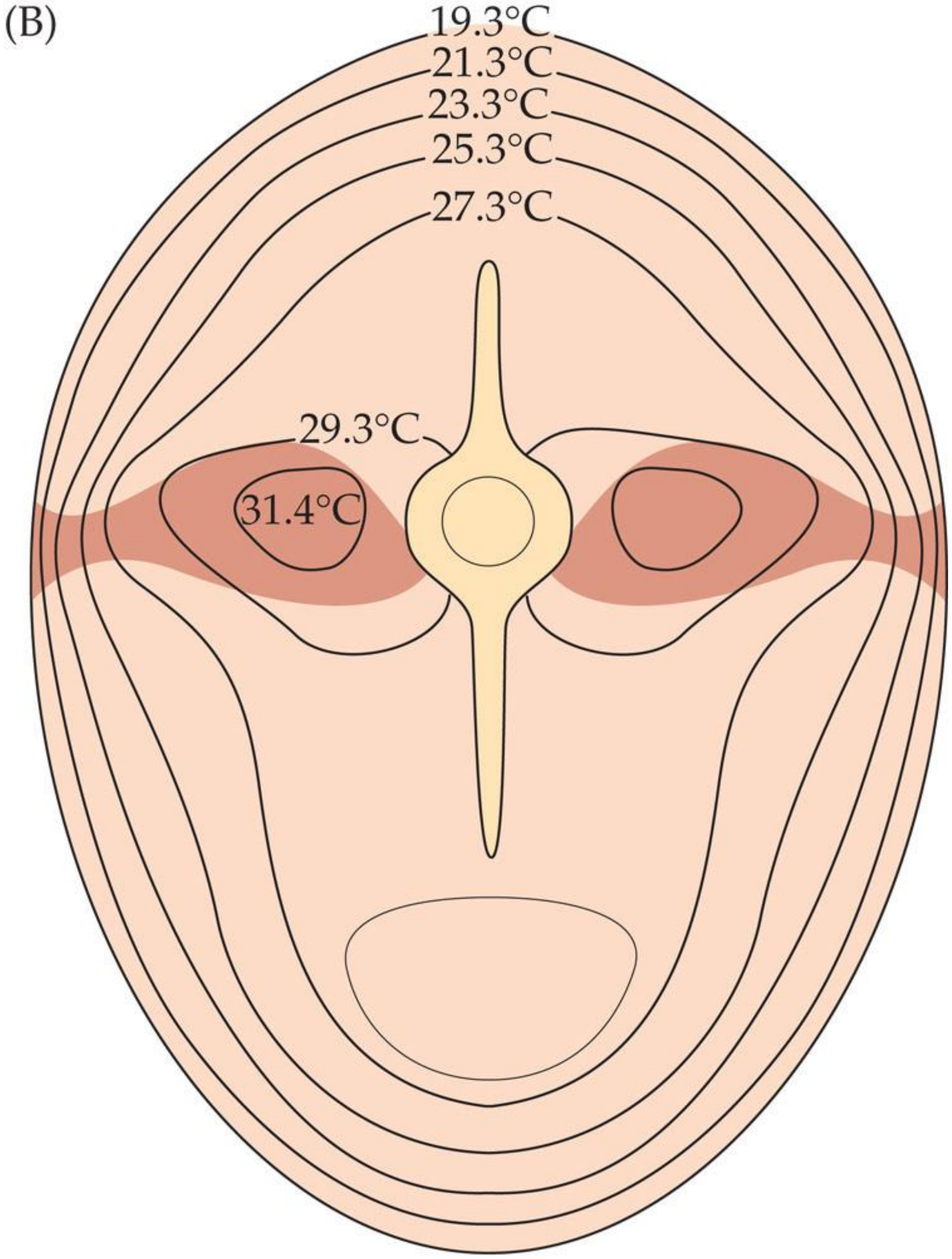
ECOLOGY 3e, Figure 4.14 (Part 1)

Figure 4.14 Internal Heat Generation by Tuna (Part 1)



ECOLOGY 3e, **Figure 4.14 (Part 1)**

Figure 4.14 Internal Heat Generation by Tuna (Part 2)



ECOLOGY 3e, Figure 4.14 (Part 2)

Variation in Temperature

Many terrestrial ectotherms can move to adjust temperature

- Many insects and reptiles bask in sun to warm up after a cold night
- Because this increases risk from predators, many are also camouflaged

On your own – review from Bio II

ECOLOGY 3e, **Figure 4.15**

Variation in Temperature

Ectotherms in temperate and polar regions must avoid or tolerate freezing

- Avoidance behavior includes seasonal migration to lower latitudes or microsites that are above freezing (e.g., burrows in soil)

On your own – review from Bio II

Elk (endotherms) also migrate from summer feeding grounds at higher elevations to warmer valleys during fall

Image by B. Tyler

http://www.greateryellowstone.org/media/issues/elk-crowd2.jpg http://www.manandmollusc.net/advanced_introduction/Images/Helix-pomatia1.jpg

Variation in Temperature

On your own – review from Bio II

Tolerance to freezing involves minimizing damage associated with ice formation in cells

- Some insects and snails contain high concentrations of glycerol, a chemical lowers the freezing point of body fluids
- Vertebrates generally do not tolerate freezing temperatures (see above for some amphibians and reptiles that do)

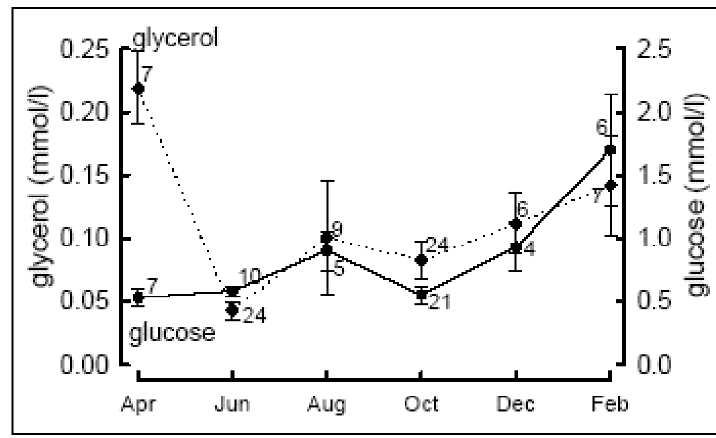


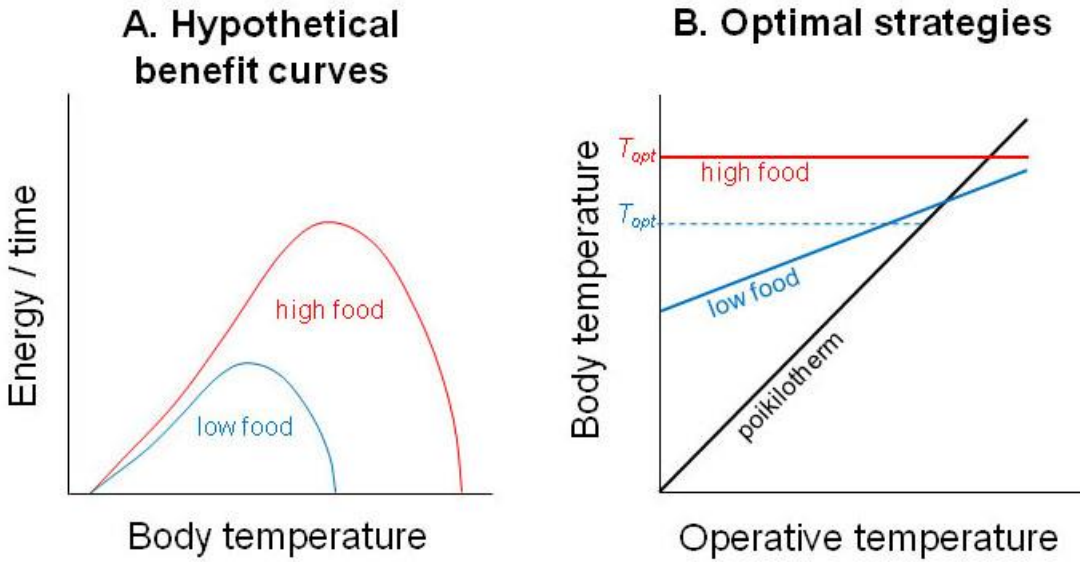
Fig. 1. Annual changes of hemolymph glycerol (diamonds connected with dotted lines) and glucose (circles connected with solid lines) concentrations (means ± SE) in *Helix pomatia* snails collected from the field at two-month intervals. Numbers indicate group sample sizes.

http://www.jpp.krakow.pl/journal/archive/1106_s8/articles/08_article.html

Variation in Temperature

Endotherms can remain active at subfreezing temperatures

- The cost of being endothermic is a high demand for energy (food) to support metabolic heat production
- Metabolic rates are a function of the external temperature and rate of heat loss.

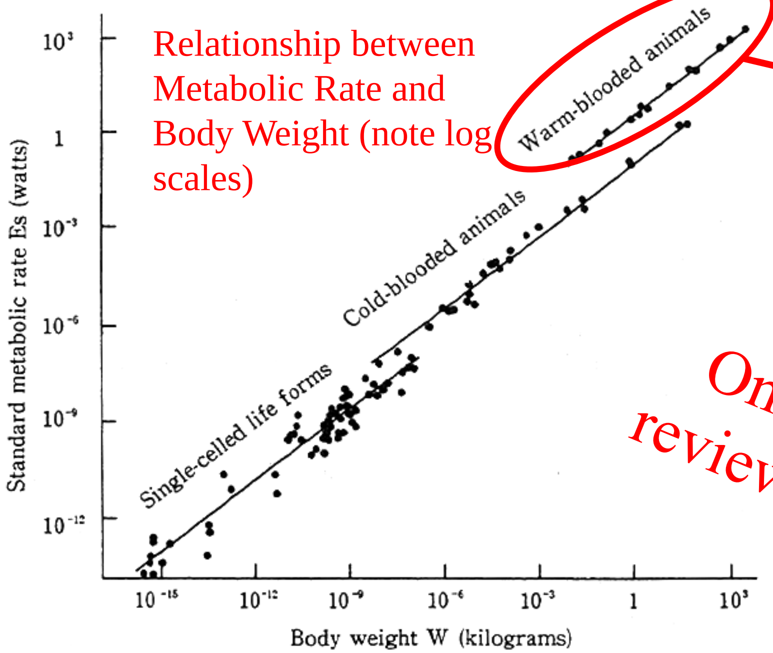


http://www.bioscience.org/2010/v2e/af/148/fulltext.php?bframe=figures.htm

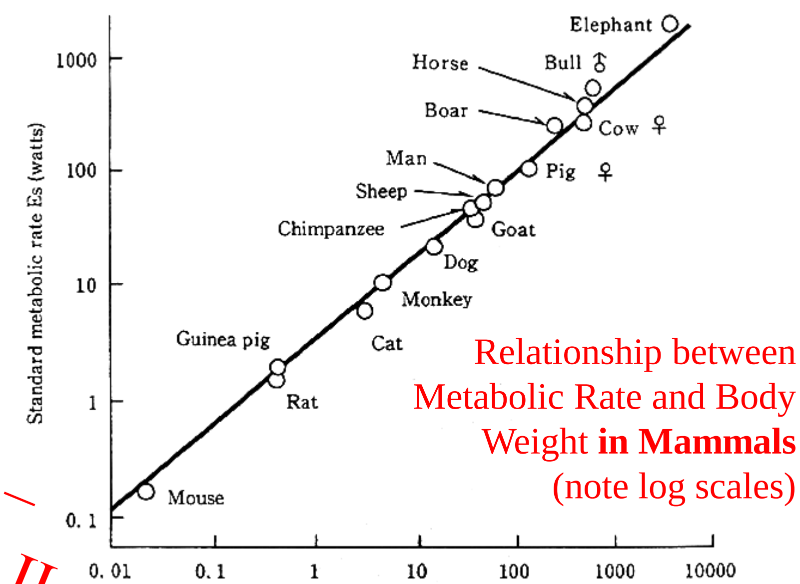
Variation in Temperature

Metabolic rate in endotherms is associated with external temperature and rate of heat loss

- Rate of heat loss is related to body size due to surface area-to-volume ratio
- Small endotherms have higher metabolic rates, and require more energy and higher feeding rates than large endotherms



Relationship between Metabolic Rate and Body Weight (note log scales)



Relationship between Metabolic Rate and Body Weight **in Mammals** (note log scales)

On your own – review from Bio II

Variation in Temperature

Thermoneutral zone

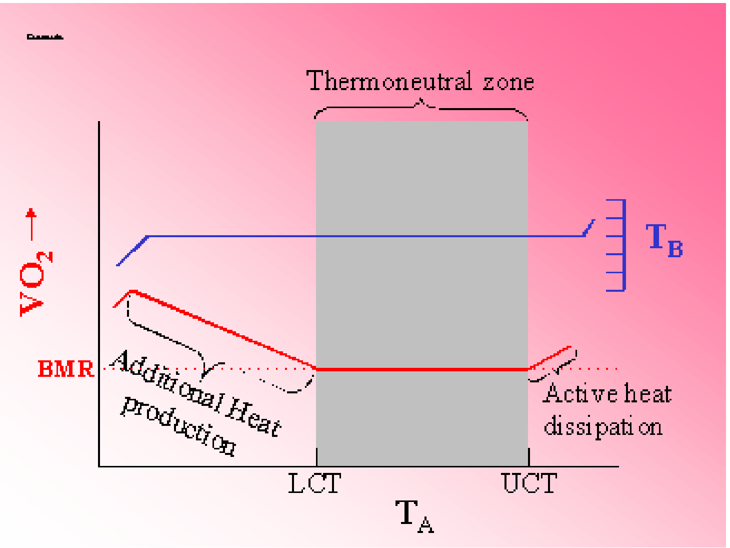
- Constant resting metabolic rate over a range of environmental temperatures

Lower critical temperature

- When heat loss is greater than metabolic production
- Body temperature drops and metabolic heat generation increases

What happens above the "upper" critical temperature?

Know this concept!! (from Bio II)

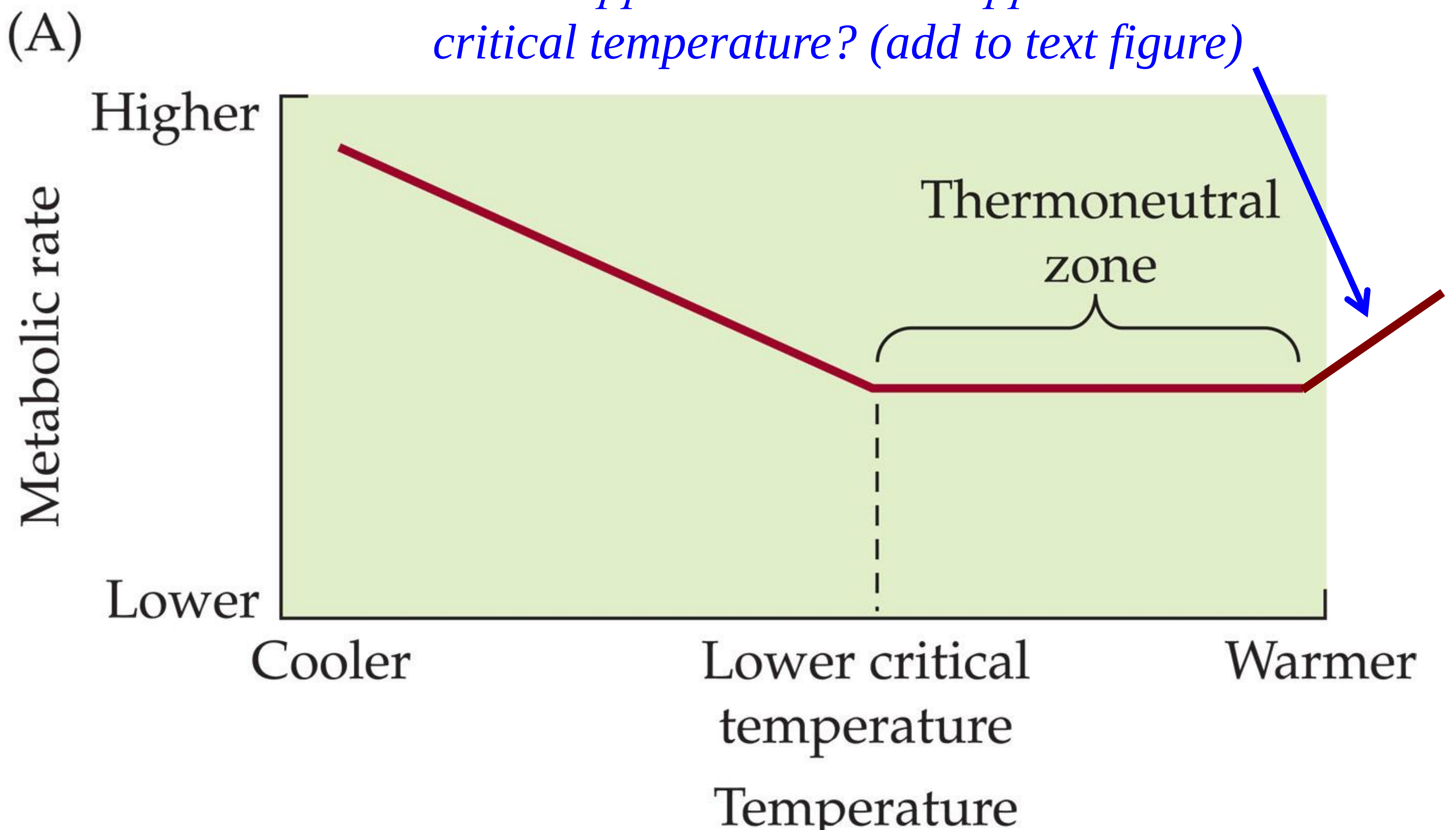


[Jump to slide #82](#)

http://people.eku.edu/ritchisong/RITCHISO/thermoneutralzone2.gif

Figure 4.16 A Metabolic Rates in Endotherms Vary with Environmental Temperatures

What happens above the "upper" critical temperature? (add to text figure)



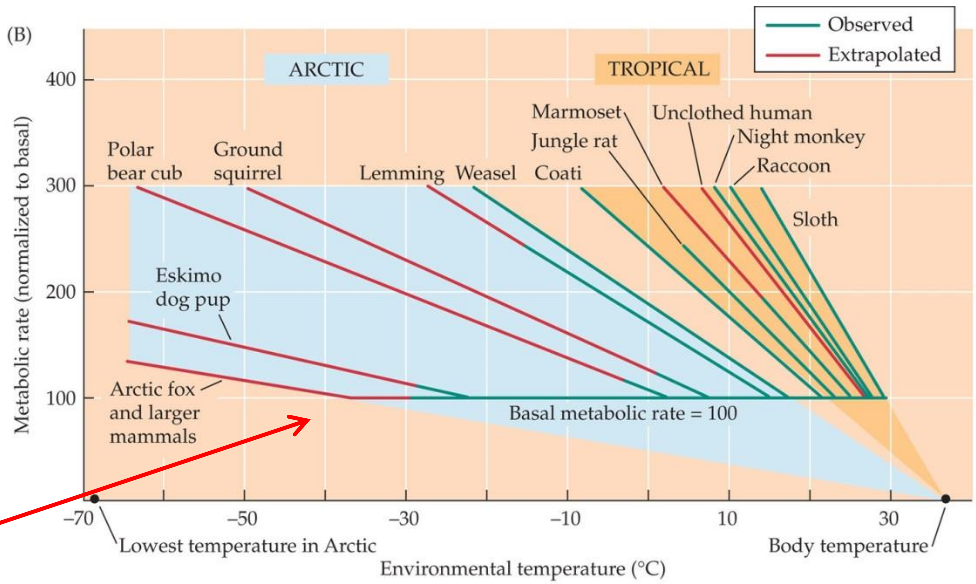
Add to figure
in text

Variation in Temperature

Animals from Arctic have lower critical temperatures than those of animals from tropical regions

- Note also that rate of metabolic activity (slope of lines) increases more rapidly below lower critical temperature in tropical as compared to Arctic mammals

Figure shows increased metabolic rate below lower critical temperature of selected Arctic and Tropical mammals

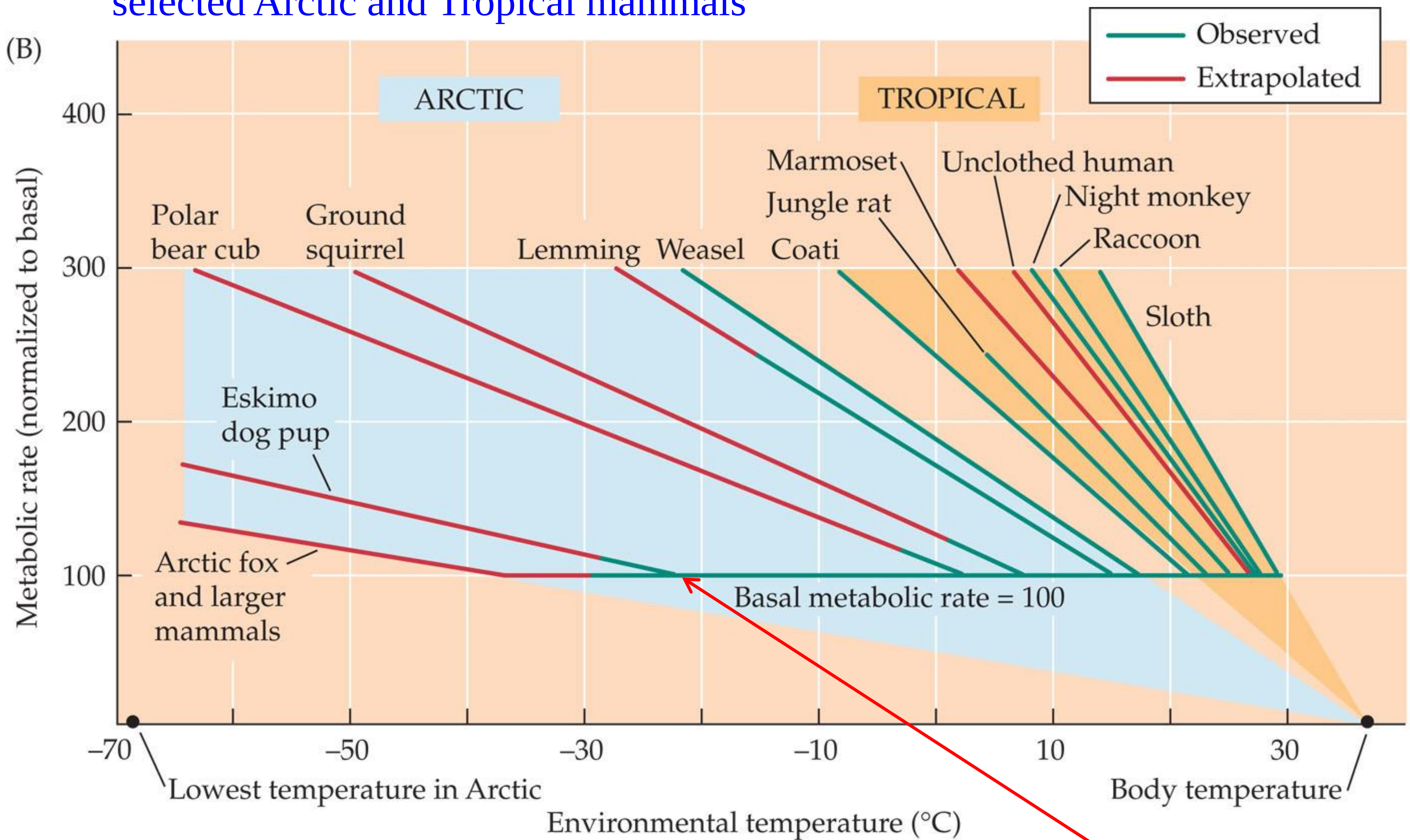


ECOLOGY 3e, Figure 4.16 (Part 2)

Note: Basal metabolic rates (this is rate at thermal neutral zone) have been normalized for all species to allow for easier comparisons

Figure 4.16 B Metabolic Rates in Endotherms Vary with Environmental Temperatures

Figure shows increased metabolic rate below lower critical temperature of selected Arctic and Tropical mammals



ECOLOGY 3e, Figure 4.16 (Part 2)

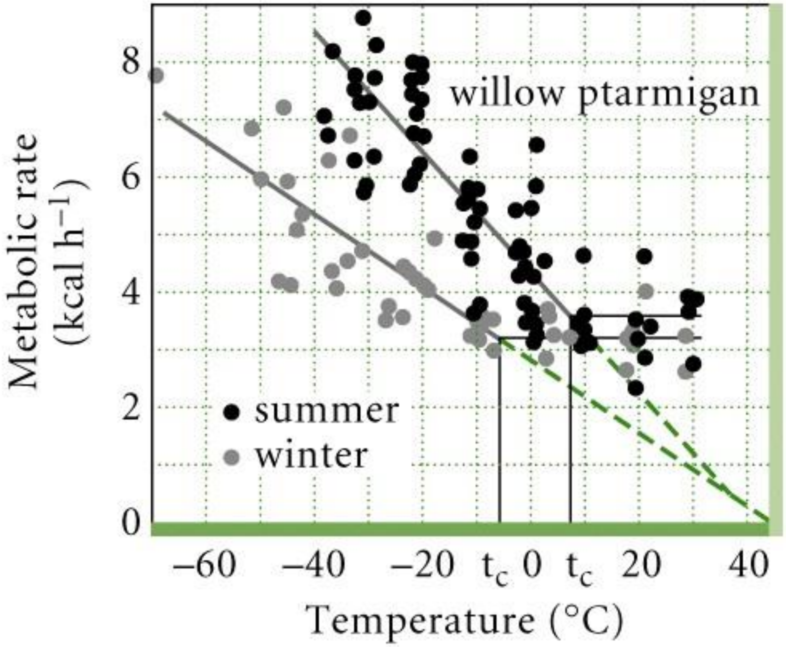
Note: Basal metabolic rates (this is rate at thermal neutral zone) have been normalized for all species to allow for easier comparisons

Thermoneutral zones and basal metabolic rates may vary with season (e.g., West 1972)

- Example of acclimatization in willow ptarmigan

On your own – know this!!

Willow Ptarmigan (*Lagopus lagopus*)
in summer and winter plumage



http://www.greglasley.net/willptar.html

http://people.eku.edu/ritchisong/RITCHISO/birdmetabolism.html

Variation in Temperature

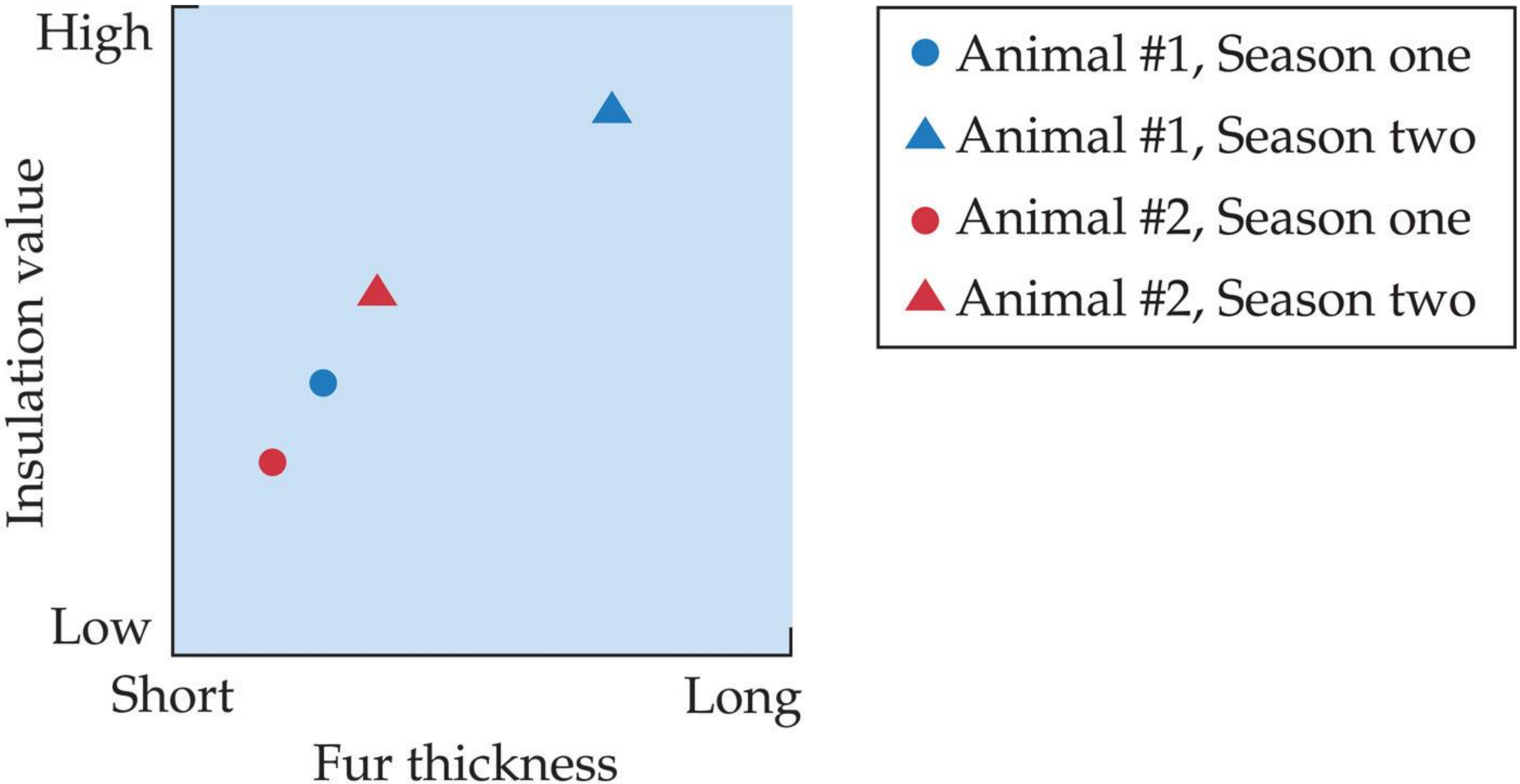
Evolution of endothermy required insulation — feathers, fur, fat

- Insulation limits conductive and convective heat loss
- Fur and feathers provide a layer of still air adjacent to the skin (produces insulatory boundary layer)
- Some animals grow thicker fur for winter

Snowshoe Hare (*Lepus americanus*): Summer and winter pelage

http://www.vermontmammals.org/hares.jpg

Analyzing Data 4.1, Figure A How does fur thickness influence metabolic activity in endotherms?



ECOLOGY 3e, Analyzing Data 4.1, Figure A

Variation in Temperature

Problems of small endotherms (.e.g. mammals) at low temperatures

- high demand for metabolic energy below the lower critical temperature
- low insulation values of their fur
- low capacity to store energy

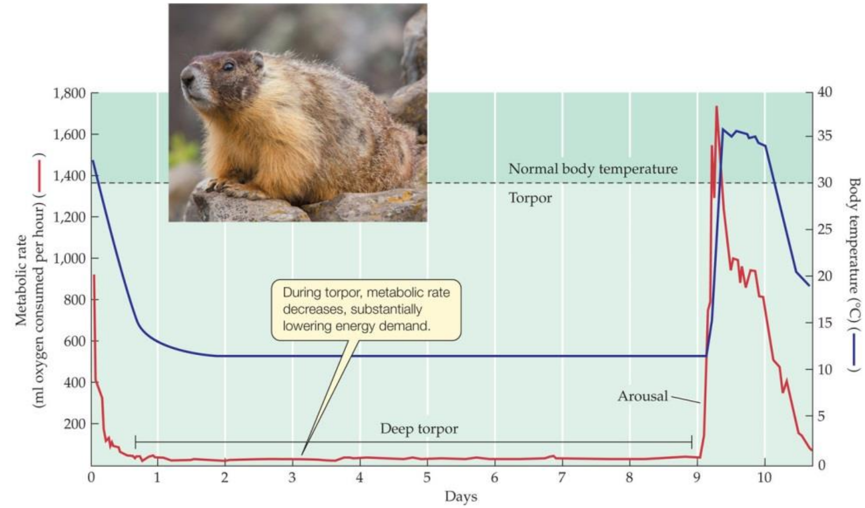
On your own – review from Bio II

- How can they survive in cold climates?...
  - Alter lower critical temperature by entering state of dormancy known as **torpor**

Torpor

- Body temperature may drop as much as 20°C below normal, and metabolic rate can be 50%–90% lower than normal
- Energy reserves are needed to come out of torpor
- The length of time an animal can remain in torpor is limited by its reserves of energy

On your own – review from Bio II



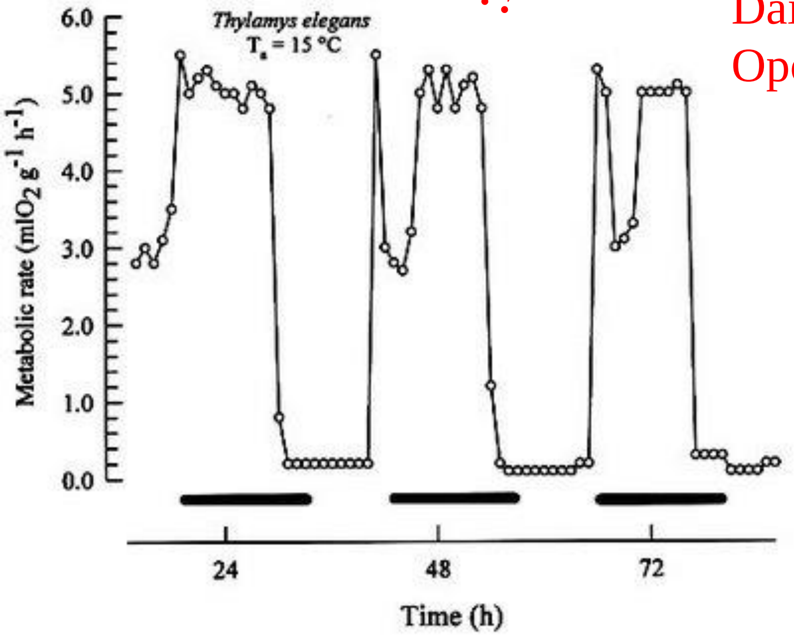
ECOLOGY 3e, Figure 4.17

http://www.bio.davidson.edu/people/midorcas/animalphysiology/websites/2007/Wells/Ownby_Rufous2.jpg

Variation in Temperature

- Small endotherms may regularly undergo daily torpor to minimize energy needed during cold nights (shrews, hummingbirds)

On your own – know this!!



Daily torpor in the Elegant Fat-tailed Mouse Opossum (*Thylamys elegans*)

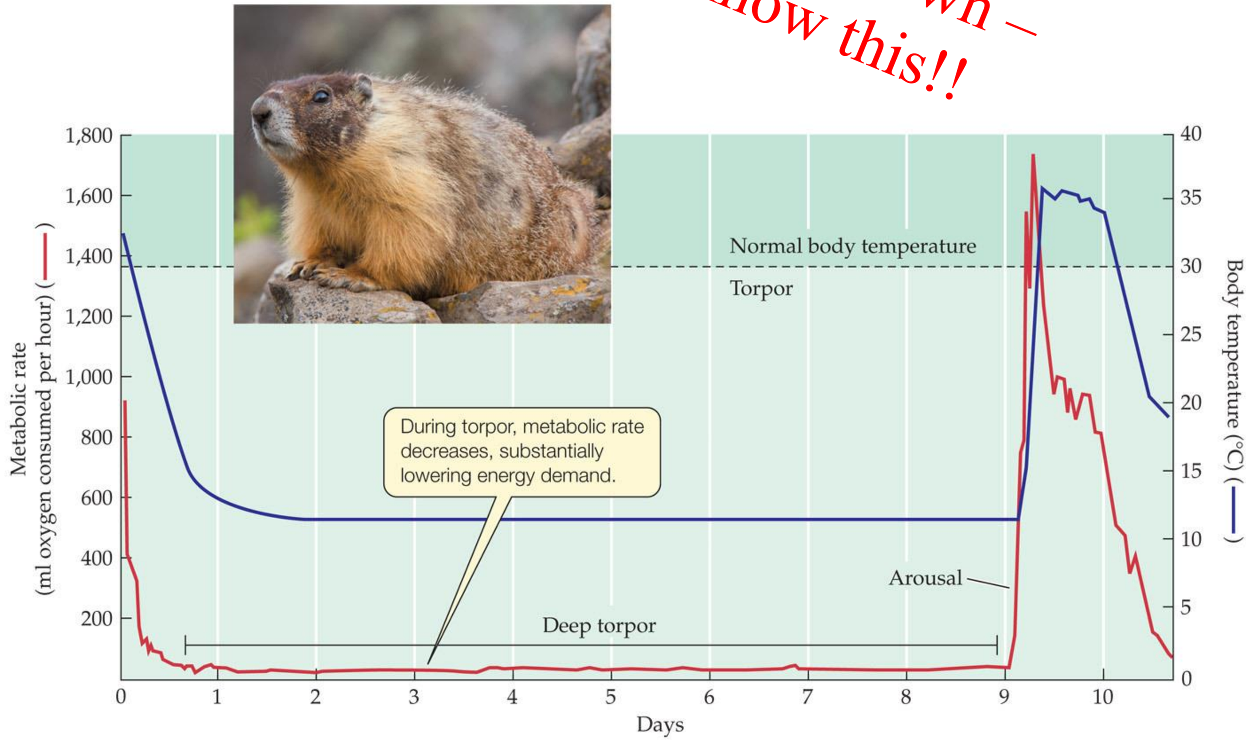
http://scienceblogs.com/clock/2006/08/chossats_effect_in_humans_and.php

http://www.knowyoursto.com/images/genusopossums/thylamys-elegans03.jpg

Variation in Temperature

- Long-term torpor is possible only for animals that have enough food and can store enough energy reserves, such as marmots (below is the yellow-bellied marmot, *Marmota flaviventris*)

On your own – know this!!



ECOLOGY 3e, **Figure 4.17**

Variation in Temperature

http://www.bio.davidson.edu/people/midorcas/animalphysiology/websites/2007/Wells/Ownby_Rufous2.jpg

Clarification of terminology

- **Torpor** is often used to indicate a short-term dormancy (daily) but is used in this text as a general state of dormancy with decreased metabolism and controlled hypothermia

- **Hiberation** is a long-term winter dormancy

- **Estivation** is a summer dormancy in some desert animals

On your own – know this!!

Concept 4.3: The water balance of organisms is determined by exchanges of water and solutes with the external environment.

Water is the medium in which all biochemical reactions necessary for life occur

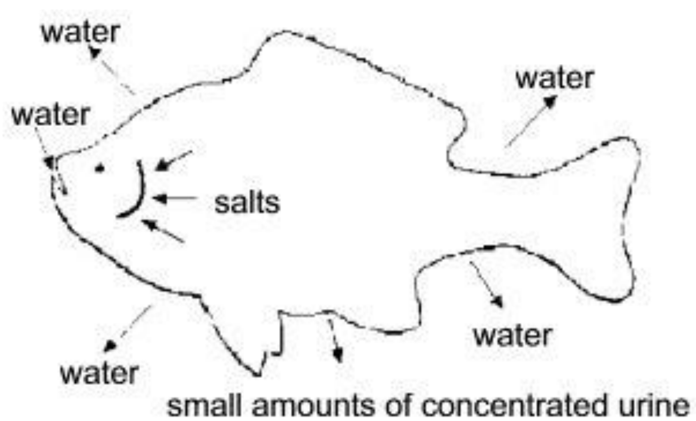
- Water has unique properties that make it a universal solvent for biologically important solutes
- Review Section 4.3 (rest of chapter) on your own (much from Bio I and II)

Variation in Water Availability

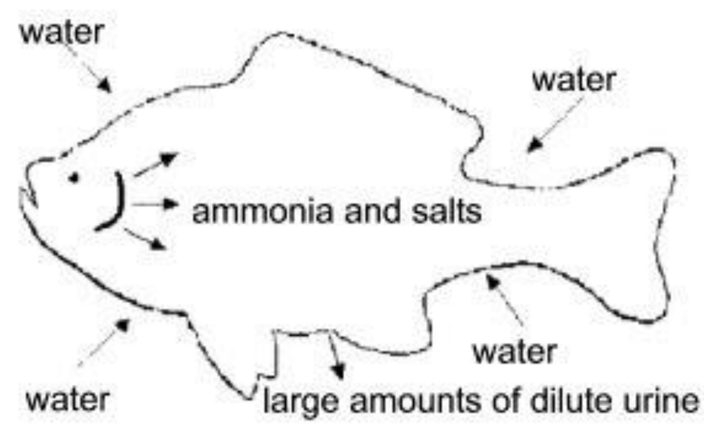
Maintaining optimal water content is a challenge for freshwater and terrestrial organisms

- Ocean waters maintain water balance of marine organisms
- Terrestrial species lose water to dry atmosphere
- Freshwater organisms lose solutes to, and gain water from, their environment

Saltwater fish



Freshwater fish



http://www.thefishsite.com/articles/314/a-fish-farmers-guide-to-understanding-water-quality-part-1

Variation in Water Availability

Water flows along energy gradients

- **Gravity**
  - Water flows downhill
  - Associated energy is **gravitational potential**

- **Pressure**
  - Water flows from area of higher pressure to lower pressure
  - Associated energy is **pressure** (or *turgor*) **potential**

Variation in Water Availability

- **Osmotic potential**
  - Water flows from a region of high concentration (low solute concentration) to a region of low concentration (high solute concentration)

- **Matric potential**
  - Energy associated with attractive forces on surfaces of **soil particles** or on surfaces of large molecules inside cells

Variation in Water Availability

Water potential is the sum of all these energy components. It can be defined as:

$$\Psi = \Psi_o + \Psi_p + \Psi_m$$

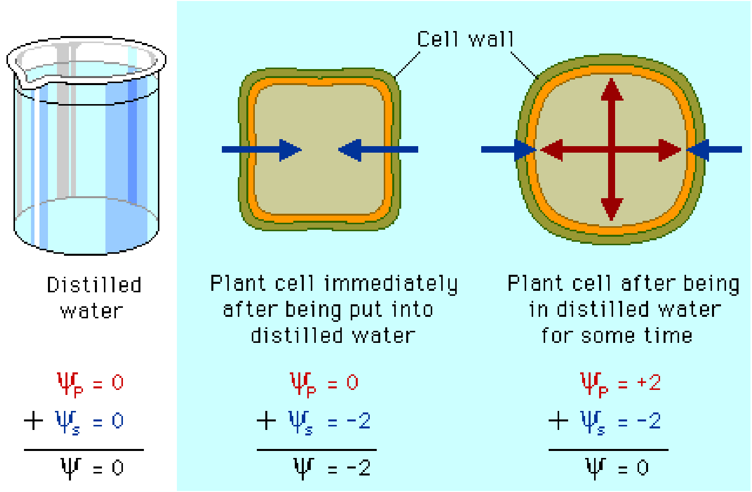
Ψ_o = osmotic potential (negative value)

Ψ_p = pressure potential

Ψ_m = matric potential (negative value)

Variation in Water Availability

- Water always moves from a system of higher Ψ to lower Ψ, following the energy gradient
- Atmospheric water potential is related to relative humidity
  - If less than 98% humidity, water potential is low relative to organisms
  - Terrestrial organisms must thus prevent water loss to atmosphere



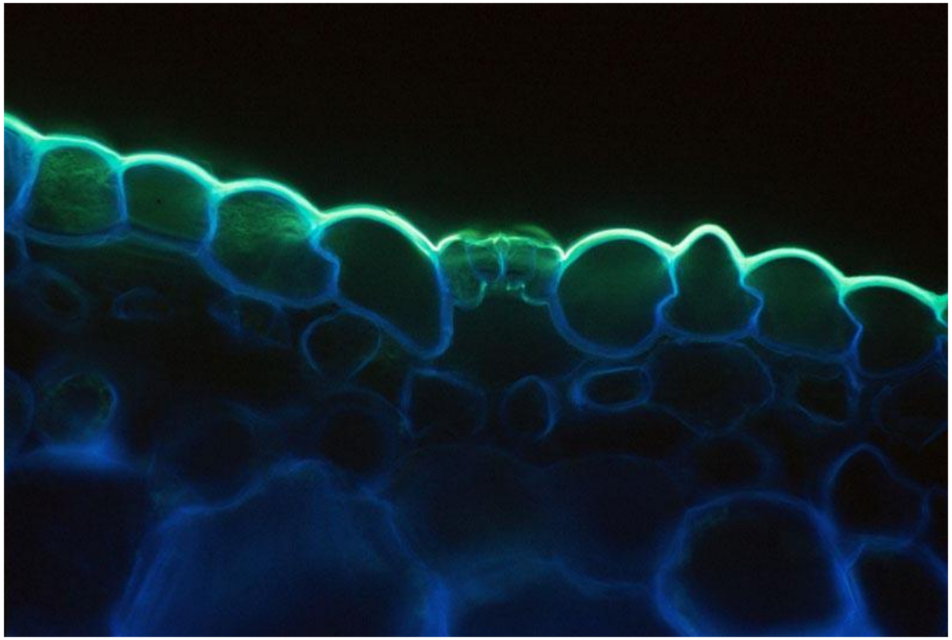
Ψ_S = solute potential

http://www.phschool.com/science/biology_place/labbench/lab1/images/watpot.gif

Resistance

- Force that impedes water movement along an energy gradient
- To resist water loss, terrestrial organisms have waxy cuticles (insects and plants) or animal skin

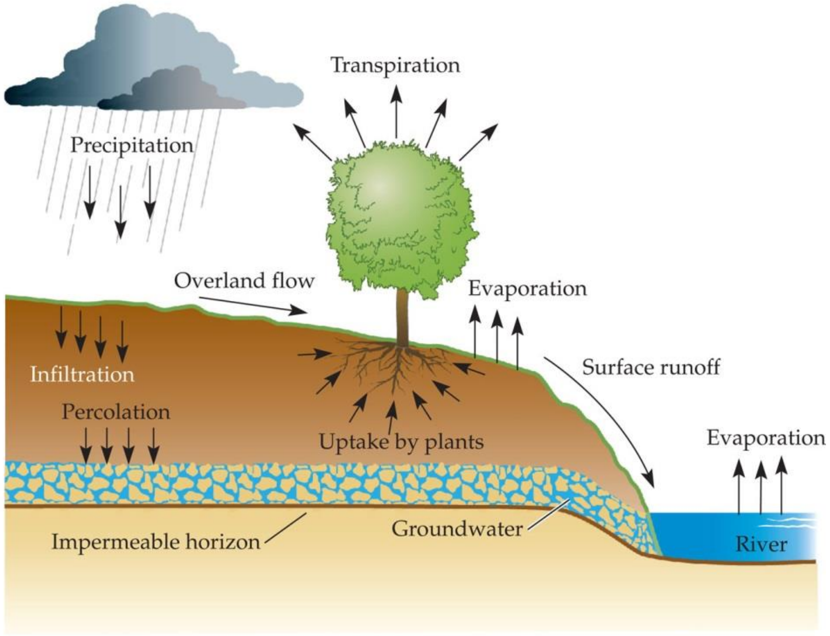
Brassica napus, leaf cross section: cuticle (yellow), stoma, guard cells. Fluorescence LM



Variation in Water Availability

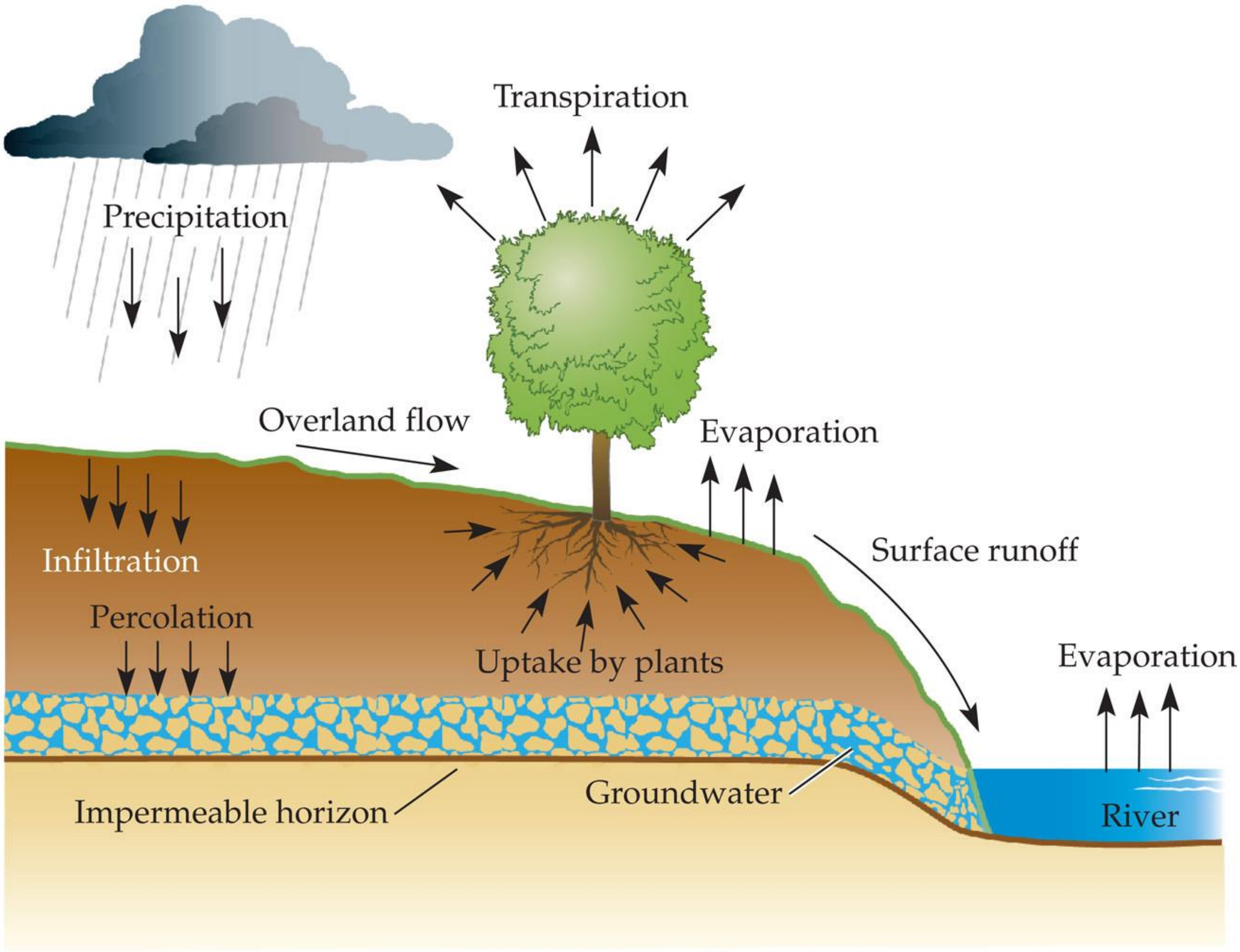
Terrestrial plants and soil microorganisms must take up water from soil to replace water lost to the atmosphere

- Water potential of soils is mostly dependent on matric potential (related to surface area and type of soil particles)
- Amount of water in soil is determined by balance of inputs and outputs, soil texture, and topography



ECOLOGY 3e, Figure 4.18

Figure 4.18 What Determines the Availability of Water from the Soil?

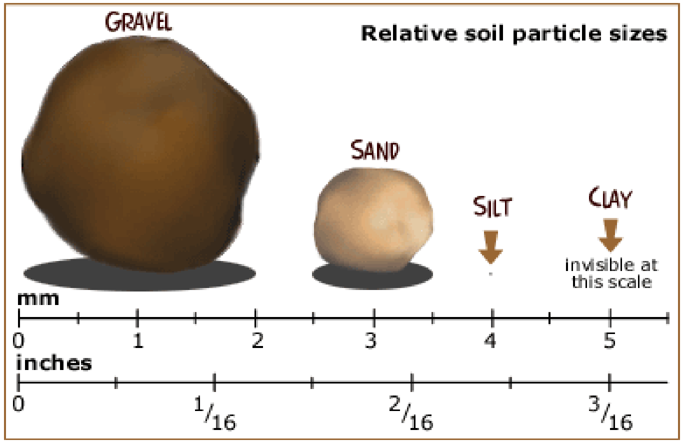


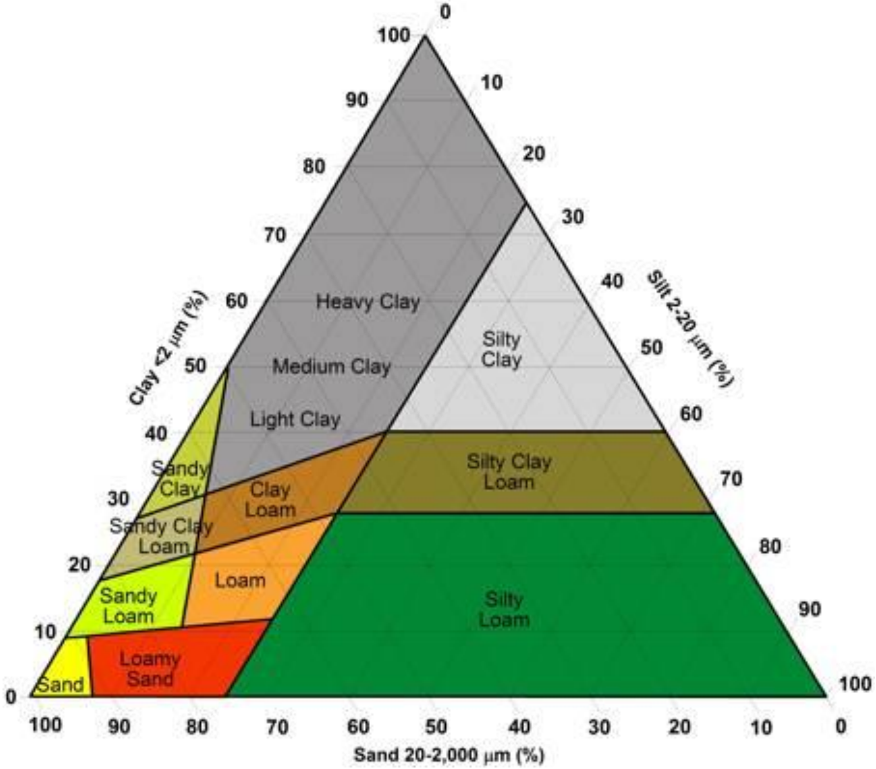
ECOLOGY 3e, **Figure 4.18**

http://school.discoveryeducation.com/schooladventures/soil/images/particle_sizes1.gif

Variation in Water Availability

- Sandy soils store less water than fine-textured soils (like silt and clay)
  - Fine soil particles also have a higher matric potential, and hold onto water more tightly (cling to soil particle surfaces)
  - Soils with mixed coarse and fine particles are generally most efficient in storing water and supplying it to organisms





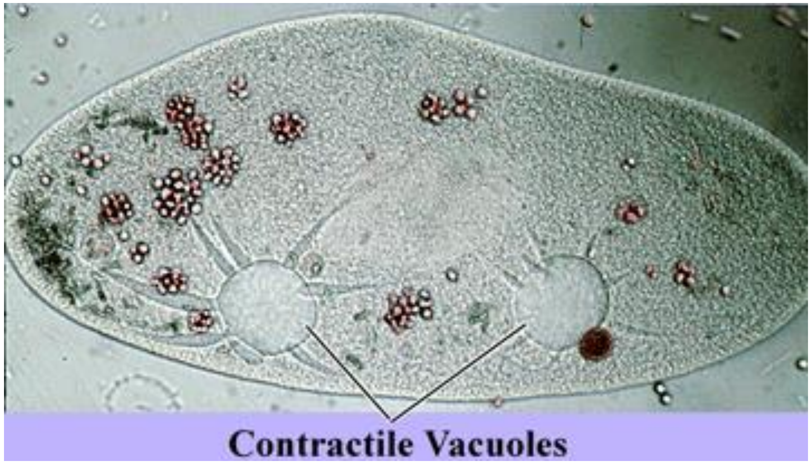
http://www.terragis.bees.unsw.edu.au/terraGIS_soil/images/sp_texclip_image002.jpg

Variation in Water Availability

Water balance of single-celled aquatic organisms is mostly determined by osmotic potential

- In most aquatic environments, osmotic potential doesn't change much over time, except in tidal pools, estuaries, saline lakes, and soils

Paramecium with contractile vacuoles



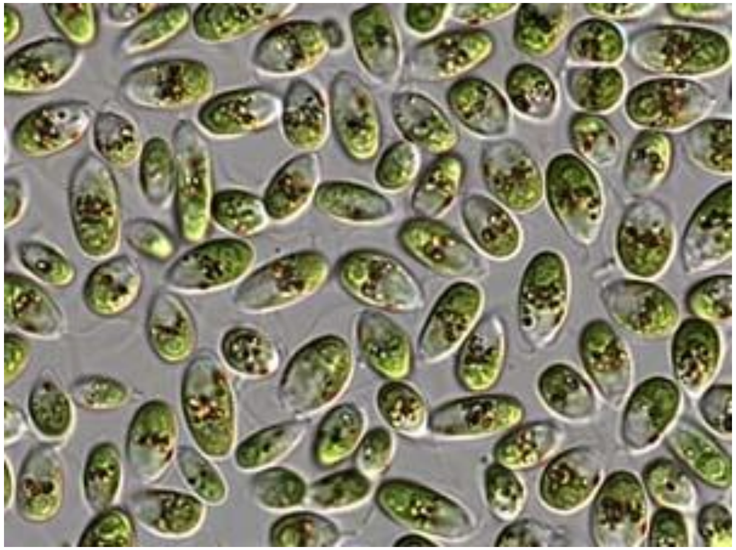
http://www.linkpublishing.com/parame_contract.gif

Variation in Water Availability

In variable environments, cells must alter their osmotic potential to maintain water balance — **osmotic adjustment**

- Solute concentration in a cell can be increased by synthesizing solutes, or by taking up inorganic salts
- Not all microorganisms can do this, while some can adjust to extreme saline conditions

Halophilic prokaryotes



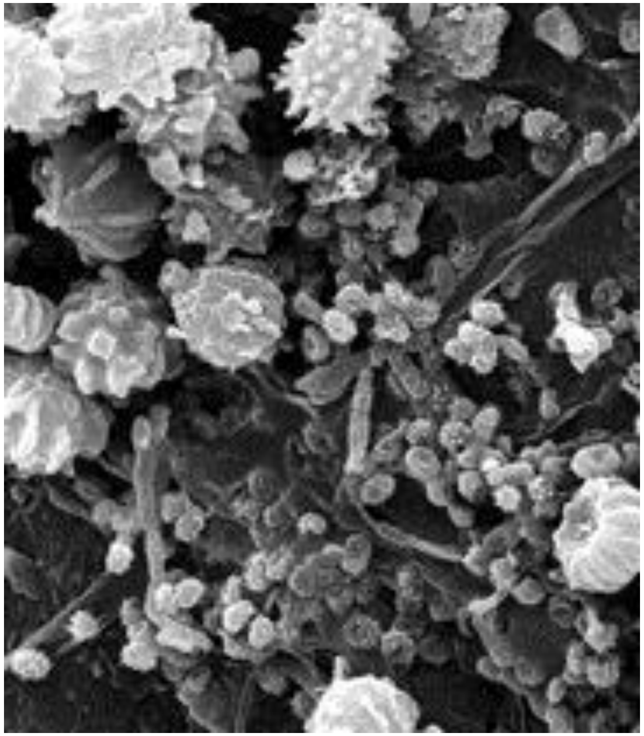
http://serc.carleton.edu/images/microbelife/Dunaliella.jpg

Variation in Water Availability

Some microorganisms avoid dry conditions by forming resistant spores encased in protective coatings

- Some filamentous forms are tolerant of low water potential and live in dry habitats
- But most terrestrial microorganisms are found in moist soils

Soil microorganisms

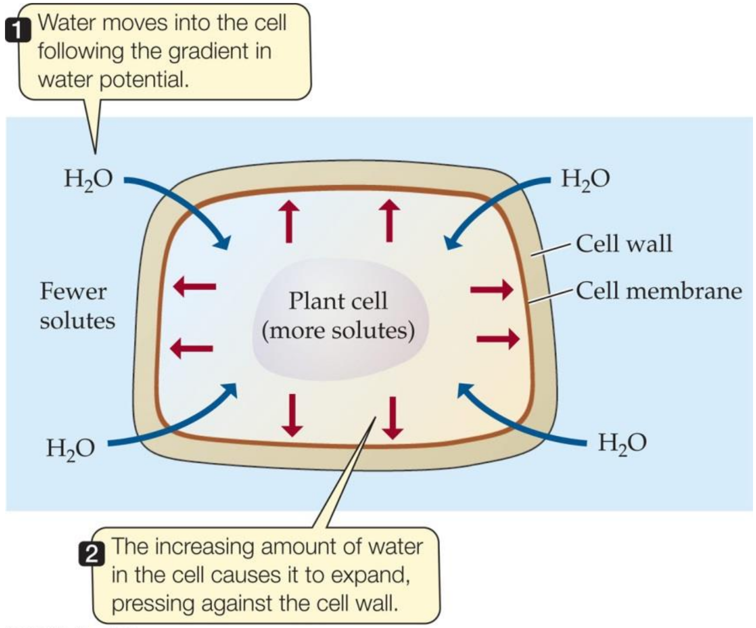


http://www.csiro.au/files/images/pczl.jpg

Variation in Water Availability

Plants have rigid cell walls of cellulose, fungi have cell walls of chitin, and bacteria have cell walls of peptidoglycan

- Cell walls allow development of **turgor pressure** — when water moves into cell, expanding cell presses against the cell wall



ECOLOGY 3e, Figure 4.19

Variation in Water Availability

Turgor pressure helps give form to plants

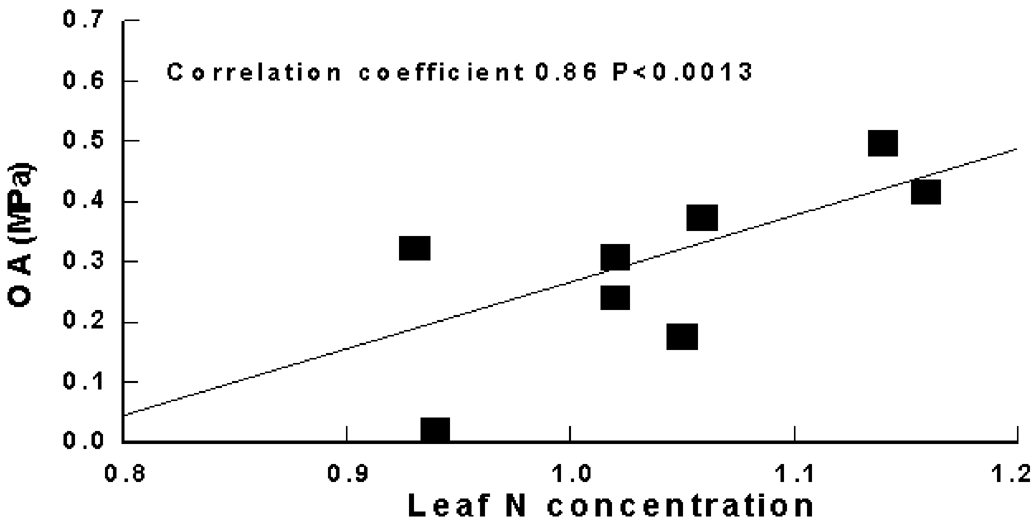
- Important force for growth, promoting cell division
- When non-woody plants lose turgor pressure, they wilt
  - Wilting is indication of water stress

Turgid and wilted tomato plants

Variation in Water Availability

Plants must take up water from a source with higher water potential than their own cells

- In freshwater plants, solutes in the cells create the water potential gradient
- In marine plants and terrestrial plants in saline soils, cells make *osmotic adjustments* by synthesizing solutes or taking up inorganic salts



Osmotic adjustment of sorghum genotypes under differing nitrogen levels in the field

http://www.regional.org.au/au/asa/1998/4/253mortlock.htm

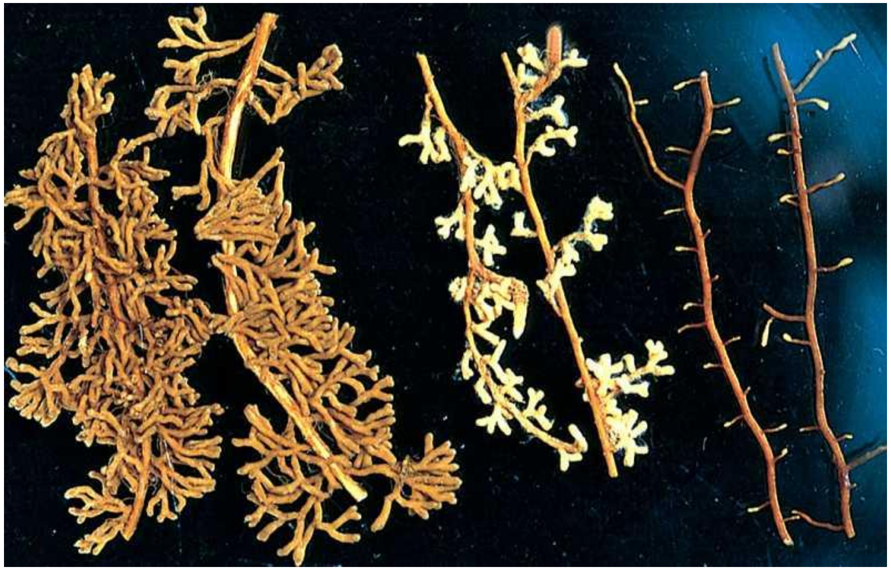
Variation in Water Availability

Terrestrial plants take up water through their roots, and by beneficial fungi called **mycorrhizae**

- Older, thicker roots have a waxy cuticle that limits water uptake
- Mycorrhizae provide *greater surface area for absorption of water and nutrients*, and allow exploration for these resources
- The fungi get energy from the plant

Mycorrhizae on the roots of pines. From left to right are…

- **yellow ectomycorrhizae** formed by *Pisolithus* ("horse dung fungus "),
- **white ectomycorrhizae** formed by *Rhizopogon*, and
- pine roots not associated with a fungus.

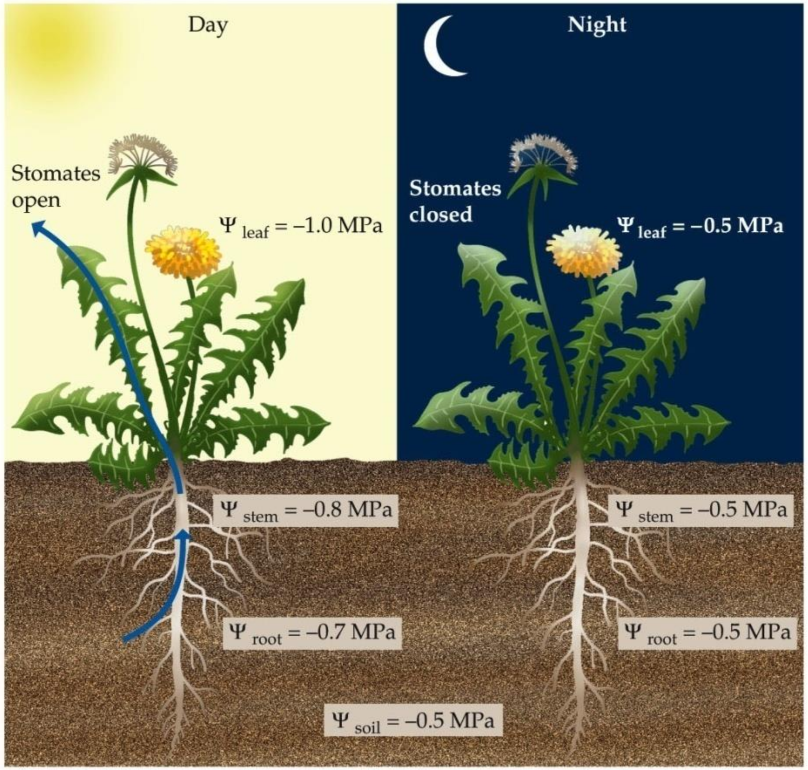


http://bio1100.nicerweb.com/Locked/media/ch17/17-12_mycorrhizae_on_t.jpg

Variation in Water Availability

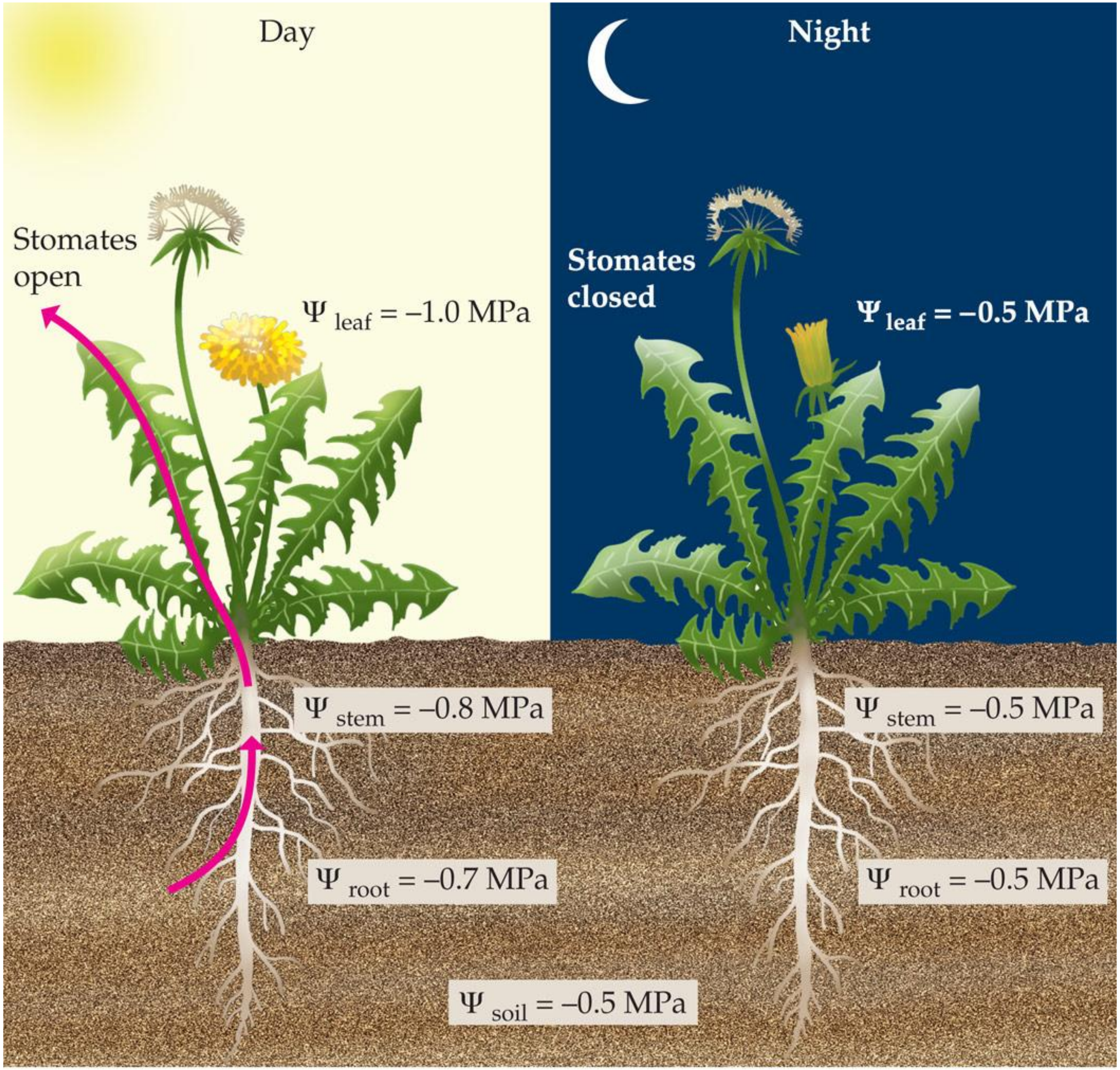
Plants lose water by transpiration when stomates are open for CO_2 uptake – **trade-off**

- Inside leaf, humidity is 100%, so water potential inside the leaf is higher than the atmosphere
- Plants must replace this water → **bulk flow of water**
- As leaf loses water, water potential in cell decreases relative to xylem in stem, so water moves from stem to leaf



ECOLOGY, Figure 4.20

Figure 4.20 The Daily Cycle of Dehydration and Rehydration

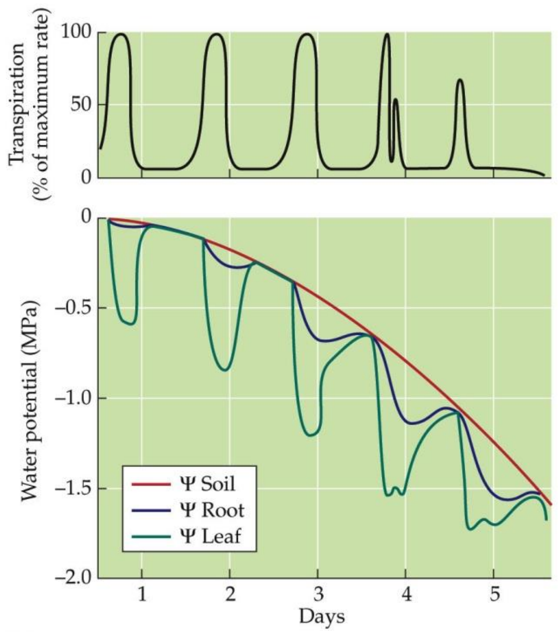


ECOLOGY 3e, Figure 4.20

Variation in Water Availability

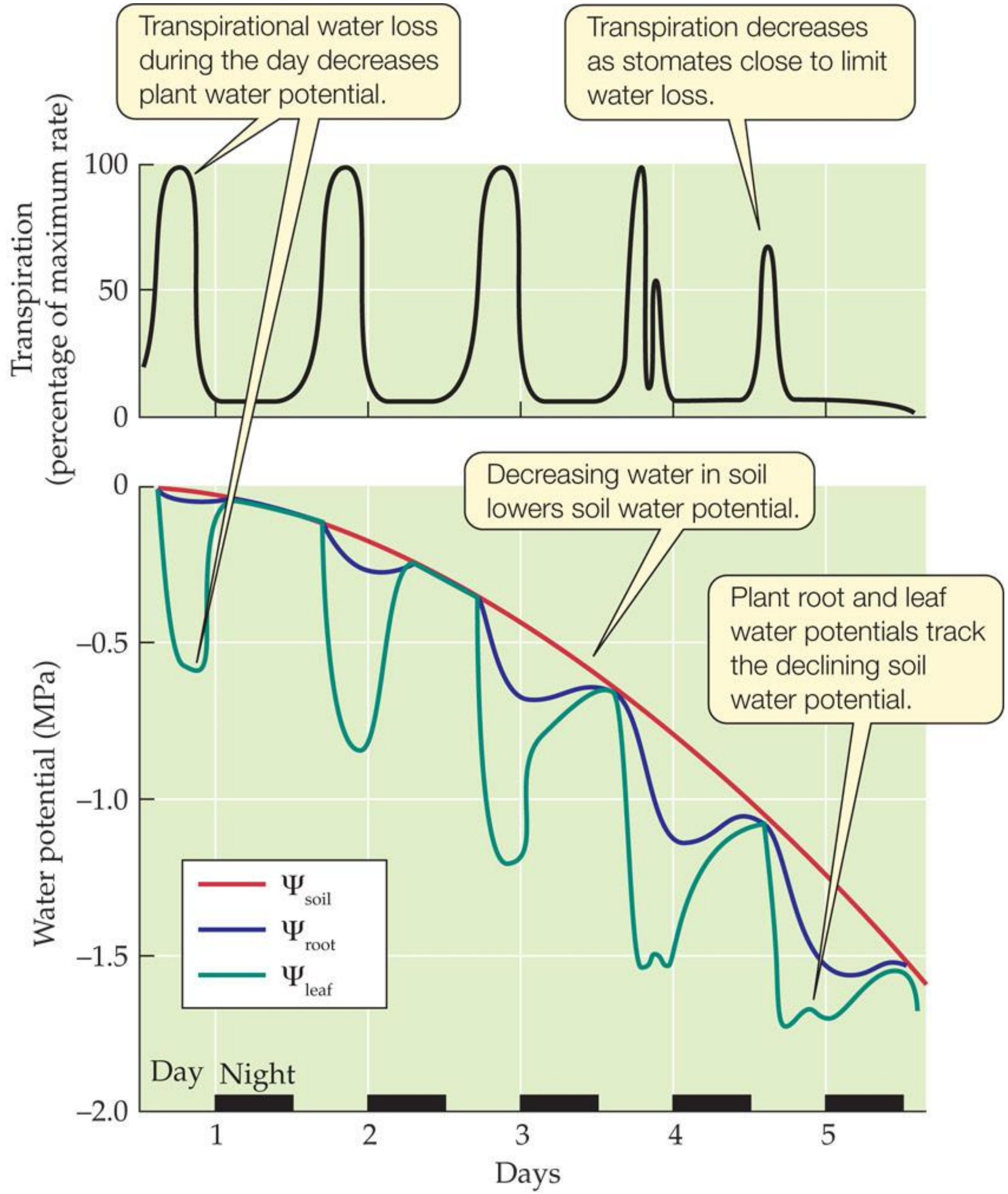
Root uptake lags behind transpiration rates during the day, so plant water content decreases

- At night, stomates close and plant water increases until it reaches equilibrium with soil water potential
- If lack of precipitation decreases soil water
  - water content and turgor pressure of plants will decrease
  - → plant will wilt



ECOLOGY, Figure 4.21

Figure 4.21 Depletion of Soil Water

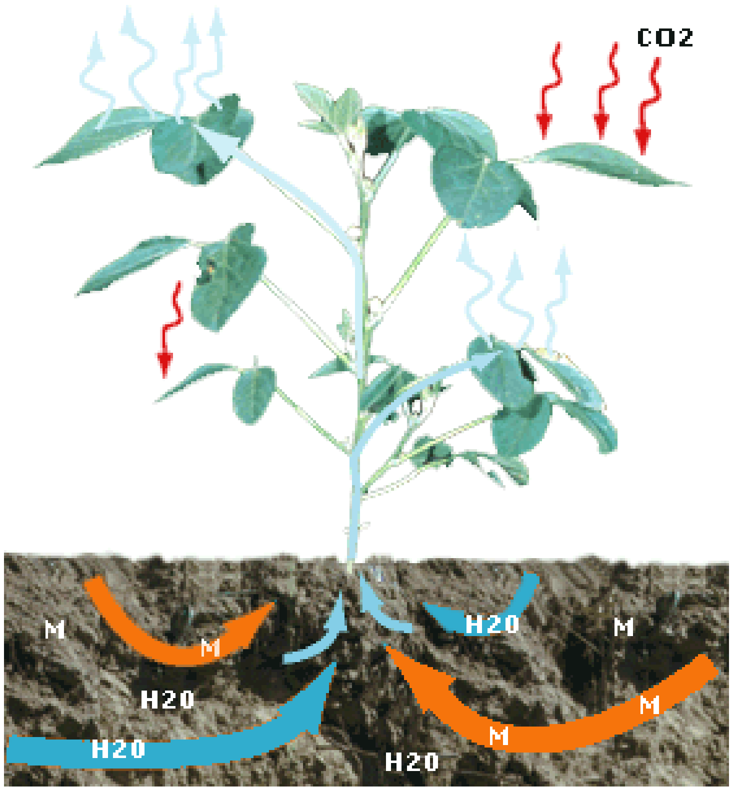


ECOLOGY 3e, Figure 4.21

Variation in Water Availability

Plants restrict water losses from transpiration in several ways due to trade-offs

- If turgor pressure is lost, stomates close
- This also impairs photosynthesis
- Some plants send a hormonal signal (abscisic acid) that causes stomates to open less
- Some plants shed leaves in dry seasons

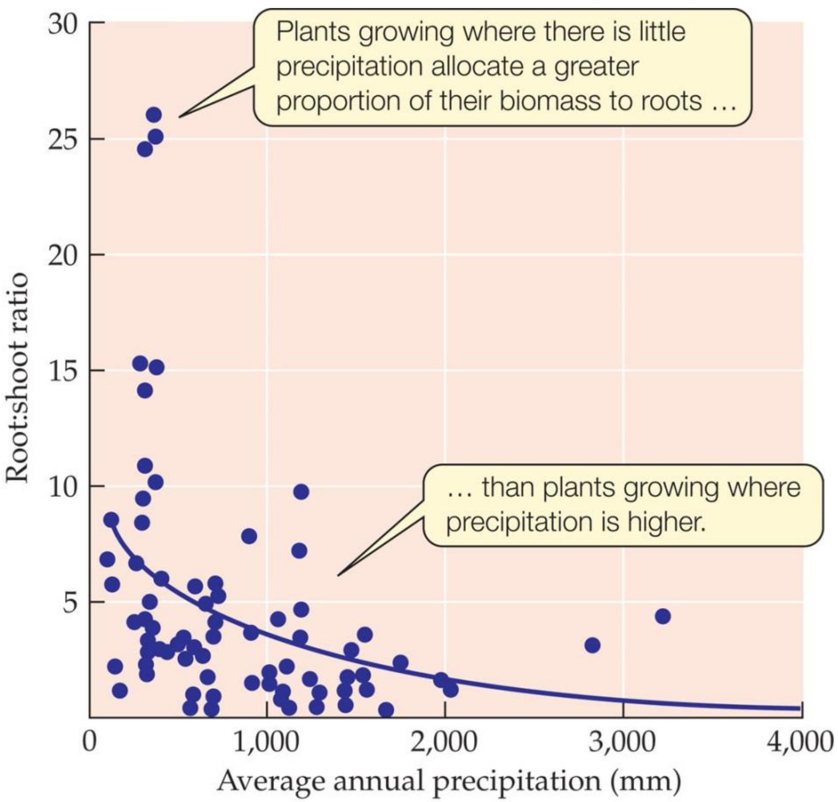


http://masters.agron.iastate.edu/classes/501/intro/images/transpiration.gif

Variation in Water Availability

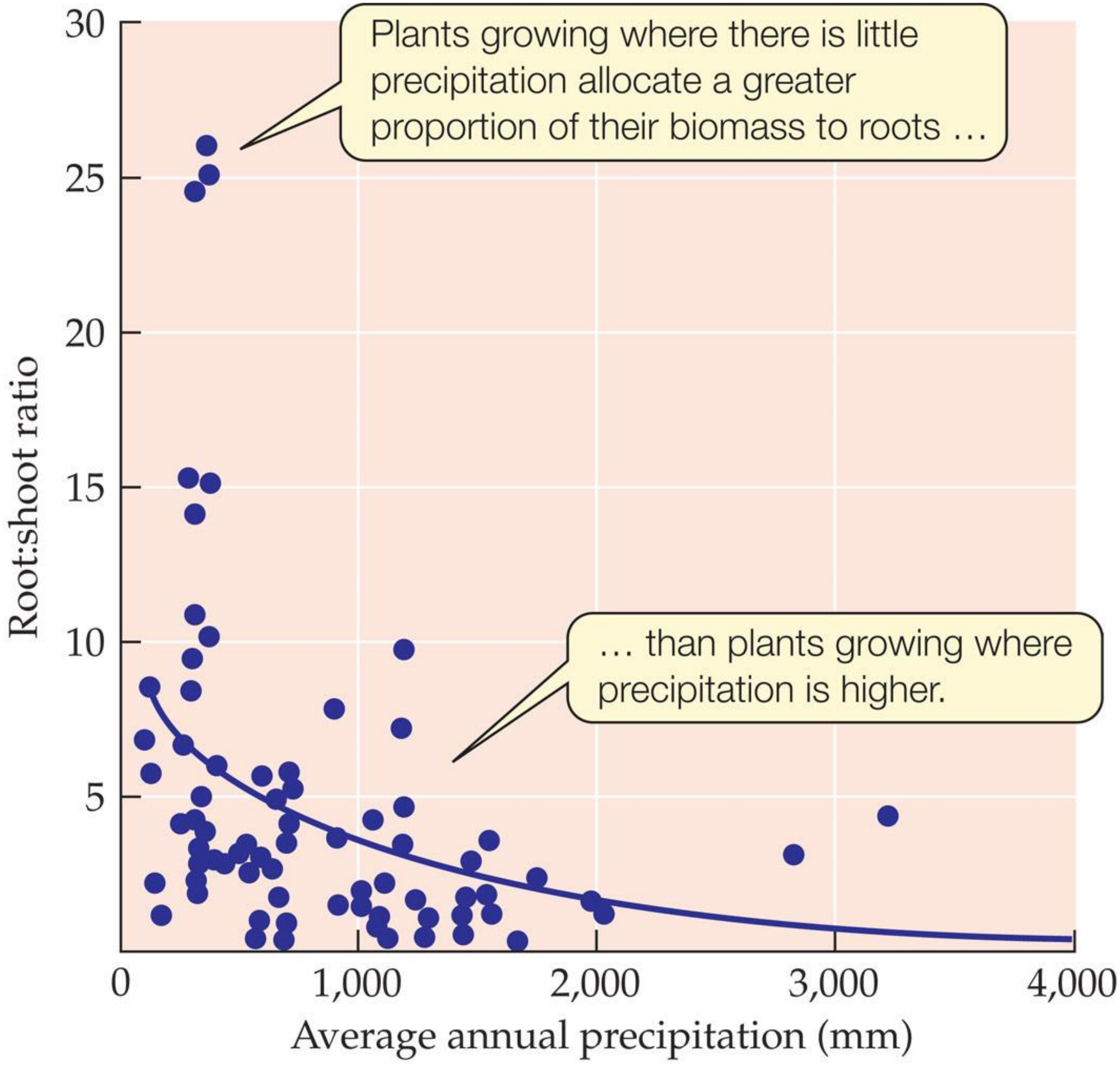
Plants in dry environments may also have thicker cuticles

- Higher ratio of root biomass to rest of plant (**root-to-shoot ratio**) enhances the rate of water supply.
- Some plants can acclimatize by altering growth of roots to match moisture and nutrient availability of soil



ECOLOGY 3e, Figure 4.22

Figure 4.22 Allocation of Growth to Roots versus Shoots Is Associated with Precipitation Levels

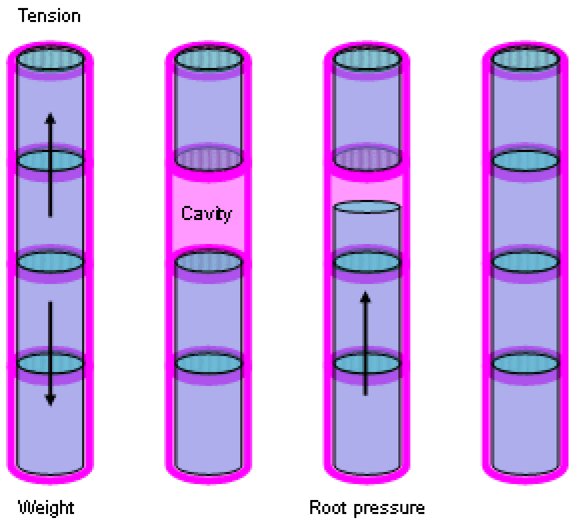


ECOLOGY 3e, **Figure 4.22**

Variation in Water Availability

In extremely dry conditions…

- Xylem can be under high tension (negative Ψ_p), which can pull air into the water column, called **cavitation**
- Cavitation can occur in woody plants in winter when water in the xylem freezes and bubbles form
- Most plants have multiple xylem tubes – if cavitation occurs in many tubes, tissue death can result



The cavity formed by cavitation is prevented from spreading to neighboring vessels by the surface tension of water at pit membranes and perforation plates of xylem. Root pressure is able to refill some cavities (depending on the plant and cavity location) and restore normal xylem function.

http://www.steve.gb.com/images/science/xylem_cavitation.png

Variation in Water Availability

In wet soils, oxygen diffusion is limited

- Waterlogged soils inhibit aerobic respiration in roots
- Moist soils can also promote growth of harmful fungi
- Root death can result, and ironically, plants can wilt in waterlogged soils

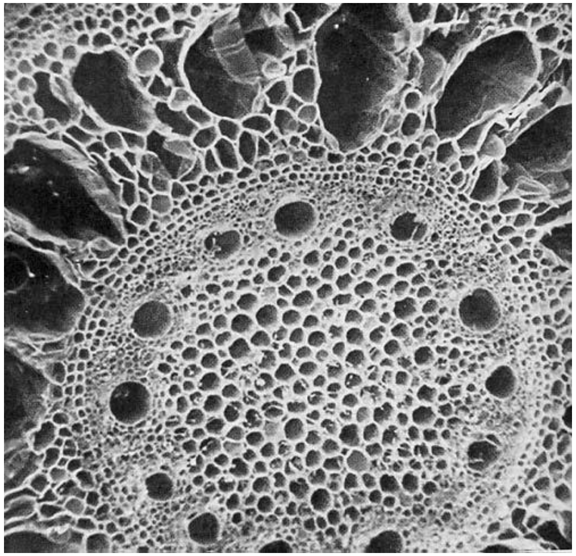
Wilted broccoli in waterlogged soil

http://topveg.com/wp-content/uploads/2007/07/wilting-broccoli.jpg

Variation in Water Availability

Plant adaptations to wet soils

- ***Aerenchyma*** – air channels (spongy tissue) in roots to alleviate oxygen stress



- ***Pneumatophores*** – specialized vertical roots (e.g.,) that allow air to enter roots

- Mangroves which grow vertically above water or in waterlogged soil are an example

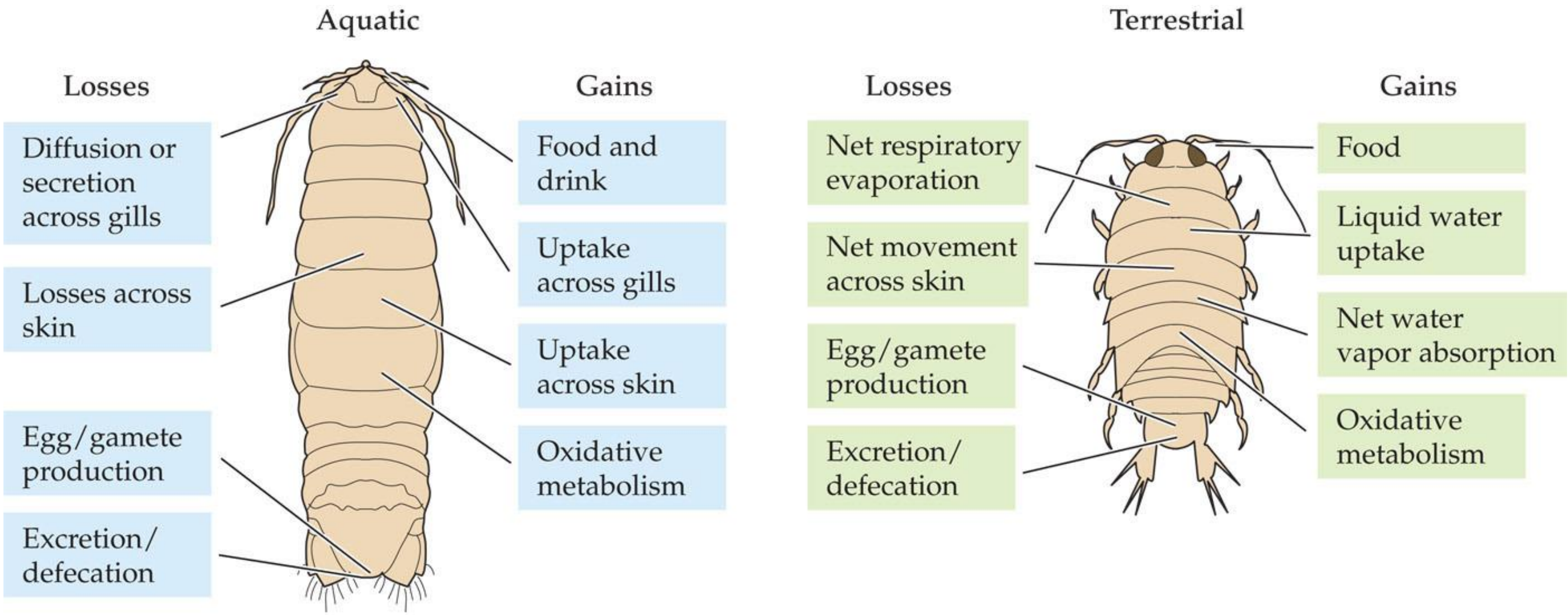
Black Mangrove pneumatophores

http://www.sfrc.ufl.edu/4h/other_resources/contest/highlighted_ecosystem/MangroveEnvfac.htm

Variation in Water Availability

Water losses and gains in multicellular animals are more complex

- Many have organs for excretion and other functions — local areas of water and solute exchange, and gradients within body can occur
- Most animals are mobile and can move to different environments to maintain water balance

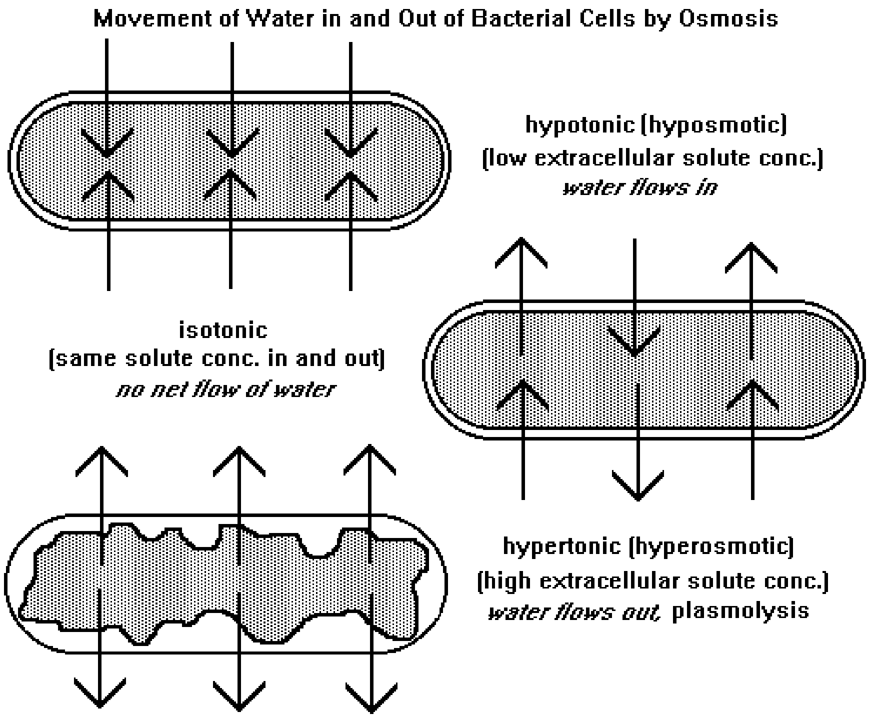


ECOLOGY 3e, **Figure 4.23**

Variation in Water Availability

For aquatic animals, the water can be:

- ***Hyperosmotic*** — more saline than the animal's cells
- ***Hypoosmotic*** — less saline than the animal's cells
- ***Isoosmotic*** — have same solute concentration as animal's cells



http://www.mansfield.ohio-state.edu/~sabedon/010plasm.gif

Variation in Water Availability

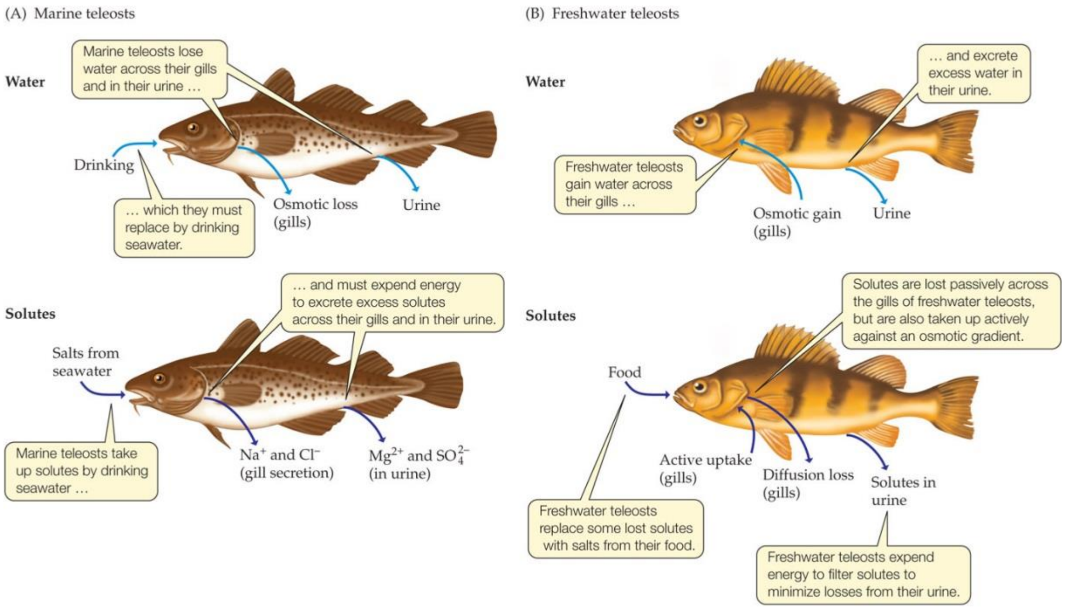
Most marine animals tend to be isoosmotic to seawater

- Marine invertebrates capable of osmotic adjustment do so by exchanging solutes with environment
  - For example, jellyfish have Na^+ and $Cl^–$ concentrations similar to seawater, but their $SO_4^{2–}$ concentrations may be one-half to one-fourth that of seawater

http://www.treehugger.com/lots%20of%20jellyfish.jpg

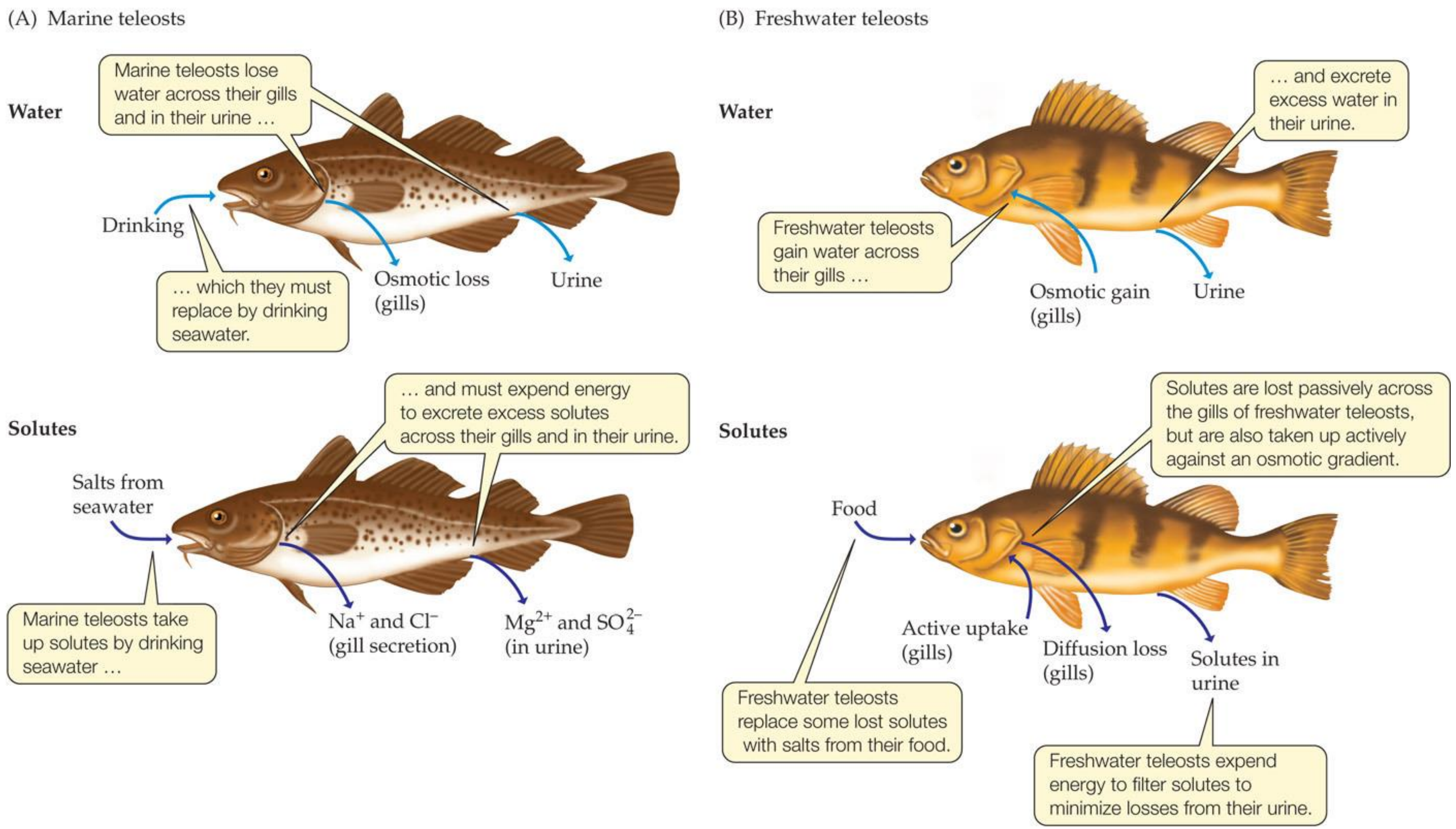
Variation in Water Availability

- In marine cartilaginous fishes (e.g., sharks, rays), blood is isoosmotic to seawater due to high concentrations of urea and trimethylamine N-oxide (TMAO)
- Marine bony fishes evolved in freshwater and their blood is hypoosmotic to seawater
  - Fish in general, exchange salts across the gills, and by eating and drinking



ECOLOGY 3e, Figure 4.24

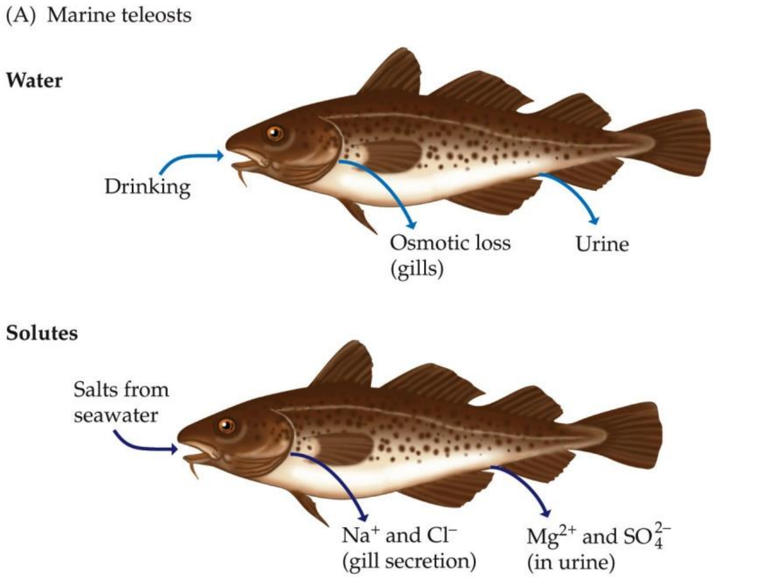
Figure 4.24 A Water and Salt Balance in Marine and Freshwater Teleost Fishes



ECOLOGY 3e, Figure 4.24

Variation in Water Availability

- Salts that enter marine bony fishes must be continually excreted through urine or across the gills, against an osmotic gradient (requires energy)
- Water is replaced by drinking

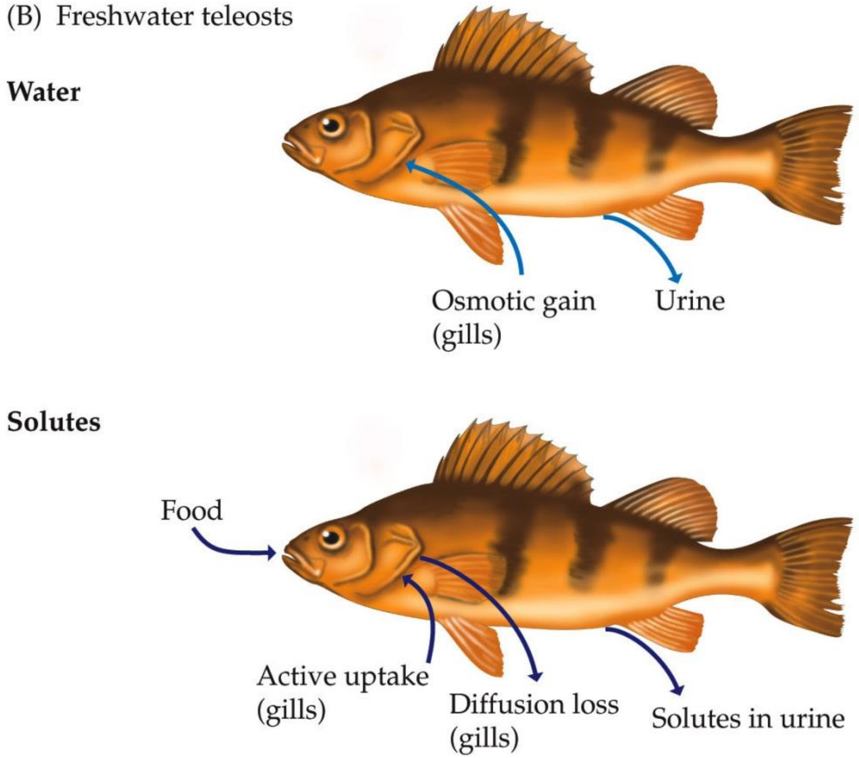


ECOLOGY, Figure 4.24 (Part 1)

- Marine mammals do not drink seawater, and produce urine that is hyperosmotic to seawater

Freshwater animals are hyperosmotic to water

- Tend to gain water and lose salts from skin or respiratory surfaces
- Solutes taken up in food or across gills, against osmotic gradient
- Excess water is excreted as dilute urine



ECOLOGY, **Figure 4.24 (Part 2)**

Variation in Water Availability

Terrestrial animals must exchange gases with a dry environment

- To minimize water loss, some live in moist environments, while some increase skin resistance
- Resistance to water loss limits amount of gas exchange possible
- Tolerance for water loss varies

TABLE 4.1

Ranges of Tolerances for Water Loss in Selected Animal Groups

Group	Weight loss (%)
Invertebrates	
Mollusks	35–80
Crabs	15–18
Insects	25–75
Vertebrates	
Frogs	28–48
Small birds	4–8
Rodents	12–15
Human	10–12
Camel	30

ECOLOGY 3e, Table 4.1

TABLE 4.1

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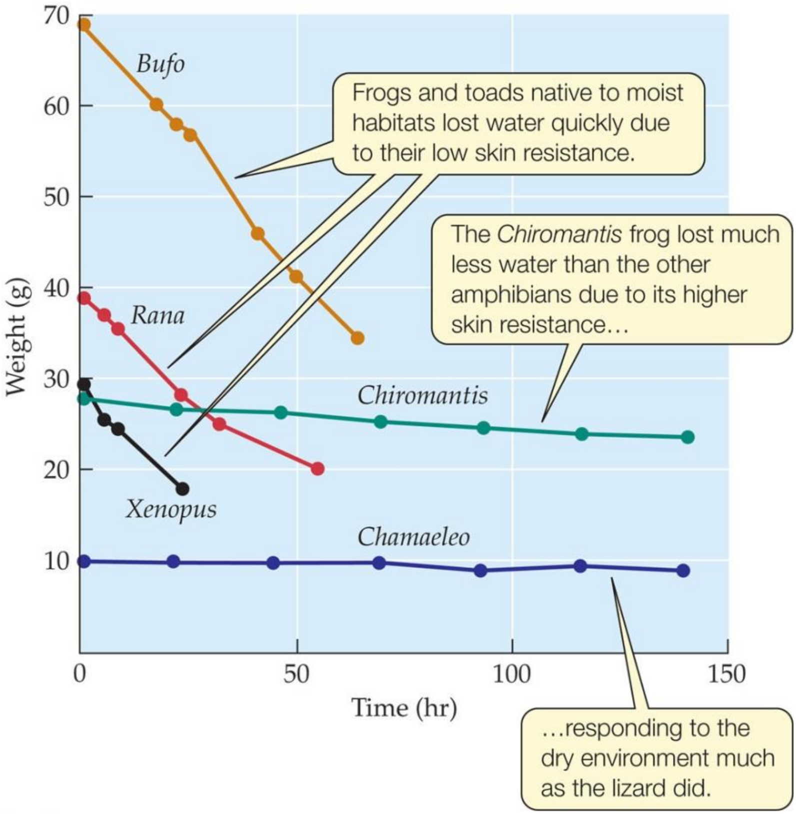
ECOLOGY 3e, **Table 4.1**

Variation in Water Availability

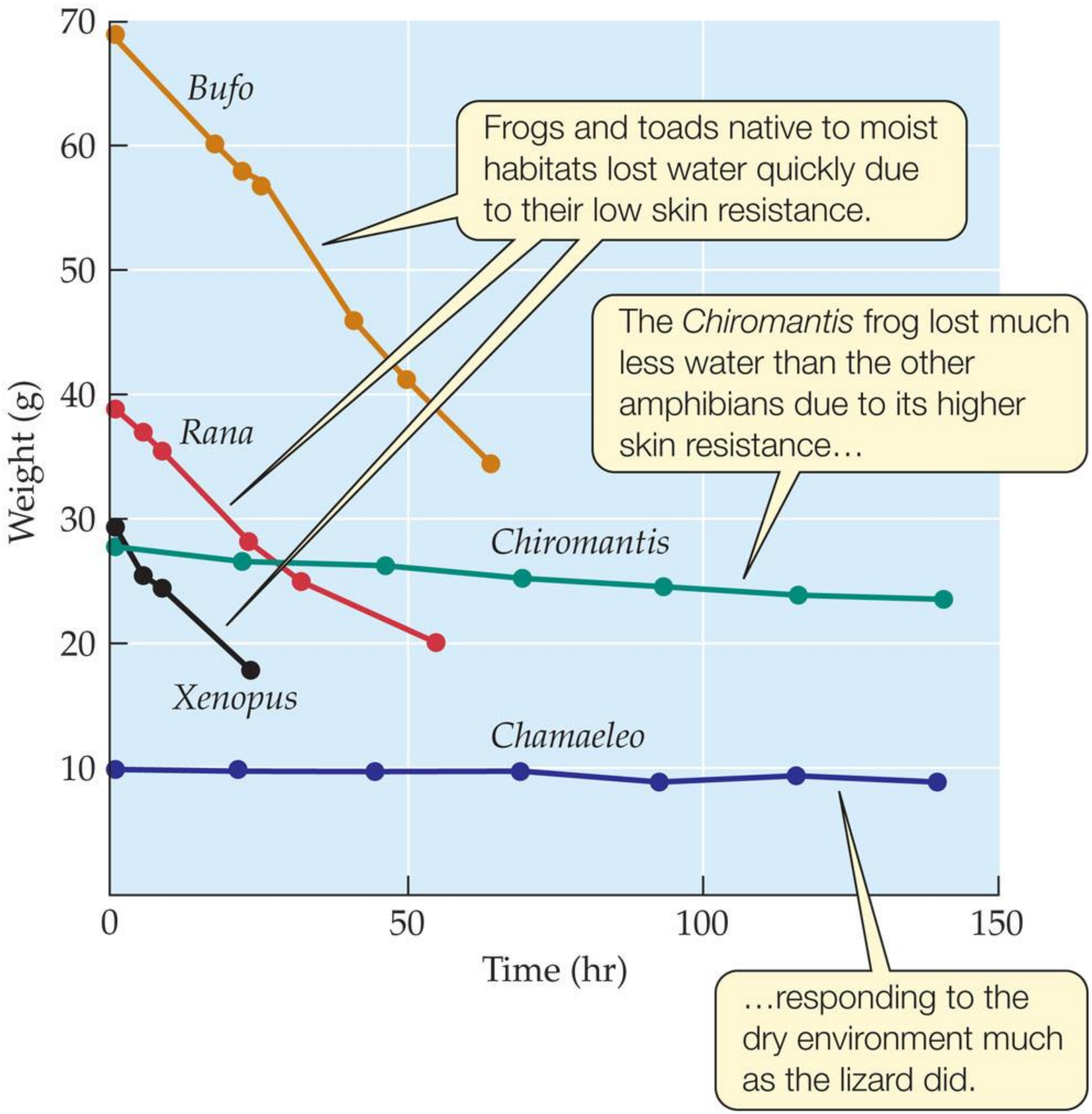
Amphibians rely primarily on a stable water supply to maintain water balance

- Occur in variety of habitats, even deserts, as long as there is reliable water — rains or pools
- Some gas exchange occurs through skin, so skin is very thin, with low resistance to water loss



ECOLOGY 3e, Figure 4.25

Figure 4.25 Resistance to Water Loss Varies among Frogs and Toads



ECOLOGY 3e, Figure 4.25

Variation in Water Availability

Some amphibians in dry environments have thicker skin

- To compensate for decreased gas exchange, they may have higher breathing rates
- During estivation, some form “cocoon” of shed skin or mucous secretions consisting of proteins and fats that lower their rates of water loss

Couch's spadefoot toad, *Scaphiopus couchii*, is a native of arid regions of American southwest

http://http-server.carleton.ca/~kbstorey/estivate_files/image020.jpg

Variation in Water Availability

Reptiles have been very successful in dry environments

- They have thick skin with layers of dead cells, fatty coatings, and plates or scales
- Mammals and birds have similar skin, and fur or feathers to minimize water loss

Blacktail jackrabbit (*Lepus californicus*); Fresno, CA

Collared lizard (*Crotaphytus collaris baileyi*), basking in a raised-up position

Variation in Water Availability

Desert invertebrates have the highest resistance to water loss

- Outer exoskeleton of chitin is covered by waxy hydrocarbons that are impervious to water

Giant desert hairy scorpion (*Hadrurus arizonensis*)

http://spiderpharmlive.com/Images/hadrurus_arizonensis.jpg

TABLE 4.2

Ranges of Resistance of External Coverings (Skin, Cuticle) to Water Loss

Group	Resistance (s/cm)
Crabs (marine)	6–14
Fish	2–35
Frogs	3–100
Earthworms	9
Birds	50–158
Desert tortoises	120
Desert lizards	1,400
Desert scorpions, spiders	1,300–4,000

ECOLOGY 3e, Table 4.2

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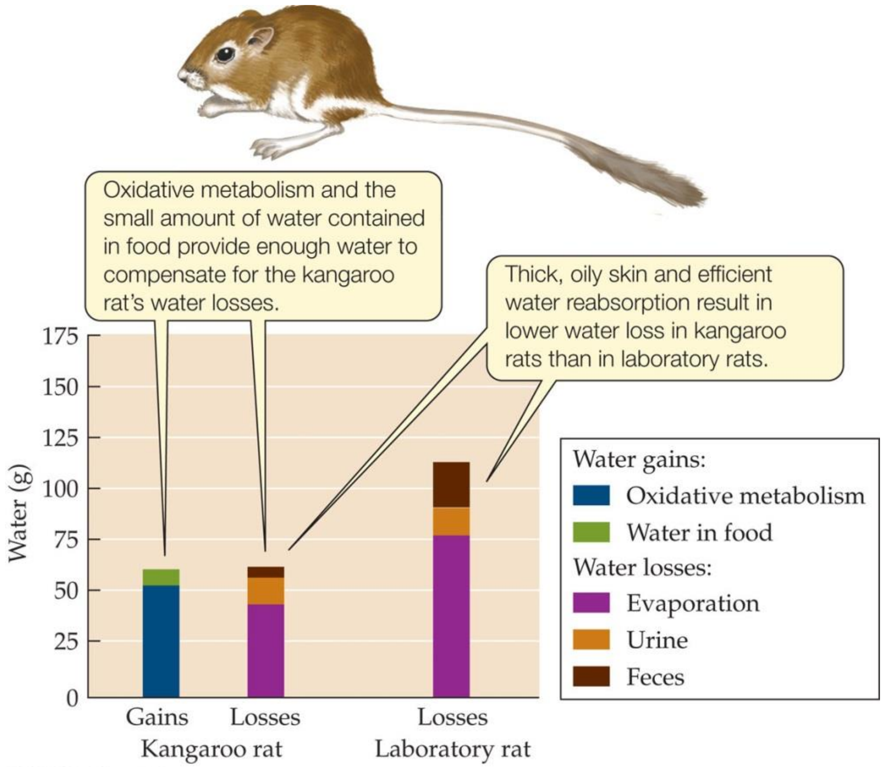
ECOLOGY 3e, Table 4.2

Variation in Water Availability

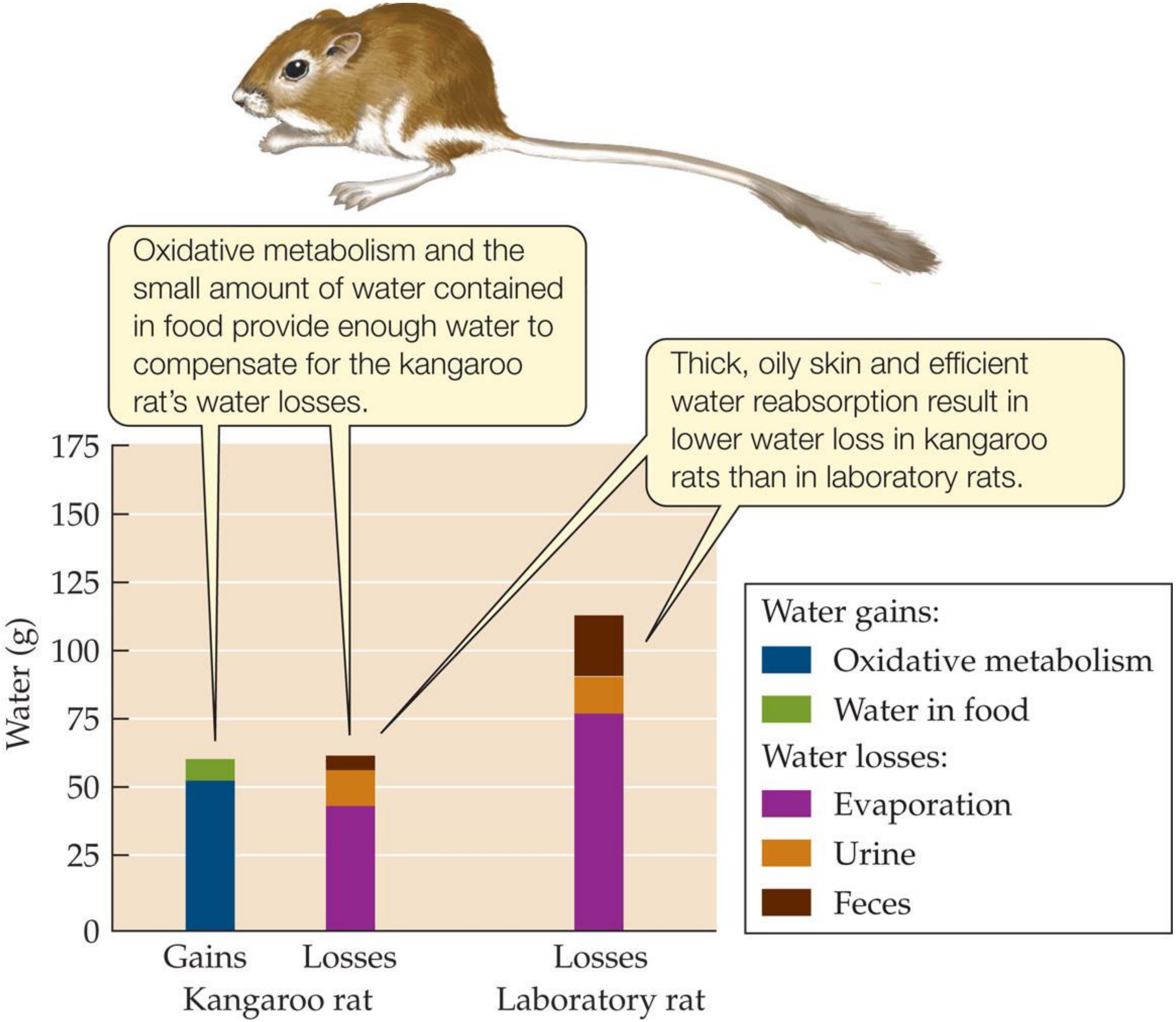
Kangaroo rats (*Dipodomys* spp.) use variety of adaptations to cope with arid environments

- Water is obtained from dry seeds oxidatively — carbohydrates and fats are converted into CO_2 and water
- Food with more water is sometimes available (insects and plants)



ECOLOGY 3e, Figure 4.26

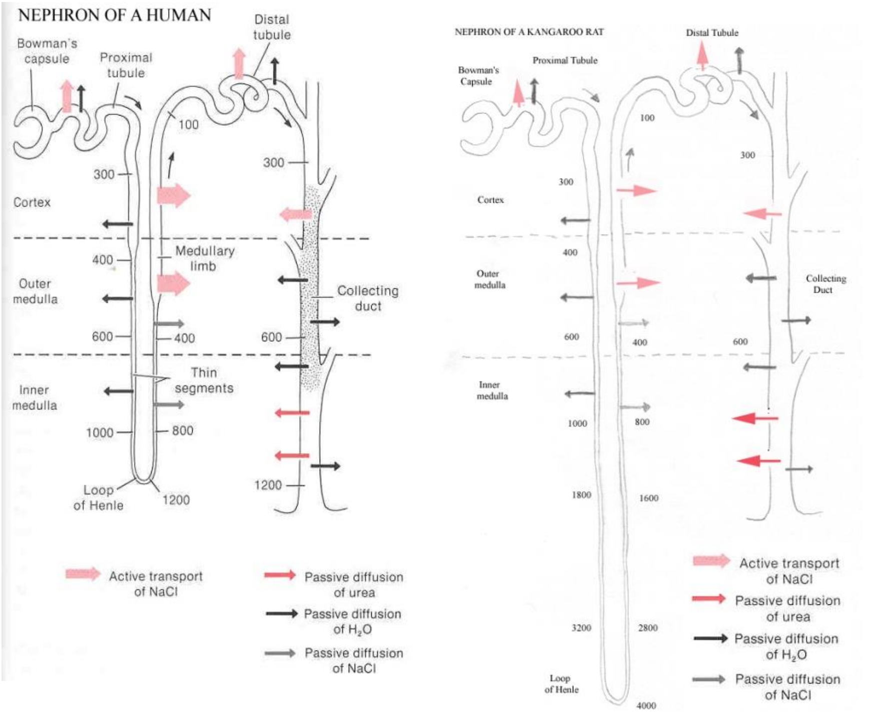
Figure 4.26 Water Balance in a Kangaroo Rat



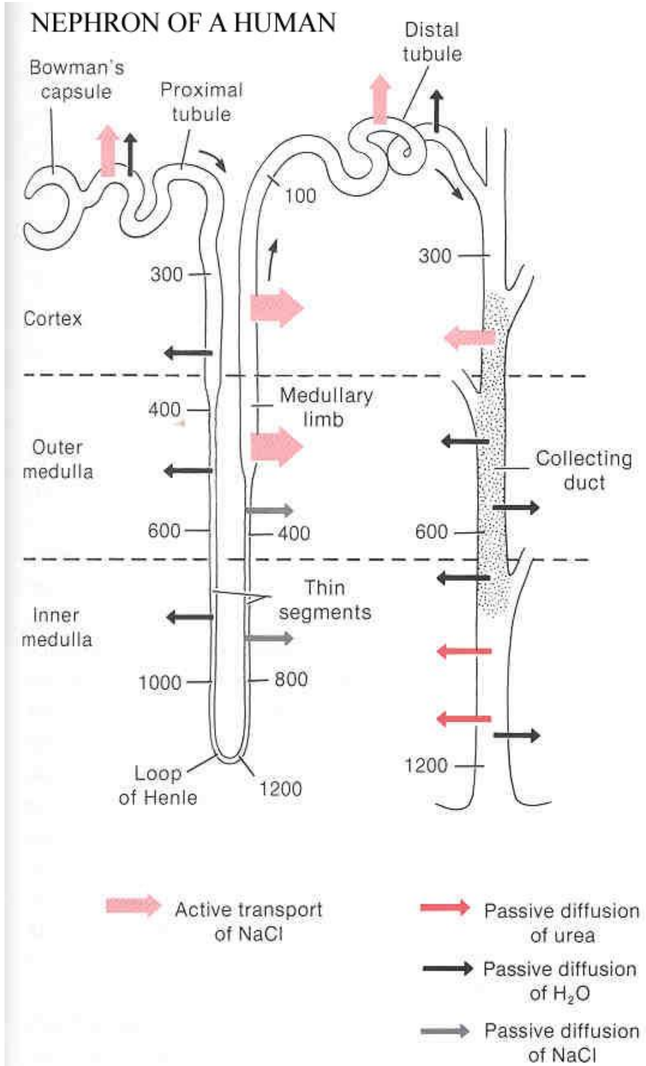
ECOLOGY 3e, Figure 4.26

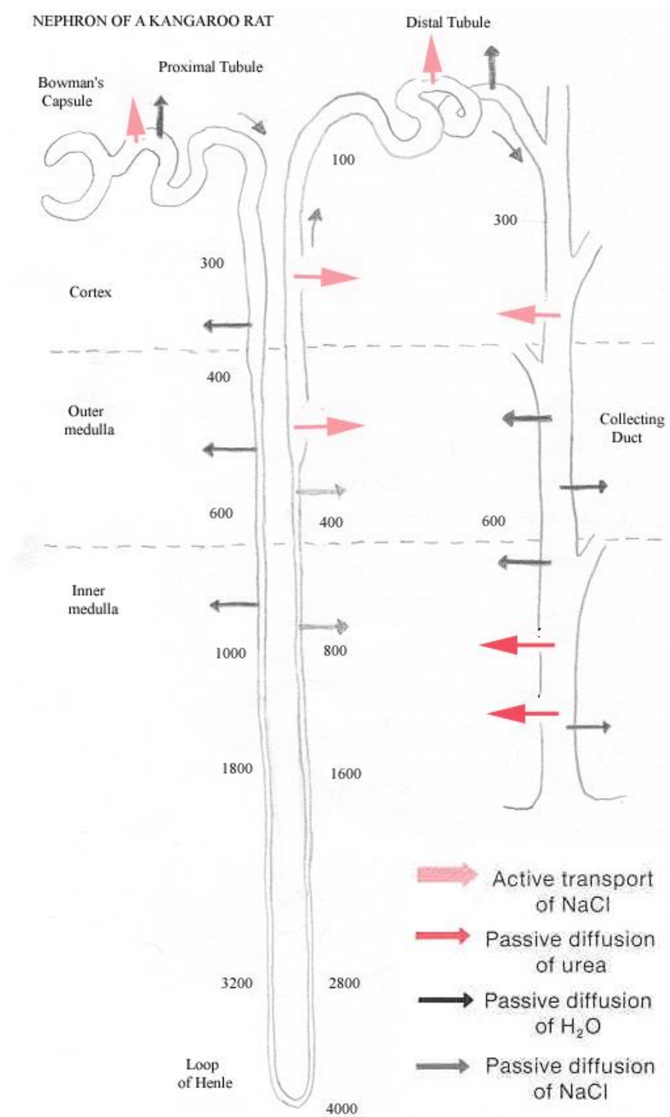
Water loss is minimized by:

- Active at night, staying in cooler burrows during day
- Thicker, oilier skin and fewer sweat glands than other rodents
- Excreting very little water in urine and feces – extremely long **Loops of Henle** make highly concentrated urine



Humans concentrate their urine up to 4X that of their blood (1200 mOs); kangaroo rats concentrate their urine about 18X that of their blood (5500 mOs). The loops of Henle are so long in Kangaroo rats, they extend down into the kidney's medullary region.





http://www.bio.davidson.edu/courses/anphys/1999/Chisholm/renalphys.htm http://upload.wikimedia.org/wikipedia/commons/thumb/6/65/Pyrrharctia_isabella.jpg/150px-Pyrrharctia_isabella.jpg

Case Study Revisited: Frozen Frogs

Three problems must be overcome for an organism to withstand freezing:

- Water forms needle-like ice crystals that can pierce cell membranes, rupturing cell
- Oxygen supply to tissues is restricted due to lack of breathing and circulation, and lack of fluid for diffusion
- When ice forms, it pulls water from cells, dehydrating them

Isabella tiger moths (*Pyrrharctia isabella* - above) overwinter in the caterpillar stage (below). The caterpillars can survive freezing at just below zero by producing a cryo-protectant chemical (Layne and Kuharsky 2000).

http://www.cirrusimage.com/Moths/woolly_bear_tiger_moth_larva.jpg

Case Study Revisited: Frozen Frogs

In animals that withstand freezing, freezing water is limited to the space outside cells

- **Ice-nucleating proteins** outside cells serve as sites of slow, controlled ice formation
- Additional solutes, such as glucose and glycerol inside cells lower the freezing point

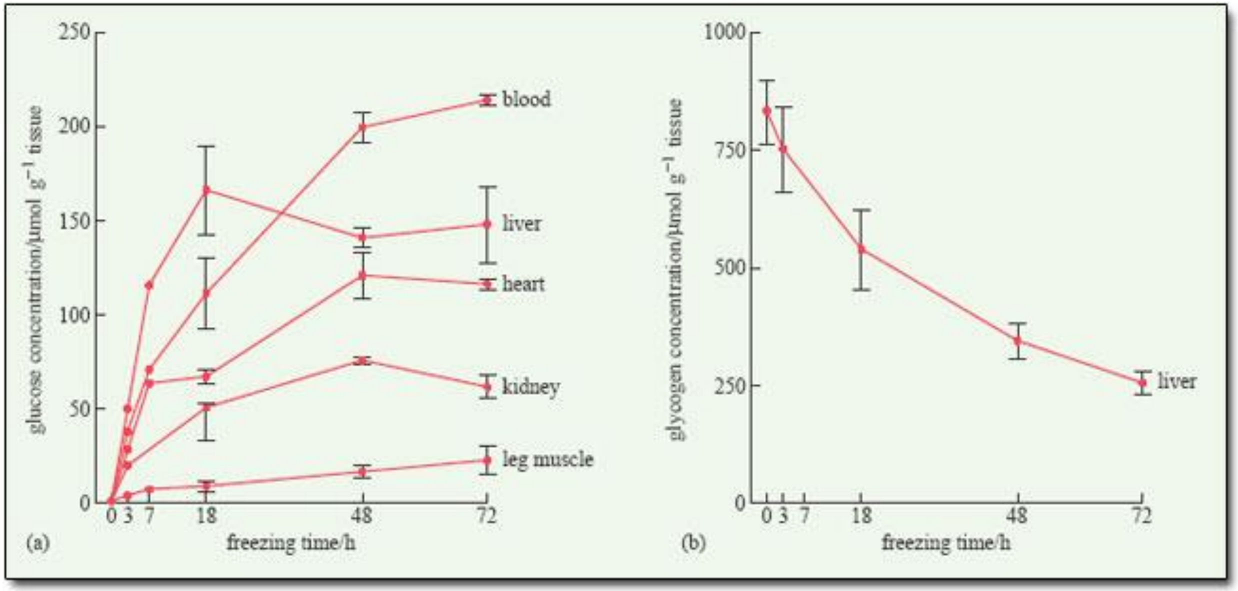


Figure 1.14 (a) Changes in the concentration of **glucose** in various organs of the wood frog (*Rana sylvatica*) over 72 hours of freezing at −2.5°C in the laboratory. (b) The corresponding depletion of liver **glycogen reserves**. Note that the horizontal axes are non-linear. Data from Pinder *et al*. (1992).

Case Study Revisited: Frozen Frogs

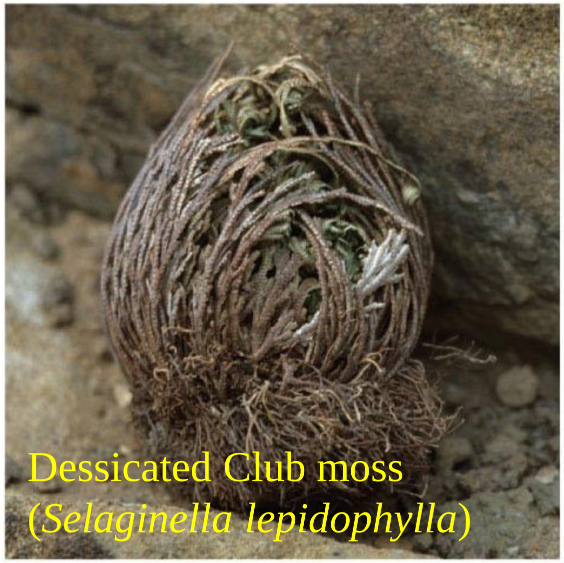
Winter burrows covered with layers of leaves and snow keep temperatures above –5°C (the lower limit for their survival)

- Freezing occurs over several days to weeks, but thawing can be rapid

http://www.units.muohio.edu/cryolab/projects/images/WoodFrog_female_000.jpg

Connections in Nature: Desiccation Tolerance, Body Size, and Rarity

(A)



(B)

Arid conditions are a more wide-spread challenge for organisms

- Some tolerate dry conditions by going into suspended animation
  - Many microorganisms do this, as do some multicellular organisms

(C)

***ECOLOGY*, Figure 4.27**

Connections in Nature: Desiccation Tolerance, Body Size, and Rarity

As cells dry out, the organisms synthesize sugars that form a glassy coating over the cellular constituents

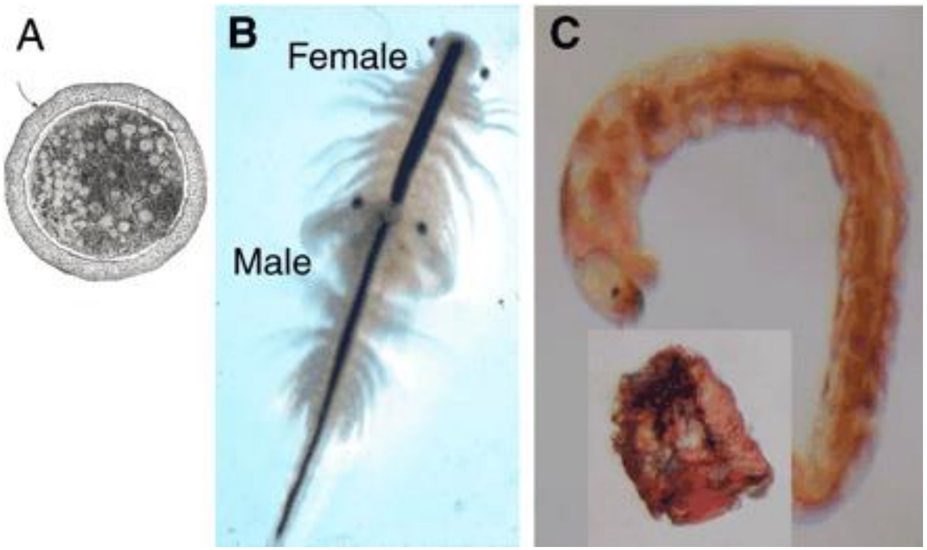
- When moisture returns, metabolic functions are regained rapidly

(C)

Why aren't more organisms tolerant of drying?

- Small organisms do not require structural reinforcement, such as a skeleton, which would restrict necessary shrinking of organism as it dehydrated

In animals that have skeletons as adults, desiccation tolerance is restricted to juvenile stages:
(A) SEM of a tolerant, encysted gastrula (diameter, 0.2 mm) of the …
(B) desiccation-sensitive adult brine shrimp *Artemia franciscana*; (length 1 mm);
(C) active and desiccated larvae of the fly *Polypedilum vanderplanki*. Photos by James Clegg (A,B) and Takashi Okuda (C).



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Water loss must be slow enough to allow sugars to be synthesized, but not too slow

- Small organisms have surface area-to-volume ratios and thicknesses favorable for the water loss rates required

http://genomebiology.com/content/figures/gb-2000-1-2-reviews1010-1.jpg

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Small size is often associated with slow growth rate and poor competitive ability under conditions of low resource availability

- Natural selection for desiccation tolerance may involve trade-offs with other ecological characteristics, such as competitive ability

http://genomebiology.com/content/figures/gb-2000-1-2-reviews1010-1.jpg