Lecture 15:
Physiological ecology

1. How can organisms deal with the stresses posed by the abiotic environment?
   a. Two examples of limiting factors: temperature and water
   b. Trade-offs and constraints

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Core ideas in physiological ecology

- Ranges of tolerance (Lecture 13) ultimately limit distribution
- Organisms are complex chemical reactions
- Reactions occur (enzymes function) best at optimum temperature and osmotic conditions, where fitness is maximized
- Many mechanisms for homeostasis have evolved to challenge hostile environments
- Maintenance of homeostasis requires energy and is often limited by constraints & tradeoffs

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One limiting factor to distribution: heat exchange

- Radiation—heat transfer by electromagnetic radiation
- Conduction—transfer by direct contact with substrate (*e.g.,* feet lose heat to ground)
- Convection—heat transfer mediated by moving fluid (usually air or water)
- Evaporation—efficient cooling from wet surfaces
- Redistribution—circulatory system redistributes heat among body parts, esp. core to appendages

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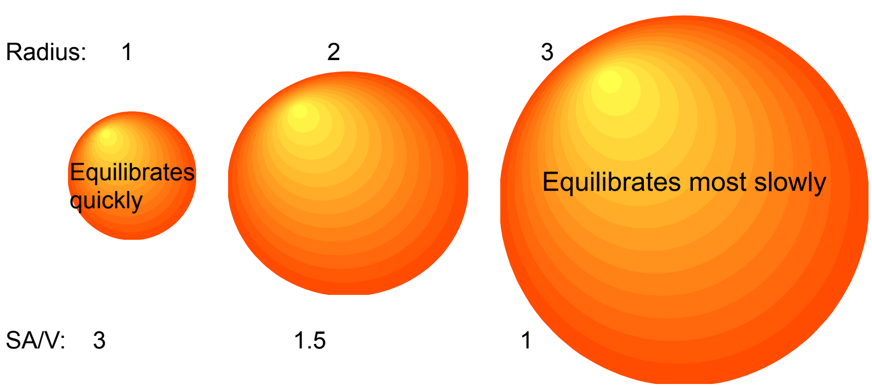
Size matters to heat balance (and other balances of gains and losses)

- Homeostasis and surface area:volume ratio
- Surface area determines equilibration rate
- Volume provides the inertia



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Heat balance especially important to homeotherms (birds, mammals)

- Poikilotherms (most reptiles, amphibians, fish, inverts) lack **physiological** means to deviate from environmental temperature (although they use **behavioural** means): their temps fluctuate
- Homeotherms must regulate heat balance to keep internal temperature within a narrow range: many traits contribute

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Size matters

- Bergmann's rule: Homeotherms tend to be larger at higher latitudes (colder)

Helarctos malayanus
65 kg, short fur

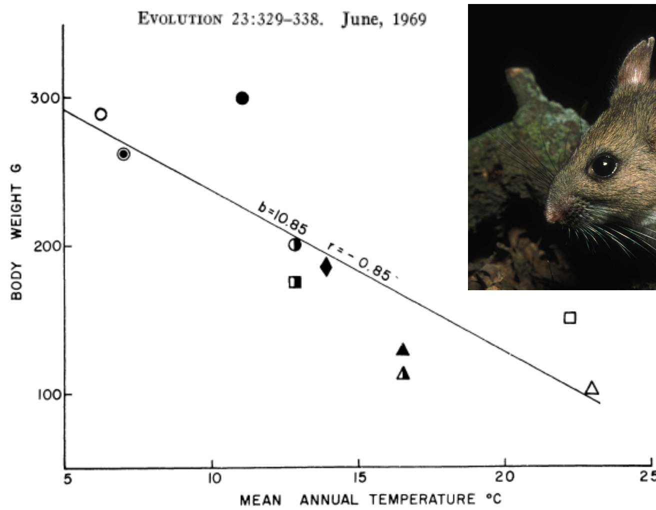
Ursus americanus
275 kg, medium fur

Ursus maritimus
650 kg, long fur

BERGMANN'S RULE AND CLIMATIC ADAPTATION IN WOODRATS (*NEOTOMA*)

JAMES H. BROWN AND ANTHONY K. LEE
Department of Zoology, University of California, Los Angeles
Department of Zoology, Monash University, Clayton, Victoria, Australia

EVOLUTION 23:329–338. June, 1969



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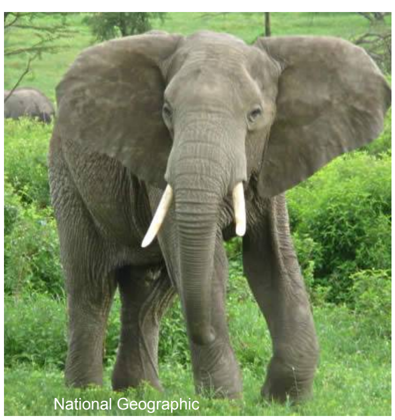
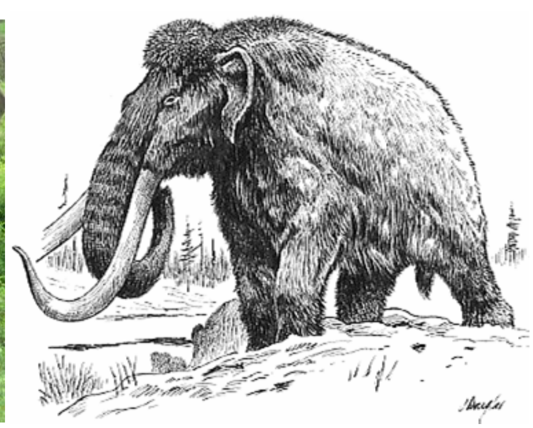
An exception?





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Shape matters:

- Sphere has least SA:V, so why shouldn't homeotherms be spheres in cold climates?
- Sometimes SA is needed for function
- Sometimes particular shapes are needed for function
- Tradeoffs and adaptive compromises
- Thought experiment: Imagine the extremes

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Who has the maximum SA:V ratio? *Chrysopelea* gliding snake, Borneo; restricted to warm tropics

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Who has the minimum SA:V ratio?

Pika, *Ochotona princeps*: alpine tundra rabbit; restricted to cold habitats; note spherical shape, reduced ears (for a rabbit relative)

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Shape matters

- Allen's rule: Homeotherms tend to have smaller appendages at higher, colder latitudes

Arctic fox
Vulpes lagopus

Red fox
Vulpes vulpes

Fennec fox
Vulpes zerda

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Allen's rule: appendages reduced in cold climates—arctic and desert hares

Lepus arcticus (Art Wolfe)

Lepus californicus (www.pestproducts.com)

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What else matters? Insulation is even more important than size/shape

Thick insulation: Half-sheared sheep

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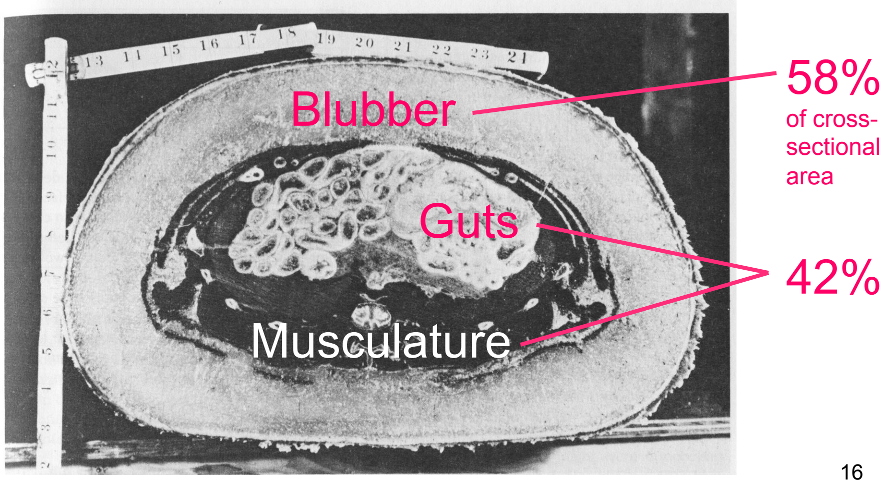
Thick insulation without drag from fur: Cross-section of seal

SEAL BLUBBER This cross section of a frozen seal shows the thick layer of blubber. Of the total area in the photo, 58% is blubber and the remaining 42% is muscle, bone, and visceral organs. [Courtesy of P. F. Scholander, University of California, San Diego]



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Feathers act as insulators

Female northern cardinal (*Cardinalis cardinalis*)

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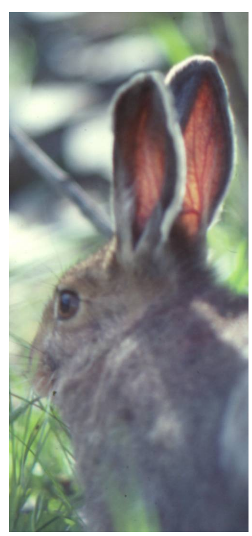
What else matters? Convective cooling enhanced by vascularization

Lepus californicus (National Geographic)



L. americanus (JD)

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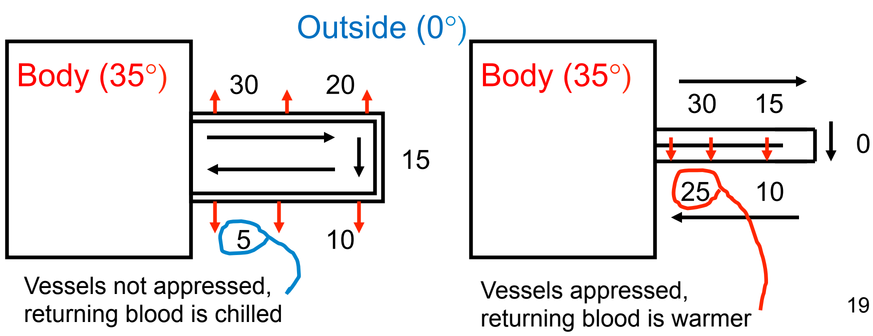
What else matters? Countercurrent circulation to limbs conserves heat

- Arteries and veins should be appressed in appendages to conserve heat; separated in appendages designed to shed heat
- Countercurrent flow maintains gradient, so heat is always flowing from outgoing blood to incoming blood



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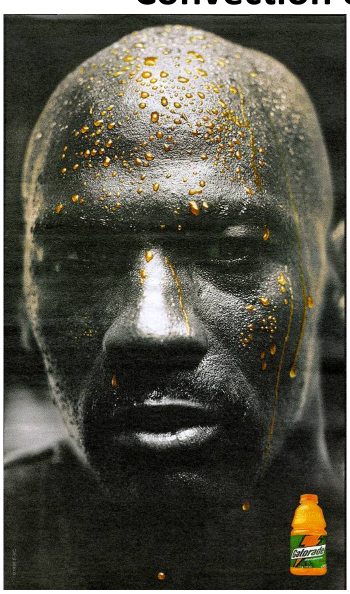
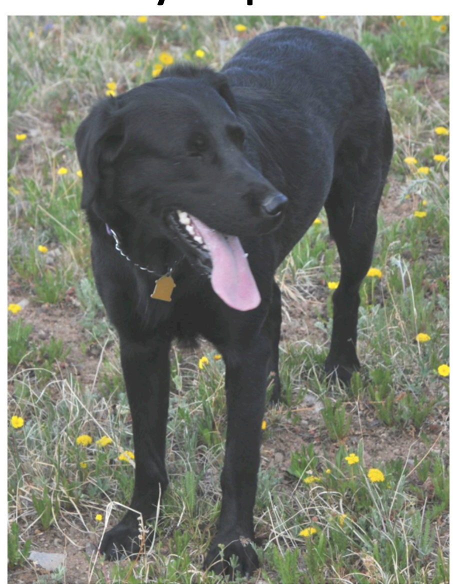
What else matters? Convection enhanced by evaporation





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Behaviour counts, too:
Convection enhanced by evaporation

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Behaviour counts, too:
Conduction enhanced by finding cool spots

A thermal image (cooler temperatures are in purple) reveals how a lolling koala can weather a heat wave.

Basic conclusions for "physiological ecology" of animals

- It's more than physiology! Also
- Gross anatomy (size, shape, insulation, vascularization) plus microanatomy and molecular variation
- Behaviour (including parental care) is usually an essential component
- Adaptations work together in coordinated ways
- Diverse solutions for common problems (e.g., cold seasons)

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Physiological ecology is different for (typical, terrestrial) plants because they are:

- Sessile, with little scope for behaviour
- Autotrophic, with few options for insulating the organism from harsh conditions

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Plant ecophysiology of carbon balance: tradeoffs & constraints abound

- Autotrophs: depend on net photosynthesis (= gross Ps minus respiration); conversion of CO_2 to fixed carbon:
- $CO_2 + H_2O \underset{\text{Respiration}}{\overset{\text{Photosynthesis}}{\rightleftharpoons}} \text{Carbohydrate} + O_2$
- Must bring together light, gases, & water in functioning photosynthetic tissue
- Functioning requires OK temperature, osmotic balance, enzymes, dissolved nutrients from soil, etc.
- Any of these components can limit fitness
- Anatomy & physiology reflect constraints

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Photosynthetic structures embody adaptation to environmental stresses

- Photosynthetic (green) structures are usually leaves (but can be stems)
- Leaf size and shape: SA:V ratios important again, as for animals
  - Benefits of large leaf surface area: good for harvesting light, CO_2
  - Costs of large leaf surface area: bad for overheating, water loss by evapotranspiration through stomata

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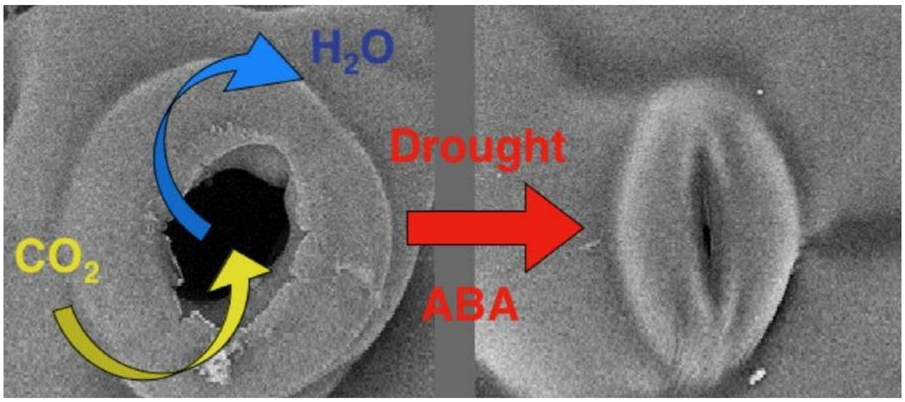
Plants with large leaves combat overheating by:

- Growing in shady habitats
- Evaporative cooling by opening stomata



www.isv.cnrs-gif.fr/jg/images/stomata.jpg

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Evaporative cooling needs plentiful water—not always available. Plants with large leaves combat water loss by:

- Closing stomata…
- …but that shuts off all gas exchange, including CO_2 input, so photosynthesis shuts down. Plant stops growing…
- …and risks overheating & tissue damage.
- Therefore, fundamental tradeoff between water conservation and rapid growth
- Consequences most obvious in desert plants

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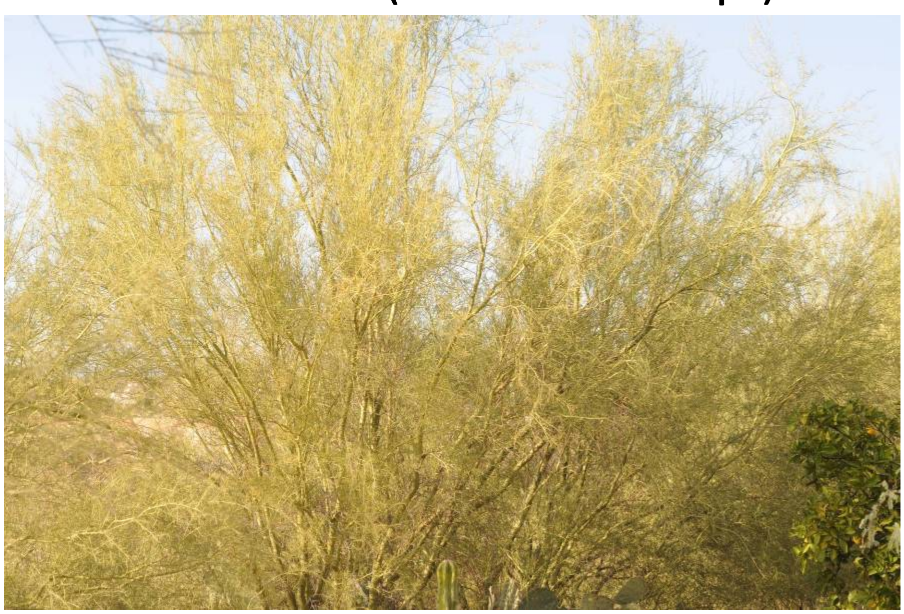
Keeping cool *while conserving water*:
Sonoran Desert, Arizona

Palo Verde (*Parkinsonia* sp.)



Palo Verde = "green stick"
Photosynthetic bark on trunks & branches; can grow without incurring heat load & water loss through leaves

Microphylly in Palo Verde

Cacti: extensive but shallow roots

Episodic patterns of H_2O availability in Sonoran desert:
Rillito River, Tucson, Arizona

Saguaro cactus (*Carnegiea gigantea*)
Restricted to Sonoran desert, adapted to episodic rains

- Grows to 15 m,
  200 yr, 5+ tonnes
- Extensive, shallow roots
- Accordion-pleated trunk allows expansion
- Can absorb 800 L of water from one storm, use it gradually for growth

Animals can evade stress through behaviour: what about plants?

- Deciduous habit: dropping leaves during dry or cold seasons can reduce water stress and tissue damage

Tropical deciduous forest, Guancaste Province, Costa Rica

Dry season

Rainy season

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Terminological clarification: "evergreen"

- The most important groups of land plants are angiosperms and conifers. Loosely, "evergreen" is used as a synonym for "conifer,"…
- …but some conifers are **not** evergreen…
- …and many evergreens are **not** conifers (especially in wet tropics)!

Red pine, *Pinus resinosa*, evergreen conifer

Tamarack, *Larix laricina*, deciduous conifer

Rosemary, *Rosmarinus officinalis*, evergreen angiosperm

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A more useful terminology for leaf structure and persistence: mesophytic vs. sclerophyllous

Mesophyte, sugar maple, *Acer saccharum*

Sclerophyll, red pine, *Pinus resinosa* Joker's Hill

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Mesophytic

- Leaves large
- Thin, papery, flexible
- High SA:V
- Flimsy, fragile
- Frequently deciduous, last only 1 season
- Prominent local examples: hardwood trees such as maples, oaks

Sclerophyll

- Leaves small
- Thick, needles or scales
- Low SA:V
- Tough, leathery
- Frequently evergreen, last several seasons
- Prominent local examples: coniferous trees such as pines, firs, spruces

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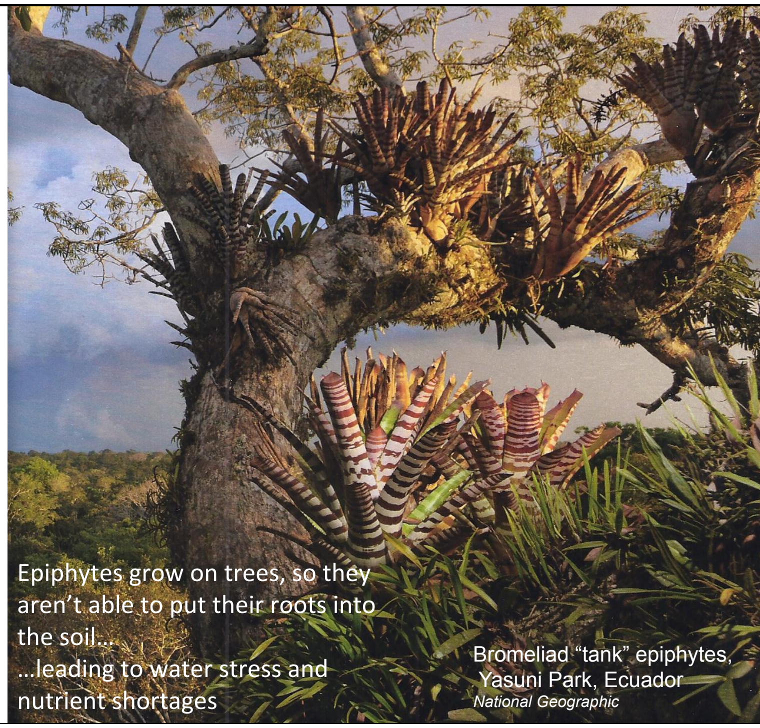

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Many tank epiphytes on palm tree hosts
Luquillo Forest, Puerto Rico

Epiphyte tangle fallen off host branch
La Selva Biol. Station, Costa Rica

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