Thermoregulation

Much of the biology of birds and mammals is influenced by their energetics; to understand endothermy in these species, it’s helpful to understand ectothermy in some detail as well.

I. Ectothermal regulation
   A. All organisms exchange energy with the environment
   B. Routes of heat exchange
   C. Principles of ectothermal regulation
   D. Mechanisms of ectothermal regulation
   E. Costs, benefits, and consequences of ectothermal regulation

II. Endothermal regulation
   A. Four characteristics of avian/mammalian energetics
   B. Consequences of avian/mammalian energetics
   C. Mechanisms of endothermal regulation
   D. Evolution of endothermal regulation

I. Ectothermal regulation (Ch. 11 pp. 326-334)
   A. All organisms (poikilotherms, ectotherms, endotherms) exchange energy in the form of heat with the environment
   B. Routes of heat exchange include:
      1. **solar radiation**, which includes
         a. **direct** radiation – results in heat gain
         b. **indirect** (reflected) radiation – results in heat gain
         c. **infrared** radiation – may result in gain or loss, depending on the heat gradient between organisms and the environment
      2. **convection** = heat exchange with air
         a. will result in gain or loss, depending on temperature gradient
         b. rate of convective loss also depends on wind speed
      3. **conduction** = heat exchange via direct contact with substrate
a. substrate includes both solid substrate (ground, e.g.) and water
b. will result in gain or loss, depending on temperature gradient
c. for animals in water, rate of conductive gain/loss also depends on rate of water movement

4. **evaporation** = loss due to the conversion of water from liquid to gas
   a. always results in heat loss
   b. only mechanism permitting animal to maintain $T_b < T_a$
   c. water can potentially be lost from any moist surface

5. **metabolic heat** = heat generated via body’s internal chemical activity
   a. major sources include
      (1) basal metabolism (largest source)
      (2) specific dynamic action
      (3) specialized muscle movement: shivering, e.g.
      (4) non-shivering thermogenesis (NST) = oxidation of brown fat for heat production rather than ATP production
   b. usually trivially small for poikilotherms, ectotherms, because they have very low basal metabolic rates

C. Principles of ectothermal regulation:

1. For ectotherms, "target temperature " of thermoregulation is called the **active temperature range**, rather than $T_b$ (because $T_b$ is going to fluctuate)
   a. active temperature range presumably represents temperature at which performance across body’s systems is optimized

2. regulation depends on ability to regulate heat exchange with environment
   a. depends critically on **high thermal conductance** of integument = ability of integument to transfer heat between animal and environment
   b. note that high thermal conductance is exactly the opposite of high insulation, which reduces heat exchange between object and environment (this will be important later)
D. Mechanisms of ecothermal regulation

1. use lizards as examples, as they have the largest repertoire and "tightest" regulation

2. remember that regulation will mean manipulating routes of heat exchange

3. It's common to classify regulatory mechanisms as behavioral and physiological - note, though, that classification below is somewhat arbitrary – some mechanisms can logically fit in multiple categories

4. Behavioral mechanisms:
   a. movement among microhabitats (e.g., between sun and shade)
      (1) controls direct, indirect solar radiation
      (2) controls convection (by, e.g., moving to sheltered places where wind isn't blowing)
      (3) controls conduction
   b. changing orientation of body relative to sun changes amount of direct, indirect solar radiation
   c. changing body contours changes the body’s surface area
      (1) controls solar radiation
      (2) also controls conduction
   d. changing body position (e.g., belly down, or up on toes)
      (1) controls conduction
      (2) controls convection

5. Physiological mechanisms:
   a. change color from dark-light – controls solar radiation
   b. regulate peripheral blood flow
      (1) regulates the rate of temperature change by regulating the rate at which heat is transferred from body core to environment
      (2) can get very complex – read example of marine iguanas p. 331

E. Costs, benefits, and consequences of ectothermy
1. major cost = dependence on solar radiation to be active
   a. some habitats may offer insufficient solar energy to permit animals to
      maintain sustainable populations
   b. within otherwise viable habitats, there may be times when insufficient heat is
      available to sustain activity
   c. inactive periods may also be periods of vulnerability
2. benefits stem from overall low "cost" of ectothermy
   a. because their total "expenditure" of energy for maintenance is reduced,
      ectotherms need absolutely less energy than do similar-sized endotherms
      (1) can live in habitats with relatively little food
      (2) can live in habitats in which food is seasonally scarce (a little food goes a
      long way!)
   b. low metabolic rates coupled with low energy requirements permits much
      smaller body sizes than endotherms can achieve:

![Distribution of body mass](image)

(1) allows ectotherms to exploit "small body size" niches that are unavailable
   to endotherms
(2) e.g. s of "small body size" niche dimensions include
(a) small habitat patches (e.g., cups formed by tropical bromeliads can support several individual frogs)
(b) small food items
(c) small shelters (e.g., cracks in bark)

3. Ectothermy has consequences for whole ecosystems as well (Ch. 12 pp. 356-359)
   a. because their maintenance budget is low, ectotherms have very high
      **conversion efficiency** (= energy absorbed/energy converted to growth) is very high
      (1) means that larger % of food is converted to new biomass than would be the case in ectotherms
      (2) see table 12.5 p. 359 in text – average efficiencies for
         (a) 12 species of ectotherms = 50
         (b) 19 species of endotherms = 1.4!
      (3) e.g., at Hubbard Brook experimental range, salamanders consume 20% of the energy that mammals do, but produce the same increment of biomass
   b. consequence is that ectotherms are critical links in food webs: they essentially "repackage" energy from small prey items into forms that larger species (including endotherms) can exploit
   c. means that, without ectotherms, the abundance and diversity of endotherms would be much lower!

II. Endothermy (Ch. 21 pp. 582-585)
   A. Differences between avian/mammalian energetics and those of ectotherms are more complex than are summarized in the "endotherm vs. ectotherm" terminology – so it's more useful to consider four basic characteristics of avian/mammalian energetics:
      1. **homeothermy** = can maintain constant $T_b$ across a broader range of
environmental conditions than can ectotherms (but never across all environmental conditions)

2. **endothermy**
   a. use energy from own metabolism (ultimately, from food) to regulate \( T_b \)
   b. benefit = greater degree of independence from environmental conditions than possible for ectotherms

3. **relatively high body temperatures** compared to the active temperature ranges of most ectotherms and poikilotherms (see table 4.6 p. 130)
   a. in general, birds and mammals have \( T_b > T_a \), often by 10°C or more
   b. reason is probably related to water conservation:
      (1) adding insulation is "cheap and easy" way to keep \( T_b > T_a \)
      (2) but, the only way to keep \( T_b < T_a \) is to use evaporative cooling
      (3) for smaller species, can’t drink enough water to maintain evaporative cooling across temperature difference of that magnitude

4. **relatively high metabolic rates** (tachymetabolism)
   a. even at the same \( T_b \), the basal metabolic rate for mammals is ~ 5 times higher than for a similar-sized lizard (ectotherm)
   b. when active, metabolic rate may be 10-30 times greater
   c. this is where the huge cost of "endothermy" comes in: it isn’t the endothermy per se, but the the high metabolic rate that’s expensive
   d. interestingly, the reason for the high metabolic rates of endotherms isn’t clear
      (1) may be that high MR is necessary to maintain large temperature differentials, especially for smaller species
      (2) may be that high MR increases aerobic scope: allowing animals to sustain aerobic activity over longer periods of time

B. Consequences of these characteristics (especially the high metabolic rate) = the anatomy, physiology, behavior, etc., of birds and mammals must be adapted to
1. acquire, digest, assimilate large amounts of food efficiently
2. deliver energy, nutrients, and oxygen to tissues very efficiently
3. convert and remove metabolic wastes (including carbon dioxide) very efficiently
4. means relatively large investment in building, maintaining, complex and efficient
   organ systems!

C. Mechanisms of endothermal regulation

1. For endotherms, body temperature and metabolic rate change in specific ways
   across environmental temperatures:
   a. although exact temperature ranges vary, basic pattern stays the same
   b. **Zone of normothermia** = range of environmental temperatures across
      which body temperature stays constant
   c. **Thermoneutral zone** = TNZ = range of environmental temperatures across which body temperature can be
      maintained at basal metabolic rate (minimal metabolic rate)
   d. \( t_2 \) = **lower critical temperature**
      (1) below this temperature, must increase MR to maintain body temperature
      (a) via NST
      (b) by shivering
      (2) \( t_1 \) = **lower lethal temperature**
      (a) below this temperature, animals can’t generate enough heat to
      maintain \( T_b \)
      (b) animals go into positive feedback loop: drop in \( T_b \) –> drop in MR –>
       drop in \( T_b \) –> drop in MR, etc.
      (c) leads to death due to hypothermia (see zone of hypothermia on
e. \( t_3 = \textit{upper critical temperature} \)

   (1) above this temperature, animals must use evaporative cooling to maintain \( T_b \)

   (2) note that this causes an increase in MR (to produce the secretions, move air, etc.)

f. \( t_4 = \textit{upper lethal temperature} \)

   (1) above this temperature, animals can’t cool enough to maintain \( T_b \)

   (2) animals go into positive feedback loop: increase in \( T_b \) \( \rightarrow \) increase in MR

      (why?) \( \rightarrow \) increase in \( T_b \) \( \rightarrow \) increase in MR, etc.

   (3) results in death due to hyperthermia (see zone of hyperthermia on graph)

2. Note that basic parameters (\( t_1 - t_4 \)) vary among species:

   a. get variation in absolute temperatures (e.g., arctic foxes have lower \( t_2, t_3 \) than do desert foxes)

   b. get variation in the "width" of the TNZ

D. the evolution of endothermy remains unclear (Ch. 15 pp. 409-410)

1. basic paradox:

   a. ectotherms have low MR and high thermal conductance

   b. endotherms have high MR and low thermal conductance (almost all are insulated to some degree to retain body heat)

   c. without high MR, insulation would be deleterious

      (1) low MR requires ectothermal regulation

      (2) ectothermal regulation requires high thermal conductance

   d. without insulation, high MR would be deleterious

      (1) heat generated would simply be lost to environment – it would be "wasted" energy

   e. scenarios for the evolution of endothermy must be able to do one of two things:
(1) explain how both metabolic rates and insulation evolved at the same time
   (unlikely)
(2) explain the evolution of either high metabolic rates or insulation for some
   function(s) other than endothermy – this would permit them to evolve
   independently

2. current hypotheses suggest different routes for birds and mammals (see
   discussion p. 138)
   a. for birds: "insulation first" hypothesis
      (1) feathers arose from scales modified for ectothermal regulation (long
          scales could be raised and lowered to regulate solar radiation on skin)
      (2) long enough scales/protofeathers would also serve to trap warm air
      (3) this would set stage for selection to favor higher metabolic rates, as that
          heat could be retained
   b. for mammals, "metabolic rate first" hypothesis
      (1) earliest mammals/protomammals were most likely small, active foragers
          (based on fossils)
      (2) this would favor moderate increase in MR to allow animals to sustain
          aerobic activity
      (3) this would then lead selection to favor the development of insulation to
          trap metabolic heat produced during aerobic activity

3. note that both scenarios suggest that the evolution of endothermy was largely
   fortuitous by-product of selection for other things (sound familiar???)