Goals:
- Understand concept of “mass balance.
- Know how food intake (and gut area) scale with mass?
- Appreciate differences in feeding rate (and in gut processing capacity) of endotherms vs.
  ectotherms
- Appreciate how the digestive system responds to metabolic challenges (e.g., cold)
- Recognize the importance of secondary compounds of plants

I. Introduction

A. Animals require food for
   1. Energy just to stay alive (maintenance metabolic requirements)
   2. "Discretionary" energy (i.e., excess energy), which can be used for activity,
      growth, repair, reproduction, storage (e.g., fat), keeping parasites well fed

B. Almost all animals obtain energy from plants or from other animals that have eaten
   plants. Nutrition refers to the specific needs of an animal in terms of energy or types
   of foods (nutrients) required.

II. How much food does an animal need?

A. One can think of "mass balance" the same way as "heat balance"

\[
\text{food in} - \text{food metabolized} - \text{food excreted} = \text{food stored (for growth, reprod.)}
\]

B. If an animal isn't growing, food stored = 0, thus the amount of food taken in must be
   balanced exactly by food metabolized and excreted.

C. Food intake is remarkably well regulated. A human may eat 1/2 ton of food/yr with
   little or no gain in mass.

D. Therefore, endotherms of a given size MUST eat more than an ectotherm of the same
   size (and they do). Why must this be true?

E. Moreover, food intake must scale roughly in same way with body mass as does
   metabolic rate (~ b = .75). In fact, food intake shows the following allometric
   relationships, with exponents close to 3/4

   \[
   \begin{align*}
   \text{herbivorous mammals} & \quad \text{intake} = 971 M^{0.73} \\
   \text{carnivorous mammals} & \quad = 975 M^{0.70} \\
   \text{birds} & \quad = 962 M^{0.71}
   \end{align*}
   \]

F. So how does food intake scale per gram of tissue? Obviously, (using herbivorous
   mammals an example),

\[
\text{intake/mass} = 971 M^{(0.73 - 1)} = 971 M^{-0.27}
\]

G. Here’s another equation for herbivorous mammals, where food intake (kg/day) scales
   as 0.157 M^{0.84}. You should be able to derive an equation that enables you to predict
   the percent of a herbivores own body mass that it eats per day, and plot this
   relationship. What you’ll find is that tiny mammals (e.g., a shrew) must eat roughly
its own body mass in food per day, whereas larger mammals (e.g., humans) fortunately do not need that much!

II. How does the surface area of the gut scale?

A. Recall flux is always proportional to surface area. Thus, the amount of nutrients that can be absorbed by the gut should be proportional to gut surface area.
B. Small intestine surface area is huge -- very convoluted with microvilli, which greatly increase surface area (by 500 X!) relative to that of a simple cylindrical tube. Hence, potential rate of absorption is greatly enhanced by the complex topography.
C. Total intestinal surface area (hard to measure, and so rarely measured) increases with mass (M^{0.77} for rabbits).
D. What would you guess for the scaling exponent for log gut surface area vs log mass?
E. Can also increase uptake by increasing density of nutrient transporters. Which term in the general flux equation would be affected by this?

III. Do endotherms eat more than ectotherms?

A. Given the much higher metabolic rates of endotherms, one would expect that food intake of mammals should be greater than that of an equivalent sized lizard. In fact, a mammal does eat c. 5 - 10 X more per day than a reptile of similar size. [In field situations, the difference is probably a much larger. Why?] Mammals have well developed jaws and teeth, to process lots of food. How do birds do this?
B. Transit time of food through gut is 10X faster in mammals than in reptiles
C. Intestinal surface area of mammal is c. 6X that of reptile of equivalent mass.
D. Thus, the evolution of endothermy (with high demand for energy) has been accompanied by a major increase in digestive capacity.

IV. How long should an animal hold onto food before excreting the residual?

A. Should it wait until it has digested 100% of the nutrients? It this will be its only meal for a the near future, it should probably digest it fully. But if food is easy to get, it should digest food only as long as the average net energy gain is increasing. This can be solved graphically, by plot net energy gained from food over time. The average rate of energy gain is maximized by drawing a tangent line from the origin to the curve, that gives the maximum average rate (or maximum slope of line line). [If you don’t believe that this graphical trick works, use Excel, make up a curve with some numbers, and compute net energy gain PER TIME for various time periods.]
V. Does an individual’s feeding rate (and gut) respond to changing energy demands?

A. What happens to feeding and to guts as energy needs change?
B. If, for example, work level increases, an increase in metabolism can persist only if food intake is increased (unless, of course, the animal relies on stored fat).
C. Cold -- expose mouse to cold, its metabolic rate increases to maintain heat balance, and its food intake increases to maintain "mass balance." Moreover, it starts to build more intestine, liver, kidney. In addition, transporter molecules, which transport sugars and amino acids (AA) across the gut lumen, also increase. But increase in feeding rate is larger for small than for big mammals – why?
D. In very cold weather, feeding is a full-time occupation. Chipping sparrow in winter spends 95% of its day feeding (a seed every 1 - 2 s). Juncos on cold day spend 75% of time hunting, but only 55% of time on warm day.
E. What about effects of changes in diet, such as from high carbohydrate to high protein? In tadpoles fed meat, gut size much smaller than in tadpoles fed plant matter. Should also see increase in number of protein transporters.
F. Nursing. Lactation requires high energy expenditure, and not surprisingly, a nursing mouse eats 3 - 4X more food per day than a non-nursing (non-pregnant) female. Both intestinal mass and transporters increase during lactation.
G. Recall the pattern of period feeders like pythons, that catch food only rarely
   1. Within 1 day of a meal, sidewinders and pythons increase metabolic rate by many fold! Their nutrient uptake capacity increases 4 - 20 X, and intestinal mass increases by 2X. Obviously, the specific dynamic effect for a python is huge, and involves enlarging the gut so that digestion can take place.
   2. Why doesn't the python just maintain its gut "ready to go?" Presumably the cost of maintenance (integrated over the long time between meals) is much greater than the cost of re-construction.
H. Natural anorexia (NOTE: the following wasn’t covered because of lack of time, but I included it for your interest – you will not be held responsible for this, however.)
   1. Anorexia involves reduction in food intake. Is considered pathological in humans. But it is a natural phenomena in many animals.
   2. Many hibernating animals have empty guts, in part because otherwise food would rot in their guts.
   3. Curiously, even some active mammals reduce food intake in winter, and rely largely on stored fats.
   4. Australian mouth-brooding frogs -- female shuts off digestion entirely while brooding her tadpoles in her gut. [Alas, this species is sadly extinct.]
I. Evolutionary changes. Chickens evolved over last 5000 years by artificial selection from red jungle fowl. Traits selected for include rapid growth rate from egg to roasting pan. Interestingly, chicken has evolved a larger intestine than the ancestral jungle fowl, suggesting that the intestine has been a major site of selection.
J. Given that food intake can be modulated in response to energy needs, is there a maximum on food intake? In other words, does food intake set a maximum on energy available for activity, growth, reproduction, etc.?
   1. Hummingbirds are very small and have huge mass-specific metabolic rates. Hence they must have high mass-specific feeding rates. Ironically, the birds spend only 20% of their waking hours feeding, and about 75% of their time "doing nothing." Are they being lazy?
   2. No. Humming birds eat nectar, and can fill their guts very quickly (about 1 minute). However, it takes then about 15 minutes to empty their guts! Despite very fast emptying time (most birds take 1 - 3 h, mammals and lizards 2 - 150 h), the gut emptying time may thus limit maximum energy intake, and hence maximum activity, etc.