General introduction:

1. Focus for the course (as for the text) will be on
   a. differentiating among different types (levels) of underlying causes of behavior (note these levels apply to other kinds of phenotypic traits as well!)
   b. using theory of natural selection to develop hypotheses for the evolution of behavior
   c. using cost/benefit approaches to behavioral analysis (can be used both to generate and to test adaptive hypotheses about behavior)
   d. how to develop and test alternative hypotheses about behavior
2. Material will be divided (more or less) into two parts: chapters 2-6 dealing with proximate mechanisms; 7-16 on ultimate (evolutionary) questions
3. You should be sure to skim each chapter before it's covered, with special attention to natural history/behavior descriptions on which discussion are based; I won't review them in detail in class.

CHAPTER 1: AN EVOLUTIONARY APPROACH TO ANIMAL BEHAVIOR

A. Questions about behavior fall into two general categories: proximate/mechanistic and ultimate/evolutionary
   1. Use "wing-flipping" in moths as example
   2. **Proximate/mechanistic** questions address mechanisms and structures within an animal that give rise to behavior (often called "**how questions**")
      a. examples (p. 3):
         i. what is the causal relationship between the animal's genes and its behavior?
         ii. is the trait to some extent inherited from the moth's parents?
         iii. How has the development of the moth (e.g., formation of neural pathways, organization of muscles, etc.) affected its behavioral abilities?
         iv. what stimuli trigger the response, and how are these stimuli received?

   b. proximate questions can be divided (with some gray areas) into two general groups:
      i. **genetic/developmental** (e.g., i-iii above) address the "construction" of the anatomical/physiological systems that produce the behavior, with attention to
         a) how do genes,environment, and developmental processes interact to produce the "final" sensory-neuro-muscular systems that produce behavior
         b) how do variations in genes/environment/development affect behavior
      ii. **physiological** (e.g., iv above) address the functioning of the sensory-neuro-muscular systems that produce behavior, including, e.g.,
         a) how stimuli are perceived, integrated with other information
         b) how decision-making systems ("brains", ganglia, etc.) sort information and respond
         c) how effector systems receive/respond to information generated by decision-making systems
3. **Ultimate/evolutionary** questions try to identify and reconstruct the evolutionary history of a behavior (using many of the same kinds of approaches used to reconstruct histories of anatomical traits, e.g.) (often called "**why questions**" -- but I don't find this a very useful taxonomy -- see below))
   a. examples (p. 4)
      i. has the behavior evolved over time?
      ii. if so, why did the changes (from "original state") take place?
      iii. what was the original step in the historical process that led to the current behavior?
      iv. what is the purpose or function of the behavior (what immediate consequence does it have for the animal)?

v. does the behavior help individuals overcome obstacles to survival and reproduction?

b. Evolutionary analyses of behaviors often begin with the basic question: is the trait adaptive? To begin, we need to

i. identify the current function of the behavior (iv above)

ii. determine whether or not the behavior has adaptive value -- whether or not it enhances the ability of individuals to survive and reproduce, and how it does so (v. above)

c. based on those answers, we can attempt to reconstruct the evolutionary history of the behavior (i-iii above), bearing in mind that

i. not all traits (behavioral or otherwise) of organisms are adaptive (more on that later!)

ii. traits (behavioral and otherwise) may change function over time (in fact, this is likely the rule, not the exception), so current function may not be original function.

4. A full analysis of any behavior must take both levels of explanation into account. E.g., capuchin monkeys rub citrus fruits on themselves -- why?

a. rubbing themselves with citrus may have adaptive value by helping to heal skin wounds (ultimate explanation)

b. rubbing themselves with citrus may feel good (proximate explanation)

c. Assume that both are correct -- if so, then a full explanation might be something like:

Individual capuchins whose sensory systems are such that they feel pleasure when rubbing citrus fruits on their skins are more likely to do so than are other monkeys. Because rubbing heals skin wounds and thus increases fitness (by making energy that would otherwise be used for healing wounds and secondary infections available for reproduction, e.g.), those monkeys will reproduce more than do others -- i.e., selection favors those monkeys whose *neuro-sensory-muscular systems incline them to feel pleasure when they engage in this specific behavior. Consequently, the genes that underly the "pleasure sensation" and those that underly the "rubbing" behavior will increase in frequency in the population and the behavior will become generalized for all individuals.*

B. The scientific method of question-observation-hypothesis-prediction-test-conclusion is used to address both proximate and ultimate questions about behavior.
   1. Note that scientific inquiry usually begins one step "earlier" -- with observations that prompt the initial question!
   2. E.g. of using the scientific method for answering proximate questions: Tinbergen's beewolves
      a. beewolves = digger wasps; females dig burrow with multiple brood cells, provision each cell with paralyzed bees, then lays eggs -- larvae feed off paralyzed bees.
      b. Tinbergen's intial observations were that
         i. females dig and provision a single burrow at a time
         ii. females covered up nests before leaving to hunt
         iii. females were able to return to own burrows without mistakes, even though
            a) "hunting grounds" were over a km away
            b) burrows were covered with sand before females left
            c) hundreds of burrows were located in the same general area
      c. **Question**: how did females find their own burrows?
      d. **Observation** bearing on question: when females left burrows, they flew circles around the burrow before leaving.
      e. **Hypothesis**: females use visual cues = landmarks to identify the location of their own burrows

f. **Prediction/test #1**:

   i. P: removing landmarks will prevent females from locating their burrows

   ii. T: removed landmarks: returning females couldn't recognize burrows from the air

g. **Prediction/test #2:**

   i. P: moving the landmarks will lead females to mistake location of their burrows

   ii. T: moving landmarks 1' southeast caused female to land 1' southeast of her burrow

h. (on your own, identify third prediction/test)

i. **Conclusion**: because predictions all met, hypothesis was supported. Note, though, that this is only first step: we still could ask many proximate questions about this behavior bees (e.g., what kinds of visual cues do they use? how long can they remember landmarks? etc.)

3. Example of using the scientific method to answer ultimate question: Tinbergen's black-headed gulls

   a. ultimate questions generally involve two "levels" of questions:

      i. the more general question is usually "**is the behavior adaptive**"? -- the general hypothesis is that it is adaptive (and that's why the trait spread)

      ii. the more specific (and the hypothesis that's generally tested first) is "**what is the selective advantage**"?

      iii. when a specific selective advantage is identified (by tests that support a specific hypothesis), that acts as support for the more general hypothesis that the trait is adaptive.

   b. Tinbergen's original observation was that black-headed gulls remove broken eggshells from the nest, leaving chicks unguarded (for short periods of time, but still apparently "risky" behavior given the large number of potential predators in these habitats)

c. **Question**: why:?

d. **general hypothesis**: behavior is adaptive; it provides selective advantage to those gulls engaging in it -- gulls who remove eggshells have enhanced reproductive success; therefore, the alleles underlying their behavior increase in frequency in the population (pay attention to precise reasoning as explained on p. 12).

e. **Observations**:

  i. outer eggshells, chicks, and, to the extent possible, nests are camouflaged

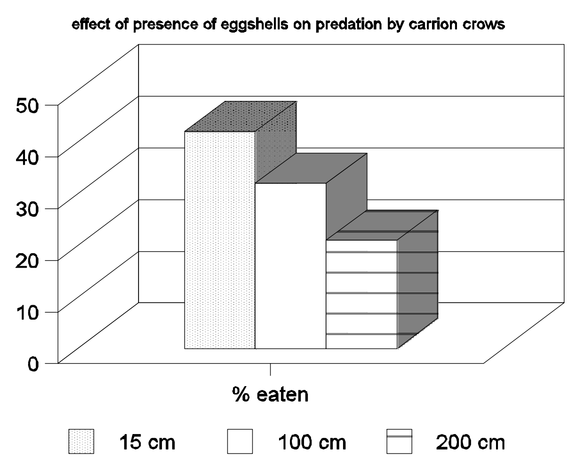
  ii. interiors of eggshells are white and highly conspicous

e. **specific hypothesis**: behavior reduces predation by removing a visual cue predators can use to locate nests and unhatched eggs, nestlings

f. **Prediction/test**:

  i. P: the closer an egg is to a broken eggshell, the greater the likelihood it will be found and eaten by predators

  ii. T: placed unbroken eggs at varying distances from eggshells and compared predation rates: closer the eggs, the higher the predation rates



g. **Conclusions**:

  i. Prediction met: specific hypothesis that removing eggshells reduces predation is supported.

  ii. Because reducing predation is likely to increase fitness (relative ability to survive and reproduce), this finding also supports the general hypothesis that the trait is adaptive.

h. Note, though:
   i. this finding more tentative than earlier conclusion (why?)
   ii. leaves us with many questions still about the evolutionary history of the behavior (e.g., what was the original form of the behavior? was it the same? how great is the selective advantage of the behavior? etc.)

C. As in the example of Tinbergen's gulls, ultimate questions about behavior are generally based on **Darwin's theory of natural selection**.
   1. Review of natural selection:
      a. Darwin based his theory on 3 observations and a prediction -- because the prediction has been confirmed repeatedly, the 4 are often called "Darwin's postulates":
         i. organisms vary: no two are genetically or phenotypically alike
         ii. variation is, at least in part, heritable: individuals pass their genes, and consequently their particular traits, to their offspring
         iii. individuals engage in a "struggle for existence": more die than reproduce
            a. in every environment, at least some resources are limited
            b. more individuals of any species are born every generation than their environment can support --> intraspecific competition
            c. individuals of different species may require the same resources --> interspecific competition
            d. predators, parasites, pathogens are present for most species
         iv. fitness varies: some individuals, by virtue of their specific variations, will be more successful in the struggle for existence: they'll survive and reproduce better than do others of their species
      b. the inevitable consequence of i-iv is that "favorable genes" (alleles that produce traits that improve relative reproductive success) will increase in frequency within populations over time

   c. this process -- natural selection -- "works" as well for behavior as it does for other kinds of traits

2. An early and conceptually important alternative to Darwinian natural selection, especially for social behaviors, was promoted by V.C. Wynne-Edwards and is now generally referred to as "**group selection**"
   a. Wynne-Edwards suggested that many social behaviors had evolved to regulate population size
   b. groups that had individuals whose behaviors led them to "sacrifice" their own reproduction would be more successful than would groups of "reprouctively selfish" individuals because the "selfish" groups would run out of resources -- and all individuals would die
   c. This idea was convincingly criticized (and defeated) by George Williams
      i. Williams argued that, in any population, initially rare "selfish reproducers" would always leave more offspring than would "altruistic non-reproducers" -- consequently, "selfishness" would become common, and "altruism" couldn't persist over time.
      ii. e.g., langurs
      iii. more specifically, Williams provided convincing arguments that Darwinian selection acting on individuals "for the good of individuals" is almost always going to be stronger than group selection.
   d. Consequently, initial hypotheses about behavior should begin with "individual selection", rather than group selection

3. Although "individual selection" arguments will generally be favored over "group selection" arguments, Darwinian explanations must still be tested against appropriate alternative hypotheses -- not all traits (behavioral or otherwise) are adaptive:
   a. selectively neutral or even mildly disadvantageous traits may persist if they're "linked" (genetically, developmentally, physiologically) to adaptive traits

b. a trait may be a maladaptive byproduct of an otherwise adaptive proximate mechanism (e.g., using gypsy moth pheromones as trap bait; using sweet-tasting poisons)

c. the behavior in question may be an anomaly caused by extreme environmental conditions (e.g., social pathologies caused by extreme crowding)

D. For both proximate and ultimate questions, the usual “rules” of scientific certainty apply:

1. Hypotheses can never be “100% proven” -- they can only gain in support
2. Hypotheses become better supported as
   a. plausible alternatives are eliminated by careful testing
      i. The best studies test multiple alternative hypotheses leading to mutually exclusive predictions (on your own, identify mutually exclusive predictions for Darwinian vs. group-selection hypothesis for infanticide in langurs)
      ii. “Process of elimination” is very important form of support (e.g., natural selection is only plausible mechanism currently available to account for adaptation -- among other important kinds of evidence!)
   b. numerous predictions of the same hypothesis are supported by careful testing = individual hypotheses subjected to multiple tests
      i. e.g., Tinbergen’s beewolves; Hrdy’s work on infanticide
      ii. the more predictions are met, the greater the support for the hypothesis
   c. for adaptive hypotheses (for behavior and for other kinds of traits) in particular, hypotheses become better supported when we find convergence = comparable adaptations in different species under comparable ecological conditions