Lecture 9
Studying Adaptation:
Evolutionary Analysis of Form & Function

I. Introduction to the “adaptationist programme” and testing for natural selection.

1) The use of the words adaptive, and adaptation is a short cut for explaining a much larger evolutionary journey.

2) Unfortunately, biologists and laypeople alike use the words ‘adapted’ and ‘adaptation to mean various, quite different things.

The phrase ‘X is adapted to live in Y’ may not mean more than:
   a. X lives in environment Y. The word ‘adapted’ says nothing about how these properties were acquired, only the positive outcome of possessing them.
      o The above statement may mean that properties of X constrain it to live only in Y.
   b. For an evolutionary ecologist, X is adapted to live in Y will usually mean that environment Y has provided forces of natural selection that have affected the life of X’s ancestors and so have molded and specialized the evolution of X.
   c. For an ecologist with physiological leanings the statement can mean that individuals of X have themselves had some prior experience. Adaptation here is definitely not genetic, but is phenotypic change, but this is not evolution.
   d. Alternatively, the statement ‘X is adapted to live in Y’ can mean that a property (an adaptation) has been identified that X possesses and that has been shown to (or at a reasonable guess might) explain why X can live in Y. Such a property could be either genotypic or phenotypic.

3) There are literally thousands of explanations for why organisms can live where they live, or make a living using the means that they do.
   a. But relatively few of these explanations have been rigorously tested.
   b. As John Endler has stated, “Natural selection is not easy to detect.”

4) Many studies that attempt to demonstrate natural selection may be flawed in one of several ways:
   a. The study does not estimate the full fitness of individuals over their complete lifetimes (very difficult to do with long-lived organisms!)
   b. The study considers only one or a few traits.
   c. The traits under study have unknown or inadequately known functions.

5) Pitfalls of the adaptationist programme – it can be overexploited. It assumes that all traits have been selected for some fitness value.
   a. The existence of goal-directed phenomena are often explained by teleological statements. (fr. Gk. teleos, “end”) which seem cause directed.
   b. E.g. He went to the store in order to get milk.

6) But the adaptationist programme does a poor job of determining whether the presence of a trait is really the product of selective forces that do not work towards some end.
   a. That is, natural selection cannot predict the future, so it cannot anticipate the needs of the organism.
II. The case of giraffe necks and foraging – another ‘Just So’ story.

1) It is fairly easy to contrive an evolutionary story to explain a particular trait of an organism.
   a. The greater difficulty is to ascertain whether that the trait as any adaptive value.
   b. And whether our hypothesis of the nature of that adaptive value is supported.

A. How the Giraffe got its long neck

1) If indeed, the long necks of giraffes are meant for foraging above the reach of competitors, we
   would predict that at least in times of food scarcity, giraffes should spend the majority of their
   time feeding near the maximum height possible.
   a. But a study in Kenya by Truman Young and Lynne Isbell (1991) demonstrated that giraffes
      of both sexes prefer to feed at shoulder height.
   b. Using natural history information gleaned from direct observation, Robert Simmons and
      Lue Scheepers (1996) noted that bull giraffes used their necks and heads as clubs in
      fighting other males for mating opportunities, often with lethal effects.

2) Observational data is consistent with this hypothesis.

3) Consistent with the observations of Simmons and Scheepers, David Pratt and Virginia Anderson
   (1985) also observed that that neck size plays a role in mating success.

B. Pitfalls and caveats to studying adaptations.

1) As Gould and Lewontin point out in their article, there are two steps that the adaptationist
   programme takes:
   (1) The traits of an organism are separated into the components, independent of the other traits,
       which are then explained as being optimally designed for their function.
   (2) If the deconstruction approach does not work, then the interaction of traits is acknowledged,
       and the limitations of adaptation are explained by trade-offs with the associated trait.

2) Dr. Pangloss from Voltaire’s Candide: “Things cannot be other than they are….Everything is
   made for the best purposes.”

3) Caveats to keep in mind when studying adaptations. (i.e. alternate explanations)
   a. Differences among populations or species are not always adaptive, but may be the result of
      fixed mutations.
   b. Not every trait is an adaptation.
   c. Not every adaptation is perfect.

III. Studying Adaptation.

1) We will cover 5 different methods used to infer that a feature is an adaptation for a particular
   function (note that natural selection is inferred).
   a. Two of these are actually the products of inference, and do not demonstrate any advantage
      of a trait. They are not in your book, (Futuyma).

A. Complexity.

1) Even if we cannot immediately guess the function of a trait, we often suspect it has an adaptive
   function if it is complex, for complexity cannot evolve except by natural selection.
   a. A peculiar, highly vascularized structure called a pectin projects in front of the retina in the
      eyes of birds.
   b. Although its function is uncertain, it is generally assumed to play some important functional
      role, both because of it’s complexity, and because it is ubiquitous among bird species
      (conserved).
B. Design.
1) The function of a morphological structure is often inferred from its correspondence with the design an engineer might use to accomplish some goal, such as locomotion, or the dissipation or retention of heat.
2) Very often, models are devised to describe the kinds of features organisms might be expected to have, to achieve a specified function in a particular context.
3) For example, mathematical models, based on principles of engineering, explain why, if fleetness is advantageous, horses should have evolved the one-toed condition.
4) Among related species or conspecific populations of mammals and birds, those in cold environments often are larger in body size (Bergmann’s rule) and have shorter ears and legs (Allen’s rule), both of which, by decreasing the ratio of surface area to body mass, reduce the rate of loss of body heat.
   a. **Bergmann’s rule** – the relationship between body size and latitude.
   b. **Allen’s rule** – populations of homeotherms in colder climates have shorter appendages.
   c. These patterns, because they appear in so many species, provide evidence of **adaptive geographic variation** due to natural selection since they are too consistent to be attributed to chance.
5) It is necessary though, to ask if the trait we are examining was the result of adaptation in the species in question, or whether it was selected for different reasons in an ancestor.
   a. Often this requires a phylogenetic perspective.
   b. *Artemisia carruthii* and *A. ludoviciana*

C. Experiments –
1) Experimental design on the Tephritid Fly, *Zonosemata vittegera*.
2) If the performance of different genotypes is compared, a researcher runs the risk of assuming that the superiority of one genotype over the other is not due to the particular character examined, a. or to the function it seems to serve.
   b. But rather to another, unknown correlated difference caused by linked genes.
   c. Or by **pleiotropic effects** – the phenotypic effect of a gene on more than one characteristic.
3) There is also difficulty in demonstrating that the trait in question does indeed affect survival or reproduction in nature.
4) Even if the trait does play a role as predicted, it is sometimes difficult to demonstrate that it indeed enhances fitness.

D. Observational Methods.
1) These are necessary when the conditions or the traits of the organism cannot be experimentally manipulated, e.g. giraffe necks.
2) However, some observations do not necessarily lead to cause and effect.

E. The Comparative Method.
1) Comparative methods take advantage of natural evolutionary experiments provided by convergent evolution.
2) If a trait evolves independently in many lineages because of a similar selection pressure, then it suggests that the trait has some adaptive value.
3) So the comparative method may be defined as the use of comparison of sets of species to pose or test hypotheses on adaptation and other evolutionary phenomena.
IV. The spandrels of San Marco and the Panglossian paradigm.
1) Gould and Lewontin’s criticism of the excessive use of natural selection and adaptation to explain the purpose of all traits.
2) The adaptationist programme regards natural selection as such a powerful force with few constraints.
3) Consequently, the adaptationist view is that every trait of an organism is considered as being optimally designed by natural selection for its function.
4) A key criticism of Gould and Lewontin is that the adaptationist programme fails to recognize alternative explanations.
5) The narrowness of their interpretation of how traits arose results in the following progressive set of explanations for a given trait.
   a. If one adaptive argument fails, try another. (Zig-zag commissures of clams, once considered as strengthening devices, now become sieves.)
   b. If one adaptive argument fails, assume another exists, albeit weaker.
   c. In the absence of a good adaptive argument, point out the lack of understanding of the organism and its interactions with its environment.
   d. Emphasize immediate utility, and exclude other attributes of form.
      e.g. the small fore limbs of T. rex. Yes, G & L argue, they are probably used for something, but they didn’t arise de novo for that end. The are more likely the reduction of a homologous structure in ancestors.
6) The problem is, the adaptationist programme often amounts to nothing more than story telling, and does not have a structure in place that would permit the rejection of the story in the face of evidence.
7) G. & L. propose alternatives to explain traits such as form, function and behavior.
   a. The null hypothesis: No adaptation and no selection at all. That is, is the presence of polymorphisms the result of selection or mutation and genetic drift?
   b. No adaptation and no selection on the trait in question, but a change in the trait is a consequence for selection occurring on another trait elsewhere, hence the correlation between selection and the trait in question.
   c. Decoupling selection and adaptation.
      ♠ Selection may occur to favor individuals with high fecundity, but it will not have adaptive value for the population – not enough food, or the high population numbers attract predators.
      ♠ Adaptation may reflect phenotypic plasticity to the environment, and hence may not be selected for (since it is variable).
   d. Adaptation and selection occur, but there is no selective basis for differences among adaptations. Related species may develop different solutions to the same problem in different areas. One solution is not necessarily better than another –ergo, there is not a perfect solution.
   e. Adaptation and selection occur, but the adaptation is a secondary utilization. E.g. the spandrels of san Marco.
8) The adaptationist programme breaks organisms down into parts and genes.
   a. G. & L. argue for a more holistic perspective.
V. More pitfalls in studying adaptation.

A. Phenotypic plasticity.
   1) If phenotypic expression varies due to the environment, there is **phenotypic plasticity**.
   2) Luc De Meester measured phototactic behavior of Daphnia from 3 lakes in Belgium.
      a. 10 genotypes per lake (30 genotypes total). Tested under laboratory conditions in a graduated cylinder.
      b. Tests the same *Daphnia* using water that had previously been occupied by fish.
   3) Much variation in the phototactic response among genotypes and source lake.
      a. The difference in response among source lakes indicates phenotypic plasticity.
      b. But, there is also a genotype effect. Within an environment (source lake) there is variation among the 10 genotypes.
      c. Such genetic variation for phenotypic plasticity is called **genotype-by-environment interaction**.

B. Preadaptation.
   1) Because traits evolve from pre-existing traits, the features a species can evolve depend strongly upon its phylogenetic position history.
      a. And the potential for these traits to be modified varies among lineages.
   2) A **preadaptation** is a feature that fortuitously serves a new function.
      a. A character that was adaptive under a prior set of conditions and later provides the initial state (is co-opted) for the evolution of a new adaptation under a different set of conditions.
      b. Preadaptations do not imply any preconceived evolutionary plan, or preparation for an event in the future, but simply an adaptation in response to natural selection that happens to also become an adaptive advantage in a subsequent environment.
   3) For example, the swim bladders of fish, an organ selected for its purpose of flotation becomes converted to a wholly different purpose, one for respiration (breathing).
   4) An **exaptation** is when characters that evolved for other functions, or for no function at all (they are neutral characters), but which has been co-opted for a new use.
      a. This is the view put forth by Gould and Vrba.
   5) How do pre-adaptation and exaptation differ?
      a. Pre-adaptation is applied when a large change in function is accomplished with little change of structure.
      b. Exaptation is when an organ changes its function but retains a fairly constant structure.

VI. Trade-offs and Constraints.

A. Energetic constraints.
   1) Doug Schemske and Jon Ågren sought to distinguish between two hypothesis to determine what the selection force (by bees) was on female flowers.
      **Hypothesis 1**: The more closely female flowers resemble male flowers, the more often they are visited by bees. Selection on female flowers is stabilizing with best phenotype for females identical to the mean phenotype of males.
      **Hypothesis 2**: The more closely female flowers resemble the most rewarding male flowers, the more often they will be visited by bees. If larger male flowers offer bigger rewards, then selection on female flowers is directional, with bigger flowers always favored over smaller flowers.
   2) The results were clear, bees preferred larger flowers.
3) So why aren’t female flowers larger than male flowers? Two possibilities.
   a. Female flowers lack the genetic variation for selection of larger flowers
   b. Trade-offs between flower size and flower number.
4) Bottom line – Female flower size has been selected for by two opposing forces:
   a. Directional selection for larger flowers.
   b. A trade-off between flower number and size.

B. Physiological constraints.
   1) Why do the flowers of *Fuschia excorticata* change colors?
      Two hypotheses proposed:
      **Hypothesis 1**: Red flowers still attract pollinators to the tree, which once there, can pollinate the remaining green flowers. Thus green flowers surrounded by red flowers should receive more pollen than green flowers not surrounded.
      Tested by Delph and Lively and not supported.
      **Hypothesis 2**: Physiological constraint prevents *Fuchsia* from dropping flowers. This physiological constraint is the growth of the pollen tubes.

C. When Pigs Fly – constraints on genetic variation.
   1) The leaf beetles of the genus *Ophraella*. Why have some hosts shifts occurred, but not others?

VII. What Not to Expect of Natural Selection.

A. The necessity of adaptation.
   1) A change in the environment (a major source of selection pressure) does not necessitate that a species must ‘adapt’ or go extinct.
   2) Alternatively, new adaptations may arise (through mutation) in the absence of a changing environment, and may persist because they are better than any pre-existing variations.
      a. But, they did not arise because of the necessity to adapt to new conditions.

B. Perfection.
   1) Perfection cannot be selected for if the alleles for perfection do not exist.
   2) Moreover, even the best of all possible variants may fall short of perfection because of constraints imposed elsewhere.

C. Progress
   1) It might be argued that evolution represents progress, but perhaps we need to define progress.
   2) Progress implies a goal, and as we know, evolution is not goal oriented.
   3) Measuring any improvement, or efficiency will only be relevant to the specific task of each species.
      a. That is, a species may selected to be better at what it does, and this could be considered progressive, but the yardstick for progress used on one species cannot be used for another.

D. Harmony and balance of nature.
   1) The view that ecosystems are harmonious, integrated “superorganisms” designed to foster the living things that compose them.
   2) However, selection at the level of the gene, or organisms, is inherently selfish.
      a. Only kin selection would explain the altruistic behavior of one conspecific towards another.
      b. Because there are no shared genes, kin selection cannot operate across species.
3) Relationships or systems that rely on some sort of balance, or equilibrium, do so because the alternate is extinction, not because of any altruism towards another species.
   a. We may observe stable predator/prey numbers, suggesting some sort of mutually agreed upon coexistence.
   b. But such stability is not based upon any restraint on the part of the predators.

E. Morality and ethics.
1) The theory of natural selection, paints a dark picture of “Nature red in tooth and claw”
2) It portrays nature as utterly amoral – not immoral.
   a. Immoral implies conscious violation of ethical norms.
   b. But amoral implies the absence of any morality or ethical qualities whatsoever.
3) This is but one reason why the concept of evolution has met with vigorous and heated resistance since its inception.
   a. Some find it aesthetically distasteful,
   b. Some find it that it assaults their need to find meaning in the universe
   c. Others fear that it will be used to justify immorality in human society.
4) But neither evolutionary theory, nor any other field of science can speak of or find evidence of morality and immorality.
   a. These do not exist in non-human nature.
   b. And science only describes what is, not what ought to be.