

Bio 45 –Lect. I – 9/10- Direct and Indirect Tests of Adaptation Hypotheses

I. Direct Tests of predictions or hypotheses about natural selection

- A. **Make comparisons among existing variants** - Find variations in a population and measure their relative fitness -- e.g., survival or reproductive success. For example, do calling and non-calling male crickets have similar reproductive success?
- B. **Create variation among individuals** - For example, we might hypothesize that tail length is the cue female pheasants use to choose a mate. We could change the tail lengths of birds (scissors and glue) to create variation in tail size, and measure the mating success of these variants versus controls. What controls would be needed?
- C. **Compare the performance of the same trait do under different selective pressures** - Rather than predict which of a variety of traits will do better in one set of conditions, we could predict that the success of a trait will depend on the environmental conditions. For example:
 - Performance of the same variant under different, existing conditions -- same idea as above but here we use existing environmental (selective) conditions or create them and compare the success of a trait in them. Look for examples in Alcock.
 - Performance of the same variant under different, novel conditions -- For example, suppose we think that young fish stay in the grass along the edge of a lake when foraging because of a lower risk of predation in open water. We set up a series of ponds with and without predators and see where the fish forage and how they do.
 - **Note:** these are like transplant experiments used to determine the contributions of genes and environment to the expression of behavior. We test selection hypotheses by putting individuals into different environments. If they have the same success in both environments, we can exclude the selective effects of the differences between environments. If they have different success in the two environments, we confirm the predicted environmental influence (selection).

Are we testing if traits are adaptations? – Not usually. We are basically testing hypotheses about relative adaptiveness of trait variants. Our goal is to test hypotheses about the possible function of certain traits (behaviors, morphology, ...). Thus we are looking at how selection treats variation (existing or what we create). This is part of the process of identifying the current utility of a trait and of identifying whether or not it is an adaptation. However, simply showing that trait variants are affected differently by selection is not sufficient to show the trait (or most common variant) is an adaptation. Remember that we are generally looking at how environment shapes behavior not just at whether something has evolved to serve a specific function (is an adaptation).

II. Indirect Tests of predictions or hypotheses about natural selection -- using the past

A. Comparative Method

Testing adaptation hypotheses on an evolutionary time scale is conceptually easy, but impossible to do directly. We would have to transplant genetically different populations into similar environments and let the transplants run for thousands of years. Any future similarity among the transplants would confirm our prediction that environment was the selective factor that caused similar adaptations to evolve (all else being equal). We could also put genetically identical populations in different environments (selective conditions). They should diverge.

Problem -- we must assume that any changes we find are due only to the predicted selective forces, and we cannot control for other variables. Thus our "experiments" would be weak because they lack controls and focus on one cause (hypothesis). Besides, we cannot do an experiment over an evolutionary time scale. So what do we do?

We use the **comparative method** which involves finding and interpreting the results of transplant experiments already done over evolutionary time scales. Thus we look for accidental experiments (e.g., finches that founded a group of islands. The comparative method is now a very quantitative and statistical one. However, our focus in this course is on a conceptual way to do stronger tests with the comparative method -- testing predictions by comparisons among species. Basically, we look correlations between phenotypes and environments. There are two basic patterns:

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Pattern 1: **Convergence** among species or populations -- Similar behavior in similar environments suggests common selective influence (e.g., Infanticide - see Alcock).

- our alternative explanation is: similarity = common ancestry which we test by comparing unrelated species.
- our null hypothesis is: similarity = chance - test by doing multiple comparisons

Pattern 2: **Divergence** - Different behaviors in different environments suggests variation in selection resulted in variation in adaptations. For example: parent-offspring recognition in gulls -- colonial nesters need recognition, solitary ones do not.

- alternative explanation: divergence = proximate effects not past selection - do multiple comparisons or focus in on direct testing the causal connections.
- null hypothesis: difference = historical accidents - compare closely related species

Phylogenetic (taxonomic) similarity or difference among species is sort of a "control" for the starting point -- Comparing similar species 'controls for' a similar evolutionary starting point (related lineages) and, using different species, 'replicates' the selective factor.

We need to take into account alternative hypotheses like: Convergence was due to completely different selective factors resulting in same behavior. **or** Divergence was due to chance. **or** Lack of convergence was due to lack of genetic variation for selection to have acted on. If we start with alternative hypotheses and if we are very careful about the comparisons, then our tests can be fairly strong. Usually they will be the starting point for more detailed analyses and experiments. We will try this with hypotheses for the evolution of horns and antlers.

B. Design analysis - We'll explore this approach in detail in the next part of the course. We will predict how animals should be designed by selection to solve a problem and test our predictions with direct or indirect strong tests. We will use cost/benefit analyses (e.g., optimality theory) of how organisms ought to deal with various problems.

***** You should be sure to find good examples of these direct and indirect approaches to testing hypotheses in Alcock, the course packet readings, and lectures. *****