Bio 45 – Lectures I - 7&8 -- Comments On Adaptationist Thinking

We need to be clear about the basics of adaptationist thinking about behavior we will use in this course. We will deal at a conceptual level with a complex subject. Be sure to work out any questions you have in class, section, journals, or office hours. Do not wait for the exams to try out your level of understanding. Consider this a supplement to Alcock's discussion of adaptation.

I. Adaptation and adaptive -- some definitions

Adaptation: If we are to treat behaviors as adaptations for solving problems, we must be clear what an adaptation is. There are two controversial problems to deal with. First we must decide if we want to stress historical origins or the current utility of a behavior. Second, we must decide if we want to focus on the factors that make some behavioral variants more favorable than others (how selection acts on phenotypes) or on the question of whether these favored traits will become more common in future generations (will selection lead to evolution).

Behavioral ecologists generally assume a genetic basis for the behaviors they study and focus on their current utility -- how does their design relate to survival and reproduction. But, we have to keep in mind that we make this assumption about genetic basis and that we rarely reconstruct evolutionary history. Alcock explores the gene-behavior connection and reconstructing evolutionary histories of behavior. For this course, our approach will be one of adaptationist hypothesis making -- how **might** selection influence the relative success of variants in a population or ones that we could imagine.

Our **strict definition of adaptation** will be: *a genetically based feature of the phenotype that is (was) favored by selection for the specific function it serves*. This definition includes a connection to evolution -- “genetically based”. It also implies -- “favored ... for the specific function” -- that the trait was selected for (designed for) a specific function. The reason for “specific function” will become clear below. On a day to day basis we will use a more **general definition** that focuses on current utility: *An adaptation is a phenotypic variant that has (or has had) a higher fitness than other variants in a given environment (or in relation to a specific activity).* Notice that this definition stresses the relative fitness of traits or behaviors in the same population. When using this general definition, remember we still make the “genetic basis” assumption.

Adaptive: Behaviors or traits that enhance the survival and/or reproduction of their bearers relative to others are called adaptive. **However**, not all adaptive traits are adaptations. How can that be? Suppose that one variant of a trait is beneficial but that there is no genetic basis for it being different from other variants of the trait. It cannot be an adaptation because it cannot evolve. That is fairly straightforward and it covers our general definition. In the next section, I will add a caveat relating to the strict definition of adaptation

Why bring in this complexity? We want to avoid the trap of calling everything that is adaptive an adaptation. Otherwise we might make up an explanation for why something exists and be satisfied that we have identified it as an adaptation. **In summary; an adaptation is an adaptive trait, but an adaptive trait may not be an adaptation.**

The nature and use of definitions is often problematic. Rather than treating definitions as something to memorize, you should treat them as working hypotheses, or as parts of a procedure for avoiding errors of reasoning. Consider definitions a trade-off between theoretical exactness and practical utility.

II. Evolved function vs. incidental effect -- not everything is an adaptation

The process of adaptationist thinking can get us in a lot of trouble when we assume that because the trait exists it must be adaptive and also an adaptation.

Traits can exits at high frequency in populations and need no adaptationist explanation! Their existence may not require an explanation of why they might be adaptive. For example, some traits are common because the genes that code for them are closely linked to genes that are part of an adaptation (they are carried along by linkage, not by selection for them -- they are hitchhiking). Adaptations are special sets of adaptive traits that we assume or know were designed by natural selection (back to the strict definition). The goal here is to distinguish between evolved function and incidental effect.

A good way to understand this problem conceptually is to consider the distinction between “selection for” and “selection of” traits. Let’s use a thought experiment to illustrate this. Imagine a can full of marbles. The marbles differ in color (red and green) and size (big and small). Now imagine that we pour the marbles from the can into a sieve. The holes in the sieve are rather small. Thus only the small marbles go through and the large ones remain. The sieve has selected for size and the result is that large marbles survived (were retained by the sieve).

Now suppose that the large ones just happened to be green and the small ones red. Not only would the sieve have sorted the marbles by size, it would have sorted them by color. Can we say the sieve selected among the marbles for color? Of course not. There was selection of color but it was an incidental result of selection for size. In this analogy, size is the evolved function (selected for) and color change is the incidental effect. What kept the green marbles around was their size, not their green coloration. Keep this conceptualization in mind and you will be less likely to fall into a common trap of adaptationist thinking -- concluding that common, adaptive traits must be adaptations.

III. Clearing up some common misunderstandings about evolution

Adaptations do not evolve for the good of the species: A fundamental logical deduction from Darwinian evolutionary theory is that individuals should be reproductively selfish. However, many people talk about adaptations evolving in order to keep a species from going extinct. One popular idea, for example, is that animals have built in population control mechanisms (like territorial behavior, or lemming suicide squads) that keeps populations from getting too large and resulting in starvation. To see the problem with this way of thinking, consider a population with two genetically different types of individuals. **Type A** will, at some density, limit its reproduction to 2 kids per pair of adults but **type S** will keep producing as many kids as it can. What will happen to the relative frequencies of the two types in the population? What might happen to the population as a result? So, how could adaptations evolve to keep species from going extinct if variants arise that would work against the good of the species?

Evolution has no goal or foresight: Evolution is simply change in gene frequency, over time, which leads to change in phenotype frequency. The evolutionary process lacks foresight. Mutations are random. This means that whether or not a mutation will occur is independent of its value (how selection will act upon it). If appropriate mutations or variants do not occur when needed, then individuals may fail to survive and reproduce and species may end up going extinct. For example, an adaptation that allows increased efficiency at getting a certain type of food (specialization) at the expense of being able to get a wide variety of food might be favored if that food is limited and the specialist is better at getting it. If so, then specialization should evolve - even if the specialization might lead to extinction should the food source disappear later. Remember that the fossil record reveals two major products of evolution - adaptation and extinction.

Chance events can lead to evolutionary change: Selection among genetically based traits is a major way evolutionary change occurs, but not the only one. For example, genetic drift can be quite important. A simple way to envision evolution by genetic drift is to think of it as a kind of sampling error in "choosing" who breeds or who emigrates to a new place. Suppose 80% of the birds in a population sing their territorial song in the morning and the other 20% sing at night and that this represents a genetic polymorphism in time of singing. If we took a large number of these birds and put them on an island where none of their species existed, what proportion of the next generation would sing in the morning? Let's assume that there is no selection favoring either singing time. The answer is 80% if the traits breed true (remember Hardy-Weinberg?!).

Now suppose you randomly choose just 2 birds to start another colony on another island. Is it possible that all of the next generation on that island would sing at night or that all would sing in the morning? Yes, that would not surprise us any more than getting heads twice if we flipped a coin twice. Now send over zealous adaptationists to the two islands a few generations later. Suppose they find that on one island 80% sing in the morning and on the other island all sing at night. Doesn't that look like selection on the second island has favored night singing? Could they make a plausible argument to support their idea (e.g., assume it was adaptive to sing at night and give a reason why)? Chance events can result in situations that look just like the results of selection. How do we deal with this problem? Later I will introduce the concept of a null hypothesis (what we would expect due to chance alone). If we test our adaptationist hypothesis against this null hypothesis, we can often avoid the kind of mistake made by our over zealous adaptationists.

IV. Adaptationist Reasoning

Given all of the problems and pitfalls discussed above, how do we use adaptationist thinking? Adaptationist reasoning can take two paths: (a) a post-hoc hypothesis for how/why a particular behavior arose, or (b) a prediction of which of two or more alternatives should be more common in the future. The first approach, known as "Just So" story telling (as in the children's books about how the leopard got its spots or the rhino its wrinkled skin), is very weak science. We will try to avoid this path.

Adaptationist thinking does not give us answers, it only offers some suggestions or predictions about what has happened or might happen. Our general approach will be to do a thought experiment like: "Given a set of conditions and a problem to solve, which of two or more alternative behavioral variants in the population should become most common in the future?" I gave you an example above with population regulation. We assume the alternatives differ genetically and that selection is the evolutionary force responsible for change. We add an appropriate null hypothesis. We then make predictions from all hypotheses and test among them.

Note that we always want to compare the relative fitness or reproductive success of two or more specific behavioral alternatives (existing or hypothesized). Reproductive success means offspring produced that enter the next generation (= getting those genes "producing" the behavioral variants into future generations). Natural selection is a major factor in determining which variants are represented in future generations. However, natural selection is not an absolute process. Natural selection is the differential survival and reproduction of alternative types (e.g., individuals with differing behavior). One type can be better than another in a population, in a specific environment. However, in another environment it might not do as well.

Why include survival in the definition of selection if the end product is always differential reproduction or reproductive success? For example, suppose Ignatz has 10 kids and Gonzo has 2. Does it matter whether Gonzo had 2 because he died before he could have more or because he had 20 and all but 2 died, or because even though he lived 30 years longer than Ignatz he only had enough energy to have 2? From the perspective of what will happen in future generations to his genes it doesn't matter much. It does matter, however, if we want to find out how evolution works and exactly why some behaviors exist. Remember, we like to at least have access to the complete story. How else can we move from adaptationist thinking to testing our ideas? You should use adaptationist thinking to play with questions that arise in lecture, or while reading, or watching animals behave. Just don't use it to make conclusions.

Over zealous adaptationists often assume that everything is possible given the power of selection. However, what can happen as a result of selection depends on a number of things. We will call these things that impede, prevent or limit the evolution of adaptations **constraints**. One constraint is the existence of appropriate new genetic variants. No matter how useful a new variant might be in a given selective environment, chance (mutation, drift, recombination), not selection determines if it will appear.

How useful a new variant would be depends on how well it (relative to an existing variant) fits within the life history, morphology, physiology and energy budget of the organism. Having wings for flying is only advantageous if you also have the physiology to support flight. In addition, evolution is a tinkerer. It only modifies what is already there; it doesn't start over again with each new adaptation. All this makes it hard to predict what the evolutionary solution to a particular problem should be -- something we need to do if we are to make and test adaptive predictions.

A lot of the rest of the course will focus on how individuals ought to be designed (what behavior would be most adaptive) in order to deal best with problems created by their environment. Our next step will be to develop ways to use adaptive reasoning for studying behavior. The concept of an energy budget and cost/benefit thinking will help us here. We will develop those in next few weeks (Optimality and Game Theory models). Stay tuned.