Evolution: The Darwinian Revolutions
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What Is An Evolutionary Adaptation?

Natural selection acts at the level of **individuals**. It is the individual organism that lives or dies, reproduces or fails to reproduce. **Populations evolve** — the characteristics of the organisms of which they are composed change over time. The physical characteristics of an individual are generally fixed throughout its lifetime, whereas the average characteristics of populations change over time. **Changes in the characteristics of the individuals in a population over time** is one useful definition of evolution (there are others, as we will see).

Evolution by natural selection, as first proposed by Charles Darwin, is the result of three processes:

1) **Variety:** There must be significant differences between the individuals in populations undergoing natural selection. Furthermore, it is generally assumed that these variations are **random** (*i.e.* not purposeful). In this simulation, random variation is modeled by different colored paper dots. For the purposes of this simulation, these are assumed to be different forms of individuals of the *same* species.

2) **Heredity:** The variations that exist within the population must be heritable from parents to offspring. Darwin clearly recognized that this was the case, although he did not originally propose a genetic mechanism by which this could occur. In this simulation, inheritance is "perfect" – that is, offspring inherit the exact form of their parents.

3) **Fecundity:** As a consequence of reading Malthus's *Essay on the Principle of Population*, Darwin realized that in natural populations more offspring are born than can possibly live to reproduce. In this simulation, overpopulation is modeled by having only half of each generation's offspring survive until they can reproduce.

If these three processes operate as specified, then the following outcome is virtually inescapable:

4) **Demography:** Some individuals will survive and reproduce more often than others, and such individuals (and their offspring) will therefore become proportionally more common over time. This, in a nutshell, is evolution by natural selection.

Darwin proposed natural selection as an explanation for the origin of **adaptations**. Most people recognize adaptations as characteristics of organisms that seem to perform some function. Adaptations seem to have a **purpose**, and their apparent goal is to accomplish something of value to the organism. However, evolutionary biologists do not generally recognize functions in living organisms in quite this way. Instead, they define adaptations like this:

> "An adaptation is any trait that enhances fitness and [has been] modified by selection to perform that role." (Williams, 1966)

Despite its widespread acceptance by evolutionary biologists, this definition is somewhat muddied by the inclusion of the term "fitness." The working definition for "evolutionary adaptation" that will be used throughout the rest of this course is this:

• **An evolutionary adaptation** is any heritable phenotypic character whose frequency of appearance in a population is the result of increased reproductive success relative to alternative versions of that heritable phenotypic character.

Implicit in this definition of evolutionary adaptation is the idea that there is some real (i.e., non-trivial) *variation* in the phenotypic characteristics present among the members of a population. Indeed, it was the recognition of the existence of such variation, and the insistence that this variation is the basis for

natural selection, that was perhaps Darwin's most revolutionary discovery. Any trait that is an evolutionary adaptation will show some non-trivial variation in the expression of that trait, from individuals who express it to a very high degree, to individuals in whom its expression is virtually unnoticeable. What appears at first glance to be pan-specificity is actually the numerical preponderance of individuals whose expression of the trait is close to the population mean for that trait.

Is there other evidence that can be used to determine if a particular characteristic is an evolutionary adaptation? In addition to showing that the numerical preponderance of a particular phenotypic trait is the result of differential survival and reproduction, it may also be possible to link the phenotypic trait with an underlying anatomical and/or physiological substrate that is the efficient cause of the trait in question. For example, wings are an evolutionary adaptation for flight in birds; wings are an anatomical phenotypic trait that makes flight possible.

Another way of determining if a characteristic is an evolutionary adaptation is to correlate the population dynamics of the adaptation with its evolutionary environment of adaptation Bowlby (1969):

- **The evolutionary environment of adaptation** (or *EEA*) is the ecological milieu under which a particular adaptation has arisen as the result of selection.

The concept of an EEA can be fruitfully employed when trying to determine whether a particular characteristic is an adaptation by attempting to show how the ecological circumstances prevalent in the EEA would have resulted in differential survival and reproduction. However, application of this technique is complicated by the fact that determination of the EEA of a given adaptation can be a somewhat circular process. Ideally, the circumstances of the EEA should be determined by means other than reference to a particular adaptation, followed by an analysis of the effects of the inferred EEA on the survival and reproduction of the organisms inhabiting it.

Final verification that a particular trait is indeed an evolutionary adaptation would require all of the foregoing, plus linking the appearance of the trait to an underlying gene or gene complex and showing that the frequency of the controlling gene(s) in the population in question has indeed been altered as the result of differential survival and reproduction. This is difficult to do even with very simple genetic traits, such as sickle-cell anemia. Furthermore, it may be that the causal connection between the underlying genes and the trait for which they code may be indirect at best. However, rather than abandon the concept of evolutionary adaptation altogether, it may still be useful to apply the definition cited above with four further qualifications:

- **Qualification 1:** An evolutionary adaptation will be expressed by most of the members of a given population, *in a pattern that approximates a normal distribution*;

- **Qualification 2:** An evolutionary adaptation can be **correlated with *underlying anatomical and physiological structures***, which constitute the efficient (or proximate) cause of the evolution of the adaptation;

- **Qualification 3:** An evolutionary adaptation can be **correlated with *a pre-existing evolutionary environment of adaptation*** (EEA), the circumstances of which can then be correlated with differential survival and reproduction; and

- **Qualification 4:** An evolutionary adaptation can be **correlated with *the presence and expression of an underlying gene or gene complex,*** which directly or indirectly causes and influences the expression of the phenotypic trait that constitutes the adaptation.

References Cited:

Bowlby, J. (1969). *Attachment*. New York: Basic Books.

Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton: Princeton University Press.