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Note that, although most of the information here is the same as that in the text, the order may be a little different in places. Read section 3.5; we'll come back to it later in the semester.

I. The basic model of Darwinian natural selection

A. Natural selection is the inevitable outcome of four features of organisms, proposed as postulates ("givens") by Darwin, but now understood as basic facts about the natural world:

1. **Organisms vary**: no two living things are exactly alike. This is the result of
   a. mutation in DNA
   b. recombination during sexual reproduction
      i. crossing-over
      ii. independent assortment
      iii. combining two unique haploid genotypes into novel diploid genotype
2. **Variation is heritable**:
   a. Although many of the differences among organisms are due to differences in

their environments, much (most?) is due to differences in their genotypes.

b. Parents pass their genotypes to their offspring – so differences among adult organisms in any generation will be result in differences in their offspring.

3. Organisms face a **struggle for existence**: in every generation, far more offspring are born than ever survive to reproduce. This is due to
   a. interactions with the abiotic environment
   b. biotic interactions (interactions among organisms), including:
      i. "3 P's": predation, parasitism, pathogenesis
      ii. overproduction:
         a) more offspring are born into the environment every generation than the environment can support
         b) leads to competition within and among species for access to available resources
      iii. selective mating:
         a) in many species, some adults are more "attractive" as mates than others
         b) so, in many species, even individuals surviving to adulthood don't mate
         c) this process is called sexual selection, and we'll talk about it later
4. **Fitness varies** among individuals based on their differences
   a. Survival and reproduction is non-random: some individuals have traits that allow them to survive and reproduce better than do others in the population.
   b. The individuals with the most favorable traits will produce more offspring than do others in the population.
5. The result of these four factors is **natural selection**: favorable traits will increase in frequency in the population over time
   a. E.g., when AZT is present, the frequency of AZT-resistant HIV virions increases over time

B. Some definitions:
   1. **Fitness** = the *relative* ability of individuals to survive and reproduce
      a. fitness is measured in terms of reproductive success: so note that "most fit" isn't necessarily biggest, strongest, longest-lived, etc.
      b. note also that fitness is relative: selection isn't a matter of "all or none" (i.e., a few individuals surviving and reproducing, and the rest don't survive at all), which is why (among other reasons) it's a gradual process
   2. **Adaptation** = a trait (anatomy, physiology, behavior, etc.) that increases the fitness of an individual
      a. note that, to correctly identify a trait as an adaptation, we should be able to specify exactly how that trait increases fitness (e.g., increases resistance to parasites; increases mating frequency; improves feeding; etc.).
      b. this is not as easy as it sounds – we'll talk about how to test adaptive hypotheses later

II. Testing the basic model of Darwinian natural selection: the case of Galápagos finches

A. Background
   1. Galápagos finches = group of birds living on Galápagos islands off coast of Ecuador
   2. Intensively studied by Peter and Rosemary Grant (of Princeton) and colleagues since 1973 (Read *Beak of the Finch* for excellent look at their work), especially medium ground finches (*Geospiza fortis*) on Isla Daphne Major – excellent model system because
      a. island isolated enough that little immigration/emigration occurs
      b. population small enough (usually around 1200) that individuals can all be marked and genetic relationships known
   3. Basic biology:
      a. medium ground finches are seed-eaters
      b. within population, individuals vary in

i. overall body size
ii. size and shape of beaks

c. variation in size and shape of beaks has been shown to correlate with the size of seeds the birds eat
   i. smaller beaks –> smaller seeds – because
   ii. because differences in beak size result in differences in ability to handle seeds of different sizes – i.e.
      a) small beaks not strong enough to crack big seeds
      b) large beaks not dexterous enough to handle small seeds
d. seed production on islands strongly affected by rainfall, which can vary substantially from year to year
   i. droughts fairly common
   ii. El Niño events cause excessive rainfall

B. Testing Darwin's postulates in this system:
   1. Is the *G. fortis* population variable?
      a. yes – especially beak depth, but also other morphological traits (fig. 3.3)
      b. note that variation in morphology, biochemistry, DNA, etc., is virtually universal (more on this later)
   2. Is variation among individuals heritable? This is actually a fairly complex question – we'll take a "simple" look here and more detailed look later
      a. Variation among individuals can result from variation in
         i. genes
         ii. environment (in this case, body and beak size are correlated with the amount of food a chick gets, e.g.)
         iii. both
      b. To determine whether or not some of the variation among individuals is heritable, basic approach = measure the similarity between relatives:
         i. if variation is heritable, get strong correlation between degree of

relatedness and similarity in the trait

   ii. in Galapagos finches, heritability in beak size is high (fig 3.4)

c. note that variation in most traits can be due to *both* variation in genes and variation in environment – but as long as some of the variation is due to genetic differences, selection can operate
d. and, in fact, heritability in most traits measured in most organisms is substantial

3. Is there a struggle for existence?
   a. A series of “natural experiments” happened in beginning with drought in 1977:
      i. rainfall decreased from 130 mm to 24 mm during rainy season
      ii. ~ 84% of the population of finches died over 20 months (fig 3.5a)
      iii. correlated with strong decline in seed availability (fig 3.5b)
   b. In fact, overproduction (even without drought) is the norm: in most populations, reproductive potential is huge, but population sizes stay ~ same (table 3.1)
   c. Recall that other factors also limit the number of individuals surviving to reproduce every generation
4. Did fitness vary based on differences among individuals?
   a. Remember that, for selection to take place, survival and reproduction must be non-random: there must be some trait or traits that make some individuals better able to survive and reproduce than others.
   b. To test this, compare survivors to non-survivors: survivors had deeper (larger) beaks than did non-survivors (fig 3.6) – so yes, survival was nonrandom
   c. Can we determine why individuals with larger beaks survived better? Yes:
      i. As drought progressed, favored small seeds were eaten first, leaving mostly large hard fruits

ii. Only birds with the deepest beaks were able to crack and eat those fruits.
iii. Additionally, largest birds (who also have the deepest beaks) were better able to defend food sources

C. Did evolution occur?
1. Natural selection did occur: because of their differences, a non-random subset of the *G. fortis* population were better able to survive and reproduce than were others: large-beaked individuals increased in frequency in the population.
2. Evolution, though, requires a change in the population from one generation to the next
    a. Thought experiment: what if differences in beak depth were purely due to environmental differences?
        i. then, drought conditions could still produce differences in beak depth between survivors and non-survivors
        ii. however, when non-survivors reproduced, they would not pass their larger beaks on to their offspring: offspring would show same distribution of beak depths as the original (“pre-selection”) population
    b. Comparison of offspring of survivors to parental generation shows opposite pattern: offspring of survivors were significantly larger, on average, than population before drought
    c. So yes, evolution did occur
3. Note another parallel with AZT resistance in HIV virions: “direction” of selection depends on specific conditions:
    a. when patients stop taking AZT, frequency of resistant virions declines
    b. similarly, after major El Niño event of 1983, got superabundance of small seeds and an decrease in beak size over time

D. Summary/conclusions:
1. Natural selection is a process based originally on four premises (postulates)

about living things.

2. In general, all four premises have been tested thoroughly over the last 150+ years and have been shown to represent basic facts about how living things work.
3. The premises can (and should) be tested in specific instances when we think natural selection is operating in particular ways in particular populations.
4. Because of the extensive testing that has already been done, we are justified in accepting natural selection as the process that leads to adaptive change.

III. The nature of natural selection: Selection is a deceptively simple process that is easy to misunderstand – here we look at some of the important features of the process that often lead to confusion

A. Selection acts on individuals, but its consequences occur in populations
   1. Selection does not change individuals – e.g.:
      a. AZT doesn't produce AZT-resistant mutations
      b. drought (and cracking large seeds) didn't produce larger-beaked birds
   2. Instead, selection acts to change the likelihood of an individual organism surviving and/or reproducing.
   3. What actually changes as a result of selection is the population as a whole – specifically, the distribution of traits (and their underlying genes/alleles) changes over time.
   4. ***THIS IS REALLY IMPORTANT***: Selection doesn't cause adaptive change to arise; it just causes adaptive traits to become more frequent.

B. Selection acts on phenotypes, but evolution is a change in gene frequencies over time
   1. The likelihood of an individual finch (or strain of HIV) surviving and reproducing depends on its particular traits – and it doesn't matter whether variation in those traits is genetic or environmental.
   2. When traits have a genetic basis, selection will result in some genes/alleles

being more likely to occur in subsequent generations – those generations will be genetically different (although only slightly so) than their predecessors.

3. It's those underlying genetic differences that, in turn, produce differences in the distribution of traits in subsequent generations.

C. Selection is "backward-looking", not "forward-looking"
  1. The organisms that best succeed in surviving and reproducing are more fit because their traits are adapted to the environmental conditions present in their own generation.
  2. So the distribution of traits among offspring populations are always the result of selection acting on conditions that were present in the previous generation.
  3. No mechanism exists that would allow selection to favor traits that will be beneficial in future generations:
     a. e.g., finch beaks didn't get smaller a generation of two before 1983 El Niño event
     b. AZT-resistant virions won't decrease in frequency before an individual stops taking AZT

D. Selection can produce new traits even though it acts only on existing traits
  1. Note that there is no simple definition of what constitutes a "new trait", so we'll look at three examples
  2. Example 1: change in the state of a quantitative character
     a. in the early 1960's, investigators at the University of Illinois began an artificial selection experiment on corn
     b. trait selected for was oil content of the kernels
     c. at beginning of experiment, oil content ranged from 4-6%
     d. each generation, they selected the corn with the highest oil content to breed for the next generation
     e. after 60 generations, oil content averaged 16%
     f. this is a "new trait" because there is no overlap in the distribution of the trait

from ancestral to descendant populations (

i. i.e., no individual in the ancestral population had oil content even ½ that of the descendants
ii. put another way, the trait “16% oil” didn’t exist in the ancestral population

3. Example 2: evolution of a novel characteristic -- the panda’s thumb
    a. giant pandas use what appears to be the notch between a “thumb” and their other fingers to strip bamboo leaves from bamboo stalks
    b. anatomically, this is not a thumb: it’s an enlarged radial sesamoid (wrist bone) – fig. 3.9
    c. selection acting on variation in size of sesamoid “converted” this bone for a new function, producing a “novel characteristic”
    d. but note that process is the same as in the preceding example: selection acted on small-scale variation
    e. This is an example of a very common phenomenon in evolutionary history: a trait used for one function is “converted” to use for another function
        i. other examples from vertebrates include
            a) gills (used first for feeding, then respiration)
            b) jaws (probably used first for respiration, then for feeding!)
            c) lungs (used first for gas exchange, then buoyancy regulation in some fish)
        ii. Traits that arise for one function and are converted for another are often called **preadaptations**
            a) term unfortunately suggests that the trait arises just so it can be converted in the future – this is not the case!
            b) other terms used to describe this are protoadaptation, exaptation – these terms avoid the implication of selection for future need
4. Example 3: gradual selection can lead to the evolution of complex traits – the compound eye (read Dawkins *Climbing Mount Improbable* for more on this

topic)

a. this is a famous case because a common argument against selection is that it can't produce complex traits
   i. traits can only be preserved over time by selection if, in every generation, the trait is adaptive
   ii. traits will only change over time by selection if the changes increase fitness
   iii. for complex traits, it can be difficult to imagine how a "partially-evolved" trait could be adaptive – and we know that selection can't anticipate future conditions
b. Darwin himself  cited the eye as a complex structure for which it was hard to imagine a long, gradual series of changes leading to the final product -- but was confident would eventually be done!
c. Two investigators (Nilsson & Pelger) used computer model to ask two questions:
   i. is there a smooth gradient of changes, from a flat sheet of light-sensitive tissue to a full camera eye, such that each intermediate step is an improvement over the preceding step?
   ii. if so, how many steps (and, therefore, how much time) would be required?
d. Procedure:
   i. began with simple system of 3 cell layers (pigment, light-sensitive, transparent)
      a) this is a reasonable starting point, as simple photosensitive systems like this are very common in nature -- so must not be too hard to evolve
   ii. in each generation, allowed random changes of no more than 1% in the shape of the transparent layer

        iii. from each generation, selected the design that had the best visual acuity as calculated based on optical physics (gives an objective measure of improvement that makes sense from an adaptive standpoint)

   e. Results: (OH/HO)
      i. yes, could get gradual series of changes, each an improvement over the last
      ii. changes resulted in transformation of simple sheets of tissue in to full camera eye (like verts, octopus) in ~ 2000 steps
      iii. calculated conservative estimate of time it would take to do this:
         a) made a fairly conservative assumption about the heritability of the trait (relative to known heritabilities for other traits) – so this increases the time estimate
         b) also made conservative estimates of strength of selection, rate of variation
         c) calculated time ~ 400,000 generations
         d) even if generation time = 2 years (and it's not, for most of the kinds of organisms that would be involved in the early stages), takes < 1 million years
         e) compared to 500,000,000 years just since the Cambrian, obvious that there's been plenty of time -- not surprising, then, that eyes have evolved at least 40 times in different groups of animals
   f. additional confirmation comes from study of extant animals (OH) -- note that stages of computer model match existing structures, so they're not biologically unlikely

E. Selection is nonrandom, but also not progressive
   1. The "random" element in natural selection is genetic variation, which is random with respect to the environment
      a. the environment does not cause adaptive variation to arise

b. i.e., just because AZT resistance is useful for HIV virions in people taking AZT didn't mean that the trait would arise – it was a random mutation that produced the trait

2. Selection is deterministic (=nonrandom): the characteristics of the environment "specify" which variants will be more likely to survive and reproduce.
3. Evolution is not "progressive"
   a. In a general way, selection has resulted in organisms that are more complex, organized, and specialized than the earliest forms of life on earth (but that's not surprising: if you start with the simplest forms of life possible, an increase in complexity etc. is the only type of change possible!)
   b. That pattern is nowhere near universal: "simplification" has happened in many lineages of many kinds of organisms (e.g., loss of internal organ systems in parasites)
   c. Evolution is not "progressive" in the sense of leading to some pre-determined goal: the evolution of human intelligence, e.g., was not inevitable
   d. Note also that, in the sense that all extant organisms are the result of the same ~3.5 billion years of evolutionary history, no organism is "more evolved" or "more highly evolved" than any other!

F. Selection is not "perfect" – i.e., selection cannot result in "perfect adaptation" because of several types of constraints or limitations:

1. Time lags:
   a. as we noted earlier, every generation of organisms is adapted to the conditions that existed in previous generations
   b. selection can act very slowly relative to the rate of environmental change
   c. result = organisms may not be "perfectly adapted" to existing conditions
2. Mechanical constraints
   a. like man-made objects, organisms are "constructed" of materials that have limits to their physical properties

   b. result is that some phenotypes are physically impossible – e.g.'s include:
      i. limits to insect body size because of external skeleton
      ii. limits to the size of terrestrial vertebrates because of properties of bone
3. Genetic/developmental "links" between traits
   a. e.g., in *G. fortis* populations, individuals with narrowest beaks survived drought better than did individuals with broad beaks
      i. so "perfect" adaptation would be birds with narrow, deep beaks
      ii. but beak width is correlated with both body size and with beak depth: birds with large bodies and deep beaks also have wide beaks
   b. more generally, a particular genetic variation may produce an adaptive change in one trait, but a deleterious ("harmful") change in another, simply because of the complex genetic/biochemical/developmental relationships among traits
   c. result often is a "tradeoff" (or compromise) between traits

G. Selection acts on individuals, not groups
1. One of the most common mistakes non-evolutionary biologists make is to think that selection can act on traits "for the good of the species" – this is especially the case when we see behaviors that would seem to decrease fitness: e.g.
   a. prairie dogs or other social animals giving alarm calls
   b. mother lions nursing offspring other than their own
2. In fact, selection always acts to increase individual fitness: if a trait benefits another individual at its bearer's expense, it will be selected against
3. When we see apparently "altruistic" traits, we're usually seeing something more complex than meets the eye – usually, the trait either
   a. benefits a close relative (which, as we'll see later, increases individual fitness) or
   b. is reciprocated – so it doesn't represent a "cost"

H. Summary/conclusions:

1. Selection is the only process that leads to adaptive change.
2. Selection is simple in general terms, but still easily misunderstood.
3. Although the model of Darwinian natural selection wasn't widely accepted until the Modern Synthesis, Darwin got it right the first time!
4. In subsequent chapters, we'll look at
   a. natural selection in more detail
   b. other mechanisms for evolutionary (but not adaptive) change