

## Evolution in action

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- Homework #1 is DUE at the next class, this Thursday!
  - Print it out from the class web page, fill it in, turn it in in class Thursday.
  - Remember: User ID: \_\_\_\_\_, password: \_\_\_\_\_.
- Recap of Darwin's theory of adaptation by natural selection
  - Darwin's theory rests on three simple postulates:
    - 1. Organisms produce many more offspring than can survive and reproduce
    - 2. Individuals vary in ways that affect how successful they are at surviving and reproducing
    - 3. Offspring tend to resemble their parents
  - The logical, necessary result is **natural selection**
    - if the parents with the most offspring are different from the average
      - then their traits will become more common in the next generation, changing the average: **directional selection**
    - if the parents with the most offspring are the average type
      - then their traits will remain the most common in the next generation, and the average will stay the same: **stabilizing selection**
- An example: Darwin's finches
  - This is simply one very clear and well-documented example case
    - that shows that Darwin's model actually does fit real life
    - there is nothing special about these finches except that Peter and Rosemary Grant went to the trouble to document them thoroughly
    - and that they are historically associated with Darwin, since he observed these birds on the voyage of the *Beagle*
    - Other cases have been studied (although few so thoroughly) with similar results
    - presumably the same kinds of things have happened around the world and throughout time, even when no scientists were looking.
  - The finch study
    - was conducted on one of the Galapagos islands, Daphne Major, in the Pacific far off the coast of Ecuador
    - The subjects are medium ground finches (*Geospiza fortis*), which mostly eat seeds
    - The Grants captured, banded, and recorded measurements and other information about almost all the birds on the island over a number of years
    - and also recorded other information about the environment, especially the availability of different kinds of seeds
  - Early in the study, the island received a lot of rain, but then it suffered a severe drought
    - This provided a great opportunity to watch natural selection in action
  - During the drought, the plants on the island produced fewer of the small, soft varieties of seeds that the finches prefer
    - The finches quickly ate most of the small, soft types of seeds

- This left mostly larger, harder seeds, which many of the birds found difficult to eat
- The food shortage caused many birds to starve to death
- Darwin's first postulate was being met: more birds were born than survived to reproduce
- The finch population declined from 1200 birds to 180 birds in just two years of drought
- This was obviously a severe case, but not that unusual in the real world
- The Grants' found that there was variation in the depth (height) of the finches beaks
- there was a normal, smooth distribution of beak depths, ranging from relatively shallow beaks to relatively deep ones
- they observed that birds with different beak depths preferred different kinds of seeds
- birds with shallow beaks preferred smaller, softer seeds
  - probably because their beaks were not strong enough to break into the larger, harder seeds
- birds with deeper beaks preferred larger, harder seeds
  - probably because there were more of them around, and these birds were able to crack them with their stronger (deeper) beaks
- So, the variation in beak depth caused a variation in fitness when small seeds were scarce
- birds with shallow beaks had trouble finding enough food
- birds with deeper beaks were more likely to find enough food
- so birds with deeper beaks were more likely to survive during the drought
- So, Darwin's second postulate was also being met: the birds varied in how well they survived, because they varied in how well they could get food during the drought
- The deeper the beak, the more likely the bird was to survive during the drought years
- the distribution of beak depths shifted from a shallower average during the early, wet years, to a deeper average after a year of drought
  - more birds with shallow beaks died, while only a few of the deep-beaked birds died
  - this left a population with relatively more deep-beaked birds
- Finally, the Grants showed that Darwin's third postulate was also working in nature: offspring tended to resemble their parents
- They showed that shallow-beaked birds tended to produce shallow-beaked offspring, and deep-beaked birds tended to produce deep-beaked offspring
- This is no surprise, of course
- but it is absolutely necessary for the theory to work
- otherwise, the offspring would not perpetuate the traits of their successful parents
- So, after two years of drought, the new generation of finches being hatched had beaks that averaged deeper than the chicks of just two years earlier
- In two years, the average beak depth increased by 4%
- This was evolution caught in the act
  - but more than that, it documented Darwin's full process of natural selection in the wild
  - we often observe evolution, but usually we just assume that the cause was directional selection
  - in this case, we know that for sure
- Even more, this is not the slow, gradual evolution we usually think of
  - Imagine what would happen to human stature if selection caused it to increase this same 4% every two generations

- In twenty generations, the average height would increase 48%!
  - (if a typical human generation is 20 years, that is just 400 years!)
- So after 400 years of selection at this rate, the average American male would be over 8 1/2 feet tall!
- Point: evolution caused by directional selection in observed, real-world conditions can actually be very fast
- Now imagine if you found one island with small-beaked finches, and another with finches with beaks 50% larger
  - you would probably call them separate species
  - You would identify two distinct kinds of birds, even though in fact they might both have been descended from the same group of parents just twenty years earlier...
  - This is what Darwin thought had happened on the Galapagos islands, although he had no idea it could be this rapid
    - that is, he thought one small population of birds had probably gotten blown out to the Galapagos chain
    - these then managed to populate most or all of the islands
    - but were relatively isolated on each one
    - so all the birds descended from the same original population
    - but the birds on each island proceeded to evolve in different directions to suit the conditions on each island
    - this model still seems to be right, almost 150 years later.
- The Grants' study had two main points
  - 1. natural selection really did occur, just as in Darwin's theory
    - all three of Darwin's postulates held true
      - more were born than survived and reproduced
      - they varied in ways that affected survival (and therefore reproduction)
      - that variation was heritable
    - and evolution really occurred, just as the theory predicts
  - 2. in severe natural conditions, evolution can be very rapid
    - they observed 4% change in two generations
    - this could add up to big changes, very fast
- You might well ask: If large beaks are so much better, why hadn't the finches already evolved deep beaks?
  - Because of stabilizing selection
  - Before the drought, the average beak size remained the same due to stabilizing selection
    - birds with smaller-than-average beaks were less likely to survive and reproduce
      - because they were less likely to find enough food, because they could eat only the smallest, softest seeds
    - birds with larger-than-average beaks were also less likely to survive and reproduce
      - true, they could eat a greater variety of foods
      - but there are costs, as well as benefits, to deep beaks
        - deep-beaked birds more often die as juveniles
        - the Grants documented this with their bird census data

- we don't really know why
  - it may be because growing a deeper, bigger beak requires more food
  - so these birds may be slightly more likely to be undernourished as juveniles, to get sick, to be less able to avoid predators, etc.
- during the normal, wet years, there was a balance between
  - the higher mortality of the shallowest-beaked birds due to their greater difficulty finding food as adults
  - and the higher mortality of the deepest-beaked birds due to their difficulty finding enough food as juveniles
- birds with average-sized beaks were the ones most likely to survive and reproduce
  - so the action of natural selection was to stabilize the population
  - to keep the most common type the most common
  - this balance of opposing forces is called an “equilibrium”
- During the drought, the benefit of having a deep beak increased, but the cost apparently did not increase as much
  - so having a deeper-than-average beak became advantageous
  - and the selection ceased to be “stabilizing”
  - instead, it became “directional”, favoring birds with deeper beaks
- Stabilizing selection and directional selection are essentially the same process
  - the only difference is whether the optimal characteristic is already the most common, or not
  - as long as there is variation among individuals, selection is always going on
    - if the most successful type is already the most common type
      - then no change occurs
      - this is stabilizing selection
    - if the most successful type is different from the most common type
      - then, as generations pass, the population average will shift towards the most successful type
      - this is directional selection
  - Boyd and Silk point out that stasis (staying the same) is no more “natural” than change
    - both require explanation, which the theory of evolution gives us
- The finch example illustrates that species are not fixed, unchanging types of organisms
  - instead, species are *populations* of organisms, composed of individuals that vary
  - what defines the species is the distribution of various characteristics among the individuals who make up the population -- what traits are common, what traits are rare, what is the average of traits like beak depth
  - this distribution of traits may change over time, if directional selection occurs, or may remain constant, if stabilizing selection occurs
- Finally, let's be careful to separate our thinking about individuals and populations
  - natural selection *acts on individuals*, not the populations
    - Individual organisms live or die, reproduce or don't
  - but natural selection's *effect is on the population*, not the individual
    - The population's average type changes

- This process of selection of individuals does have a net *effect* on the population, but the actual *process* works individual by individual, not on the group as a whole
- This distinction is important, because it shows that natural selection does *not* consider how the traits affect the group or the species as a whole
  - natural selection, acting on individuals, might favor traits that are advantageous for individual organisms, but are disadvantageous for the group as a whole
    - natural selection can even drive the whole group to extinction
- Consider Boyd and Silk’s hypothetical example of high-fecundity vs. low-fecundity females (fecundity is the ability to produce offspring)
  - high-fecundity females produce more offspring; their offspring tend to be high-fecundity as well; so female fecundity rises
  - if food is scarce, it might be better for the group to produce fewer offspring
    - with a small number of offspring, there would be enough food for most to survive
    - with a large number of offspring, many would consume food for a while but still starve to death, wasting the food they ate
    - more would survive overall if fewer offspring had been born in the first place
  - but natural selection won’t favor low-fecundity females for the net good of the group
    - because natural selection only acts on individuals
  - all that matters is that the high-fecundity females produce more offspring
    - as long as some of the offspring survive, the high-fecundity females will have produced a larger share of them
    - so there will be more high-fecundity females in the next generation, and the average fecundity will keep rising
    - even though the increasing competition for food allows fewer and fewer offspring to survive to adulthood
    - so the population gets smaller and smaller, maybe until disease, predators, or other bad luck wipes it out completely
- so natural selection does not necessarily lead to “better” organisms
  - it just perpetuates whatever variants produce the most surviving offspring at that moment
  - the end result might not be what a designer would have picked
- A useful clarification: There are two kinds of variation that selection can act on
  - **Continuous variation:** variation in the magnitude of a characteristic, like height or the depth of birds’ beaks
    - a smooth range of variation without gaps between different types
    - evolution can affect a continuously variable trait by changing its average value
      - for example, the average height of Americans might increase from one generation to the next
  - **Discontinuous variation:** variation in which there are a few discrete types, like mottled vs. black moths
    - there are no intermediate types
      - there is not a range of coloration from mottled through darker variants to black, but just two (in this case) sharply defined types
    - evolution can affect a discontinuously variable trait by shifting the frequency of the types

- so one type might start off rare, but become more common from one generation to the next
- Another useful concept: very complex adaptations can arise from the accumulation of simpler changes
  - example: people who doubt that evolution is possible often point to the human eye
    - it has many parts that all have to be there in order to work as a normal human eye does
    - the lens has to be just the right shape and position to cast a sharp image on the retina, etc.
    - just a lens, or just a retina, would not permit sight
    - so how could such a complex device evolve gradually?
      - it must have been created all together, by a grand designer!
  - but this is looking at the process backwards, assuming that the full, camera-like eye was the goal
    - natural selection was not aiming to produce a human eye
    - it was simply favoring certain variants every generation
    - each step was advantageous at the time
    - these favored variants eventually accumulated to produce the eye
  - a hypothetical scenario
    - imagine starting with an organism that could not detect light
    - if some individuals happened to have slightly light-sensitive skin, they might have an advantage
      - since plant foods grow better where there is light, they would know when they were likely to be near plants, and when they should move to improve their odds of finding plants
      - there could be many other advantages to simply distinguishing light from dark
    - so light-sensitive skin would become more common
    - if some had more light sensitivity on one part of their body than another, by moving around they could tell which direction was lighter
      - this would be advantageous, and would become more common
    - if the light-sensitive skin was concentrated in a concave part of the body, that would restrict its “view” and improve the organism’s ability to tell which in direction the light (or dark) was
      - that would be advantageous, and would become more common
    - the deeper the concave area and the smaller the opening, the better the directionality...
    - the ability to distinguish which part of the light-sensitive skin lining the pit would also improve directionality
    - improving that ability would allow detection of motion, as in the shadow of a predator moving from one side to the other...
    - a transparent layer over the skin might protect it...
    - a thicker transparent layer with some curvature might concentrate the light...
    - a thicker, curved layer might cast a very fuzzy image on the light-sensitive skin, improving the ability to detect direction and motion...
    - and so on...
  - the point is that selection simply favors the most successful variant each generation

- and these successively better variations will keep accumulating
- the end result may be very complex
- even though it was reached “by accident”, by taking the best step at each generation
- this severely limits what features evolution can develop
  - since each step has to be an improvement, there generally cannot be huge leaps
  - if something cannot be reached by a succession of gradual improvements, natural selection will never produce it
  - which is probably why living things generally do not have wheels or screws, among other seemingly useful features
- this partially answers the question I posed earlier: Why are organisms so strangely, even badly, designed?
  - because the only designs that ever develop are those that can be reached by small improvements on a previous design
- this gradual tinkering approach can lead to local optima, but not necessarily global optima
  - **local optimum:** the adaptation with the highest fitness of all the ones similar to it
    - there could be numerous good variants, better than any similar design
  - **global optimum:** the best of the various local optima
- Natural selection should push organisms to evolve towards local optima
  - but not necessarily the global optimum
  - it depends on the starting point, or rather, on the previous history of evolutionary change
- say you are in the woods and have no map, but you prefer being higher up than down in the valley
  - each step, you choose the direction that is most uphill
  - after a while, you may be high up on a mountain
  - you got there without ever having any idea of where you were going
  - but you will never get up the even higher mountain on the other side of the valley...
- example of camera-type eyes (like ours) versus compound eyes (like insects’)
  - compound eyes are essentially bundles of mirrored tubes with light-sensitive spots at the bottom; many of these tubes are mounted on part of a sphere
    - they produce an image made up of one dot from each receptor
  - compound eyes are poorer than camera-type eyes
    - they have a limited, fairly poor resolution (fewer “pixels” in the image)
    - they are less efficient at gathering light, so they don’t work as well in low light
- so why aren’t compound eyes replaced by camera-type eyes?
  - because there is no gradual path to convert one to the other that goes through ever-improving variants
- the two are results of different variants that happened to be selected for early in the evolution of the eye
  - as early eye-spots were evolving, in some lineages, variants that had larger spots were favored
  - in other lineages, variants that more, smaller spots were favored
  - both approaches improved the early eyes’ sensitivity to light
  - the larger, single spots could be gradually improved by becoming concave eye to improve directionality

- leading to pinhole eyes, and eventually camera eyes
- the multiple-spot approach could be gradually improved by becoming convex to improve directionality
  - leading to leading to compound eyes
- once the first few steps were taken, progressive improvements to each design led in completely different directions
- if there were a divine “designer”, she might pick the right early step so that gradual improvements would lead to the best possible adaptation
- but in the absence of such foresight, evolution can only work with what it has at any given moment, and can only go in a direction that immediately produces better results
- so the outcome will often be the best that could be done by improving the earlier design, not the best that could have been done by designing from scratch or by starting with a different design.
  - that is, evolution cannot work towards a long-term goal
  - it only selects for whatever leaves more offspring right now, one generation at a time
- Two ways to look at evolution
  - We can look at it up close
    - as we did with the minor variations in the beaks of finches over just a few generations
    - or even the gradual evolution of the human eye
    - What we see in the close-up, short-term, detailed view is called **microevolution**
      - **Microevolution** = evolution within a species (changes in a population that do not result in a new species)
      - Microevolution usually refers to changes that are often small and not very important in themselves
        - like the beaks of the finches on Daphne Major.
      - microevolutionary changes are often fairly easy to understand in terms of Darwin's theory the process of natural selection
  - or we can step back and look at long-term changes in populations that are visible in the fossil record
    - that is, the kind of evolution that explains why there are many different, distinct kinds of plants and animals
    - What we see in the long-term view is the appearance of new species
      - **Macroevolution** = evolution that creates new species, and groupings of related species (genera, families, etc.)
      - Darwin suggested that the accumulation of a lot of small microevolutionary changes ought to add up to bigger, more obvious differences
        - Eventually, to entirely new species
      - given enough time, the accumulation of microevolutionary changes in many different populations ought to create countless different species with all sorts of different features
    - which is precisely what Darwin originally set out to explain: the profusion of different species of plants and animals, each adapted to its environment

- Next time, we will consider macroevolution: the creation of different kinds of organisms -- that is, the "Origin of Species" that Darwin wrote about
- Now, let's take a slight detour to think about epistemology
  - **epistemology**: how you know what you know
  - There are two general ways of knowing something
    - One way to know things is by accepting authority
      - for example, memorizing what the professor says because he or she is the professor and supposedly knows what is correct
    - Another way is to be convinced by an argument
      - for example, to really understand what Darwin meant with his three postulates, and to be convinced that the only logical conclusion is that if they really occur, then evolution has to happen
  - Accepting authority is the easiest way to know something
    - but it leaves you unable to explain or defend your beliefs, much less convince anyone else
    - it does not lead you to really understand things
    - and it leaves you vulnerable to accepting things that are not true
  - Understanding *why* a claim is convincing is better
    - it means that you understand the idea and its context
    - it means that you can defend your belief if someone challenges it
    - it means that you are protecting yourself from believing things that might not be true
      - of course, you are depending on your own intelligence and reasoning to do so
      - so you might make mistakes
      - but would you rather depend on someone else?
  - In this class, I don't want you to simply accept authority.
    - I want you to understand *why* claims and arguments are convincing
      - you should be able to explain *why* you came to your conclusions, not just remember an answer
      - if you don't believe the book, me, or some other authority, you should be able to explain *why they* claim something is the case, and then *why* you find that the claim is wrong
        - this is tough to do when you are new to a field, but at least keep it in mind
    - I hope you will believe that I and the authors of the textbook won't lie about empirical observations like beak size measurements
      - but keep in mind that even seemingly concrete facts can be mistaken
  - Question authority!
    - Some claims are more questionable than others, but the judgement call is yours.
    - this is what science is about
    - and it is also what the rest of real life is about.
    - keep an open mind, but use it!
    - your intelligence is your best defense.
- So, read, understand, and think carefully about the material for the next class!
  - and don't forget to print and complete the homework assignment.