Introduction to Biological Anthropology: Notes 4

What are species and how do they arise?

- Last time, we saw how Darwin's theory of adaptation by means of natural selection can be seen from two points of view:
  - **Microevolution** = evolution within a species (changes in a population that do not result in a new species)
    - like changing beak depth in finches
  - **Macroevolution** = evolution that creates new species, and groupings of related species (genera, families, etc.)
    - like the splitting of one species of finches into two different species
- So let's now consider macroevolution:
  - that is, the "Origin of Species" that Darwin wrote about
- So, what are "species"?
  - Preliminary definition: **Species** are (usually) easily distinguishable types of organisms (I'll define this better later)
    - The notion of species has two key parts
      - individuals of the same species are *similar to each other*
      - individuals of one species are *different from* individuals of other species
    - there are (usually) no intermediate types
      - no gradation from one species to the other, but rather a gap
      - no intermediate forms that are hard to classify as one or the other species
      - there are gorillas and there are chimps, but no "gimps" or "chorillas"
    - this is curious
      - why are there distinct *kinds* of organisms (species), rather than a smooth gradation of characteristics like we see among individuals within a single species?
      - why are there no chorillas?
    - by and large, species are real categories that exist in nature
      - unlike many categories used by scientists, species aren't just invented for the sake of convenience
        - living things really fall into distinct, well-defined categories
    - There are a number of different definitions of species.
      - amazingly enough, there is actually still a lot of debate about what these distinct kinds of organisms really are
      - and although they seem easy to observe, in some cases there is still room for disagreement
      - for a summary of some of this debate, see:
        - http://www.talkorigins.org/faqs/speciation.html
      - we will consider just the two most interesting of the leading concepts of species:
        - the **biological species concept**
        - the **ecological species concept**
  - But first, we need to understand two useful ideas

- **reproductive isolation**: members of one population do not interbreed successfully with members of another population
- **gene flow**: the movement of genes among individuals and groups
  - from parents to offspring, that is, the mixing of genes through mating
  - or from one population to another, by individuals leaving one group and joining another, or by mating between members different groups

- The **biological species concept**
  - "A species is a group of organisms which interbreed in nature and are reproductively isolated from other groups"
    - this is by far the most widely accepted species concept, but not the only one
  - according to this view, members of a given species are *similar to each other* because they interbreed
    - the traits of all members of the species are continually getting mixed together, so the population remains a single, fairly uniform group
  - according to this view, species are *different from other species* because there is no interbreeding between different species
    - there is no exchange of genes between one species and another, so traits don't get mixed between them
    - there are no "chorillas" because gorillas and chimps never mate
      - so there is no way for a gorilla to have offspring with characteristics unique to chimps
    - each reproductively isolated population is free to evolve in its own direction, leading to big differences between species
  - The biological species concept emphasizes patterns of **gene flow** as the main thing that defines and maintains distinct species
    - according to the biological species concept, there is gene flow *within* species, but *not between* species
    - the gene flow keeps all organisms in one species similar; all reflect more or less the same gene pool
    - while the lack of gene flow between different species means that they remain different, without mixing together
  - a note about reproductive isolation
    - populations may be reproductively isolated in many different, often subtle ways
    - in the most obvious case, they may be so different physically that they simply cannot mate, or that even if they do, the offspring do not survive or are not fertile
    - but isolation is just as complete if they simply do not mate for some other reason
      - for example, if one population is active in the day, and the other at night
      - or if two populations of birds develop preferences for different colors of feathers, and the birds only choose mates of their own type
      - even though they could be made to successfully mate in a lab or on a farm, if they do not actually mate in nature, they are effectively isolated
- The **ecological species concept**
  - "A species is a group of organisms that is genetically distinct from other species because any hybrids between species are much less successful"
    - This is a much less common, somewhat radical view

  - but it is worth looking at
- according to this view, members of a given species are *similar to each other* due to stabilizing selection
  - stabilizing selection favors the typical type
  - while weeding out any variants
- according to this view, species are *different from other species* because
  - any hybrids with other species are less successful
  - and are weeded out by natural selection
- the net result is similar to the biological species concept, but it emphasizes stabilizing selection, rather than gene flow
  - stabilizing selection keeps members of the species similar
  - and weeds out any hybrids, maintaining the difference from other species
- this explains how even if a species is divided into physically isolated populations and there is no gene flow between them, the two populations often still remain the same
  - because they are experiencing the same stabilizing selection pressures
- the idea here is that most species are at or near an adaptive "optimum"
  - any change would reduce their fitness, so stabilizing selection keeps the characteristics of each species where they are, and keeps the various species different
- support for this still somewhat radical viewpoint:
  - 1. Many related species are known to actually hybridize in the wild, yet they don't blend together into one intermediate species
    - because selection weeds out the hybrids?
  - 2. Separate populations of the same species that are isolated from each other by geography often do not diverge
    - something keeps them the same in spite of a total absence of gene flow
    - for example, rainbow trout in different rivers cannot interbreed because they never encounter each other, yet they all remain rainbow trout
    - the populations in the different rivers don't all evolve off in different directions, even though they theoretically could
    - because stabilizing selection keeps them at their adaptive optimum?
  - 3. Asexually reproducing organisms are divided into species just like sexually reproducing ones
    - in asexually reproducing organisms, offspring bud or split off a single parent
      - the offspring is a clone of the parent, genetically identical to it except for occasional copying errors
      - examples of asexually reproducing organisms: bacteria, fungi, flatworms, many plants under certain circumstances, etc.
    - So there is no mixing up of genes throughout a population, as there is with sexually reproducing organisms
      - why don't the descendants of each asexual parent each evolve off in their own direction?
      - why do all the members of the species remain similar to each other?
      - since there is no mating, there is no gene flow to keep them similar…

- yet (asexual) shiitake mushrooms remain shiitake mushrooms wherever they are, generation after generation
- the likely answer: because stabilizing selection weeds out any variants that arise through errors in reproduction
- if this were *not* true, then
  - each lineage of asexual organisms should evolve off in a different direction
  - this would create a continuous range of variation among asexual lineages
  - rather than what we actually observe:
    - many separate lineages of the same kind (species), and no lineages with forms intermediate between species
- Which species concept is correct?
  - undoubtedly both
  - the question is only which processes are more important in a given case
  - in many cases, reproductive isolation (the biological species concept) must play a role
    - since many species ARE totally reproductively isolated
  - but stabilizing selection must play a role in many cases, too (the ecological species concept)
    - because gene flow among all members of the species is often minimal or impossible, yet they remain the same species
    - and many species remain different from each other, even though they do hybridize
- Why do these species concepts matter?
  - Your choice of which process you think is most important in separating and maintaining species in nature affects on how you explain the origin of new species

- Why do species exist at all?
  - **speciation:** the development of a new species
  - speciation is hard to study
    - it is too *slow* and/or too rare to observe easily in nature
      - most cases of speciation being observed in nature have only "observed" in the sense that new species were seen where they had not existed before; no one happened to be collecting data precisely when it happened
    - and too *fast* and/or too rare to observe in the fossil record
      - usually, fossils of a new species just appear; we generally don't find a nice sequence of fossils leading from one species to the next
        - although there are some known examples of gradual speciation in the fossil record (among marine shellfish, ancestral horses, pigs, and others)
      - this is what we would expect species normally did not change much, and speciation only happened occasionally
        - because the number of individuals involved in the transition would be very few, compared to those involved in the long period of stability
        - so the chance of finding fossils of those few transitional individuals would be low
  - Two senses of the concept of speciation: **anagenesis** and **cladogenesis**
    - **anagenesis**: the evolutionary change of a population over time
      - example: say we have a long time to watch a population of rodents

- they start off the size of mice
- natural selection favors larger ones for some reason
- after 5000 generations, they have evolved to the size of house cats
- we may want to call these a different species
- if we decide to consider the cat-sized rodents a new species, it would be a **chronospecies** (also called **paleospecies**)
  - **chronospecies**: arbitrary divisions of a lineage of a single population into two or more "species", in order to reflect gradual changes over time
    - because after enough change has accumulated, we don't want to call the later form by the same name as the earlier one, because it is clearly different
- but chronospecies do not fit the biological species concept
  - we assume that they would not be able to mate with their mouse-sized ancestors, but there is no way to check
    - since the two types never lived at the same time
    - in fact, it is meaningless to discuss reproductive isolation in this case
      - since the first and last generations could not mate with each other regardless of whether they had changed or not; they did not live at the same time
  - also, every generation could presumably mate with the ones just before and just after
    - there is no sharp dividing line between chronospecies
    - but there *are* sharp divisions of reproductive isolation between living species
- chronospecies do not fit the ecological species concept, either
  - again, the different chronospecies did not live at the same time
    - so there were no hybrids that could have been less successful, and no selection acting on hybrids
- Chronospecies are just arbitrary categories imposed by scientists
  - while species that live at the same time,
  - defined by the biological or ecological species concepts,
  - are real, distinct categories "out there" in nature
- finally, anagenesis only describes how a population changes over time; it does not explain the increase the number of different populations (species) over time
  - if this were the only process, and life originated on earth just once, there would only ever be one species at a time
- we need to explain how new species are added
  - how species split into multiple descendant species

- **cladogenesis**: the splitting of one species into two (or more) species
  - this is what we usually mean by "speciation"
  - two populations of a species diverge enough that they no longer successfully mate
    - one or both have changed
    - where there was a single species before, now there are two (or more)
    - both populations exist at the same time, but they do not interbreed
  - a **clade** is a descent group of species
    - all the species that descended from a specified common ancestral species
    - like a branch of a family tree

  – we'll get back to clades later in the course
- there are three spatial situations in which speciation (cladogenesis) might occur
  - **allopatric** speciation: "in different territories"
  - **parapatric** speciation: "in adjacent territories"
  - **sympatric** speciation: "in the same territory"
  - these differ mainly in the amount of physical separation they require between the diverging populations
- **allopatric speciation**: speciation that occurs when two populations that are geographically isolated from each other diverge far enough to form distinct species
  - "allopatric": "in different territories"
    - the two populations are separated by a physical barrier or great distance, like lizards on two different islands, or fish in two different lakes
    - causing them to be reproductively isolated from each other
  - if the selection pressures on the two isolated populations are different, the two populations are free to evolve in different directions
  - if they diverge far enough, they have become separate species
  - this process is especially likely to happen in small, splinter populations
    - because small populations can evolve more rapidly than large ones
    - in large populations, new variants tend to get diluted away by gene flow with the many other individuals
    - while a new variant in a very small population can more rapidly become the common type
  - a hypothetical bird example
    - finches from a wet island get blown to a dry island.
    - selection on the dry island favors deeper beaks, and the bird population evolves deeper beaks
    - eventually they are so different from the parent population that, even if they somehow get back together on a single island,
      - they are reproductively isolated for physiological or behavioral reasons (biological species concept)
      - or the hybrids between the two are not very successful, so the two species don't blend back together (ecological species concept)
    - speciation does not *necessarily* happen when two populations are isolated; it depends on enough evolution occurring in one or both of the populations.
      - if conditions are similar for both populations, the same kind of stabilizing selection acting on both populations may keep them the same
      - then they just remain two populations of the same species
- pretty much everyone agrees that allopatric speciation actually occurs in nature
  - this is the simplest, least controversial speciation process
- The other two spatial patterns of speciation may or may not actually occur
  - they are debated, both theoretically and with field data
  - There is some evidence that parapatric speciation may occur
    - but it is probably rare
  - It is not certain that sympatric speciation can occur at all

        - if it does, it is probably rare
    - **parapatric speciation** ("in neighboring territories"): speciation that occurs when two populations that live in adjacent, bordering territories with no barrier between them diverge far enough to become distinct species
      - for example, a population lives both in a forest and in the grasslands next to the forest
        - there is no barrier between them
        - gene flow occurs between the areas, because all are free to mate with each other
        - this should keep their traits all mixed together
      - so how could they diverge into different species?
        - individuals far from the border are more likely to mate with each other that with individuals from the other environment
          - so the two areas are partially isolated
        - the two parts of the population experience selection that favors different characteristics suited to each environment
        - and the limited gene flow between them is not enough to prevent the two parts of the population from diverging somewhat
        - near the boundaries, in the **hybrid zone**, some hybrids will be born
        - if these intermediate types are less successful than the more specialized offspring of parents that are both from the same environment…
          - then natural selection will tend to weed them out
        - leading to two new, different species: speciation
      - in fact, this relatively lower fitness in individuals from hybrid zones is actually observed in many natural cases, so parapatric speciation probably actually occurs
    - **sympatric speciation** ("in the same territory"): speciation that occurs when members of a single population occupy different ecological niches in a single area
      - (**niche**: the combination of food, habitat, behaviors, etc. exploited by an organism)
      - such as some living up in the trees, others living on the forest floor
      - the same processes as in parapatric speciation could occur
      - but many biologists doubt that a population could develop two types without some isolation to start with
      - it is not certain that sympatric speciation actually occurs in nature

- An additional useful concept
  - **adaptive radiation**: the rapid divergence of populations of a single species into numerous new species, to take advantage of many newly available ecological options (niches)
    - typically would happen when an organism is first introduced to a new environment, or the environment changes drastically
    - in this new environment, there may be many different adaptations that could work well
    - partially isolated populations of the new organism happen to diverge in many of these different directions
    - leading to numerous new species that are all descended from the original one
    - once most of the available options are taken by new, specialized species, the process of creating new species slows or stops
    - an example that apparently happened on the Hawaiian Islands

- a small population of one type of finch got to Hawaii, maybe blown in a storm
- there were no other birds there
- there were many possible ways for birds to make a living
  - specializing in small, soft seeds; or large, hard seeds, or soft fruits; or hard fruits; or flowers; or insects…
  - and all were available without much competition
- some or all of the processes of speciation took place (allopatric, parapatric, and/or sympatric)
- the bird population quickly diverged into many different species, each well adapted to exploit one ecological option (niche)
- once most or all of the niches are filled, speciation slowed down or stopped
- we will see that adaptive radiations were important in the evolution of humans

- Rates of evolution
  - **Gradualism**: a view of evolution which supposes that changes accumulate at a steady pace over time
    - the pace is generally imagined to be slow
    - implies that populations respond slowly to natural selection
    - so in this view, most populations are not yet well adapted, but are still being pushed slowly towards the optimal form for that environment
  - **Punctuated equilibrium**: a view of evolution which supposes that populations experience long periods of equilibrium (or “stasis”), occasionally “punctuated” by spurts of rapid change leading to a new, different equilibrium
    - supposes that populations sometimes evolve rapidly
      - this would be most likely in very small, isolated populations
    - implies that most populations are well adapted and are kept the same by stabilizing selection
    - while occasional splinter populations may evolve rapidly to some new configuration
      - which may be a better variant of the same species that then spreads back through the whole species through gene flow, converting it to the new, more successful form
      - or which may be a new species altogether
    - the punctuated equilibrium model has a big plus: it explains the scarcity of transitional forms in the fossil record
      - we would expect to find lots of fossils of the species from its long periods of equilibrium
      - and few or none from the brief punctuation events in which a small sub-population rapidly evolved into a new variant or new species, because so few individuals were involved in the brief period of change

- A modern view of rates of evolution - the “evolutionary jitters”, or the “evolutionary hair trigger”
  - the fossil record seems to show very slow rates of evolution
  - J.B.S. Haldane invented a unit to discuss this: a 1% change in a characteristic per 1 million years = 1 darwin
  - typical rates of evolution based on fossils are around one darwin

- but if we look at the beak depth of the finches on Daphne Major during the drought, which changed 4% in 2 years, the rate is 2 million darwins!
- this is a pattern that recurs in many cases:
  - studies of long time spans based on fossils find slow rates of evolution,
  - while studies of short time spans based on field observations or lab studies find rapid rates of evolution
- how can this be?
  - the fossil record is very incomplete
    - it gives us widely separated snapshots, rather than a continuous record
  - fossil studies usually assume that the change between snapshots was a single, constant, one-way shift
    - simply because we have no information that shows a more complex pattern
    - but we now know that populations shift back and forth a lot
    - beak depth evolves up and down on a several-year basis in Darwin's finches
    - so the real rate of change is rapid, but it keeps reversing itself, so the net change over a long period is little or none
    - so say fossils finches from one layer show birds with small beaks, and in a layer a million years later, they have larger beaks
      - the beak size may have gone up and down hundreds of times in that million years
      - we just happened to get some fossils from a wet period (small beaks) in one layer, and some fossils from a dry period (large beaks) in the other
      - so we infer very slow directional change, when it has actually been rapid but back-and-forth with no long-term trend
- what does this mean?
  - populations are not lumbering, slow-changing things
  - instead, they are constantly being bumped back and forth by minor variations in selection pressures
  - the reason that species seem relatively stable is because they are mostly already well adapted to their environments,
    - and environments tend to vary around long-term averages that (usually) change slowly
  - the implications:
    - if there *is* ever a big change in the environment that changes the selection pressures,
      - then populations are able to respond very rapidly, and quickly evolve off in new directions
    - or if a new, advantageous variant somehow arises
      - it can become common very rapidly
  - far from being fixed or slow to change, populations are on an "evolutionary hair trigger"
  - this explains why the fossil record seems to show the punctuated equilibrium pattern

- But even this newly recognized capacity for "rapid" evolution probably isn't fast enough to respond well to changes on the scale of a human lifetime
  - that is, trees and large mammals, which take many years for each generation to grow to maturity, may not be able to evolve fast enough to cope with rapid changes like global warming, which is happening over just a century or two.

- but organisms with very short generations may be able to evolve that fast
- like rodent and insect pests
- and disease organisms like *Staphylococcus* and other bacteria, that have evolved resistance to antibiotics

- But even large, long-lived mammals can evolve faster than we usually think
  - here is a real-life example of rapid evolutionary processes in a large, long-lived mammal
  - Source: BBC News, September 25, 1998
  - Elephant poaching for ivory has been intense in most of Africa since at least the 19th century
  - In 1930, about 1% of elephants in Uganda were born without tusks - what would normally be seen as a birth defect.
  - Today, in areas outside of Uganda where the elephants are effectively protected still "only 2% of the animals are tuskless."
  - But today, in areas of severe poaching:
  - "Research at the Queen Elizabeth National Park, Uganda, showed that 15% of female elephants and 9% of males in the park were born without tusks"
  - A survey of elephants in Zambia's North Luangwa National Park in 1997 found that over 38% of the elephants there have no tusks
  - what is going on here?
  - Before heavy poaching, tusks were favored by selection
    - they are useful for digging for food and water
    - for self defense
    - and attracting mates
    - "Conservationists say an elephant without tusks is a crippled elephant."
  - But because poachers kill elephants to get their tusks, selection is now severe against elephants with tusks
    - so the few tuskless individuals survive and breed without being bothered by poachers
    - "…being tuskless is better than being dead…"
  - The "tuskless" trait has gone from 1% or 2% to over 38% in 70 years!
    - and this is in a species with very long generations
      - elephants don't mate until they are 15 or 16 years old
    - so the "tuskless" trait has become at least 14 times more common in fewer than five generations!
    - this is rapid evolution, caught in the act.
  - if this continues, some wild populations of elephants may be virtually all tuskless within our lifetimes, or our children's
    - and since tusks are involved in attracting mates, members of the tuskless populations may not mate much, if at all, with the remaining tusked elephants
    - so we could actually be observing the appearance of a new, reproductively isolated species
    - and this is not a little, short-lived bird, but a big, long-lived mammal like us

- this kind of drastic, rapid evolution, due to a newly introduced threat or other environmental change, probably played a big part in the evolution of many species, including our own…