Evolution: The Darwinian Revolutions

BIOEE 2070 / HIST 2870 / STS 2871

DAY & DATE: Tuesday 2 July 2012

READINGS: • Darwin/Origin of Species, chapters 5 through 10

• MacNeill/Evolution: The Darwinian Revolutions chapters 1-4

• Ruse/Darwin and Design: Does Evolution Have a Purpose? chapters 3 & 4

Lecture 6:00-7:50: Charles Darwin and Natural Selection Section 8:00-9:00: Discussion of evidence for Darwin's theory

Announcements:

• Essay assignment #1 is due next Monday!

You should be working on it now.

If you would like me to look at a rough draft, email it to me at:

adm6@cornell.edu

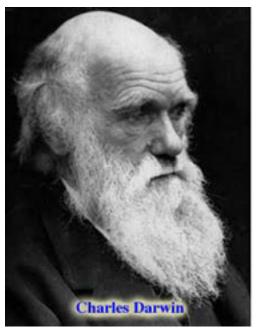
• How To Read Darwin's Origin of Species:

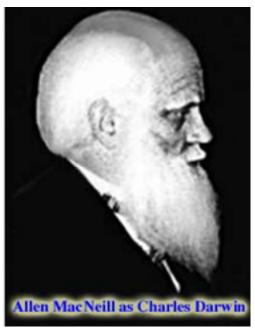
Do not be intimidated by Darwin's prose style in the *Origin of Species*! Darwin was a good writer by the standards of the Victorian period. Like all writers of that time, he writes long, complex sentences, conveying difficult ideas. To make reading the *Origin of Species* easier, follow these instructions:

- Be sure to read the chapter section headings before reading each chapter. These chapter headings provide an "outline-style" introduction to the main ideas in each chapter.
- Use the chapter summaries at the end of each chapter.
- Concentrate on the main ideas: Darwin usually presents each main idea at the beginning of each section. Most of the section is supporting evidence for this main idea you can skim this, and still get the main points.
- Reflect on the overall structure of Darwin's argument.

Charles Darwin

Darwin's work has had an enormous impact on society, perhaps more than any other single person's. His books changed the world, and will continue to change it for the foreseeable future. This is doubly remarkable, as Darwin himself was not a very good student – anyone in this course probably would qualify as a better student than Darwin.





As a young man, Darwin showed no interest in scholarship. <u>Gertrude Himmelfarb</u>, a historian of science who wrote a book about Darwin and the <u>Origin of Species</u>: said:

"Why was it given to Darwin, less ambitious, less imaginative, and less learned than many of his colleagues, to discover the theory sought after by others so assiduously?"

According to his <u>autobiography</u> Darwin studied latin, greek, and mathematics in primary school, but without distinguishing himself as a good student. His greatest interest as a boy was in collecting things – stamps, rocks, birds eggs, etc. – and in taking long walks in the country.

His primary interests in college were hunting and collecting beetles. His father, a prosperous physician, wanted him to become a doctor (his older brother, Erasmus, was already a doctor), and so sent him to Edinburg University to study medicine with his brother. However, Charles couldn't stand to witness surgery being performed on children without anaesthetic, and so he quit medical school. His father then recommended that he become a country parson, so Darwin entered Cambridge University, where he earned a degree in theology. He was an indifferent student at best, earning a "gentleman's C".

In later years he said that he had forgotten virtually everything he had learned while at Cambridge, with the exception of two books by William Paley:



- <u>A View of the Evidences of Christianity</u>, in which Paley tried to dismantle <u>David Hume's attack</u> on miracles, and
- <u>Natural Theology</u>, in which Paley presented the argument for design in nature. In this book, Paley proposed a thought experiment in which the reader is to imagine finding a watch in the path how one would determine whether the watch had an intelligent designer, as opposed to a stone, which clearly has not.

Given the foregoing, how could Darwin have written the most important book in biology, if not all of science? There are several aspects of Darwin's character that could explain this apparent anomaly:

- Darwin was an extraordinarily avid collector, especially of natural objects. For example, he once tried to capture three beetles (for his collection) by popping one in his mouth and one in each hand. Unfortunately, the one in his mouth exuded an acrid fluid, causing him to drop and lose all three beetles.
- Darwin was very deeply interested in geology, as a result of a course he had taken in Cambridge. It was not uncommon for students in training as parsons to take courses in geology and natural history, as many of them were also amateur naturalists.
- Darwin was also very interested in botany and "natural history" (what biology was called in those days). His botany teacher, Professor Henslow, thought so much of his talents that he recommended that Darwin be appointed as ship's naturalist for the voyage of HMS Beagle (a post Henslow himself had been offered, but turned down due to family responsibilities).

Darwin and the **Voyage** of *HMS Beagle*

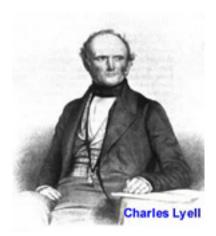


Darwin jumped at the chance to serve as ship's naturalist aboard the Royal Navy survey ship, *HMS Beagle*. However, the *Beagle's* captain, Robert Fitzroy, felt that Darwin was insufficiently qualified for the post, and hired someone else instead. However, Captain Fitzroy did consider Darwin for the position of "gentleman's companion" (someone with whom he could dine and talk who would be of his own social class). At first Fitzroy was reluctant, based on the shape of Darwin's head - Fitzroy was a believer in phrenology, the divining of a person's character and intellect by studying the shape and bumps on a person's head. However, Fitzroy eventually relented, and Darwin was taken on as Fitzroy's companion and amateur naturalist.



<u>Darwin's father</u> also balked at allowing Charles to serve on the *Beagle*, until talked into it by Charles' uncle, <u>Josiah Wedgwood</u> (head of the <u>Wedgwood pottery company</u> and father of Darwin's eventual wife, <u>Emma Wedgwood</u>).

While voyaging on the *Beagle*, Darwin read <u>Charles Lyell's</u> multi-volume text, <u>Principles of Geology</u>, which convinced him of Lyell's principle of <u>uniformitarianism</u>. Among other things, Lyell inspired Darwin to study the geology of coral reefs, about which Darwin wrote <u>an essay</u> upon his return to England.



From a reading of his journals and notebooks, it is clear that Darwin was not convinced of the reality of evolution while on the voyage of the *Beagle*. Indeed, he took so few pains in cataloging the specimens he collected that he had to consult Captain Fitzroy's collection of <u>Galapagos finches</u> to write his account of the voyage.

Darwin's voyage aboard the *Beagle* transformed him from an indifferent student to a passionate and highly skilled naturalist. He had a natural talent for collecting specimens and recording his observations. He wrote volumes of notes and sent thousands of specimens back to museums in England. His noted eventually became the basis for his first book, *Journal of the Voyages of HMS Beagle*, which he wrote with the encouragement of Captain Fitzroy upon his return to England.

Darwin's Evidence for "Descent With Modification"

Darwin was still a creationist when he returned to England after the five-year voyage of the *Beagle*. Upon his return, he started several notebooks in which he pondered the things he had observed while on the voyage. In particular, he considered three sets of observations that were eventually to lead him to the idea of evolution by natural selection. These three things were:

- the patterns he observed in the geographic distribution of animals and plants as the *Beagle* circumnavigated South America. Darwin observed that similar habitats in widely separated locations were inhabited by similar (but not the same) species; he eventually concluded that this indicated that such species had descended from common ancestors.
- the fossils of extinct animals he collected from all over South America. His careful observations
 of these fossils convinced him that they were the remains of species no longer present in South
 America, but which were related to species that still existed. Like the geographical
 distributions described above, these observations suggested that modern species had descended
 from other, similar species now extinct.
- the distribution of species he observed on volcanic islands in the Atlantic and Pacific oceans. He noticed that although these islands were located in the same types of habitat, they were inhabited by different species. Furthermore, although these species were not at all related to each other, they were related to species located on the nearby mainland, suggesting again that the island species and the nearby mainland species had descended from common ancestors.

Darwin's Ideas on Animal and Plant Breeding

Darwin had no empirical (i.e. "observational") evidence for natural selection. Instead, he used imaginary examples and analogies to animal and plant breeding.

- In about 1837, he had started thinking about the implications of what he had seen while aboard the *Beagle*, and started a series of <u>notebooks</u> on "the transmutation of species"
- He began to study the processes of animal and plant breeding very intensively, culminating in an <u>essay</u> which he wrote on the subject in 1842, and revised in 1844
- Early on, he concluded that "Any variation which is not inherited is not important..." (*Origin of Species*, 1st ed., page 12 / Wilson pg 456)

Darwin mentioned the importance of "correlation of growth," by which he meant the unintended effects on animal and plant breeds as the result of selecting for specific characteristics. He also pointed out that traits that are not inherited are not relevant to evolution by natural selection.

Pigeons as a Model for Natural Selection

He began the *Origin of Species* by pointing to the various breeds of domesticated pigeons as being analogous to natural selection. He pointed out that all <u>domesticated pigeon breeds</u> are descendants of the wild rock dove (<u>Columba livia</u>). He went on to note that, "The diversity of the breeds is something astonishing..."(<u>Origin of Species</u>, 1st ed., page 21 / Wilson pg 462)

• Although these breeds are startlingly diverse, they are *not* separate species. However, they are at least as different from each other as natural species are in the wild.

From his interviews with pigeon breeders, Darwin concluded that pigeon breeders of his time believed that all of the various breeds of pigeons were derived from separate kinds of pigeons that existed in the wild; *i.e.* that no evolution or selection had taken place to produce such breeds. Darwin concluded otherwise: that all 700+ breeds of pigeons had been derived from the wild rock dove by means of artificial selection. He asserted that pigeon breeders were denying the evidence right in front of them: that their choices of breeding pairs were shaping the breeds that exist.

Darwin asserted that most of the artificial selection done by animal and plant breeders was
probably done unconsciously, by breeders choosing desirable traits among their domesticated
animals and plants.

Darwin also asserted that there is greater variation among the domesticated breeds of animals and plants than exist among wild species in nature. He noted that domestic breeds tend to "sprout variations" when they are taken out of their natural environment. What breeders do is simply to select those new variations that strike their fancy, thereby preserving unusual forms that would almost certainly be lost in nature.

What is a Species?

How does Darwin define "species?" Does he define them in the same way that modern evolutionary biologists do? Consider this quotation from the <u>Origin of Species</u>:

"Many years ago, when comparing, and seeing others compare, the birds from the separate islands of the Galapagos Archipelago, both one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties." (Origin of Species, 1st ed., pg 48 / Wilson, pg 480, emphasis added)

Note that he is comparing birds within the various species on the Galapagos Islands, rather than comparing birds of different species on those same islands.



Furthermore, although he was referring to the finches of the Galapagos islands, he could have been speaking about most species. He goes on:

"Certainly no clear line of demarcation has yet been drawn between species and sub-species—that is, the forms which in the opinion of some naturalists come very near to, but do not quite arrive at the rank of species; or, again, between sub-species and well-marked varieties, or between lesser varieties and individual differences. These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage."(Origin of Species, 1st ed., pg 51 / Wilson, pg 482, emphasis added)

It seems that Darwin is arguing that species, as defined by naturalists, are simply a figment of the human imagination. However, later in the *Origin*, he states:

• "To sum up, I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links..."(*Origin of Species*, 1st ed., pg 177 / Wilson, pg 563, emphasis added)

Why did Darwin begin the *Origin* by pointing out that species boundaries seem "entirely vague and arbitrary", but later on conclude that species become "tolerably well-defined?" Darwin had two aims in writing the *Origin of Species*:

- To convince his readers of the reality of "descent with modification" from common ancestors; he was largely successful in this aim.
- To convince his readers that natural selection was the cause of the "beautiful adaptations" that define species; he was largely unsuccessful in this aim.

To accomplish the second aim, Darwin was forced to use an "argument from analogy," because he could not point to any real-world examples of natural selection in action. In <u>Chapter 1 of the Origin of Species</u>, he essentially argued that "breeds" under domestication are analogous to "species" in the wild insofar as both are shaped by selection.

The animal and plant breeders that Darwin consulted were of the opinion that their breeds were derived from separate species in the wild. Darwin pointed out that this opinion was incorrect: that they were all derived from one "wild type" ancestor, which was modified by artificial selection.

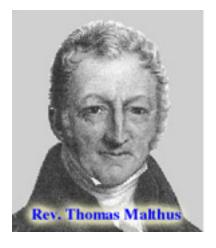
• In other words, natural selection is analogous to artificial selection.

Darwin on the "Struggle for Existence"

Although he became convinced in about 1837 that evolution had occurred, Darwin did not stumble upon a mechanism for evolution until the autumn of 1838. He says in his autobiography:

"In October 1838...I happened to read <u>Malthus on Population</u>, and being well prepared to appreciate the struggle for existence which everywhere goes on...it struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed." (<u>The Autobiography of Charles Darwin, 1887</u>)

He almost immediately realized that the excess population growth that Malthus described would result in a "struggle for existence" which he would later call "natural selection."



<u>Malthus'</u> <u>Essay on the Principle of Population</u> included several ideas that were crucial for Darwin's theory:

- that the food supply in any area increases only linearly, whereas the population increases exponentially
- that because of this, every natural population will eventually outstrip its food supply, leading to widespread starvation.

Darwin proposed that species in nature were subject to a "struggle for existence." This "struggle" is caused by the enormous reproductive potential of living organisms. As Malthus first pointed out in his <u>Essay on the Principle of Population</u>, if a population is not limited by food, space, or other resources, it will rapidly increase. In the *Origin of Species*,, Darwin pointed out that unchecked populations (of elephants, for example) could easily cover the surface of the Earth.

Darwin pointed out that the "struggle for existence" is not necessarily violent. It includes "...the dependence of one being upon another...including...success in rearing progeny." (*Origin of Species*, 1st ed., pg 62 / Wilson, pg 490) Darwin also pointed out that the "struggle for existence" is most intense among members of the same species, which have nearly identical requirements for resources:

• "...the struggle almost invariably will be most severe between the individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers." (*Origin of Species*, 1st ed., pg 75 / Wilson, pg 498, emphasis added)

In other words, the "struggle for existence" proposed by Darwin is a struggle to leave the most offspring, which over time will result in the offspring of the more successful individuals becoming more common among the members of their populations.

Darwin on Natural Selection

Darwin's presentation of the concept of natural selection was by far the most important part of the book for him, if not necessarily for his readers. Darwin viewed natural selection as a kind of "engine" of organic change, driving different variants of the same species to diverge until they became new species.

However, viewed correctly natural selection itself is <u>not</u> a mechanism; rather, it is the <u>outcome</u> of a process that has several components, including:

- Variation: That is, differences between the members of populations. These variations need not be extreme, as illustrated by the relatively large changes that animal and plant breeders have accomplished, using relatively slight differences in physical appearance and behavior.
- Inheritance: The distinct variations noted above must be heritable from parents to offspring.
- Fecundity: Living organisms have a tendency to produce more offspring than can possibly survive. Among those individuals that do survive, those that also reproduce pass on to their offspring whatever characteristics made it possible for them to survive and reproduce.

• Non-Random, Unequal Survival and Reproduction: Survival and reproduction are almost never random. Instead, individuals survive and successfully reproduce because of their characteristics. It is these characteristics that form the basis for evolutionary adaptations.

Some species (such as <u>eastern timber rattlesnakes</u>) are clearly <u>polymorphic</u>: they exhibit two or more distinct "morphs" (*i.e.* body forms and color patterns: sulfur-yellow with dark bands, versus "sooty" black). Darwin explains such polymorphisms as being the result of selectively neutral variations in populations. Modern evolutionary biologists explain it differently, usually by referring to natural selection for a heterozygous intermediate between the two morphs.





Eastern Timber Rattlesnake

On page 84 of the Origin of Species, Darwin says:

• "We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages, and then so imperfect is our view into the long past geological ages, that we only see that the forms of life are now different from what they formerly were." (*Origin of Species*, 1st ed., pg 84 / Wilson, pg 504, emphasis added)

And again on page 95:

• "Natural selection can act only by the preservation and accumulation of infinitesimally small inherited modifications, each profitable to the preserved being; and as modern geology has almost banished such views as the excavation of a great valley by a single diluvian wave, so will natural selection, if it be a true principle, banish the belief of the continued creation of new organic beings, or of any great and sudden modification of their structure." (Origin of Species, 1st ed., pg 95 / Wilson 511, emphasis added)

And once again on page 108:

• "That natural selection will always act with extreme slowness, I fully admit...that natural selection will always act very slowly, often at only long periods of time, and generally on only a very few inhabitants of the same region at the same time." (*Origin of Species*, 1st ed., pg 108/Wilson, pg 518, emphasis added)

His point? Darwin is essentially arguing that natural selection acts too slowly to be observed. He even stated (in a conversation with a colleague and passed on by word of mouth) that it would take at least 50 years to observe any kind of natural selection acting in nature.

If this is the case, then how does Darwin go about proving to the reader that natural selection occurs, and is the "engine" of "descent with modification?"

- As noted in earlier lectures, he draws analogies to artificial selection in the breeding of domesticated animals and plants.
- He provides two examples of natural selection in action: wolves preying on deer, and plant-insect coevolution (*Origin of Species*, 1st ed., pg 90 / Wilson, pg 507). However, it is important to note that both of these examples are imaginary; they are a kind of "Darwinian thought experiment."

In effect, Darwin has no direct, observable examples of natural selection, so his argument for its action must be drawn on inference alone. He states:

• "Whether natural selection has really thus acted in nature, in modifying and adapting the various forms of life to their several conditions and stations, must be judged of by the general tenour and balance of evidence given in the following chapters." (*Origin of Species*, 1st ed., pg 127 / Wilson, pg 532, emphasis added)

If Darwin were to try to get such an explanation published in a science journal today, he would almost certainly be turned down.

Darwin on Sexual Selection

Darwin states that mating among most animals is based on "female choice" - that is, females are "choosy" about who they will mate with, while males are generally "ready and waiting" for females to allow them to mate. Darwin points out that this will cause females to shape the adaptations of males, by choosing mates based on their characteristics. He calls this process sexual selection.

Darwin implies that sexual selection can be separable from natural selection, insofar as the two processes can be shown to have separate effects. Some evolutionary biologists agree, but others argue that sexual selection is merely a special form of natural selection.

• There are numerous species of birds (e.g. peacocks, magpies, etc.) in which the grotesquely exaggerated characteristics of males (produced by female choice) can actually lower the male's chances of survival.

Darwin based most of his second most famous book (<u>The Descent of Man and Selection in Relation to Sex</u>) on the concept of sexual selection, especially as caused by female choice. Darwin believed that female choice could explain the evolution of the various races of humans, as well as the more obvious differences between females and males in other species, such as peacocks.

Summary of Darwin's Argument in Chapters 1-4

Natural selection is analogous to artificial selection, in that both depend on variation, inheritance, fecundity, and result in non-random, unequal survival and reproduction. Darwin has no real, observable examples of natural selection in action. Instead, he argues that the "general tenor and balance of the evidence" in later chapters of the *Origin* will eventually carry his argument.