

Chapter 9. NATURAL SELECTION AND BIOLOGICAL EVOLUTION

Which beginning of time [the Creation] according to our Chronologie, fell upon the entrance of the night preceding the twenty third day of Octob. in the year of the Julian Calendar, 710 [i.e. B.C. 4004].

Archbishop James Ussher (1581—1656)
*The Annals of the World*¹ (1658:1)

“How stupid not to have thought of that!”

Thomas Huxley (1825-1895), about Darwin’s theory of Evolution by Natural Selection.

I. Introduction

A. Classical Discoveries of Biology

From the mid 18th Century to the early part of the 20th, a large fraction of biologists’ efforts went into two massive collective discoveries, the discovery of biotic diversity, and the discovery of evolution.

Over the period from 1750 to 1950 the careful descriptive analyses of Swedish biologist Karl von Linné and his followers showed there to be on the order of 10 million or so different types of living organisms. The differences in biotas in different parts of the world came to be appreciated, the amazing diversity of the tropics was documented, and previously unimagined major groups of organisms were discovered, including microorganisms and the biota of odd habitats like the oceanic plankton. The sometimes bizarre and always impressive adaptation of organisms to their habitats and ways of life greatly impressed the early scientific naturalists, who argued that it proved the existence of an All Seeing Designer.

Similarly, paleontologists described a huge variety of fossil plants and animals. The succession of forms, and the presence of many detailed structural similarities between living and extinct forms, as well as structural parallels between living forms, strongly suggested that living and ancient forms of life were connected by branching lines of descent. By the mid-19th century, the evidence that modern forms of life had evolved from ancient ones became well-nigh inescapable, and it became much more difficult to hold the notion that

1. Full title: *The annals of the world. Deduced from the origin of time, and continued to the beginning of the Emperour Vespasians reign, and the totall destruction and abolition of the temple and common-wealth of the Jews.*

each species had been separately created.

B. Darwin's Contribution

Natural selection is a model of how evolution works. Darwin is sometimes mistakenly credited with discovering evolution. This is misleading. Many people besides Darwin contributed to this enterprise. Darwin's real contribution was to develop models of how the evolutionary process worked, the most famous of which was his model of evolution by natural selection. Wallace independently hit on the idea. Darwin and Wallace also gave simple verbal models of evolution by chance, artificial selection, sexual selection, and by the inheritance of acquired variation. They could depend on most active scientists (laymen were another story) of his day accepting evolution. His proposals regarding the causes of this evolution, especially his hypothesis that chance and natural selection played major roles in causing evolution, were both more novel and more controversial. It is only since the mid-20th century that we can fairly confidently speak of moving Darwin's hypothesis about natural selection into the category of a discovery.

Charles Darwin developed his basic theory of evolution by natural selection in 1838, shortly after he returned from the voyage of the *Beagle* and married Emma Wedgwood (she was an heir to the Wedgwood China family, owners of the pioneering 19th century manufacturing enterprise). In his autobiography he claims the idea came to him one day, after many weeks of false starts grappling with the "species problem", while "reading Malthus for pleasure." (Darwin's autobiography is just a sketch for his family, and is known to be not very accurate. The Malthus remembrance may be apocryphal, but it is good propaganda for general education. Read broadly, a bit eclectically, think very carefully about what you read, and you too may one day make a famous discovery!) He did not publish his ideas until 1858, when A.R. Wallace sent him a paper noting the process of natural selection from the East Indies, where he worked as a professional collector of plants and animals for taxonomists. Shocked into publishing, Darwin's (and Wallace's) ideas created the immediate furor that Darwin apparently deeply feared (Gruber, 1974), although much of the scientific community was very sympathetic.

C. Population Thinking: Simple But Counterintuitive

Why had not natural selection been discovered long ago? As the epigraph from Huxley shows, Darwin's basic model was almost absurdly simple. Why was the reaction in all but prepared minds so skeptical? Why, even to this day, do many professional biologists, not to speak of laymen, have trouble with natural selection? The answer seems to be that Darwin's basic insight violates people's intuitions about how nature ought to work. The problem is that the population thinking lying at the basis of the natural selection model vi-

olates two simple thinking procedures that people use in every-day life. (Psychologists who study these things argue that intuitive thinking procedures that people use generally tend to work well for *some* kinds of problems but fairly poorly for others.)

First, people tend to be typological not population thinkers. People are very good intuitive taxonomists, but they take their categorization too literally. In everyday life, it is often very efficient to ignore all the fuzzy variation in the world and classify things into arbitrarily bounded classes. For example, the vowel sounds that people make when speaking vary continuously. However, human listeners sharply classify sounds into discrete vowels, ignoring all the fuzz and individual variation. We do the same things with color names. We saw in an earlier chapter how good hunters and gatherers were at classification. We think of things as exemplars of classes, for example species of organisms, and discount individual variation as departures from type, or as aberrations. Ethnocentrism, the classification of people by race or culture, coupled with a tendency to ignore individual differences in outgroups, is an example of typological thinking. In population thinking, by contrast, we have to learn that the individual variations are more important to the theory than the categories we put them into.

Darwin's insight that individual variation—the small departures from the “type” that previous biologists had dismissed as uninteresting error in developing the essence of the species—was fundamental to evolutionary processes and was his first stroke of genius. As it were, his mechanism derives imperfect species from variable individuals rather than imperfect individuals from a perfect type. The conceptual leap here was profound, and must be rediscovered by each new generation of students. This was the culmination of the development of population thinking started by Malthus.

Second, people are prone to believe that the causes of phenomena should have certain gross resemblances to their effects. Psychologists have discovered that people commonly use something they call the “representativeness heuristic²” to make judgments (Tversky and Kahneman, 1974). We have already met one manifestation of this thinking procedure in the “doctrine of signs”, the theory that the cures of diseases should in some way resemble their symptoms, or the organ involved. In many everyday cases the intuition that the causes of things should be like their effects is correct; a smashed house must have been struck by a large impressive object or force. Big, spectacular effects should have big, spectacular causes. In the case of evolution, the phenomena we want to explain is the spectacular diversity and adaptedness of organisms. Surely this awesome phenomenon ought to

2. Heuristics are the basic ways we approach learning, discovery, or problem-solving by experimental and especially trial-and-error methods.

have a awesome cause, say a Divine Creator of unimaginable power and wisdom. Such was invoked by Darwin's teachers under the name of the "argument from design"; the Craftsman is necessary to explain the Wonders of Nature. Darwin's population approach turned all this on its head. He looked for the cause of adaptation and diversification in the grubby events of the everyday lives of organisms. Small chance variations among individuals, the competition among these variants as they fed, fled, and mated, and a sufficient amount of time were all Darwin's theory required. Even Huxley, Darwin's "Bulldog" could not bring himself to believe that natural selection was all that was needed to account for evolution! There must be something fancier going on he felt because he could not entirely free himself of the grasp of the representativeness heuristic.

The whole trick to understanding natural selection, and indeed this part of the course, is to understand population thinking. This is fun and easy once you abandon the bad heuristics.

D. Importance of Natural Selection for Human Ecology

Many human anatomical and physiological traits are adaptations. For example, skin color varies as a function of latitude, and this variation is plausibly adaptive. Prominent hypotheses include that dark skin protects from sunburn in high light environments, and that pale skin is required for adequate vitamin D synthesis in more poleward climates. Although we will concentrate on the quantitatively more important cultural adaptations in this course, some human biological variation has to be at least assessed for its adaptive value. We return to this topic in Chapter 21 on disease.

The most important human adaptation is the capacity for culture. As we have seen in Steward's scheme, much cultural variation is correlated with environmental variation, and is certainly adaptive by common sense standards. However, it has proven very difficult to specify exactly how culture comes to be adaptive. In other words, social scientists have not had an easy time developing the analogs of biologists' models of the evolutionary process. In the subsequent chapters in this part of the course we are going to see how Darwinian ideas have been used (1) to try to understand culture as an adaptation (Chapter 10), and (2) as *methodological* inspiration for trying to formulate models of cultural evolution itself (Chapters 11 and 12). Regarding the latter, there is a school (to which we subscribe) that believes that population thinking is the key to understanding cultural evolution, just as it is in the case of organic evolution, no matter how much culture and genes differ in material terms.

II. Darwin's Basic Model

A. Malthusian Principle + Heritable Variation → Adaptation

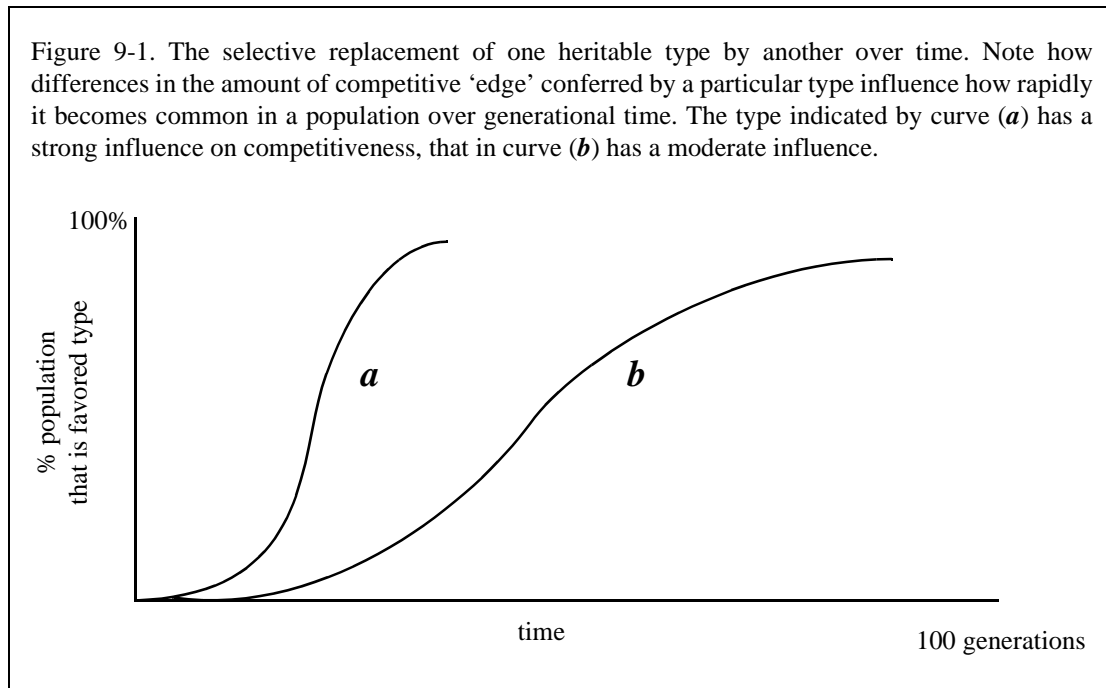
Offspring resemble their parents. Biologists say that the one important cause of parent offspring resemblance is *heritable variations*, now known to be mainly caused by genes in typical organisms. If variation can be accurately passed down the generations, then long-term evolution is possible. Usually some portion of the variation is heritable and some portion is due to non-heritable effects.

Normally organisms will have to compete for resources to reproduce. Darwin borrowed the idea of exponential increase leading to competition from Malthus. Populations are liable to grow rapidly if they are far from resource limits. If environments are permanently unstable, individuals will scramble for resources to have many children. If populations are allowed growth for long, resources will become limiting and individuals will have to struggle for resources to survive and have any offspring at all.

Darwin devoted most of the pages of the *Origin* to give empirical evidence that heritable variation exists and that competition is important. What must necessarily happen over a number of generations if these two assumptions are true? The heritable variants that cause individuals to be better competitors will increase, and the variants that cause poorer competitors will decrease. Depending on how large the competitive differentials between the variants are, and how much of the variation is heritable, the variants causing poor performance will disappear more or less rapidly. If some process is creating new variation, say at random, at some small rate, there will occasionally arise a newer and better variant, and selection will favor its increase. Unfavorable variants that arise by chance will not increase simply because they are unfavorable.

Reproductive success is the key. Natural selection will result in populations of adapted individuals by favoring those that “work better” in a given environment. Notice that “work better” has a precise technical meaning here; the differential ability to survive, and reproduce, hence to differentially propagate some heritable variants relative to others under prevailing environmental conditions. Those heritable variants that leave the most offspring are defined as conferring higher *fitness* or as being better *adapted*. However, we mustn't think of fitness itself as the cause of evolution by natural selection. Fitness is merely the result of the differences in the performance of everyday tasks that happen to result from how organisms with heritable phenotypic differences interact with their particular environments. In the end, it is reproductive success of the types over the whole life cycle (e.g., taking into account of the probability of survival) that is the key measure of fitness.

The rate of evolutionary change varies. Figure 9-1 illustrates the way selective change depends upon the magnitude of competitive difference and on the amount of variation present in the population. Notice that the **rate of change** due to selection is most rapid when the mixture of types is about 50:50, and is slow at the beginning and end. There is little heritable variation when a population is composed of almost all one type, but the maximum amount when all types are equally abundant.



Darwin imagined that the accumulation of small adaptive differences by selection generation after generation leads to even the fanciest adaptations. Natural selection is quite unspectacular, down-in-the-dirt process on the generation to generation time scale. Nothing much happens. But the fact that variation is heritable means that small changes can accumulate from generation to generation if selection is persistently in the same direction. Over tens to hundreds to thousands of generations first readily appreciable, then quite spectacular changes, result. It is like population increase in the last Chapter. Changes that seem slow from the perspective of one generation can seem quite rapid when they accumulate over a few generations.

Such a pretty piece of deductive reasoning! It can all be reduced to the idea that even the random generation of variation plus a principle of selective retention of some of those variants will result in adaptation by natural processes. The process matches anything a Divine Designer could do by way of generating adaptations.³ As we'll see in later Chapters, Darwinian theory can account for some exceedingly strange twists in evolutionary patterns.

Part of Darwin's argument was that the *imperfections* of adaptations betray a natural rather than a divine process.:

Postulate 1: Potential for exponential increase ensures competition for resources.

Postulate 2: All populations have heritable variability, at least some of which affects performance in important ways.

Conclusion: So long as the environment is relatively consistent, heritable variants that confer a competitive advantage in survival and reproduction (greater fitness) will increase. Populations must become better adapted with time as long as (1) and (2) are true.

While evolution by natural selection is incredibly complex in practice, Darwin's extremely simple model turns out to give us a tremendous amount of insight into the diverse processes by which evolution proceeds.

B. Darwin's Achievement

More than anything else, Darwin and Wallace introduced a method of studying evolution. They might have said “study the dynamics of individual variation as things happen to individuals during their lives, and as variation is transmitted to the next generation. A good account-book tracing the increase and decrease of heritable variation through time will reveal the principles of evolution.” The model of natural selection he introduced is an excellent example of population thinking, but the method is far deeper than this one model. Population biology has a huge array of models derived by using population thinking, not to mention the empirical studies that apply its precepts literally.

Note also how he looked for the cause of grand things—the vertebrate eye and the fossil record—in drab everyday events: the causes of evolution are ecological processes. This approach to evolution focused biologists' attention on problems they could investigate, the biology of inheritance and the ecology of competition among variants in nature. In a way Darwin's theory created more problems than it solved (the argument from design

3. If you would like to pursue this idea further, we suggest Richard Dawkins' *The Blind Watchmaker* (1987) which bears the subtitle “why the evidence of evolution reveals a universe without design.”

accounted for adaptations themselves well enough), but it set workable biological problems in the context of an interesting general theory that made all the little problems seem important. One might say that Darwin set up evolution as a concrete scientific problem instead of a speculative “philosophical” one. Spencer and other progressive evolutionists’ ideas suffer from this latter defect in the scientist’s mind. They don’t give us any interesting work to do, they just entangle us in a hazy gauze of vague concepts.

III. Modern Synthetic Theory (Mendelism + Darwinism)

A. The Mechanism of Inheritance

Around the turn of the 20th Century, Hugo De Vries, William Bateson, and other experimenters with heredity, rediscovered Mendel’s principles of particulate inheritance, and founded the modern science of genetics. This ushered in a period of intense confusion and controversy as biologists tried to understand how the new genetics fit with natural selection and Darwin’s general ideas about evolution. Bateson believed that the two were incompatible because genes caused large effects rather than the small ones that Darwin had postulated for the elementary units of inheritance. This all turned out to be a red herring; the early genetical experiments focused on genes with large effects, such as those that caused tall and short pea plants in Mendel’s classic experiments, because these were easy to study. As it turned out, most traits of evolutionary interest are underlain by many genetic variants, each of which does have a small effect.

It took more than 30 years, from 1900 until about 1936, before genetics and evolution were united in the Synthetic Theory. In part, the problem was the personal antagonisms between important actors. For example, among the important Darwinians were Karl Pearson and Ronald A. Fisher⁴. Pearson was hostile to genetics. He dismissed the younger Fisher’s paper showing how easily genetics could be reconciled with natural selection with an insulting letter, and used his influence to ensure that Fisher could not get a university post. Fisher was “exiled” to work at Rothamstead Agricultural Experiment Station in England, and did not get a university professorship until Pearson retired. (While at Rothamstead, Fisher invented a large fraction of modern statistics to analyze the experiments conducted there.) Eventually field biologists like Theodosius Dobzhansky, Ernst Mayr, and Ledyard Stebbins had a hand in a second Darwinian revolution 1930-50. One thing must be said about this episode. Science does not progress because scientists always act like mature adults or

4. You may remember Fisher and Pearson from your statistics classes. Sir Ronald A. Fisher (1890-1962) made major contributions to 20th century statistics, research methodology, and evolutionary theory. Pearson, of course, you remember from the Pearson product-moment correlation coefficient (more commonly referred to as Pearson’s *r*).

nice people! See Provine's (1971) history.

In the Synthesis, genes replace earlier vague and erroneous ideas about the nature of heritable variation. Modern genetics gives us an increasingly detailed picture of the structure of the inheritance system on which selection works. The earliest accomplishment was to show that individuals of many species are diploid (carry two copies of each gene), that genes occur in blocks called chromosomes, and that sexual reproduction resorts the parental contributions each generation in sexual species through independent assortment of chromosomes and crossing over within chromosomes. Later, Watson and Crick in the 1950's showed that genes are DNA, and initiated the field of molecular genetics that now gives us a huge amount of detail about the structure of the genetic inheritance system.

Genetics also furnished the tools to study evolution in detail. Actual changes in gene frequencies could be studied in the field and lab as selection regimes changed.

B. Forces of Evolution

After the Synthesis evolution was mainly studied with models assuming various kinds of structure in the genetic inheritance system. Models of inheritance come in two common types, mendelian (discrete) and quantitative. *Mendelian models* mimic the actual properties of the genetic inheritance system. We imagine that particles with certain effects are being transmitted, as in Mendel's famous tall and short pea plants with wrinkled and smooth seeds. We suppose that there are a countable number of genes underlying the trait we are interested in, each associated with a phenotypic effect. This approach works well for eye color and blood type in humans because there are only a few genes with quite distinctive effects influencing phenotypes in these traits. However, most real traits are underlain by many genes, each with a small effect. Mendel's peas notwithstanding, height is commonly a *quantitative trait*. There are so many genes affecting this trait in most organisms that we cannot recognize any specific one of them in phenotypes except in pathological examples of dwarfism and gigantism. Height varies continuously without jumps or gaps between types. In such cases, we can deal with the mean value of the trait in the population and the measured variation. Some portion of the variation is transmitted from parents to offspring (a statistic called the *heritability* measures the degree to which this is so), and some portion will be composed of environmental variation.

Geneticists discovered new evolutionary mechanisms, and redefined natural selection, that change gene frequencies over time. Thus *natural selection* increases the frequency of genes "appropriate" for a given environment via differential mortality and fertility of variants produced by mutation (ultimately). *Mutation*, resulting from random changes in DNA structure due to environmental mutagens and other copying errors, increases varia-

tion. *Drift*, which results in random changes in gene frequency due to sampling errors, increases as populations become small. It leads to reduced variation within populations, and increased variation between populations. Other important forces include *recombination* (the shuffling of genotypes each generation due to recombination in sexually reproducing species), *migration* (the movement of individuals with different genotypes from one environment to another), and *sexual selection* (resulting from competition for mates or choices among potential mates). We can get along without a detailed discussion of these for the time being. Darwin also thought that the inheritance of acquired variation was an important evolutionary force. The genetic system does not allow for this mechanism; Darwin made a number of mistakes about evolutionary processes because his theory of inheritance was wrong.

C. Three Kinds of Selective Situations

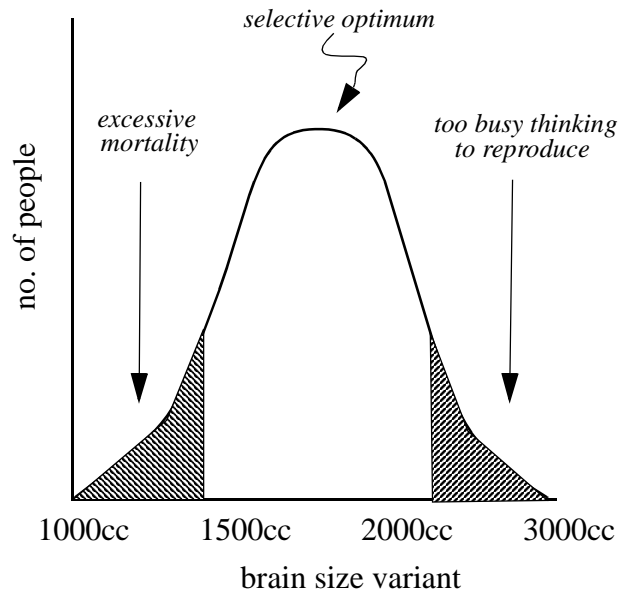
One form of selection, stabilizing selection, actually prevents evolution by random factors. Stabilizing selection works against both extremes in a population; i.e., it tends to keep a trait from becoming either too great or too small. Stabilizing selection is often thought to be very common. In other words, most populations, most of the time, are thought to be near selective optima. Human brain size provides a hypothetical example. See figure 9-2a. It doesn't seem to have increased for perhaps the last 100,000 years. We don't know exactly what forces balance the disadvantages of larger and smaller brains. It does seem to require considerable intelligence to manage the complexity of human technology, social organization, and symbolic culture. This must put some sort of selection against small brains, although the correlation between sheer brain size and intelligence is weak over the normal human range of brain size. People with very large brains (and their mothers) have difficulties at birth. Brains are physiologically costly and fragile organs. Perhaps big-brained people are more susceptible to the divergent claims of cultural as opposed to genetic fitness (see Chapters 12, 15, and 16).

Evolution occurs when directional selection acts against one tail of a distribution pushing the population toward a new optimum. Directional selection tends to push the distribution of a favored trait in a particular direction. In the example shown in figure 9-2b, *Australopithecines* had bodies that were similar in size to modern humans but had brains about the size of a chimpanzee (500 cc). For some reason, selection favored larger brains, and over the last 2 million years or so large-brained humans arose from the small-brained ancestral type (see Chapter 25).

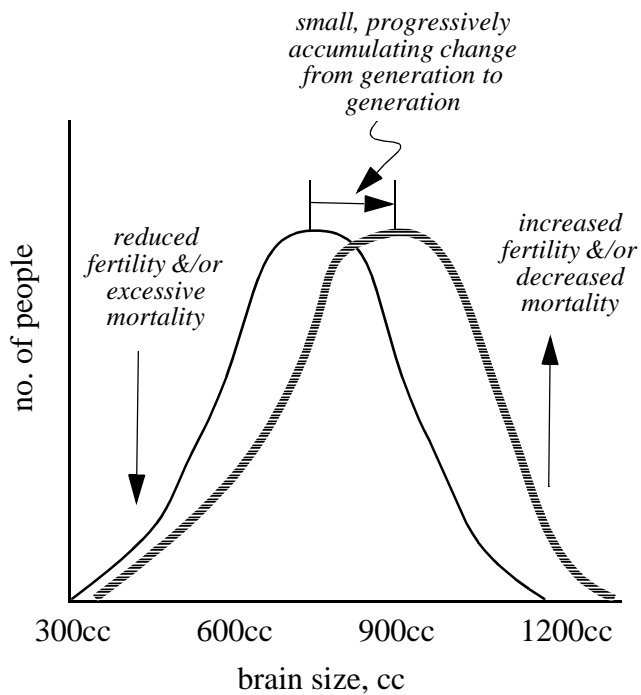
Directional selection can be very rapid on the geological time scale. Geneticists have selected corn for high oil content, for example, and gotten responses under strong selection

Figures 9-2 a & b. A comparison of the effects of stabilizing and progressive (directional) selection on human brain size. Note that stabilizing selection acts against both extremes of the population distribution while progressive (directional) selection acts against only one extreme.

(a) Stabilizing Selection:
The *Homo sapiens* case



(b) Directional Selection:
The *Australopithecine* case



of about 1/3 of a standard deviation per generation for many generations in a row (this is a quite highly heritable trait). If the standard deviation of Australopithecine brain size was 50 cc, this means a size increase of 17 cc per generation. At that rate, it would take about 60 generations to reach modern brain sizes, or about 1,500 years. Since the actual evolution of large brains took much longer, directional selection is probably very weak most of the time in nature.

It is interesting to note that in Darwin's time the age of the earth was thought to be relatively short, although little scientific opinion held it to be as short as Bishop Ussher's calculation of 4,004 years since Genesis quoted in the chapter epigraph. Darwin had to worry whether the earth had been around long enough for his relatively slow process to have "created" the diversity and complexity of life. Darwin figured he needed about 400 million years to fit in all the organic evolution in the fossil record. Lord Kelvin used physical calculations to compute the age of the earth in the 1860s. He supposed that it started out at the temperature of the sun, and estimated how long it would take to cool to present temperatures. He concluded the earth might be from a few million to about a 100 million years old, and his best guess was 25 million years. The actual figures for the length of the fossil record are about 550 millions years, and the Earth formed from solar nebula about 4.5 billion years ago. Kelvin disliked Darwinism, and used his figure to attack his ideas. His calculations were wrong because he knew nothing of radioactive elements, whose decay heats the interior of the earth. Now we know the earth is many times older than even the oldest 19th century estimate, and the embarrassment is, if anything, reversed. Natural selection in the short run is too powerful to account for why evolution in the long run proceeds so slowly. The time since life began (3.5 billion years ago) is long even compared to Darwin's estimate, and Natural Selection can work perhaps even faster than he guessed. We will return to the problems of macroevolutionary limitations on the rate of evolution in Chapter 24.

Evolutionary biologists used to suppose that weak selection was the norm in nature. John Endler (1986) has recently upset this old truism. He finds that field studies show quite a wide range of strengths of selection, but include many examples of strong directional selection. However, these are short term, local studies. Perhaps we can rescue the old generalization by imagining a lot of back-and-forth selection of some strength in different times and places, with the average result being rather weak. In any event, even very weak selection can lead to great changes *on a time scale that is short by the standards of geological time*. Natural selection is thus a potent force of nature, on a par with the geological forces

that move the continents. Biological processes like photosynthesis, “built” by natural selection, are extremely important, along with purely geophysical forces like seafloor spreading, in the evolution of the earth’s crust. Thus it seems that stabilizing selection must normally be more important than progressive selection.

Other possible kinds of selective regimes exist, such as frequency dependent selection and sexual selection. we will come to these in later Chapters.

IV. Organizational Levels and Natural Selection

Natural selection is a maximizing or optimizing principle. Because natural selection tends to increase the mean reproductive fitness of a population over evolutionary time, we can say that it works to “maximize” the net reproductive output. Because the implications of this are frequently misinterpreted, one has to be very careful to understand what it is that tends to be maximized. Let us consider evolution at three levels, genes, individuals, and groups of individuals.

Some argue that individual genes can maximize their reproductive success. The best known proponent of this view is Richard Dawkins who, in his book *The Selfish Gene*, pushes the argument for selfishly motivated genes about as far as it can go. However, because genes are packaged into individuals, and transmitted as packages between generations, it is dangerous (even from the gene’s point of view) to be too selfish. For example, a selfish gene like one that causes cancer, that optimizes its own spread at the expense of others, is ultimately selected against, at least if the cancer victim is young enough to have its production of offspring reduced. (Most cancer victims in fact are elderly. We return to the theory of why the old are especially prone to disease in Chapter 21 on disease.) Thus the conventional view is that genes do not normally compete against each other for fitness within an individual organism.

Others assert that selection at the individual level is of paramount importance--indeed this is the current majority opinion. Adaptations are the fitness-maximizing attributes of individuals. G. C. Williams (1966) made a very influential argument to this effect. There is a small caveat under the term “inclusive fitness”, which allows for the fitness help lone individuals can give their genetic relatives (see Chapter 14). The strength of this basic dogma is based on the recognition that because individuals are the basic phenotypic and reproductive units selfish individuals can very conceivably increase their reproductive success in competition with other individuals in the population. A solitary individual can carry on with the fitness enhancing business of surviving and reproduction much more independently than the solitary cell or individual gene.

A third position argues that the fitness of populations, species, or communities can be subject to selection. British biologist V.C. Wynne Edwards (1962) claimed that animals commonly sacrifice their own reproductive success, in situations in which selfishness would put the group in danger. He believed that, to some approximation, individual animals were as dependent upon the group for survival and reproduction as solitary genes are upon whole individual phenotypes. This book gave rise to the “group selection controversy” which over time was resolved with the recognition that group selection is theoretically possible if there is: (1) high variability between groups; (2) low variability within groups; and (3) substantial group extinction rates, or differential group success rates. The problem is that migration between groups will tend to spread selfish individuals into unselfish groups if any such exist. Within a group of unselfish individuals, selfish ones will have a special advantage. They can take advantage of the altruists⁵, without bearing the costs of altruism themselves.

The common conclusion is that selection usually favors individual advantage, rather than the interest of genes or of groups. Genes are selected to cooperate to make a reproductively effective individual, but individuals are not nearly so likely to be selected to make a successful group by sacrificing their own advantage for the advantage of the group. Of course, individuals who strive to survive and reproduce as individuals also tend to perpetuate their group. The rub comes when it might be useful for individuals to cooperate to reproduce the group as a functional entity the way genes collaborate to produce a body that then jointly reproduces all the genes in the genome. Nevertheless there is a recognition that group selection is not impossible, and that there may be conditions in which group selection is quite strong relative to individual selection. This is particularly the case with humans, with their high levels of cooperation. Indeed some biologists who are otherwise persuaded that group selection is unimportant see a possible role for it in humans. We will return to this topic in Chapter 14. In the meantime, beware of the picture of animals cooperating in their collective interest. This theme is common in TV nature films and childrens’ books. It sets modern evolutionary biologists’ teeth on edge!

V. Many Complexities

As was mentioned already, evolution by natural selection can get very complicated when we begin to attend to details and raises some intriguing puzzles. Even so it is amazing how far you can get by patiently and carefully applying simple models. Remember, it is also

5. *Altruism* is defined as behavior by an individual organism that is either not beneficial or is harmful to itself, but that benefits the survival of others.

these peculiarities that often give the best evidence about the operation of natural selection. Lots of processes--such as a Divine Creator--might produce perfect adaptations. But what process besides selection could do some of the following things:

Sex ratio is a phenomenon that provides a wonderful Darwinian puzzle: Why do most species have such an excess of males? In most animals, the ratio of the sexes is 50:50, or close to that number. As anyone who has had experience with livestock raising is aware, the large number of males in a population is far more than are needed. The rule for beef bulls on the range is that one bull per 20 cows is perfectly sufficient. Why doesn't selection normally adjust the sex ratio to something like 1:20? It seems like a much smaller portion of males would be more adaptive; cattlemen and dairymen certainly think so. (A similar point has been made by a number of feminists in recent years!)

R. A. Fisher worked out the basic selective logic. Suppose there are two sexes, and both are necessary for reproduction. This pattern characterizes many, but by no means all, organisms. Each offspring will have one male and one female parent. Now, suppose one sex is rare, say males. Then, *the average male will have many more offspring than the average female.* (As animal breeders say, your bull is half your herd.) If there is any heritable variation for sex determination the rare sex will have more reproductive success than the common one. The two sexes will be equally fit only when the sex ratio is 50:50. Once animals or plants are committed to sexual reproduction they will suffer the burden of excessive males.

The male excess leads to another question: Why have sexual reproduction at all? Consider the problem from the female's point of view. In most species, the female contributes almost everything to the offspring (egg mass, parental care, etc.). Yet she accepts sperm in sexual reproduction and cuts the number of genes she transmits to the next generation in half. Why don't females always reproduce asexually, so as to double their fitness? There actually are many species that can reproduce asexually, so switching is not a big biological problem. Why do females tolerate males in the world at all? This is one of the "hot topics" of the last dozen or so years, and there is not yet a universally accepted answer⁶. The most basic reason seems to be that sexual reproduction reassorts genes, creating variable offspring. Individuals with variation are perhaps more likely to resist disease (see Chapter 21). Females may be able to take advantage of male competition to pick fathers with good genes on behalf of their kids (see Chapter 15). Populations with recombination

6. Lynn Margulis, (perhaps one of the most creative biological scientists of this generation) and her son, Dorian Sagan, have published an interesting and accessible book on this topic entitled *Mystery Dance: on the evolution of human sexuality* (1991).

can respond more rapidly to variable environments, because favorable mutations can be brought together to create especially superior types. This last mechanism requires a bit of group selection to work; sexual populations would out-evolve asexual ones, even if sex was an individual fitness disadvantage for females.

Here is a puzzle for you to try your hand at related to the sex ratio question. The y sex determining chromosome is transmitted only by males in mammals (females in birds). Mitochondria are transmitted only by females. Both of these structures contain a little DNA, but much less than a regular chromosome. What would happen if a mutation favoring alteration of the sex ratio appeared on one of these structures? Can you give a selective reason why these structures contain so little DNA compared to the regular genome? The famous evolutionist W. D. Hamilton (1967) wrote a nice paper outlining the simple selective logic here about 20 years ago. Hint: think in terms of Dawkins' selfish genes. What would you do about the sex ratio to maximize your fitness if you were a selfish gene on a y chromosome?

VI. Conclusion

Darwin's proposed mechanisms of natural selection and the inheritance of acquired variation gave biologists interesting scientific hypotheses to explain the diversity, adaptedness and evolutionary history of the earth's biota. It made these topics for real scientific investigation, as opposed to support for metaphysical notions like a divine creator. Some of Darwin's ideas turn out to be wrong; the inheritance of acquired variation mechanism turns out to be unimportant in the genetic system of inheritance, but that is the work scientific hypotheses do. In stimulating critical empirical inquiry, some ideas fall by the wayside. As far as genetically transmitted adaptations are concerned, only natural selection *causes* adaptation. Other processes, for example mutation, cause evolution in the sense of a change in a population through time, but only natural selection "guides" or "directs" this change in ways that create complex adaptations. Since the ecological study of contemporary organisms fundamentally involves their adaptations, ecology derives from evolution. Perhaps an even better way of stating it is that *ecological processes actually cause evolution.*..

**Ecological processes actually *cause* evolution.
Selection is just everyday ecological processes,
repeated for many generations.**

Natural selection is a proper materialistic explanation for evolutionary change and adaptation that can be investigated in the field and lab. In this regard it is quite different from progressive evolutionary schemes, such as Steward's, which have no causal referents to investigate. There is just the evolutionary trajectory, which is what is to be explained; the only evidence for the progressive force is the pattern which is to be explained. The "theory" doesn't specify any independent observations that would help us decide whether there is a progressive force or not. This is circular reasoning: a pattern cannot explain itself! Typical progressive evolution theories are thus bankrupt as causal explanations on purely logical grounds.

In coming chapters, it will be important for us to take a step back from the model of selection itself to the methodological principle that lies behind it, population thinking. By paying close attention to individual variation within populations and the propagation of this variation through time, evolutionary biologists have come to understand a lot about organic evolution. In the human case, much individual variation is cultural, and cultural variation obeys "laws" of inheritance quite unlike Mendel's, but the trick of focusing attention on the plain everyday events of individual lives pays the same scientific dividends. This is the method we will adopt in the next few chapters.

VII. Bibliographic notes

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