

The Five Forces Behind Human Evolution

Five different forces have influenced human evolution: *natural selection*, *random genetic drift*, *mutation*, *population mating structure*, and *culture*. All evolutionary biologists agree on the first three of these forces, although there have been disputes at times about the relative importance of each force. The fourth and fifth forces are new in the sense that they are not explicated in more traditional texts. This is not an attempt to develop a “new” theory of human evolution. Instead, the forces of population mating structure and culture are arbitrary categorizations used to organize several different phenomena of human evolution. Scientists agree on the phenomena themselves, although there not as accepted way of organizing them.

Each of the five forces will be explained in turn. This is a risky approach because it can lead to the false impression that the five operate quite distinctly and differently from each other. In fact there are important interactions among these forces, a topic that will be discussed at the end of this chapter.

Natural Selection

Natural selection is defined as *the differential reproduction of organisms as a function of heritable traits that influence adaptation to the environment*. There are three essential components to this definition—(1) differential reproduction, (2) heritable traits, and (3) adaptation to the environment.

Darwin noted that most species reproduce at a rate that, if unchecked, would lead to exponential population growth. However, such growth is seldom realized in nature because many organisms fail to reproduce. Darwin reasoned that if this differential reproduction was associated with adaptation to an environmental niche and if the adaptive traits were transmitted to a subsequent generation, then the physical and behavioral traits of a species will change over time in the direction of better adaptation.

Genetic variation fuels natural selection and genetic inheritance transmits adaptive traits from one generation to the next. If all the members of a species were genetically identical, then there would be no genetic variation and hence no natural selection. The organisms in this species could still differentially reproduce as a function of their adaptation, but they would transmit the same genes as those who failed to reproduce.

Biologists index natural selection by *reproductive fitness*, often abbreviated as just *fitness*. Reproductive fitness can be measured in one of two ways. *Absolute reproductive fitness* may be defined as the raw number of gene copies or raw number of offspring transmitted to the subsequent generation. It may be expressed in terms of individuals (e.g., George has three children), phenotypes (e.g., on average the red colored birds produce 3.2 fledglings), or genotypes (e.g., on average genotype *Aa* has 2.4 offspring). For sexually reproducing diploid¹ species like us humans, a convenient way to calculate absolute fitness is to count the number of children and divide by 2. For example, someone with 2 children would have an absolute fitness of 1.0, indicating that the person has left one copy of each allele to the next generation.

¹ Diploid refers to a species that has two gene copies in its genome. Some plants are tetraploid, meaning that they have four gene copies.

The second way of measuring reproductive fitness is *relative reproductive fitness*. Relative fitness is simply the absolute fitness of an individual, phenotype, or genotype divided by the absolute fitness of a reference individual, phenotype, or genotype. For example, suppose that the absolute fitnesses of genotypes *aa*, *Aa*, and *AA* are respectively 1.8, 2.4, and 2.5. If *AA* is the reference genotype, then the relative fitness of *aa* is $1.8/2.5 = .72$, the relative fitness of *Aa* is $2.4/2.5 = .96$, and the relative fitness of *AA* is $2.5/2.5 = 1.0$. It is customary, but not necessary, to express the relative fitness of genotypes in terms of the most fit genotype.

It is crucial to distinguish reproductive fitness from desirability. The fastest, the most agile, the longest lived, and the most intelligent do not need to be the “fittest” in a reproductive sense. Fitness is defined solely and exclusively in terms of gene copies left to the subsequent generations. There is no mention of social values in this definition. A genotype that promotes longevity is more fit than one leading to a shorter lifespan only if leaves more copies of itself.

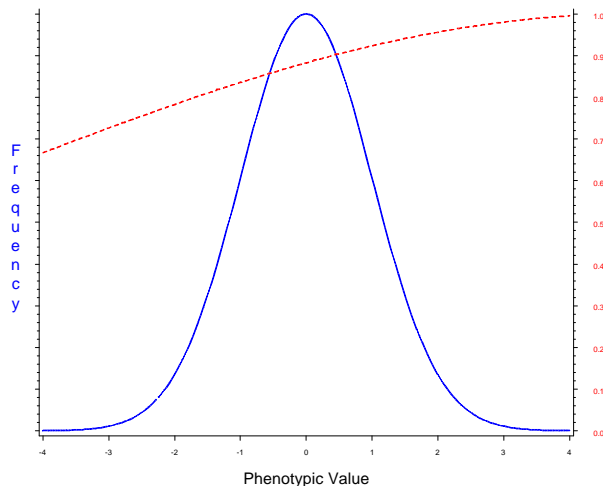
Similarly, fitness is correlated with survival but it is not synonymous with survival. Unfortunately, popular culture has equated natural selection with the term “survival of the fittest,”² implying a tooth and claw struggle in the jungle. Natural selection often involves subtle mechanisms, some of which may actually end in the organisms death! After a perilous journey from salt water to the headwaters of a stream, salmon reproduce and then die. The male preying mantis is literally devoured by the female while in the very act of copulation.

An important part of fitness and natural selection is competition with other *conspicifics* (other members of the same species). The environment for an organism is much more than physical surroundings. It also includes the behavior of conspecifics. Hence, reproductive fitness for many organisms is defined less in terms of the organisms physical capacity to reproduce and more in terms of being able to outreproduce other conspecifics. A male gorilla, for example, can survive, be healthy, and be physiologically capable of producing many offspring. His main problem with reproductive fitness lies with other males. Unless he can entice fertile females away from an established male, his reproductive fitness will be low.

The Three Modes of Natural Selection

For continuous traits, there are three modes of natural selection—*directional*, *stabilizing*, and *disruptive*. In directional selection, fitness increases with trait value. An example of directional selection is presented in Figure X.X.

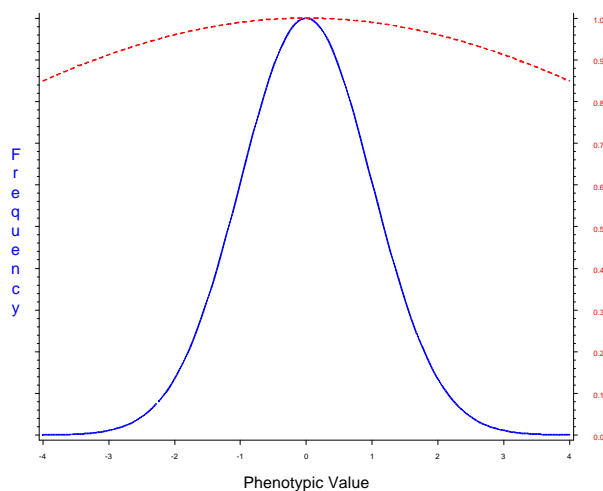
² The actual term was coined by the philosopher Herbert Spencer not by Charles Darwin.



Here, the phenotype has a normal distribution (solid blue line). The fitness function (aka *selection function*) is given by the dashed red line and the relative fitness is expressed on the right hand vertical scale. Fitness is lower for low values of the phenotype and becomes progressively larger for larger phenotypic values. After several generations of selection, the mean of the distribution will shift towards the right, in the direction of increased fitness.

Most human evolutionists suspect that human brain size underwent directional selection. About 4 million years ago (mya), the brain size of our probable ancestors, the *Australopithecines*, was around 450 cc (cubic centimeters), only slightly larger than that of a contemporary chimpanzee. Around 2 mya, brain size almost doubled with the emergence of *homo habilis* and later *homo erectus*. Brain size increased so that modern humans average between 1300 and 1400 cc.

The second mode of natural selection is *stabilizing selection*. Here, trait values that are close to average have the highest fitness and fitness decreases as one moves away from the mean (Figure X.X).

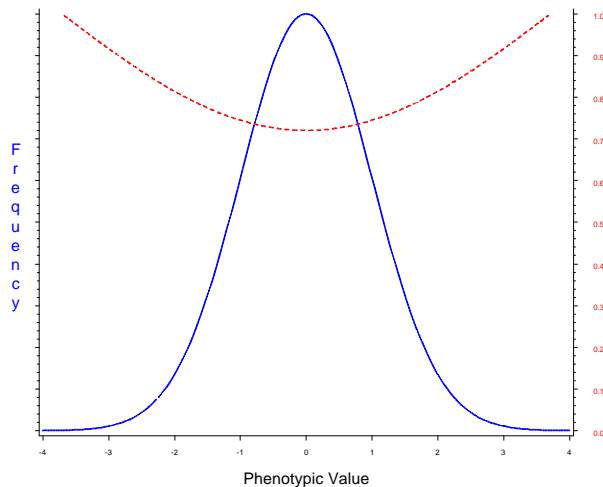


In the popular mind, natural selection is almost always equated with directional selection. Yet most biologists suspect that stabilizing selection is the most frequent mode of natural

selection. Most species are well adapted to their ecological niches—otherwise, they would have gone extinct many eons ago—so being somewhere around the average is more likely to be beneficial than having an extreme phenotype. Stabilizing selection will not change the mean of a distribution but it may reduce the genetic variance over time.

Human birth weight is a classic example of stabilizing selection. Before modern medical interventions, low birth weight neonates had high mortality. Similarly, neonates much larger than average posed serious problems for their mothers and themselves. In terms of infant survival, it was preferable to be near the mean rather than at the extremes.

The third mode of natural selection is *disruptive selection* (Figure X.X). Here phenotypes close to the average have reduced fitness compared to phenotypes at the extremes. Disruptive selection appears to be the rarest form of natural selection and, indeed, there are few well-documented cases of it. There does not appear to be a good example of disruptive selection in human evolution. Despite its rarity, however, disruptive selection may be very important for the emergence of species. After suitable time, disruptive selection can lead to bimodal distributions which might eventually lead to different species.



The Effect of Natural Selection

The ultimate effect of natural selection is to *change allele frequencies*. It operates only on what is already present in the genome of a species and makes some alleles (and combinations of alleles) more frequent and other less frequent. Nevertheless, the appearance, anatomy, and physiology of a species may change over time simply because some alleles become rare after lengthy natural selection. Programs in artificial selection where humans control the selection process are the best illustrations of the tremendous genetic variability hidden in a species' genome. All contemporary strains of dogs had their origin in the wolf. The fact that dogs come in all sizes (from chihuahua to wolfhounds), color patterns (dalmations to golden retrievers), and temperaments (high strung terriers to phlegmatic basset hounds) is due to deliberate selection of rare allelic combinations in the wolf genome³. Yet despite these differences, many dogs can still reproduce with wolves.

³ Of course, a few mutations here and there have probably helped along the way.

Genetic Drift

Genetic drift is defined *as the change in allele frequencies over time due to chance and chance alone*. To illustrate drift, imagine the change over time in allele *A* in a small isolated population of 10 individuals. Suppose that the frequency of *A* is .50 and the frequency of the other allele, *a*, is also .50. Hence, with 10 individuals, there will be 20 alleles—10 *A* alleles and 10 *a* alleles. In transmitting alleles to the next generation, the probability of transmitting *A* is the same probability as flipping a fair coin 20 times and getting 10 heads and 10 tails. This is the most likely of all possible outcomes, but the probability of this outcome is only .17; the probability of an outcome *other than* an even 50/50 split is $1 - .17 = .83^4$.

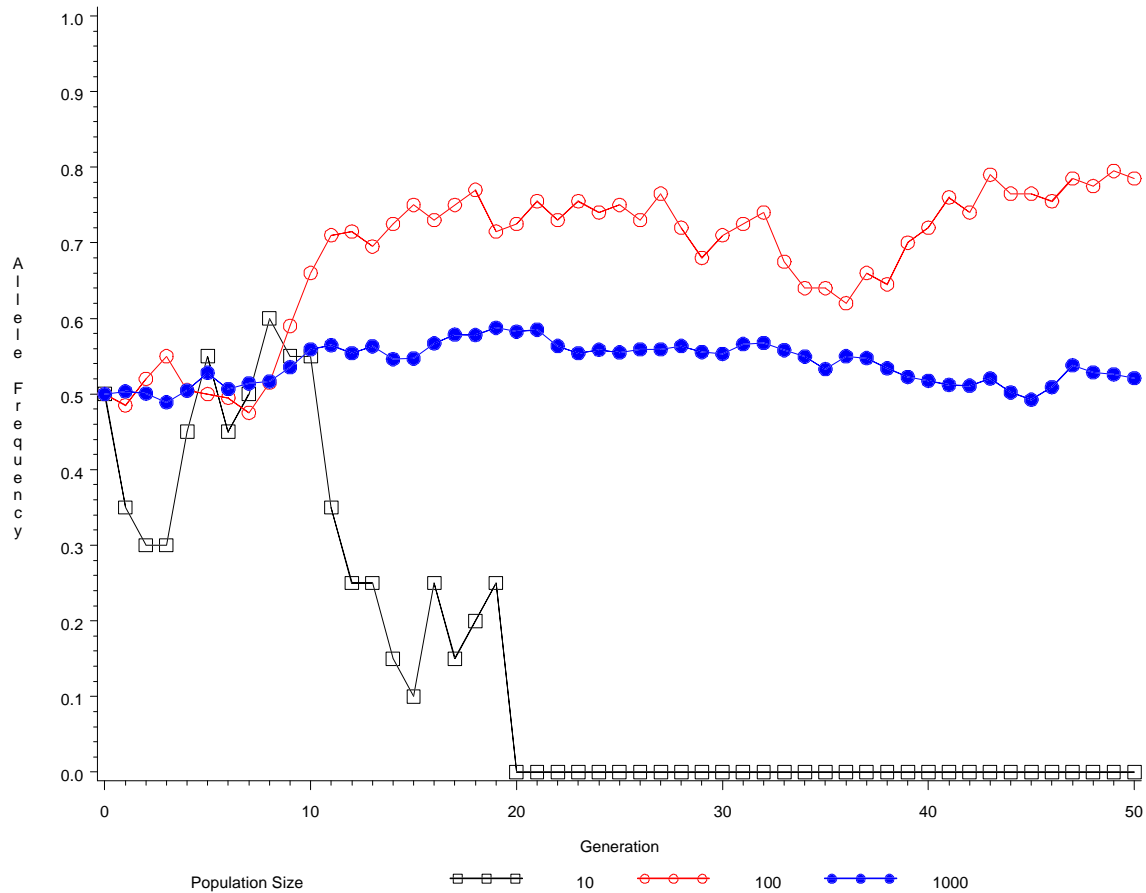
Suppose that we actually flipped the fair coin and ended up with 12 heads (or *A* alleles) and 8 tails (or *a* alleles). The frequency of *A* is now .60. The probability of transmitting allele *A* to the next generation is equal to flipping a *biased* coin that has a 60% chance of heads and a 40% chance of tails. In 20 flips of this biased coin, the most likely outcome is 12 heads and 8 tails, but once again the probability of this single event is only .18. Again, we are more likely to experience an outcome *other than* a 60/40 split.

Suppose that we flipped this biased coin and ended up with 13 heads and 7 tails. In this generation, the frequency of *A* is .65. In the next generation, the probability of transmitting *A* is equal to the flip of yet another biased coin, but one that has a probability of heads being .65.

You can see how chance changes in allele frequencies in one generation alter the probability of transmitting the allele to the next generation. The process of genetic drift is equivalent to tossing biased coins in each generation. The degree of bias is determined by the allele frequency in that generation. As a result, a plot of the frequency of allele *A* by generation should show that *A* usually changes in frequency from one generation to the next.

Figure X.X illustrates the principle of genetic drift in three populations—one of size 10, one of size 100, and one of size 1,000. There are two salient issues about drift illustrated in this Figure. First, note how the line for the smallest population “bounces around” more than that for the population of size 100 which in turn is more variable than the line for the largest population. This phenomenon is due to the fact *that the most important factor influencing genetic drift is population size*. Drift will be greater in smaller populations. As population size increases, the effects of drift diminish.

⁴ For the mathematically inclined, the probability of any outcome follows a binomial distribution.



The second important issue in Figure X.X involves the line for the smallest population. At generation 19, there were only 5 *A* alleles and 15 *a* alleles, so the probability of transmitting an *A* allele is $5/20 = .25$. By dumb luck, no *A* alleles were transmitted to the 20th generation. Once this occurs, allele *A* is lost from the population. Geneticists call this phenomenon *fixation*. In this case allele *a* is fixed in the population. The only way to get allele *A* back is by mutation or immigration of an individual with *A* into the population.

Whenever the population size is small, the ultimate effect of drift will be to fix alleles. That is, if the process of drift continues over a large number of generations, then eventually one of the two alleles, *A* or *a*, will become fixed. Which of the two alleles becomes fixed is a matter of chance.

The role of drift in evolution has been hotly debated. If we find a polymorphism in a gene among contemporary humans, does that polymorphism reflect the effects of drift, the effects of natural selection, or some combination of drift and natural selection? Because we lack a time machine to travel back and sample DNA, there is no easy answer to the question. Geneticists weigh substantive issues (“what is the gene product for?”) and educated guesswork about early human evolution (“how useful was this gene product in the millenia when humans were hunter-gatherers?”) to arrive at a common sense solution. Clearly, the genes responsible for the development of the eye and the neural circuitry and mental computations that result in vision were heavily influenced by natural

selection. But the same may not apply to those polymorphisms that influence contemporary myopia (near sightedness).

Mutation

Mutation is defined as *an error in copying the DNA*. There are several different ways to classify mutations. Here, we use two different classifications, the first depending upon the type of cell and the second on the amount of DNA. In terms of the type of human cells affected by mutation, geneticists distinguish *somatic mutations* from *germinal mutations*. Somatic mutations influence somatic cells—i.e., all cells of the body other than those that directly produce the gametes (sperm and egg). Germinal mutations affect the cells that directly turn into the gametes.

Because there are many more somatic than germinal cells in us humans, the vast majority of detectable mutations are somatic. Somatic mutations may have no discernible effect on an organism when, for example, they take place in a unused section of DNA, or they can influence the physiology of the cell (and the cell's daughter cells) when they occur in a coding region or a regulatory region of DNA. In some cases, somatic mutations result in abnormal cell growth, ranging from benign moles to malignant carcinomas. Although somatic mutations can affect the reproductive fitness of the organism experiencing them, they cannot be passed to offspring.

Germinal mutations, on the other hand, are the life force behind evolution. The ultimate effect of mutation is to *introduce new genetic material*. Without germinal mutation, there would be no genetic variation, no natural selection, no genetic drift, and hence, no evolution. According to contemporary evolutionary theory and modern reproductive biology, germinal mutations are the only method of introducing *new alleles* and *new arrangements of DNA* into a species. All of the other forces of evolution change allele and/or genotypic frequencies; they do not introduce new genetic material.

The amount of genetic material affected by mutation can range from a single nucleotide (as in the sickle cell allele for β hemoglobin) to a whole chromosome (as in most cases of Down's syndrome). Mutations that influence a single nucleotide are called *point mutations* and have generated an important class of polymorphisms termed SNPs (for Single Nucleotide Polymorphisms). Here, we will lump all mutations that influence more than a single nucleotide into a single category and term them *gross mutations*. Mutations can result in the substitution of one nucleotide for another, delete one or more nucleotides, insert a series of nucleotides, or even duplicate a series of nucleotides.

The effect of a mutation depends on where the mutation occurs in the genome. If the mutation occurs in a section of DNA that does not contain code for a peptide chain, does not regulate the production of a peptide chain, does not influence subsequent replication of the DNA molecule etc., then it may have no influence on the organism or the organism's progeny. Some mutations that actually occur in coding regions may also have no effect. For example, a mutation that changes the DNA codon from AAA to AAG will still result in the amino acid phenylalanine being placed in the peptide chain. Mutations that do not influence the ultimate reproductive fitness of an organism are called *neutral mutations* and give rise to what are called *neutral alleles*. Although neutral alleles may not be important for the evolutionary change, they are of extreme important to geneticists tracing the evolution of populations and species. For example, if two human populations

diverged recently, the frequency of the neutral alleles should be similar in the two groups. But if they separated a long time ago, then the allelic frequencies of neutral alleles should differ. Similarly, the older human populations should have accumulated more neutral alleles than populations that have more recently fissioned from one another. Hence, genetic similarity as well as genetic variation on neutral alleles can assist in reconstructing human evolutionary trees.

The most likely effect of a mutation that actually has an effect on a phenotype is to reduce fitness. Proteins and enzymes have been honed and shaped by generations of natural selection to make sure that they work appropriately for the organism. An abrupt, random change to a protein or enzyme is akin to tossing an extra gear into a finely tuned motor or capriciously rearranging a circuit on a computer chip. Most such random acts harm rather than help functioning. If the affected allele is recessive, the loss of functioning is not critical. In all likelihood, the other allele will produce a functioning protein or enzyme. Consequently, deleterious mutations can build up for recessive alleles. This is probably the reason why several hundred different deleterious alleles have been identified for any single recessive disorder.

Occasionally, however, mutations can be beneficial and increase in fitness. On the primate X chromosome, the gene for green retinal cone pigment is located quite close to the locus for red cone pigment. It is suspected that at one time there was only one gene, but a gross mutation resulted in its duplication. Further mutations altered the gene product in the duplicated locus (or perhaps the original one) so that it responded to light of a different wavelength. Natural selection favored the resulting increase in color discrimination and ultimately gave us the color vision that we primates have today.

Mutations are both rare and common depending on how they are typed. We have seen that gross chromosomal mutations are quite common in fertilizations, but the majority of embryos die in utero. Mutation rates for a single allele are very difficult to quantify. Those that occur in coding regions for dominant alleles that influence an organism's prenatal development may suffer much the same fate as chromosomal anomalies and hence be undercounted. Most geneticists, however, agree that mutation rate for an allele is rare and is on the order of one mutation for several thousand or several tens of thousands of gametes.

Population Mating Structure (aka Population Structure)

Although the concept of population mating structure is implied in all texts on evolution, the actual term *population mating structure* is seldom encountered. Here, population mating structure is defined as all those factors—physical, temporal, anatomical/physiological, and behavior—that result in nonrandom mating among members of a species. To understand this concept, we must first understand the meaning of a population. A population is *a group of individuals who belong to the same species, have a characteristic set of allele frequencies, usually reside in the same geographic area, and mate among themselves*. Some examples may help to clarify a population and how population structure influences evolution.

Marmots are a genus of rodent and several species are found in only in alpine ecologies (i.e., areas far above sea level). Imagine two populations of marmots in the Rocky Mountains, one group inhabiting the alpine region of Long's Peak in Rocky

Mountain National Park, the other group residing on neighboring Meeker's Peak. In order for a marmot born on Long's Peak to mate with a marmot living on Meeker's Peak, the first marmot must leave the alpine region of Long's Peak, traverse a valley, and then climb into the alpine region of Meeker's Peak. Although this may actually occur, it happens rarely. Most Long's Peak marmots are born on Long's Peak, live their whole lives on Long's Peak, and mate with marmots who have been born and raised on Long's Peak. The same occurs with marmots on Meeker's Peak. In short, the marmots on Long's Peak are one population while the marmots on Meeker's Peak are another population. Hence, *geographical separation* of populations is a major factor influencing the population structure of a species.

In some cases, different populations may actually reside in the same geographical area. Mayflies spend two years living as nymphs in the bottom of lakes and streams before they metamorphose into winged insects, reproduce, and die. Imagine mayfly nymph Elmer who has just met the love of his life, mayfly nymph Esmeralda. Elmer could be the persistent suitor who wines and dines Esmeralda every night for a year. But if Elmer is scheduled to metamorphose in an odd year while Esmeralda is programmed to change in an even year, the two will never be able to mate. Consequently, even year mayflies are one population while odd year mayflies are another population, even though the two may physically reside next to each other.

Physical and temporal separation permit different populations to evolve in different ways. Imagine that an unusually large avalanche on Long's Peak that decimates the local marmot population. With lowered population size, genetic drift may be accentuated for a few generations and alter allele frequencies. Similarly, a drought in one year may deplete the number of hatching mayflies, again intensifying natural selection and accentuating the effects of drift.

Another factor in population structure is the *founder effect* which occurs when only a few members of a species colonize a new territory. The South American finches that originally colonized the Galapagos islands (and provided Charles Darwin with an excellent example of natural selection) were probably few in number. Genetic drift, the effects of natural selection in adapting to a new environment, and their geographical isolation contributed to their evolution.

The amount of *immigration and emigration* among populations also influences allele and genotypic frequencies—large amounts of immigration/emigration reduce the differences between local populations while small amounts of immigration/emigration permit the populations to diverge.

The evolution of human populations has been dramatically influenced by physical population structure. Even today, the physical separation of human populations maintains genetic diversity that would otherwise be absent. For example, people born and raised in the tropical rain forests of the Amazon basin are more likely to mate with other people born and raised in the same geographical area than they are with, say, North American Eskimos. Even within national boundaries, there are local populations. Someone living in Nebraska is more likely to mate with a fellow cornhusker than with a Yankee from Maine.

Psychological Effects on Population Mating Structure.

One of the clearest examples of psychological influences on population structure is the phenomenon of *mate preference*. Mate preference occurs when members of one sex prefer to mate with individuals with certain phenotypes in the opposite sex. Evolution occurs when these preferences result in *actual* differences in fitness—the preferred phenotype does, in fact, leave more gene copies than the less preferred phenotypes. One account of how the peacock's tail evolved invokes mate preferences. We have all witnessed the display of a male peacock during which he fans his long tail out into a semicircle of brightly colored “eyes.” The reason for the display, however, has nothing to do with human esthetics—the male wants to attract a female and mate with her. The story says that at some point in time, female peacocks developed a preference for males with large and colorful displays. Hence, they preferentially mated with males of these phenotypes. The males passed their genes on for large, colorful displays while the females passed their own genes on for *preference* for large, colorful displays. The process in which mate preferences in one sex result in differences in fitness for phenotypes of the opposite sex is called *sexual selection*⁵.

The evolutionary psychologist David Buss and his colleagues report strong similarity across cultures for mate preferences. When people are asked to rate or rank traits in terms of preference in a potential spouse, almost all place a “nice person” as the number one quality. Kindness, sincerity, and compassion consistently rate high. Intelligence is second[see Buss]. Not all traits, however, show cross cultural uniformity. The desirability for premarital chastity in a spouse varies considerably from one culture to another.

Buss's research clearly demonstrates that on average differing cultures agree on the traits that are desirable, neutral, or not desirable in a mate. But do people actually *do* what they *say*? And do (or did in the past) mate preferences result in *real* differences in fitness?

Here, the evidence is mixed. If males and females have similar mate preferences, if these preferences are strong, and if they are actually acted upon, then there should be strong spousal correlations for preferred traits. For example, if a woman—let us call her Diane—is a very nice person, highly intelligent and physically attractive, she should be a highly sought after potential spouse. Because many different men are pursuing Diane, she can have her own choice of a partner. Because Diane has her own mate preferences and has a choice of Tom, Dick, and Harry, she is likely to select a male who is also nice, smart, and good looking. A woman lacking Diane's attributes is less likely to attract someone like Diane's husband as she is a guy with her own level of mate desirability. As a consequence, we should find positive correlations among spouses for niceness, intelligence, and physical attractiveness.

⁵ Some regard sexual selection as different from natural selection, but the distinction is semantic and depends upon how one defines “environment.” If the female peacock's preference is considered part of the environment to which male peacocks must adapt, then sexual selection is a variant of natural selection. If one does not accept this definition of the male peacock's environment, then sexual selection may be considered a difference phenomenon from natural selection.

Empirically we do find significant spousal correlations for intelligence and cognitive ability⁶ (about .40) and for physical attraction (about .30). The problem comes with niceness. Virtually all the empirical data on spouses show that they are completely uncorrelated on personality traits! Consequently, contemporary personality inventories fail to tap the construct of “niceness,” and/or there is really no spousal correlation in the first place. Other evidence suggests that there is no spousal correlation.

When people are asked about mate preferences, almost all agree that “personality” is the most important issue before even intelligence and physical attractiveness. In addition to niceness, people also express preference for a mate who is happy, outgoing, active, and talkative. These are attributes of the dimension called extroversion or positive affect and no studies have reported significant spousal correlations for this trait. People also express preferences against having a mate who is anxious, high strung, and worrying. These attributes comprise the dimension of emotional stability, negative affect, or neuroticism, and once again, there is no spousal similarity for this trait. In addition, few people report that social and political attitudes have any importance on mate selection. Yet spousal correlations for social and political attitudes are higher than those for intelligence!

Hence, some aspects of mate preference might reflect discrepancies between self-report and actual behavior. People may think and even genuinely feel that an outgoing mate is more desirable than a shy one, but in the actual, day-to-day encounters with a specific person, the overt and concrete behaviors that constitute extroversion do not matter much in choosing a mate. Similarly, the failure to rate social and political attitudes highly may be due to our own underappreciation of these traits. We may think and even genuinely feel that they are arbitrary behaviors of little consequence, but when faced with a person whose attitudes are very different from our own, then attitudes become an issue in mate choice.

Culture

Culture is not unique to humans. Species of monkeys and apes—and quite possibly other mammals and some birds—can transmit information and behavior from one generation to the next. Examples include termite fishing in chimps, potato washing among macaques, and even swimming! But culture has influenced human evolution to a degree unprecedented in any other species⁷.

Medicine is a clear example. Our contemporary knowledge about public sanitation and antibiotics has dramatically reduced death and disability from infection, and it is ludicrous to believe that the engineering plans for an urban sewer or the chemical formula for erythromycin are encoded directly in our DNA. Instead, clever people developed new insights into the causes of infection transmitted this information horizontally to their colleagues and vertically to the next generation. And the result in all likelihood has been a reduction in the pressure from natural selection.

⁶ The spousal correlation for intelligence and cognitive ability in industrialized countries is also influenced by the social propinquity created by the educational system. For example, the social milieu of college makes it easier for college students to meet, date, and eventually marry other college students.

⁷ Human culture has also profoundly influenced the evolution of species other than our own. Unfortunately, an all too frequent consequence of us humans has been the extinction of other species.

There are many other examples of culture's effect on human evolution. The social and religious attitudes that are a part of culture influence allele frequencies. Feelings and beliefs on population growth, birth control, and abortion clearly influence reproductive fitness, and social and religious attitudes, like virtually all behavior, have a moderate heritability. Similarly, social attitudes about who to marry and who not to marry influence mating structure. Military culture obviously has influenced the reproductive fitness of individuals continually since recorded history began. Travel technology has made it possible for people in different parts of the world to meet and mate, removing the reproductive isolation of human populations. Domestication of the horse and camel intensified population migrations, and developments in oceanic transportation removed the reproductive isolation between Native Americans and Europeans. Even our new information age is influencing evolution. People on different continents can now meet over the Internet.

The prospect of genetic engineering is a developing cultural event that may have profound effects on human evolution. It is still much too early to predict the long term consequences of genetic engineering. For some traits, genetic engineering, even if it is technologically feasible, may not be the option of choice. For example, suppose that you had a child with a growth hormone deficiency. Would you pay \$100,000 for genetic engineering or pay \$2,000 to give your child injections of growth hormone at important stages of development?

Other aspects of genetic engineering inspire awe and dread. In the past, the overwhelming effect of human culture on human has been to alter allele and genotypic frequencies⁸. Genetic engineering could open what may be Pandora's box by allowing science to actually create new alleles, thus changing mutation from a random phenomenon into a deliberate, scientifically guided enterprise. Suppose for example that altering the regulatory region of a few genes could allow them to operate for a longer time during fetal development and increase the number of neurons in the brain and human cranial capacity? We would have the potential for creating humans with *new and novel* genotypes that do not currently exist in the human genome. Prognosticating on the long term future is best left to science fiction writers, astrologers, and crystal ball gazers, so there is no immediate urgency to act. If history is any judge, then some parts of contemporary science fiction will turn into science while others remain fiction. In the case of genetic engineering, it is impossible at the present time to distinguish the two.

The Five Forces: Integration

The five forces of evolution do not operate in five individual vacuums with each force doing its own thing independently of the other four. Instead the five forces have dynamic interactions, making it very difficult for us humans to conceptualize evolution. (We humans have problems visualizing with 5 dimensional space!) The most elaborate attempt to combine the forces is called *shifting balance theory* developed by the famous geneticist Sewall Wright.

Wright's synthesis of shifting balance theory was presented in no less than four volumes, but he offered a simple analogy for understanding it. Imagine a three

⁸ An exception would be mutational effects from X-rays, atomic energy and certain chemicals.

dimensional map of a mountainous region that has been flipped over 180 degrees so that the peaks of mountains become deep pits and the original valleys turn into ridges. This three dimensional terrain represents the adaptive landscape of a species—the pits are regions of strong adaptation to the environment while the ridges are areas of poor adaptation. A species is represented as a blob—not a rigid and firm structure like a pin ball, but a heavily viscous blob like a dollop of heavy grease with all types of dust and dirt particles in it. Natural selection is the force of gravity.

When a species is well adapted to its environmental niche, the species (blob) resides in a pit. As the environment for the species changes, the landscape itself alters. When the environmental changes are small, the pit changes only slightly, rising a bit here or sinking a bit there. Some movement is imparted to the blob so that it appears to rock back and forth a bit, but the overall change in terrain is too modest to expel the blob from its pit. This is a situation known as *stasis* in which a species remains the same for a long period of geological time.

However, the environment can sometimes change in a big way, sometimes physically (e.g., an ice age) but often from competition from other species. When this happens, there is uplift in adaptive pit so that the terrain changes from a deep pit to a shallow bowl to, eventually, a ridge. In such circumstances, population size decreases so that the effects of random genetic drift come into play. In this scenario, drift is equal to shaking the whole landscape in an unpredictable way, and population size equals a change in the size of the blob.

As the uplift changes the pit into a ridge, the blob—much smaller and lighter than it used to be—begins rolling downhill (i.e., natural selection is moving it toward a point of adaptation). The effect of genetic drift, however, can shake the landscape so that blob is ejected from shallow depressions where gravity would otherwise keep it. Eventually the blob will be rolled and jostled into deeper and deeper pits. The species is adapting to the environmental changes. It will grow in size, reducing the effect of drift. As the shaking subsides and as the environment stabilizes, the blob will remain in the pit and another period of stasis occurs.

The blob, however, is no longer the same. During the period of intense change, the blob will have lost some particles of dirt and dust while other particles of dirt and dust have replicated themselves. This represents allele loss and the increase in frequency of rare advantageous mutations. Effectively, the blob has changed into a new species. In some cases, the blob may have split into two different parts, each eventually settling into its own adaptive pit. This is where a line branches in evolution.

The effects of population structure and culture may be incorporated into Wright's model by imagining that we place the adaptive pit under a powerful microscope. Magnification shows that what appeared to be a single blob is in fact a large series of "bloblets" that have settled into the tiny crevices among the boulders in the deep pit. Some bloblets are connected by small channels of the viscous material while others are physically separated. This denotes the spatial and temporal aspects of population structure. Mate preferences may be represented as different forms of magnetism that attract certain dust particles to others. When the landscape changes, the appearance from far away is that of a single, large blob moving when in fact it is the movement of a large number of these bloblets, all responding to the gravity.

Culture changes the bloblets from inanimate matter into something that can move and act on their own accord. They can now dig downwards by themselves, becoming better adapted and allowing the population size to increase. As population size increases, bloblets grow larger and merge together. Eventually, they can grow so much that they split and a portion spills over into a new unoccupied piece of territory.

Like all analogies, this account of shifting balance is not perfect. But it does demonstrate the important interactions of the various forces of evolution. When selection pressure is intense, population size decreases, allowing a greater role for drift. Viewed from a distance, the blob may appear to split apart, but under the microscope, the fusion is really an isolated bloblet going its own way. The ultimate fate for most isolated bloblets is extinction—they get trapped in small local pits where the decrease in population size is too rapid to permit them to slide into deeper adaptive areas. But occasionally, one bloblet makes it into one adaptive pit while another ends in a second pit where both increase in size until another upheaval takes place.

Common Mistakes in Evolutionary Thinking

Evolution Has a Goal

Evolution is a *description for a process* that lacks consciousness, intentions, or goals. Tigers do not have stripes because evolution wanted them to blend in against a forested background where the sun highlights one area but leaves an adjacent area in deep shade. Tigers have stripes because at some point in their past striped tigers outreproduced other tigers. If things had gone differently, tigers may well have had spots like leopards and jaguars. Writers speak of evolution as “working towards this” or “acting against that” because it is difficult to speak about a process without attributing some sense of agency to it. “The sun warms the earth” is a descriptive statement; it does not mean that the sun consciously changes its physics in order to keep the earth warm. Similarly, “evolution made us humans smart” is also a descriptive statement. Evolution did not “intend” for that to happen. It just happened.

Evolution Works for the Species

Older writings and TV documentaries often spoke of the working of evolution as being “for the good of the species.” Lacking sentience, evolution does not work for the good of anything, even individuals. Species are a necessary consequence of evolution because of genetic transmission and, in sexual species, because of the requirement that one have the anatomy, physiology, and behavior to allow successful mating with others.

In *The Selfish Gene*, Richard Dawkins argues that evolution is really a case of some forms of DNA being able to outreplicate other forms of DNA. In the process, DNA can develop any type of mechanism that assists in its own replication, even when the mechanism involves inhibiting rival forms of DNA from replicating. A chicken’s egg was not developed for the good of the good of chicken species. Instead, the chicken is an egg’s way of making another egg.

One Dimensional Thinking

Few humans can visualize anything more than three dimensions at one time, so when systems involve a number of different interacting forces, we cannot simply close our eyes and picture the landscape. In such cases, there is a temptation to keep everything else constant and allow only one dimension to vary. In general, there is nothing the matter with this approach, but it may run into problems in a highly interactive and complex system like evolution.

Natural Selection Explains Everything

There is a tendency to take aspects of human anatomy, physiology, and behavior and explain them in terms of natural selection having acted *directly* upon them. In the long run, it *may* turn out that the direct effects of natural selection explain most everything, but our knowledge of human evolution is so embryonic that we cannot make that claim today. Indeed, contemporary knowledge of genetics encourages a skeptical wait-and-see attitude.

Sewall Wright argued for the principle of *universal pleiotropism*—the fact that any single gene influences several different phenotypes. Even if this principle is not universal, it certainly applies to a large number of loci. Consequently, if natural selection operates on one trait, there are likely to be changes in several other traits. Deliberate and controlled experiments on selection in plants and animals bear this out. For example, John DeFries derived two lines of mice, one selected for high activity, the other for low activity. It turned out that the two lines also differed in defecation rates, even though there was no direct selection for defecation. We humans defecate about once a day, not many times a day like many other mammals. Undoubtedly, one can concoct some selective advantage for our behavior, imagining for example that it reduced the scent trail left by a group of protohumans moving through the savanna. But historically, once a day defecation may have been a byproduct from selection on a different trait.

Similarly, many traits today may be secondary byproducts of evolution, a phenomenon that Darwin referred to as *pre-adaptation*. It is unlikely that early hunter gatherer populations experienced direct selection for operatic talent or the ability to memorize long lists of nonsense syllables. Instead, the evolution of cognitive abilities and a sophisticated vocal system opened the door for these behaviors to emerge as secondary consequences.

The effect that genetic drift had on human evolution is impossible to establish at the present time because drift is a random and chance process. Some anatomical differences among various human populations may have arisen simply by dumb luck because the populations were initially established by a small number of migrants.

Evolution and Optimization

Heron, pelicans, osprey, and loons all catch fish for a living, but they do so in quite different ways. A heron stands motionless in shallow water patiently waiting for a fish to swim by. When this happens, the heron swiftly grabs the fish with its long, extended beak. Pelicans fly ten to thirty meters over water looking for fish near the surface. When the pelican spots a fish or a school of small fishes, it goes into an abrupt dive and crashes into the water, attempting to scoop up the prey in its pouch. Ospreys

soar high above water. When the osprey finds a fish near the surface, it goes into a deep dive and grabs the fish with its talons. Loons paddle on the surface like ducks. When the loon spots a fish swimming underneath, the loon dives and swims after the fish.

The different strategies for fishing illustrate that evolution does not find the global optimum. Instead, it finds *solutions*, some of which may be *local* optima. To use the shifting balance landscape, evolution has resulted in the heron, pelican, osprey, and loon living in their own adaptive pits. It does *not* guarantee that all four species *must* end up in the deepest pit in the whole landscape. There is no “best” solution for a bird to catch fish. Instead, there are several different solutions and as long as a species finds *one* of them, it is perfectly ok.

To complete the analogy, when there is upheaval in the adaptive landscape, a blob is more likely to end up in a pit close to the one in which it started rather than a pit at the opposite end of the landscape. This reflects the fact that natural selection is constrained by the genes and the phenotypes that already exist in a species. If ospreys have to become better at fishing, then natural selection is likely to work in the direction of better eye sight, stronger talons, and more fluid aerodynamic design. It is not likely to reengineer the osprey to make it look and behave like a pelican.

Confusing Relative with Absolute Fitness

The confusion between relative and absolute fitness can lead to false inferences about evolution. When there is continuous selection against a genotype over time, then that genotype will decrease relative to the more fit genotypes. However, this *does not necessarily imply that the less fit genotypes will eventually be removed from the population*. That may be the case, but it is *not necessarily* the case. Why? Because the extinction of an allele or of a genotype depends on population size and absolute fitness, not on relative fitness.

To illustrate this principle, consider the data on relative fitness presented in Table X.X. Here, allele *A* confers more fitness than allele *a*. In the current generation, it is assumed that the frequency of *A* is .60. With the relative fitnesses given in Table X.X, the frequency of *A* in the next generation will increase to .605. After 100 generations of such selection, the frequency of *A* would be .92.

Genotypic Frequencies:				
Genotype	Relative Fitness	Current Generation	Next Generation	After 100 Generations
<i>AA</i>	1.00	.36	.366	.845
<i>Aa</i>	.98	.48	.478	.158
<i>aa</i>	.96	.16	.156	.006

Now consider the same data expressed in terms of absolute fitness (Table X.X). here, it was assumed that there was an initial population of size 100 and that individuals in this population transmitted, on average, 1.05 copies of their genes to the next generation. Hence, the absolute fitness of a genotype equals the relative fitness multiplied by 1.05.

Notice how genotype *aa* increases in absolute numbers over time. After 100 generations, *aa* is quite rare *relative* to *AA*, but its actual numbers have quadrupled.

Genotype	Absolute Fitness	Number of Genotypes:		
		Current Generation	Next Generation	After 100 Generations
<i>AA</i>	1.050	36.0	38.4	11116.1
<i>Aa</i>	1.029	48.0	50.2	1948.6
<i>aa</i>	1.008	16.0	16.4	85.4

As you might guess, the critical variable in all of this is *the rate of population growth*. When this rate is high relative to the relative fitness of genotypes, then lesser fit genotypes can increase in absolute numbers. Once their number increase sufficiently to overcome the effects of drift, then the alleles for lesser fit genotypes can remain in the population. When the rate of population growth is low relative to the relative fitness of the genotypes (or, of course, when population size is stable or decreasing), then the lesser fit alleles are likely to be removed from the population.

Since recorded history—and probably before that—the pattern of human evolution has been one of high population growth. Although natural disasters, famines, epidemics, and warfare act to the contrary, the reduction in population is local and temporary—they are irregular blips compared to the long term trend. Hence, the human genome may still contain a number of alleles that would have been eliminated had not the population been growing.

Human Evolution

Anyone reading this section 50 years from now will laugh at its naiveté, and the reason for their bemused state will be justified. The discovery of new fossils, the sequencing of the human genome, and the completion of the human genome diversity project will provide new insights that alter currently cherished beliefs. This has been the history of science in human evolution, so there is no reason to suspect that the trend will change. Still, we are stuck in the present and must do the best with the available data.

Most biologists suspect that humans, chimpanzees, and bonobos (pygmy chimps) split off from a common ancestor as recently as 4 to 5 million years ago (mya). The split occurred in Africa. The ancestors of chimps and bonobos remained in the forested areas of central Africa while our own ancestors began adapting to life on the savanna—the open spaces of the African plain. One of the first evolutionary developments was upright posture. The earliest protohuman fossils, those of the Australopithecines, a Latin term for “southern ape,” walked upright and had modified hands, but in many other ways resembled a chimp. They were small (between 3 and 4 feet tall), had curved fingers, and a skull with a protruding jaw, a recessed cranium, and heavy ridges behind what are now the eyebrows.

The reason for the development of upright posture is unknown, but it certainly had the advantage of permitting the Australopithecines to travel long distances and freed their

hands to carry objects. It is possible that they used tools and very likely that they were a highly social species as we, chimps and bonobos are today. Over the course of 2 million years, several varieties and species of Australopithecines may have cohabited together and possibly even competed with one another on the savanna⁹. Between 1 and 2 mya, fossils appear of two species, now termed *homo habilis* (handyman) and *homo erectus*. The upper cranium of the skull expanded and assumed a more rounded shape, permitting brain size to increase from about 450 cc to between 800 and 1200 cc. (Or perhaps, brain size increased, putting selective pressure on the cranium to increase.) The protruding jaw receded a bit, teeth became smaller, and height increased slightly. But two phenomena are striking—(1) tool use is now well documented in the form of flint and stone fashioned to act as chopping and scraping tools; and (2) our ancestors migrated out of Africa. Fossils of this species have been found in what is now China, southeast Asia, and southern Europe. It is assumed that these species retained the sociality of their ancestors.

Over time, the cranium and brain size increased, the jaw receded, the thick brow ridges shrank, teeth became smaller, and height increased. Several different species may have coexisted in different parts of the world. As recently as 50,000 ya groups of heavily boned hominids (*Neanderthals*¹⁰) lived in certain areas of Europe and the Middle East together with a more gracile (i.e., slender) form of *homo*, assumed to be our direct ancestors.

The actual origin of anatomically modern humans (amh) has not been firmly established. The most favored theory has the support of the ever growing body of molecular genetic data on human origins. It holds that amh developed quite recently, someplace in the order of 100,000 to 200,000 ya, probably in Africa, and then migrated to other areas of the Old World where they competed with and/or interbred with existing hominids, leading to the resident hominids' extinction and/or absorption.

The alternative theory, dubbed the candelabra theory, is proposed by a small number of physical anthropologists. This theory holds that amh are the result of convergent evolution of geographically dispersed human populations that originated from the migration 2 mya from Africa. That is, after colonizing much of the temperate and tropical zones of the Old World 2 mya, the various human populations faced the same selective pressures and consequently evolved in the same way.

Although the two theories disagree as to *when* the migration from Africa occurred, both agree on the particulars of recent human evolution (i.e., evolution from 200,000 ya to 50,000 ya). Cranial capacity had increased to a range from 1200 to 1700 cc and the skeletal structure attained a gracile form very close to modern humans. Tool use—or at least the evidence of tool use—suggest that it developed into an art. Spearheads are evident as well as bone instruments fashioned to perform needlework, pictorial drawings

⁹ Preoccupation with the savanna environment may be a classic case of looking for the keys under the lamppost because the light is better there. Bones in humid, forested areas decay rapidly while those in drier climates can fossilize.

¹⁰ Named after the Neander Valley in Germany where their fossils were first discovered. Although the term Neanderthal today carries the connotation of a brutish and stupid barbarian, Neanderthals had the noble qualities of esthetics and respect for the dead evident in their careful burials. Why they disappeared has not been clearly established. They may have interbred with a more numerous variant of *homo* and lost their distinctive anatomy and/or been driven towards extinction by competition.

appear in caves, and some implements show evidence of engraving. Undoubtedly, verbal language has developed. But human evolution was not finished by 50,000 ya. The skeleton continued its gracile development and cranium capacity still increased to give its present day range of 1000 to 2000 cc, the average today being somewhere between 1300 and 1400 cc.

Most scientists believe that early amh were foraging hunter-gathers. They lived in small, cooperative groups that would settle in a single location and hunt, dig roots, pick fruit, and possibly harvest grain until the immediate resources were depleted. Then they would move on. Many hypothesize strong sex-role differences during this period—the guys hunted, the gals gathered. The small human groups—like virtually every other mammalian omnivore—adapt to seasonal change, migrating to areas of optimal foraging and hunting at the appropriate time of year. Somewhere in the history of this—and whether it started 4 mya or 40,000 ya is anybody’s guess—the mating structure changed. Some form of *homo* eventually recognized a relative permanence in mating that said something to the effect that this guy (or these guys) have a recognized relationship with this gal (or these gals) that permits them to mate, call them “their own,” and transfer property and prestige to their offspring. Early *homo* also became cognizant of genealogy. Barak was not just Barak. He was also Thrug’s and Amalog’s son.

Everyone agrees that the increasing human cranial capacity was accompanied by an increase in intellect—memory, symbolic manipulation, learning capacity, etc. The largest anatomical differences between human and chimp brains is in the frontal lobes—those areas suspected of executive functioning, evaluation, and reason. The increase in frontal material permitted our recent hominid ancestors to develop culture beyond the simple social learning cultures of macaques, chimps, and bonobos. Our monkey and ape cousins have only the “monkey see—monkey do” cultural transmission. *Homo*’s ability to transmit culture includes simple imitation but expands into symbolic instruction. At some point *homo* could communicate the idea “don’t do it that way, do it like XYZ” without ever physically demonstrating the “XYZ” behavior. Barak is no longer just Barak, and is no longer just Thrug’s and Amalog’s son. He is also Gortog’s grandchild, even though Gortog, dead for several years, is a person unknown to the listener.

The reasons behind the evolutionary increase in brain size are not known, although there is no shortage of speculation. The need to fashion better tools, the requirements for sophisticated social interaction with conspecifics, the benefits of symbolic thought, language, and competition between human groups have all been postulated as the reason for the intelligence of hominids. It is also possible that the causes for increased brain size shifted over time, say from social communication to symbolic and rational thought to competition. Whatever the reason(s), they must have been quite important. Metabolically, the brain is a very expensive organ. Although it comprises only 2% of body weight, it consumes about 20% of the body’s metabolic resources. Such an expense does not come without important evolutionary trade offs. Also, the increased brain size posed (and still does pose) difficult problems for mothers who must squeeze such a large structure from the pelvis and vagina during childbirth.

Two cultural inventions altered the environment for amh. The first (i.e., the first to be explained here, not necessarily the first temporally) was the domestication of certain animal species. A few human populations no longer had to hunt for meat. They could

simply tame the “meat,” lead it to green pastures, slaughter it at will, and use its milk, wool, etc. The second invention was agriculture. It is thought that agriculture was developed sometime around 10,000 ya, probably independently in several different area of the world. But the pattern of its discovery and diffusion unclear. No matter. The end result was the same—agriculture limited the nomadic wandering of some human populations. They had to stay in a single geographical area to plant, tend, and harvest crops.

It is assumed that agricultural populations increased in number. This had two important effects. First, some agricultural populations migrated into the adjacent areas occupied by hunter-gatherer societies. Because the agriculturalists grew in size while the population size of their hunter-gatherer neighbors remained stable, the number of agriculturalists would eventually overwhelm the hunter-gatherers. Through interbreeding, population growth, cultural assimilation, and/or competition, the agricultural societies would become dominant in many fertile areas.

The second effect of population growth under agriculture was an elaboration of social roles. As the technology of raising crops improved, in very fertile areas it was no longer necessary for everyone to toil in the fields. Some people could become what today’s economy call service and manufacturing employees while others became supervisors. The result was an integrated web of codependent roles and occupations, leading to the development of cities and what we now call civilization¹¹, the first evidence of which appeared 5,000 ya.

The archeological record clearly shows that civilization did not start in one place and then spread unchecked throughout the world. Civilization appeared here and there in a series of starts and stops and not from a slow, inexorable diffusion from a single central origin. In a manner still obscure to science, civilizations develop in an area, flourish, and dissolve. To the best of our knowledge, the actual humans do not change, at least in any dramatic way—the cranial capacity of those who start and develop a civilization appear to be no different than those who disperse and engage in less sophisticated social, political, and occupational roles after the civilization’s demise. Indeed, the reasons for change in civilizations is one of the great mysteries of social science.

¹¹ The term “civilization” has several meanings. Here, it is meant as an elaborate system of interacting social, political, and occupational roles that coincides with the development of cities. It is not meant to imply “cultural refinement” in either a moral or esthetic sense, nor is it meant to imply that nonagricultural societies are “uncivilized.” *All* human population have a culture, but not all human populations have a culture that involves cities.