Chapter 8

The Nature of Natural Selection

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Evolution as such was not original with Charles Darwin, but his theory of how evolution happens was. The concept of natural selection was Darwin's (and Alfred Russel Wallace's, independently) wholly original idea, and it is the centerpiece of *The Origin of Species*. This is the theory that accounts for the complexity of organisms and for their adaptations, those features that so wonderfully equip them for survival and reproduction; this is the theory that accounts for the divergence of species and thus for the boundless diversity of life. It is one of the most important ideas in biology, and one of the most important in the history of thought. The philosopher Daniel Dennett (1995) calls it "Darwin's dangerous idea," because it replaces an entire worldview. It accounts for the appearance of design in living things.

Design in organisms had previously been imagined to be the product of an intelligent, omnipotent creator, and indeed was one of the most important arguments for the existence of such a being. Today's antievolutionists rally to the idea of intelligent design, arguing, as had their pre-Darwinian forebears, that the features of organisms are too complex, and too well fitted for their functions, to be explained by natural causes; they must, instead, have been caused by miracles. But natural selection (together with the origin of genetic variation) is indeed a sufficient explanation for organisms' complex adaptations—and for a good many other features of living things as well. So this is a concept with immense philosophical implications, and it is at the center of the creation-versus-evolution battle.

Given the importance of the concept, it is critical that it be conveyed as clearly and as accurately as possible in teaching students science. It is a simple concept, but it nevertheless works in many and sometimes subtle ways. Moreover, many people (even some biologists) carry misconceptions that make it all the more difficult for them to understand natural selection clearly. I will cite what I think are the most important points to understand when coming to grips with natural selection. Much of what follows has been clearly explicated by George Williams (1966), Richard Dawkins (1986, 1989), and others, and draws on passages in *Evolution* (Futuyma, 2005).

Natural Selection *Is* a Consistent Difference in the Rate of Increase of Different Genotypes or Genes (and No More Than That)

Natural selection is not "caused by" differences in rates of survival or reproduction: it *is* a difference of this kind. If the average rate of increase of one genotype (or gene) is consistently greater than that of others, natural selection exists. Such a genotype (or gene) is likely to increase in *frequency* (i.e., its proportion in the population) and may replace all others (i.e., become *fixed*).

The simplest example of such a process is an increase or decrease in frequency of a mutation in a laboratory culture of a species of bacteria; for example, mutations in the gene encoding galactosidase (the enzyme that provides energy by metabolizing lactose) have been studied in cultures of *Escherichia coli* (Dean, Dykhuizen, & Hartl, 1986). Mutations have been found that either reduce or enhance enzyme activity; these result in slower or faster cell division and thus growth in numbers compared with the wild type allele (figure 1). This is the very essence of natural selection. A mutation that enhances galactosidase activity would improve the level of adaptation of an *E. coli* population to a lactose-rich environment. There is nothing intelligent or thoughtful about the process; *it is nothing more than a statistical difference in reproductive rate,* that is, in *reproductive success.*

The Slogan "Survival of the Fittest" Should be Discarded, Abolished

This slogan, often used as a definition of natural selection, is wrong and misleading on several grounds. First, natural selection is differential reproductive success, not merely survival. Survival to reproductive age is

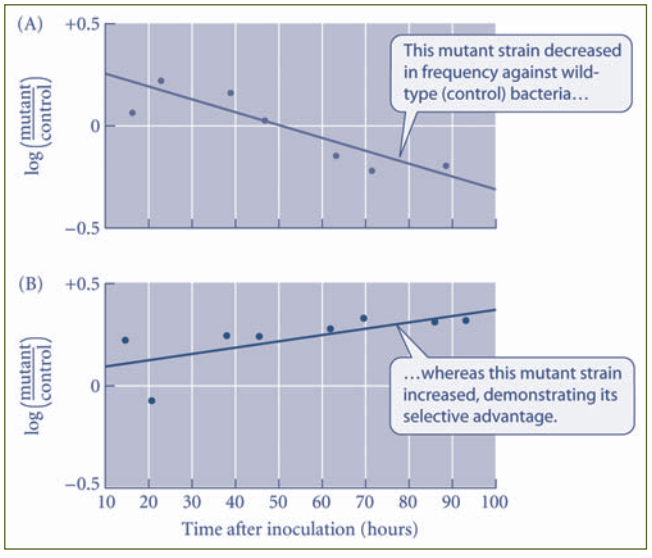

Figure 1. Natural selection illustrated by changes in the frequency of two mutations of the ß-galactosidase gene of *Escherichia coli,* in separate laboratory cultures with the control (wild-type) allele. One mutation decreased in frequency, and the other increased, because of their effects on the rate of cell division. (From Futuyma 2005, after Dean et al. 1986.)

clearly a prerequisite for reproductive success, but a sterile genotype, however great its survival, has no future (except by virtue of kin selection, as in social insects, but that is another topic.) A great deal of natural selection consists of genetic differences in reproductive rate, by both sexes.

Second, there is not always a "fittest": there can be stable coexistence of several genotypes, for any of several reasons. For example, each of several genotypes may be better adapted than the others to a different microhabitat, or to using a different resource, and all of them may be able to persist in a suitably variable environment.

Third, this slogan has been used to claim, falsely, that natural selection is an empty tautology. (Which type is the fittest? Answer: Why, the one that survives.) But this claim of tautology is false for two reasons:

1. We often can specify, or predict, which allele or phenotype will be the fittest, based on information other than simply seeing which takes over a population. I will explain this in the next section.

2. The allele that becomes fixed may not be the fittest: it may just have been "lucky." It may have been fixed by genetic drift, which is simply random fluctuations in the frequency of alleles or genotypes, owing to sampling error. Two alleles may not differ at all in their effect on the organism (i.e., they are neutral), but it is a mathematical certainty that their frequencies will fluctuate from generation to generation, and that one of them will eventually be fixed, purely by chance (figure 2). In another population, the other allele may well be fixed instead. We can calculate the probability that one or the other allele will be fixed, just as we can calculate the chance of drawing four aces from a randomly shuffled deck of cards. Thus evolutionary change can occur by chance (genetic drift) *or* by natural selection (or both). We must distinguish chance from natural selection!

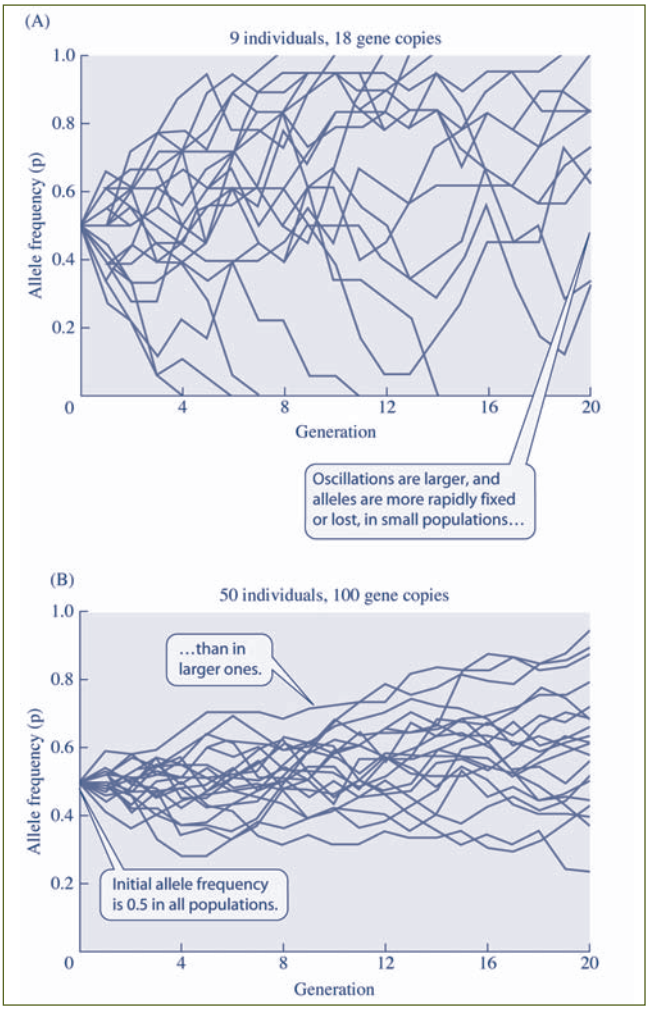

Figure 2. Computer simulations of random genetic drift in small (nine) versus larger (50) populations. In each case, 20 populations begin with identical allele frequencies (50 percent of each of two alleles, say *A* and *a),* and the frequency of one (say, *A*) is followed for 20 generations. The allele's frequency fluctuates at random toward zero and one, and ultimately will end at one of those boundaries. (From Futuyma 2005, after D. L. Hartl and A. G. Clark, *Principles of population genetics,* Sinauer 1997.)

Natural Selection Is the Antithesis of Chance

The distinctive property of natural selection is that in a given environment there is a consistent difference among genotypes, and therefore consistency of the pattern of evolutionary change (given those genotypes and that environment). Consistency

implies that a nonrandom cause is at work. For example, replicate experimental populations, if initiated with the same set of genotypes, typically show similar patterns of change in genotype frequencies. (Note that "chance" in science refers to unpredictability, not to lack of purpose, as it sometimes means in everyday discourse. Scientists do not invoke purpose in any natural phenomenon (outside of human behavior), but nevertheless, they do not say that all natural events happen by chance.)

Chance means unpredictability, but we can often make rough predictions of the evolution of a characteristic, at least in the short term, if we know enough about the function of the character and about the environment in which the organism must function. For instance, we know that in many birds and insects, the effectiveness with which an individual feeds depends on the fit between its beak (or mouthparts in general) and the size or location of its food. (A famous example is provided by studies of the adaptive fit of beak size to seed size and hardness in the Galápagos ground finches [Grant, 1986].) The soapberry bug feeds most effectively on seeds if its beak is the right length to reach the seed through the enveloping fruit wall. Its native host plants are now much less common than several Asian species that have either larger or smaller fruits, depending on the species. Within the last few decades, the bugs' beak length has independently evolved in Texas and Florida to match the fruit radius of different Asian plants that are now abundant (figure 3; Carroll & Boyd, 1992). Beak length has evolved, *predictably*, toward a new optimum that differs, depending on the ecological situation. This is not a matter of chance!

Natural Selection Makes the Improbable Probable

The frequency distribution of beak length in soapberry bug populations now has shifted mostly beyond the range of variation that the populations had before new food plants were introduced (figure 3). This is a very common observation for characteristics in which alleles at several or many different gene loci contribute to variation. For a "quantitative character," such as size, there may be at each locus "plus" alleles that increase size and "minus" alleles that decrease it; a genotype's size then depends on how many + and – alleles are in its genetic makeup. (If, for instance, there were four loci, A–D, the largest and smallest genotypes might be denoted + + + + + + + + and – – – – – – – –, respectively. Intermediates have various mixtures of + and – alleles. If the population consists mostly of fairly small individuals, the + allele at each locus is quite uncommon. Then the probability that both a sperm and an egg will have many + alleles is very low, so the production of an extremely large offspring is very improbable. (That is, extremely few gametes would have a ++++ set of alleles, i.e., the + allele at every locus.)

If we were to breed mostly the largest individuals (those with more than the average number of + alleles at these loci), we would produce F_1

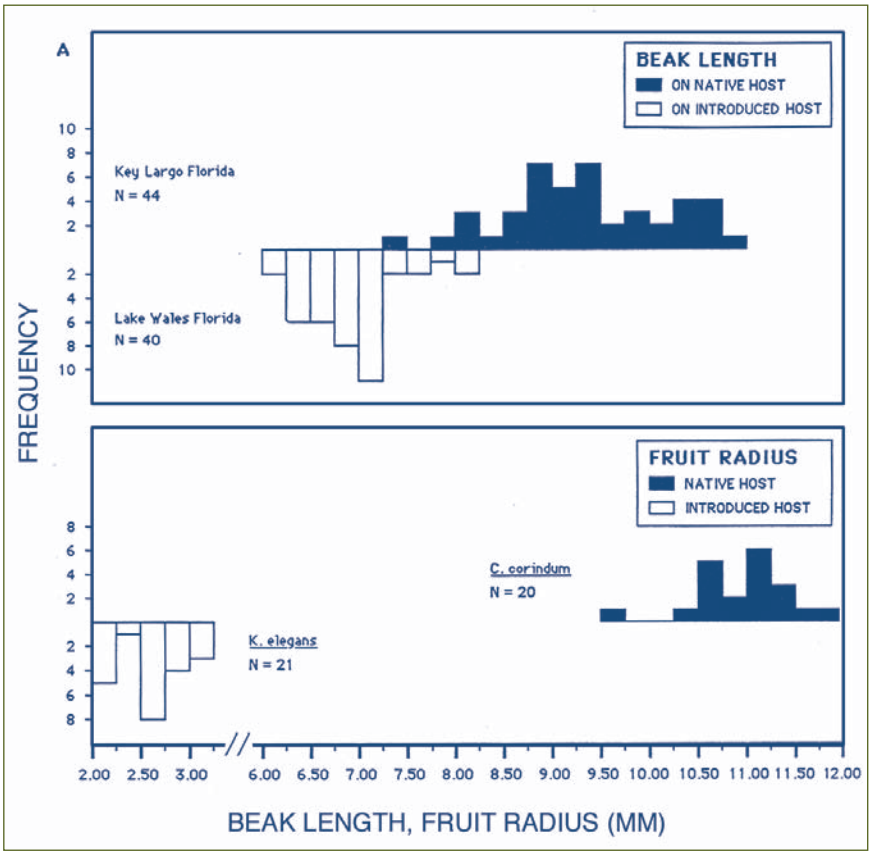

Figure 3. Rapid evolution of beak length in the soapberry bug in Florida. The bottom panel shows the frequency distribution of the radius of the fruit of the native host (*C. corundum*, black histogram at right) and of the much smaller fruits of an introduced host *(Koelreuteria elegans)* that is now abundant in a different region of Florida (white histogram at left, flipped upside down). The top panel shows that the beak length of bugs that feed on the introduced host is much shorter than that of bugs associated with the native host (black histogram). The average beak length is shorter than any that were measured in the population that still feeds on the native plant, and which represents the ancestral condition. (After Carroll & Boyd, 1992.)

offspring in which the frequency of + alleles is higher than it was in the general population in the previous generation. Then the "concentration" of + alleles would be higher in the gametes of these individuals than it had been in the previous generation—and it would be higher still if only the largest members of the F_1 generation bred. So the probability of gametes, and therefore F_2 offspring, with many + alleles (and therefore larger size), would be increased. The selection process acts as a distiller or sieve for + alleles, making formerly improbable gene combinations (such as +A+A+B+B+C+C+D+D) more probable.

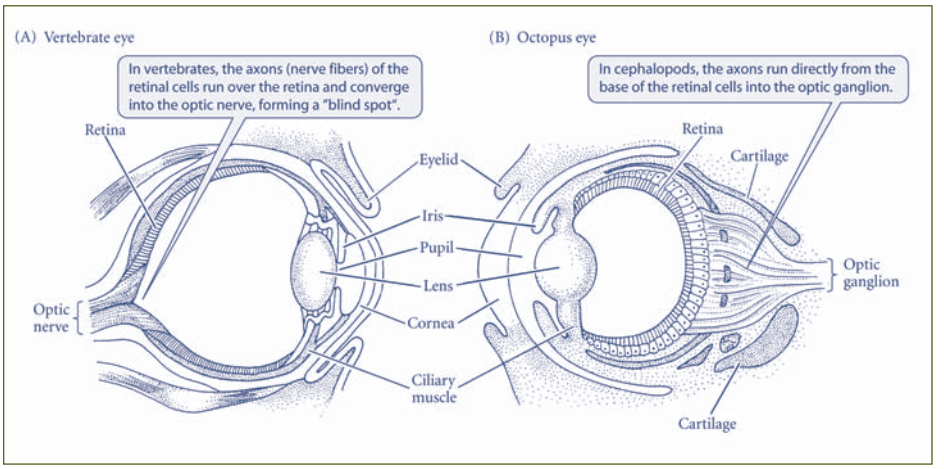

Figure 4. Sections through the eye of a vertebrate (a) and a squid or other cephalopod (b). In the vertebrate eye, the optic nerve forms a blind spot, the kind of design flaw that is common in organisms and which the mindless processes of mutation and natural selection can be expected to produce. (From Futuyma 2005, after R. C. Brusca and G. J. Brusca, *Invertebrates,* Sinauer Associates, 1990.)

This is exactly what has occurred when plant or animal breeders, or researchers, have deliberately selected for characteristics in domesticated organisms or in experimental subjects such as fruit flies. Within a few generations, extreme phenotypes that were never seen in the base population become abundant, based on selection of genetic variation that was already present in the base population. The breeders have used selection to make the improbable probable. Darwin did not know about genes, but he was very familiar with this process, and he saw that natural environmental agents of selection could have exactly the same effects. If the reproductive success of the longest- (or shortest-) beaked bugs is greatest because they have better access to a new kind of seed, the frequency of relevant alleles will increase, and unlikely gene combinations become more likely.

This principle explains, very simply, how features with the appearance of design—including complex features based on the input of many genes—are formed by a natural process. Natural selection is the creative factor in evolution. However…

Natural Selection Is Not Another Name for God

Natural selection is not even a name for Luther Burbank, a 19th-century horticulturist who used deliberate selection to develop stunningly novel strains of plants. That is, natural selection isn't intelligent; it isn't even a being, much less an intelligent one with goals and foresight. So there is no guarantee that it will produce optimally designed organisms.

Examples of suboptimal design are legion (as anyone who suffers from wisdom teeth or lower back pain will agree). For example, the axons of the retina cells in a vertebrate eye arise from the front of the cell and trail over the surface of the retina, converging into the optic nerve, which creates a blind spot where it plunges back through the retina and out the rear side of the eye as it extends to the brain (figure 4). There is no logical necessity for a blind spot, especially since cephalopods (e.g., squid) have evolved a very similar eye in which the axons sensibly arise from the rear of the retinal cells, and which therefore doesn't have a blind spot.

Such examples seem to speak of unintelligent design. The unintelligent designer, natural selection, is limited by the availability of the right genetic variations (which the mutation process may not have supplied), by historical legacies (for selection can act only on variations of whatever features an organism already has), and by trade-offs that limit adaptation. (For example, the elements of the male vocalization of the túngara frog that most appeal to females also attract frog-eating bats [Ryan, 1985].)

Moreover, because natural selection has no forethought (or any other thought), it cannot prepare organisms for future contingencies that differ from the regular pattern of environmental change that a species has experienced in the past. Arctic geese prepare for winter by flying south, because goose genotypes that didn't do that in the past have been eliminated. But natural selection cannot build features that are useless now but might prevent extinction in the future. For example, some parasites thrive by castrating

their host, redirecting host energy and materials from host reproduction to parasite reproduction. The possibility that the host population may go extinct in the future, by failure to reproduce adequately, cannot prevent the parasite from evolving the habit of castration. Likewise, many species produce great numbers of offspring not for the sake of the survival of the species population, but because under many circumstances, highly fecund (fertile) genotypes leave more descendants than less fecund genotypes.

Conversely, features that are advantageous here and now may evolve by natural selection even if they enhance the risk of future extinction. Many species have evolved specialized ecological requirements, such as the Kirtland's warbler, which is on the brink of extinction because it will nest only in stands of jack pine of the right age, with just the right shape. In a species with a 1:1 sex ratio, asexual (parthenogenetic) females have twice the rate of increase as sexual genotypes, because all the offspring of an asexual female are daughters that make more daughters, whereas only half of a sexual female's offspring are daughters. Quite often, therefore, a mutant genotype that is asexual will take over the species. (A familiar example is the common dandelion.) We know that the vast majority of these asexual species become extinct before very long, probably because they do not have the genetic flexibility that recombination in a sexually reproducing species provides. But that does not prevent populations from evolving asexual reproduction.

Natural Selection Is neither Moral nor Immoral

Since it is nothing more than a statistical process of differences in reproductive success, natural selection cannot be said to be either moral or immoral: it is *amoral*.

If a designer were to equip species with a way to survive environmental changes, it might make sense to devise a Lamarckian mechanism, whereby genetic changes would occur in response to an individual's need. Instead, adaptation is based on the combination of a random process (mutation) that cannot be trusted to produce the needed genetic variation (and often does not) and a process that is the epitome of waste and seeming cruelty: natural selection, in which the increase of an advantageous allele requires the demise or reproductive failure of vast numbers of organisms with different genotypes. Some African human populations have a high frequency of the sickle-cell hemoglobin allele because heterozygotes are more resistant to malaria than normal homozygotes. Sickle-cell homozygotes usually die before they reach reproductive age. It would be hard to imagine a crueler instance of natural selection, whereby part of the population is protected against malaria at the expense of hundreds of thousands of people who are condemned to die because they are homozygous for a gene that happens to be worse for the malarial parasite than for heterozygous carriers.

Any property that enhances the reproductive success of one genotype compared with others can enable that genotype to become fixed—to take over a population. This, as Richard Dawkins (1989) made clear in his book *The Selfish Gene*, is also true of one gene (allele) compared with others.

As my colleague George Williams (1989) has said, "natural selection is a mechanism for maximizing short-sighted selfishness." This intrinsic "selfishness" of genes and genotypes has many consequences that are repugnant from a moral point of view. For example, cannibalism can be advantageous to an individual. Flour beetles (*Tribolium*) eat eggs and pupae, and this tendency has been observed to increase in experimental populations, even though it reduces the growth rate of the population and could increase the chance of extinction (Wade, 1977). Male lions and langurs that take over a group of females kill the nursing offspring of the previous male, since this brings the mother back into reproductive condition and the male can father his own offspring faster. The seminal fluid of *Drosophila melanogaster* fruit flies is toxic to females (Chapman, Arnqvist, Bangham, & Rowe, 2003). They live long enough to lay the eggs that the male has fertilized, but they may not live long enough to mate again and lay other males' offspring. There is conflict between mammalian mothers and their fetuses: it is advantageous for the fetus to obtain as much nutrition from the mother as possible, but advantageous to the mother to withhold some, which can be used for her own subsequent reproduction. Accordingly, a paternally inherited gene in mice, encoding an insulin-like growth factor, enhances the fetus's ability to obtain nutrition from its mother, but a maternally inherited gene degrades this growth factor, opposing the paternal gene's effect (Haig, 1997).

This is an example of conflict between different genes in the same genome, of which many examples are coming to light (Hurst, Atlan, & Bengtsson, 1996). For example, mitochondria are transmitted only through female gametes in plants (and in most animals), so any mutation that can increase the production of eggs at the expense of pollen or sperm has an advantage. Almost all thyme plants carry a mitochondrial allele that prevents the development of

anthers and pollen; the resources that would go into their development are used instead for higher seed production. However, natural selection has favored a chromosomal gene that completely counteracts the male-sterility gene, so that most thyme plants have normal stamens and pollen. (It is advantageous for chromosomal genes if the plant has both male and female function, since these genes are spread through both pollen and seeds.) The result is a standoff between genes that cannot be called an adaptation, since the function of one gene is simply to nullify the effect of the other—but it is nevertheless an easily comprehended result of natural selection.

Discussion

Of course, natural selection can lead to the evolution of cooperation, not just conflict. I have focused on the results of "selfishness" to emphasize that natural selection can produce characteristics that are downright offensive to anyone's sense of ethics (or at least would be, if humans were displaying these features). But, of course, infanticide by lions and toxic seminal fluid are no more unethical than volcanoes that erupt and kill, because there is neither morality nor immorality, neither ethical nor unethical behavior, outside the human realm. From these examples and this realization, we can draw two major consequences:

1. Organisms have many characteristics that you would not want to attribute to an intelligent, beneficent designer, and in fact they have many characteristics that make no sense at all from a design point of view—such as toxic semen, cub killing, or dueling genes that exactly counteract each other. But they make a great deal of sense if you understand evolution by natural selection.

2. Evolution provides no foundation at all for a code of human behavior. What is natural among other animals is totally irrelevant to ethics or morality. There is no foundation for the naturalistic fallacy, that what is natural is good.

The points I have emphasized concern the overall nature of natural selection and its implications. I have not treated the details of natural selection, such as the many forms it takes (kin selection, group selection, sexual selection, soft selection, hard selection, and so on). I have not discussed the evidence for natural selection (literally hundreds of studies, most of which have demonstrated selection in its many forms). Nor have I discussed the importance of natural selection for human affairs. It is imperative that students understand that evolution by natural selection can sometimes occur rapidly, and that it can occur in organisms that really matter to us (Palumbi, 2001). The soapberry bug does not attack plants we care much about, but other insects have evolved to attack our crops (e.g., the apple maggot, which became a major pest of apples a little more than a century ago), and hundreds of insect pests have evolved resistance to chemical insecticides. Above all, probably the most serious crisis in medicine is the failure of antibiotics to control some of the pathogens they were designed to combat. This stems, of course, from the ongoing evolution of antibiotic resistance—in organisms ranging from HIV to the tuberculosis bacterium—due to natural selection that we impose by widespread (and often unnecessary) antibiotic use. Students simply must learn about evolution by natural selection, if for no other reason than self-protection. The applications of evolution are many, and they are steadily increasing. We cannot afford another 145 years of denial that Darwin was right.

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