NATURAL NECESSITY

See **Laws of Nature**

NATURAL SELECTION

In modern evolutionary biology, a set of objects is said to experience a selection process precisely when those objects vary in *fitness* (see Fitness). For example, if zebras that run fast are fitter than zebras that run slow (perhaps because faster zebras are better able to avoid lion predation), a selection process is set in motion. If the trait that exhibits variation in fitness is *heritable*—meaning, in our example, that faster parents tend to have faster offspring and slower parents tend to have slower offspring—then the selection process is apt to change trait frequencies in the population, leading fitter traits to increase in frequency and less fit traits to decline (Lewontin 1970). This change is the one that selection is "apt" to engender, rather than the one that must occur, because evolutionary theory describes processes other than natural selection (e.g., mutation, recombination, migration, drift, inbreeding) that can change trait frequencies and can nullify the effects that selection is disposed to bring about (see Evolution). This is why heritable variation in fitness is neither necessary nor sufficient for evolution (Brandon 1990).

The logical schema just described is very abstract; the zebra example involves conspecific organisms, but it also is possible that the "objects" in a selection process might be genes, or groups of conspecific organisms, or communities of organisms from different species. The schema also leaves open how often selection actually brings about the effects that it would cause if there were no counteracting forces. Thus, the question of how the schema applies to the living world gives rise to many empirical questions, some of which have interesting philosophical dimensions.

Adaptationism

At the close of his introduction to *On the Origin of Species*, Darwin [1859] 1964, 6 says that natural selection is "the main but not the exclusive" cause of evolution. In reaction to misinterpretations of his theory, Darwin felt compelled to reemphasize, in the book's last edition, that there was more to evolution than natural selection. It remains a matter of controversy in evolutionary biology how important natural selection has been in the history of life. This is the point of biological substance that presently divides adaptationists and anti-adaptationists. The debate over adaptationism also has a separate methodological dimension, with critics insisting that adaptive hypotheses be tested more rigorously (Gould and Lewontin 1979; Sober 1993).

Although it is widely agreed that natural selection has been an important cause of the similarities and differences that characterize the living world, the question remains of how important nonselective processes have been. For example, the underlying genetic system can "get in the way" of natural selection, preventing the fittest of the phenotypes found in a population from evolving to fixation. The simplest example of this is heterozygote superiority: If there are three genotypes at a locus and the heterozygote is the fittest, the genetic system will prevent that genotype and its associated phenotype from evolving to 100% representation. Adaptationists tend to minimize the practical import of this theoretical possibility (saying, for example, that heterozygote superiority is rare), whereas anti-adaptationists often take it very seriously indeed.

Gould and Lewontin (1979) criticized adaptationists for inventing "just-so stories," in which claims about adaptive significance are accepted only because they seem intuitively plausible. They also complained that adaptationism was unfalsifiable, since a new adaptive explanation could be invented if an old one were empirically disconfirmed; unfortunately, this point also applies to the pluralism about evolutionary processes that anti-adaptationists have favored. Gould and Lewontin also criticized adaptationists for taking a naively atomistic approach to how traits are individuated. Although few biologists would regard five fingers on the left hand as a different trait from five fingers on the right (because they do not evolve independently), adaptationists have argued that female orgasm in humans evolved independently of male orgasm, subject to its own selection pressures. It is a characteristic anti-adaptationist suggestion that female orgasm is to male orgasm as male nipples are to female nipples; the traits in each pair are products of the same developmental processes. Both evolved because there was selection in one sex for the trait, and the trait emerged in the other as a correlated consequence (Lloyd 2003).

Adaptationists have replied to these criticisms in several ways. One reply has been to insist that the idea of natural selection is an indispensable tool for biological investigation (Dennett 1995). A second has been to assert that selection is the only natural process that can account for adaptive complexity (Dawkins 1982). It is noteworthy that these adaptationist replies do not address the methodological objections that the critics advanced.

One positive outcome of the controversy has been the development of more rigorous methods for testing adaptive hypotheses—for example, controlling for the influence of nonselective processes (Harvey and Pagel 1991; Orzack and Sober 2001). It is to be hoped that biologists will recognize that global affirmations or denials of the importance of natural selection are not required *before* one studies the evolution of a particular trait in a particular group of organisms. Adaptationism and anti-adaptationism, as general biological claims, are summary *conclusions* that might be drawn after the evolution of a range of traits is understood; they are not needed as *premises*.

The Units of Selection Problem

Although Darwin usually thought of natural selection in terms of different organisms in the same species competing with each other, he also thought there were traits in nature that should be explained by postulating a process of *group selection*, wherein different groups in the same species compete with each other. This idea came in for severe criticism during the 1960s, and it remains controversial to this day (see Altruism). The logical schema for the process of evolution by natural selection also has been applied to the genes that exist in a single organism; this is the process of *intragenomic conflict*. The genes in a single organism often sink or swim together—they are equal in fitness, in that each has the same chance of finding its way to the next generation. However, genes in the same organism sometimes compete. For example, in the process of *meiotic drive*, heterozygotes produce gametes that bear one allele disproportionately more than the other. *Multilevel selection theory* (Sober and Wilson 1998) is the idea that there are different "units of selection"—that natural selection occurs among genes in the same organism, among organisms in the same group, among groups in the same species, and perhaps even among species in the same monophyletic taxon (Gould 2002). This idea contrasts with the doctrine of the *selfish gene*, which says that natural selection should be thought of as a process that exists exclusively at the genetic level (Dawkins 1976; Sterelny and Kitcher 1988).

When Darwin discussed the evolution of altruistic characteristics, he saw that there could be a conflict of interest between what was good for the individual and what was good for the group. More recent work has shown that this type of conflict can arise at levels of organization that Darwin was unable to consider. For example, driving genes in the house mouse are favored at the intragenomic level but are selected against at the level of whole organisms, since they render males sterile when found in double dose. There also is selection against the driving gene at the group level, since groups whose males are all homozygotes go extinct, and the copies of the gene found in females are thereby taken out of circulation (Lewontin 1970). It is intuitive to think of selection processes at different levels as component vectors that serve to increase or reduce the frequency of a trait; the net effect of selection at all levels is the result of combining these vectors into a single resultant.

Gradualism

Darwin thought of natural selection as acting on variations that have small effects—a complex adaptation, like the vertebrate eye, does not appear all at once. This point pertains to the question of how a trait first originates in a single individual—whether its parents had 99% of an eye, or no eye at
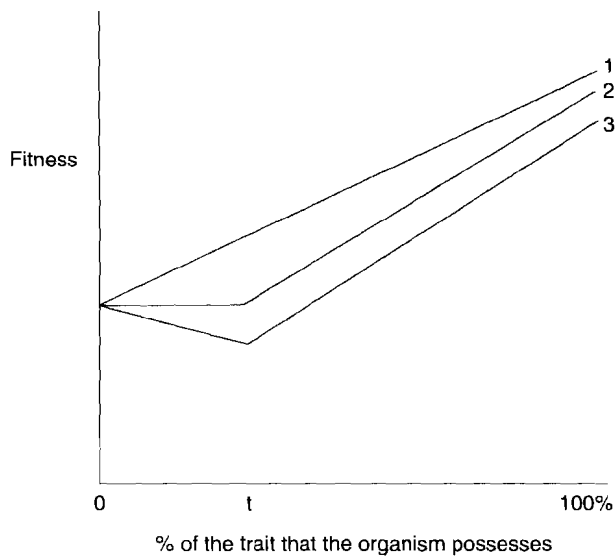
Fig. 1 What are the fitness consequences of having n% of a wing or an eye, as opposed to having $(n-1)$%? According to line 1, each small increase represents an increase in fitness. According to line 2, having more of the trait makes no difference in fitness until a threshold (t) is crossed. Line 3 also depicts a threshold effect, but here having more of the wing or eye is deleterious, not neutral, until the threshold is crossed. Evolution via the pure process of Darwinian gradualism requires the monotonic increase that line 1 exhibits and cannot occur if the fitnesses are those represented by lines 2 or 3. However, evolutionary theory countenances processes additional to that of "pure Darwinian gradualism," so, in fact, the theory says that it *is* possible for a trait to evolve under all three scenarios.

all. In either case, once the complex trait is found in a single individual, the question must be faced of how the trait is to become common in the population. Both saltationists (those who believe that evolution involves "jumps") and gradualists may want to invoke the process of natural selection to account for this. Saltation, therefore, is not an alternative to natural selection. Although Darwin did not know about Mendelian genes, much subsequent work in genetics has vindicated his gradualism. However, recent work indicates that single mutations sometimes produce large effects—for example, the *HOX* gene can cause a leg to appear on the head of a fruit fly. Contemporary biologists usually do not see this as diminishing the importance of natural selection.

If Darwinian gradualism, strictly construed, is to transform an ancestral population in which the organisms have no eyes at all into a descendant population in which all organisms have 100% of an eye, it is essential that n% of an eye represent an advantage compared with $(n-1)$%. In terms of the fitness functions depicted in Figure 1, Darwinian

gradualism can occur when the fitnesses obey the pattern in line 1, but not when they conform to lines 2 or 3. However, recall that contemporary evolutionary theory describes processes other than strict Darwinian gradualism (for example, drift, to be described later, allows a less fit trait to replace one that is fitter), and so the evolution of traits whose fitness profiles conform to lines 2 and 3 is by no means impossible.

In thinking about whether a trait can evolve in conformity with the rules of Darwinian gradualism, it is important to consider the possibility that a trait might start evolving for one reason and then continue evolving for another. Perhaps rudimentary and complex eyes both evolved for the same adaptive reason, because they help the organism process information about the environment that is contained in light (Dawkins 1996). However, this pattern seems less plausible for the case of wings. Even if later wing evolution was driven by the usefulness of flying, it is hard to see how the evolution of rudimentary wings could have proceeded in this way, since 5% of a wing provides no lift at all; being able to fly is a threshold effect. Kingsolver and Koehl (1985) argue that insect wings began evolving as devices for regulating temperature and continued to evolve as devices for flying.

Progress

Is the process of natural selection an instrument of progress? This question must be divided in two, distinguishing the issue of moral progress from that of improvement in fitness. With respect to the former, Darwin clearly recognized that the process of natural selection involves a mountain of suffering and death; indeed, he sometimes expressed revulsion at the adaptations that natural selection produces. One grisly example that repeatedly drew his attention was the ability of parasitic wasps to paralyze their hosts and lay eggs in them; when the eggs hatch, the young feed on the living caterpillar, leaving its brain for last (Gillespie 1979). At the same time, Darwin often expressed approval of the changes that selection brings about in nature, and he often did so as well in connection with the workings of selection in human evolution. Whatever moral ambivalence Darwin may have felt about natural selection, it is interesting that Darwin's "bulldog," Thomas Henry Huxley (1893) thought that there was a profound conflict between what is good for us in terms of fitness and what is good for us in terms of morality, with morality obliging us to control the instincts that natural selection has put in place. These critical assessments of the moral

significance of natural selection contrast starkly with the wholesale endorsement of the process that the political movement called Social Darwinism supplied. Social Darwinism used Darwin's theory to construct a moral justification for ruthless capitalism, according to which the weak had to be crushed to make way for the strong. Many modern biologists, sobered by the political misuses of Darwinism, now draw back from this ideological endorsement. They want their science to be *value free;* that is, a scientific theory has the job of saying what changes occur in nature and why, but it is not a scientific problem to say whether those changes represent good news or bad. (See Ruse 1997 for more on how the concept of progress figures in the thinking of different evolutionists.)

With respect to the second sort of progress—the effect of selection on fitness—Darwin thought of the process as an improver. He says that "as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection" (Darwin 1859, 489). Modern evolutionary theory makes it clear, however, that the process of natural selection need not improve the fitness of organisms. Quite apart from whether improving fitness is a good thing, selection can reduce the average fitness of the organisms in a population, even when the physical environment is static. If altruists compete against selfish individuals in a single persisting population, selfishness will go to fixation, with the result that the individuals in the population at the end of the process are less fit than their ancestors were when the process began. Adam Smith's optimistic picture of an invisible hand increasing the wealth of nations has been supplemented (though not replaced) by the pessimistic picture of the tragedy of the commons. Selection can improve average fitness, but it also can reduce it (Sober 1993, 97–99).

The Propensity Interpretation of Fitness

Alfred Russel Wallace, the codiscoverer of the theory of evolution by natural selection, suggested to Darwin that he drop the expression "natural selection" because it misleadingly suggested conscious choice; Wallace preferred Herbert Spencer's phrase "the survival of the fittest" to characterize the theory (Hodge 1992). Darwin embraced this summary slogan; however, it gave rise to the criticism that the theory is a tautology. If the fit are defined as those who survive, one cannot explain why one set of organisms survived to reproductive age while another did not by saying that the former were

fitter. The first step in replying to this criticism is provided by the propensity interpretation of fitness (Mills and Beatty 1977; Brandon 1990; Sober 1984). Fitness is to reproductive success as solubility is to dissolving—fitness is a dispositional property. In particular, it is a probabilistic disposition, a propensity. A fair coin is disposed to land heads more often than one that is biased in favor of tails. If one organism is fitter than another, then the first will *probably* be more reproductively successful. The natural way to represent this mathematically is in terms of the idea of a probabilistic expectation. If an organism has a probability p_i of having exactly i offspring ($i = 0, 1, 2, 3, \ldots$), then its expected number of offspring is $\sum i(p_i)$. The expected number of offspring is not the exact number one should expect the organism to have; rather, it is the average number the organism would have if it got to live its life again and again under identical circumstances. Thus, the first line of reply to the charge that the statement "a is fitter than b if and only if a is more reproductively successful than b" is a tautology is to point out that the statement is not even true. If the rejoinder comes that it is then a matter of definition that "a is fitter than b if and only if a has a higher expected number of offspring than b," the reply here is that every theory contains definitions. Even if this is the proper definition of fitness, it does not follow that the entire theory is tautologous; evolutionary biology is full of empirical claims. (For discussion of whether fitness should be defined as a probabilistic expectation, see Sober 2001.)

Chance in Evolution

One reason that fitness should be understood as a probabilistic quantity and not as an organism's actual degree of reproductive success is that evolutionary theory describes a nonselective process that can lead organisms to enjoy different degrees of reproductive success. This is the process of random genetic drift, which Motoo Kimura (1983) developed to explain the huge amounts of molecular variation observed in natural populations. Drift occurs when traits change frequency by random walk; this occurs when they are identical, or nearly identical, in fitness. Here we find a disanalogy with a deterministic propensity like solubility: If a and b are both immersed and a dissolves while b does not, then a must have been soluble and b must have been insoluble. But if a is more reproductively successful than b, it is not inevitable that a was fitter than b.

When should a difference in reproductive success be attributed to natural selection? If two identical

twins are on a mountaintop and one is killed by a lightning strike while the other is not, should we conclude that the second twin was fitter (Beatty 1991)? One way to answer this question in the negative is to argue that there is no phenotypic difference between the two twins that could form the basis for saying that they differed in fitness. This brings out another feature of the propensity interpretation—just as a tossed coin has a given propensity to land heads by virtue of its physical makeup, so an organism has whatever degree of fitness it has in a given environment by virtue of its genetic and phenotypic characteristics. However, the fact remains that the first twin was standing in one place while the second was standing in another when the lightning struck. Is this not a phenotypic difference? It is not relevant that the property of standing in a given place on a given day is not heritable; selection does not require heritability, though evolution by natural selection does. A different approach to the twins problem is to think of it statistically. If two coins are each tossed once, and the first lands heads and the second tails, standard statistical practice does not allow one to reject the null hypothesis, which says that they are identical in their probabilities of landing heads. A similar conclusion can be drawn about the twins. Notice that it does not matter that the two individuals happen to be genetically identical.

To understand the relationship between selection and drift, it is important to distinguish process from product. Evolution in finite populations always includes the process of drift, whatever change in trait frequencies may result. In similar fashion, the possibility of sampling error exists when a fair coin is tossed ten times, regardless of whether the outcome is nine heads and one tail or five of each. And no matter which outcome occurs, it is a mistake to ask "how much" of the outcome was due to the coin's fairness and how much was due to finiteness of sample size. It is useful to have both selection and drift in evolutionary theory because both categories are needed to describe relevant similarities and differences. Two populations may be characterized by the same suite of trait fitness values even though they differ in size, and two populations may have the same size even though they are characterized by different suites of fitness values.

Chance is said to enter evolutionary theory in two ways. First, mutations are said to occur "by chance." Second, random genetic drift is described as a "chance process." The term "chance" has different meanings in these two remarks. The point about mutations is just that they do not arise because they would be useful. This has nothing to do with whether mutations are deterministically caused or arise by an irreducibly probabilistic process. The relation of random genetic drift to the possibility of an underlying determinism raises issues that are more subtle. When we talk about different organisms having different probabilities of surviving and different expected numbers of offspring, how are these probabilities to be interpreted? Reasoning about Newtonian theory, Laplace ([1814] 1951) famously opined that if determinism is true, then probabilities (other than 0 and 1) are merely subjective—they reflect an agent's lack of information, not the objective chanciness of events. If this is right, then interpreting the probabilities used in evolutionary theory depends on facts about microphysics (Rosenberg 1994). However, it is worth contemplating a possibility not dreamt of in Laplace's philosophy. Perhaps nonextreme probabilities at the macro level can be objective even if determinism is true at the micro level. The actual relative frequency interpretation of probability allows for this possibility, although it is inadequate in other respects as an interpretation of the probability concepts used in science. Perhaps other, more adequate, interpretations of probability can allow macroprobabilities to be both objective and independent of whether microdeterminism is true.

What Does Natural Selection Explain?

If selection (in the form of lion predation) over many generations has favored fast zebras over slow ones, selection can explain why all present-day zebras run fast. But does it explain, in addition, why this or that individual runs fast? Sober (1984) answered this question in the negative: Selection explains only the frequencies of traits in a population, not why individuals have the traits they do. Selection is like an entrance exam—if you are required to speak English to gain admission to a room, the test explains why the room is composed entirely of English speakers. However, the test does not explain why the individuals in the room (Sam, Aaron, etc.) speak English. The phenotypes that individuals develop are to be explained by their genes and environment, not by the process of natural selection. Neander (1995) criticized this position on a number of grounds. One criticism involves an appeal to transitivity: If selection can explain why all the individuals in a given generation have a trait, and if the individuals in the next generation have the traits they do because they inherited them from the previous generation, then by transitivity, selection helps explain why the offspring have the traits they do.

Are There Laws in Evolutionary Biology?

Beatty (1991) argued that biological regularities hold only because this or that contingent event occurred in the evolutionary process. For example, if a population obeys Mendel's "law" of assortment, which says that Aa heterozygotes produce equal numbers of A- and a-bearing gametes, this is because there has been sufficiently strong selection against meiotic drive in ancestral populations for this fair Mendelian mechanism to evolve. However, it is a historical contingency that this type of selection pressure actually occurred. Sober (1997) replied that even if a regularity of the form "All Hs are F" is a contingent consequence of the earlier evolutionary event E, it still can be the case that "if E is true earlier, then it will be true later on that all Hs are F" is an evolutionary law. Rosenberg (1994) develops a different set of reasons for thinking that there are no biological laws other than the principle of natural selection. A separate puzzle about the status of laws in evolutionary biology concerns the fact that they appear to be a priori mathematical truths when spelled out carefully (Sober 1984). This distinguishes them from physical laws like the law of universal gravitation, which is empirical. A possible explanation for why the dynamical laws of evolution should be a priori may be found in the fact that fitness and other biological properties are multiply realizable (see Sober 1999 for discussion).

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See also **Adaptation; Altruism; Evolution; Fitness; Population Genetics; Species**