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Theory Really Matters: Philosophy of Biology and Social Issues

1.1 The Science of Life Itself

The results of the biological sciences are of obvious interest to philosophers because they seem to tell us what we are, how we came to be, and how we relate to the rest of the natural world. The media often report that “scientists have discovered” the original purpose of some common human trait—morning sickness during pregnancy is designed to prevent malformed fetuses (Profet 1992). Or a traditional but controversial claim about society is found to be a “biological fact”—boys are more prone to violence and in greater need of formal social training than girls. And the “gene for” this difference has been localized—the genes for good social adjustment are on the paternally derived X chromosome, which only girls receive (Skuse et al. 1997). In all these cases biology seems to yield clear factual answers to questions of enormous moral and social significance.

In the late nineteenth and early twentieth century many philosophers looked to biology for answers to basic questions of ethics and metaphysics. Herbert Spencer’s evolutionary “synthetic philosophy” was the most influential philosophical system of its time. Friedrich Nietzsche, hero of today’s “post-modernists,” believed that Darwin’s theory could demolish traditional views of humanity’s significance in the overall scheme of things. In America, the pragmatist Charles Saunders Peirce investigated the implications of evolution for the nature and limits of human knowledge. But mainstream philosophy in the universities of the English-speaking world took a very different view. At the opening of the twentieth century Bertrand Russell declared that the theory of evolution had no major philosophical implications. The sciences that had something to teach philosophy were mathematics (particularly mathematical logic) and physics. Physics was to serve as a role model for the other sciences, and for the next fifty years philosophers nagged biology for

its failure to live up to its example. The well-known philosopher of science and mind J. J. C. Smart compared the biologist to a radio engineer. Biologists study the workings of a group of physical systems that happen to have been produced on one planet. Smart thought that such a parochial discipline was unlikely to add to our stock of fundamental laws of nature (Smart 1963).

Mainstream philosophy has taken an equally dim view of the significance of biology for ethics. In the nineteenth century Darwin's theory was thought to have all sorts of moral implications. Darwin himself remarked that if "men were reared under exactly the same conditions as hive-bees, there can hardly be a doubt that our unmarried females would, like the worker-bees, think it a sacred duty to kill their brothers, and mothers would strive to kill their fertile daughters; and no one would think of interfering" (Darwin 1871). The view that our moral ideas are an accident of biology seems inconsistent with, for example, the Kantian idea that morality is binding on all rational beings. If human morality is an adaptation for survival in human ancestral conditions, perhaps we should not take it quite so seriously. Drawing very different lessons from evolution, Spencer and others identified social progress with the universal progressive tendency that they claimed to find in nature (Ruse 1996). Even at the time, some philosophers were skeptical about these claims. Thomas Huxley, for example, thought them wrong-headed (Paradis and Williams 1989). Many twentieth-century philosophers have been even more damning, seeing all such ideas as fundamentally misguided. Biology cannot settle ethical issues because it speaks to matters of fact, not value. According to this view, inferences from purely factual claims to moral ones commit the *naturalistic fallacy*. Normative claims about what ought to be true can never be validly inferred from factual claims about what is true. Debate about the naturalistic fallacy continues. But although some philosophers still try to derive ethical results from evolution (Ruse and Wilson 1986), the consensus is that this cannot be done (Kitcher 1994).

It has always seemed obvious to the wider community that biology has the potential to challenge our most treasured beliefs about ourselves and the way we should live. This view is probably correct. Even if moral principles cannot be inferred from purely factual biological premises, the biological sciences can discover morally relevant facts. Those discoveries can interact with existing moral principles to produce radical new practical policies. For example, early in the twentieth century, morality was connected to evolution via the supposed need to maintain the evolutionary pressures that have adapted humans to their environment. The result was a case for *eugenics*—policies intended to maintain or improve human fitness through selective breeding. The eugenicists put forward purely biological claims about the

effects of the relaxation of natural selection on humans in technologically advanced societies. These claims were supposedly, in themselves, factual. But conjoined with standard moral ideas about the importance of human welfare, the resulting eugenic case seemed compelling to people of every moral persuasion, from socialists to liberal capitalists to fascists. Before the Second World War almost every advanced society had made some legal provision for eugenics (Kevles 1986). Only its enthusiastic adoption by the Nazis brought eugenics into disrepute. More recently, E. O. Wilson and other biologists have claimed that human economic practices are driving species extinct at rates comparable to the great mass extinctions of earth's history. They further claim that these extinctions have the potential to disrupt the ecological processes on which human life depends. They call for radical changes in social and economic policy (E. O. Wilson 1992).

There are many uncontroversial biological claims that are relevant to our moral and social views. Starving children stunts their growth and ruins their health, and that is one reason not to starve them. But biological claims that have *novel* social and moral implications are usually highly controversial. Media reports of "genes for" homosexuality or evolutionary explanations of female orgasm are followed the next day by contradictory claims by equally well qualified authorities. Controversy is possible because the exciting conclusion is usually linked to actual experiments and observations by complex, and far from obviously sound, chains of argument. This is one reason why there is *philosophy* of biology. Philosophers try both to disentangle these chains of reasoning and to evaluate the broader conceptual frameworks that make biological results yield these significant social lessons. In *Wonderful Life*, Stephen Jay Gould describes for the general reader the recent reclassification of a group of Canadian fossils. But he also draws from these fossils the lesson that human intelligence is an accidental product of history rather than an essential feature of the natural world (Gould 1989). In chapter 12 of this book we look at the arguments connecting the fossil data to this extraordinary conclusion and examine the broader views in biology and philosophy upon which these arguments rely.

So philosophy is important to biology because biology's exciting conclusions do not follow from the facts alone. Conversely, biology is important to philosophy because these exciting conclusions really do depend on the biological facts. *Biological determinism* is the family of views that share the idea that important features of human psychology or society are in some way "fixed" by human biology. Many moral and social philosophers would dearly love a guarantee that nothing like biological determinism could possibly be true. But philosophy cannot provide such a guarantee. We believe that most

of the doctrines that go under the name of biological determinism are false, but they are false because of the facts of evolutionary theory and genetics. It is true that some defenders of these views suffer from philosophical confusions, but these confusions cannot be diagnosed without coming to terms with the biology involved. The role that genes play in evolution and development is the subject of part 2.

Another reason philosophers are interested in biology is that, like much of science, it expands our sense of the possible. We think that far too often metaphysics and philosophy of science have been dominated by models drawn from physics and chemistry. An impoverished list of possible answers will often lead to an invalid conclusion. For example, a standard distinction in our culture is that between “learned” and “innate” behavior. Thus many parents are worried that young boys’ delight in weapons is innate. Moreover, this distinction has played an important role in philosophy (Cowie 1998). One of the great divides in the theory of knowledge has been between empiricists, standardly regarded as thinking that very little is innate because almost everything is acquired from experience, and rationalists, standardly regarded as supposing that we come equipped with much that is innate. We think it would be very unwise to attempt to resolve this debate without understanding how modern ethology has transformed the concept of learning and why many biologists consider the concept of innateness to verge on incoherence. These issues are discussed in many parts of this book, but particularly in chapters 13 and 14. To choose another example, the concept of *biological species* figures extensively in ethical discussions of our obligations to the environment. Most philosophers learned Ernst Mayr’s definition of a species in high school: a species is a group of organisms potentially capable of interbreeding with one another. They will cite this definition when asked what species are, despite discussing in the next breath plants and asexual species, neither of which fit the interbreeding criterion. The nature of species is one of the most hotly disputed areas of biology (9.2), and the alternative definitions have very different implications for environmental ethics.

The aim of this book is to introduce the major areas of discussion in philosophy of biology, not to directly address the broader philosophical questions to which these discussions are relevant. In this introductory chapter, therefore, we sketch some of the links between the issues discussed in later chapters of the book and some broader philosophical questions, namely:

- Is there an essential “human nature”?
- Is genuine human altruism possible?
- Are human beings programmed by their genes?

- Can biology answer questions in psychology and the social sciences?
- What should conservationists conserve?

These questions have both empirical and conceptual strands, and it is this mixed character that makes philosophy of biology relevant to them.

1.2 Is There an Essential Human Nature?

What makes someone a human being? The idea that each human being shares with every other human being but with nothing else some essential, human-making feature goes back at least to Aristotle. He thought that each species was defined by an “essence”—a set of properties found in each individual of the species, but only there. That essence makes it the sort of creature that it is. Today most people suppose this essence is genetic, and that the job of the Human Genome Project is to reveal the genetic essence of humans.

In reality, however, there is no such thing as the “genetic essence” of a species. A central aspect of modern evolutionary theory is *population thinking* (Mayr 1976b; Sober 1980). Each population is a collection of individuals with many genetic differences, and these differences are handed on to future generations in new combinations. Populations change generation by generation. In many contemporary views of the nature of species, there is no upper limit to the amount of evolutionary change that can take place within one species. Over many generations a species may be transformed in appearance, behavior, or genetic constitution while still remaining the same species. Diversity is normal, and perhaps even functional, for lack of diversity makes a species vulnerable to parasitism and to extinction due to environmental change. So uniform populations in the natural world are unusual. Such populations do exist in the laboratory. For experimental purposes, biologists often want, and have generated by inbreeding, “pure” strains of fruit flies and mice. These strains are “standard” in the sense that they are the same in every laboratory, not in the sense that they are the “normal” or “correct” genome of the fly or the mouse. These invariant strains have to be carefully constructed by selective breeding; nature does not supply them for free.

It is not easy to repair Aristotle’s idea in the face of this variation within species. That may seem surprising, for anyone familiar with field guides, identification keys, or floras will be familiar with the idea of “identifying traits.” A *Field Guide to the Birds of Australia* will appeal to the characters of voice, plumage, and behavior to distinguish, say, one babbler species from another. But these identifying features are rarely truly universal at any time, let alone across

time. A statistically atypical white crowned babbler is still a white crowned babbler. It may be the forerunner of the typical babbler of the future or a survivor of the typical babbler of the past. So from the fact that we can *reliably recognize* many species it by no means follows that there is an *invariant essence* of a species. Even more to the point, as we shall see in chapter 9, there is no good reason from biology to try to repair Aristotle's idea. Contemporary views on species are close to a consensus in thinking that species are identified by their histories. According to these views, Charles Darwin was a human being not by virtue of having the field marks—rationality and an odd distribution of body hair—described (in Alpha Centaurese) in *A Guide to the Primates of Sol*, but in view of his membership in a population with a specific evolutionary history.

The implications of this transformation of our view of species have been much discussed in philosophy of biology, although they have been surprisingly neglected in ethics. David Hull, in particular, has argued that nothing in biology corresponds to the traditional notion of “human nature” (Hull 1986). This idea is significant, for the concept of human nature has been historically important. It has underwritten the view that there is some way that human beings are supposed to be, and that other ways of being are deviant or abnormal. This view is still central to the thought of some contemporary moralists (Hurka 1993). Biology is often supposed to provide some backing for this notion of normality: that there is a way that members of any species—including *Homo sapiens*—are meant to be, and that deviations from this are abnormal. But Darwinian species are continually evolving clusters of more or less similar organisms. There is nothing privileged about the current statistical norm.

So no general biological principle suggests that human moral feelings, mental abilities, or fundamental desires should be any more uniform than human blood type or eye color. On the contrary, human cognitive evolution seems likely to have involved an evolutionary mechanism that produces variation within a population, called *frequency-dependent selection*. In frequency-dependent selection, the fitness of a trait depends on the proportion of the individuals in a population that have that trait. In a classic thought experiment to illustrate this idea, John Maynard Smith invited us to consider the interaction between two types in a population: an aggressive, hard-fighting “hawk” and a timid, quick-to-retreat “dove.” Hawks win any contest against doves, and so succeed wonderfully well when most of the population are doves. But in hawk-dominated populations, hawks bear the severe cost of frequent fights, and doves do not (10.6). So in many circumstances both types will survive indefinitely in the population (Maynard Smith 1982). In general,

frequency-dependent selection often gives rise to the coexistence of distinct types within a population. The evolutionary psychologist Linda Mealey has argued that psychopaths may represent one “minority strategy”—a variant form of the human species that can reproduce as effectively as the other types as long as it remains a small minority (Mealey 1995). According to this picture, if there were more psychopaths, there would be stronger selection against psychopathy than there is now. Of course, Mealey's particular idea is speculative, and we are not endorsing it here. Our main point is that the amount of morally and cognitively significant variation in the human population is an open empirical question. The fact that we recognize one another as members of a single species neither establishes that there must be some enormously significant characters distinctive of humans nor excludes that possibility.

Just as our species, like other species, consists of a varied population of individuals, so too do groups within a species. Human beings form overlapping pools of genetic variation, not distinct races, each with its own distinctive genome. Because our genetic material dates back to the beginning of the evolutionary process, and because human populations have typically been separate for only tens of thousands of years, only a small proportion of variation is distinctive of particular human populations. It can be argued that the average genetic distance between two individuals within a population is typically larger than the average genetic distance between two populations (Lewontin 1972, 1982a; Cavalli-Sforza, Menozzi, and Piazza 1994). Phenotypic differences may follow the same pattern. So we should not assume that the “races” that have been so important in human ethnic politics correspond to well-defined biological populations. They may instead be illusions generated by a focus on features that are more common in some geographic location or social group than in others, so creating a stereotype that is more applicable in that group. If we look only at these specially chosen features and ignore the exceptions to the stereotype, the members of another race seem to be a single, different type of human being. But even if these races are well-marked subpopulations with distinctive local adaptations—if, for example, Inuit facial structure really adapts them for life in the cold—we should not suppose that such subpopulations are invariant. The Inuit will only sample the full range of human variation, but they will still be a varied and evolving sample. Modern technology probably has to some extent eased selection pressure for adaptations to cold, so their facial features may well be in the process of change. In sum, the only real subdivisions of the human species are its many populations: groups that have been genetically isolated from one another for a longer or shorter time. These populations often do

not fit traditional “race” categories very well. The people of Finland are very historically distinct from other Northern European populations, but they share with those populations the socially prominent feature of white skin, so the differences are ignored.

Much of this book will help make clear how central the doctrine of the ubiquity of variation is to modern biological thought. In chapter 13 we discuss some recent evolutionary psychologists who have argued that the human mind is an exception to the rule. They have argued that all healthy humans inherit the same mental potential. Other parts of chapters 13 and 14 examine approaches to human evolution that fully embrace the ubiquity of variation and the possibility that distinct types coexist in a single human population.

1.3 Is Genuine Altruism Possible?

Richard Dawkins’s *The Selfish Gene* (1976) has been one of the most successful works of popular science. It argues that people, like other organisms, are “survival machines” built by their genes. These survival machines have no function in life but to produce as many copies as possible of the genes that built them. Dawkins was not the only person to advocate this view. The 1970s were the decade of *sociobiology*—the attempt to extend evolutionary explanations to human behavior. Like Dawkins, many sociobiologists saw humans as survival machines for genes. Most of them also agreed with him that all evolved human behavior must be designed to benefit those genes.

The idea that organisms are survival machines for genes rests on the view that genes are the only things that are passed on when an organism reproduces. So everything that one generation inherits from the last must pass down this genetic highway. An organism can inherit its mother’s long neck or its father’s knowledge of what is good to eat only if these characteristics are somehow stored in the genes. If individuals with long necks or sensible food preferences become more common in future generations, it is only because the underlying genes are surviving and proliferating. This view is known as *gene selectionism*, and the arguments for it are assessed in part 2, chapters 3–5.

Dawkins thought there was an important connection between gene selectionism and another important debate in biology—the debate over the evolution of *altruism*. An altruistic act is an act performed by one individual to benefit another. The question that biologists have debated is, if organisms exist only to benefit their genes, could evolution create altruistic organisms?

Gradually biologists came to realize that there was a problem in supposing that particular behaviors—for example, warning others of the presence of a predator—were altruistic adaptations. An *adaptation* is a feature of an organism whose presence today can be explained by the fact that it served some useful purpose in previous generations. A cat’s claws, for example, are adaptations for catching prey. How could evolution lead to adaptations that were costly to the animal engaged in the behavior but beneficial to other individuals? This problem was initially masked by a failure to distinguish clearly between adaptations that assist the survival and reproduction of individual organisms and adaptations that assist the survival and reproduction of the species or group of which that organism is a member. Because early evolutionists did not make this distinction, they were quite happy to explain some fact about an organism by pointing out its value to other individuals of the same species. For example, when a bird calls out a warning about a predator, it draws attention to itself. Surely a bird that stayed silent would do better in the struggle for existence, and so warning behavior could not evolve. One solution is to say that this behavior benefits the whole population of birds. Groups of birds that warn one another survive longer than groups in which birds sacrifice one another, and the superior survival of altruistic groups explains the warning behavior we see today. This is a “group selective” explanation.

George C. Williams is famous for his rejection of group selective explanations (Williams 1966). He argues that evolution cannot build an adaptation that is good for the group because of “subversion from within.” Organisms within a group are in competition with one another. Suppose that there are two kinds of organisms in a group: those that act for the good of the group, and those that do not. The “selfish” individuals would get all the benefits that occur because of the “altruistic” behaviors, but would bear none of the costs. So evolution would favor the selfish individuals. Therefore, a feature cannot evolve because it is good for the group, only because it is good for the individual.

Williams developed a second argument that connects the debate about altruism to Dawkins’s idea of gene selectionism. Williams argued that an adaptation can evolve only if it is reproduced in each generation. But only genes are passed on intact across the generations. So an adaptation can evolve only if it is produced by some underlying gene or genes. If this is true, then an adaptation can evolve only if it favors the gene(s) that produce it. Suppose that the bird giving warning calls makes its own “warning genes” less likely to be passed on, and the “silence genes” of other birds more likely to

be passed on. Under those circumstances, we would expect the “warning genes” to become rarer and rarer in the population, and “silence genes” more and more common. Eventually, calling would disappear from the population.

The ideas sketched in this section suggest that insofar as human behavior is a product of evolution, it is created by certain underlying genes, and is designed solely to assist the reproduction of those genes. The message that many social scientists have taken from these theories is that if they are to respect the biological facts, they face a dilemma. They must either insulate a large part of human behavior from biological explanation, or they must explain all human behavior in terms of individual self-interest. Both of these unattractive alternatives have been extensively explored.

However, the original biological theory is subject to much debate. The dilemma may well be false, for the case against group selection has been revisited. Perhaps the problem of “subversion from within” is not fatal. A potentially similar problem arises in the evolution of adaptations that are for the good of the organism. Organisms are groups of cells, and each cell carries groups of genes. Building an organism is a community project. So why isn't it undermined by selfish struggles between genes and cells to get into the cell lineages that become the gametes and perhaps ultimately new individuals? As it happens, such struggles sometimes do happen, and they are bad news for the organism. But usually they do not. Organisms possess features to guard against subversion. For example, in many animals a particular cell lineage—the *germ line*—is fixed as the source of all future gametes early in the growth of the embryo. A human female is born with a fixed number of potential eggs already in place. This phenomenon is known as the “segregation of the germ line.” A mutant “selfish” cell that is outside the germ line cannot hope to survive the death of the individual organism. We are familiar with just such “selfish” cells, which replicate freely without regard to the interests of the organism as a whole. They are known as cancers, and they have a very limited life span. If a cell is outside the germ line, its only reasonable strategy is to contribute to the general welfare of the organism in the hope of reproducing those copies of the genes within it that *are* in the germ line. By this means, most cells are forced to act for the good of the whole organism (Buss 1987).

Recent advocates of group selection have argued that groups, like individual plants or animals, possess a mechanism for enforcing cooperation and preventing subversion from within. This mechanism is population structure. Subversion from within relies on the fact that a selfish individual can associate with altruistic individuals and derive benefits from their altruism. If the dis-

tribution of individuals in a population makes altruists likely to associate with altruists and nonaltruists with nonaltruists, subversion from within may not be effective. We focus on altruism in chapter 8.

1.4 Are Human Beings Programmed by Their Genes?

Some human psychological characteristics are nearly universal. Almost all humans speak some language or other. Other features vary widely across cultures. Food taboos, for example, are often quite uniform within cultures, but not across them. Most people with a European cultural background find the thought of eating insects and their larvae repellent, though many will happily scoff raw oysters by the dozen. These preferences are reversed in other cultures. Still other features vary even within a culture. What explains these patterns, both of variability and of invariance?

A central problem within many contemporary debates on this subject is the relationship between human psychology and human genetic endowment. There are those who think both that our genetic endowment plays a central role in the development of many of our most important characteristics, and that this central role of genes in development implies that these characteristics are resistant to change by the manipulation of the developing individual's social environment. Sometimes this view is framed as an explanation of invariant, or allegedly invariant, features of human cultures. We all possess, say, genes for aggression, and hence aggression is found in all human cultures and will be found in all possible human cultures. Sometimes it is framed as an explanation of differences. In some views of intelligence, certain genes predispose their bearers to a lower IQ not just in statistically typical environments, but in all possible environments. *Genetic determinism* or *biological determinism* are labels for views of this general character.

A caricature version of biological determinism is the view that there are biological factors (usually genes) whose presence in an organism means that, no matter what other factors are present, a certain outcome will result. Thus, for example, a gene linked to the production of certain hormones in males might be thought to guarantee that its bearers will be aggressive, no matter what upbringing they are given. There are no biological determinists in this extreme sense. With the exception of mutations that are lethal no matter what, it is universally acknowledged that no feature of an organism will develop unless suitable environmental inputs are present. No one supposes that a plant will grow in just the same way no matter what sort of light or nutrients it receives. So the term *biological determinism* is often applied to more moderate, and often vaguer, views. Such a view might be that some trait will

emerge in any organism that has the right gene and that has a “normal” environment. A “normal” environment might be defined as one suitable for producing viable organisms of that sort. So to create an organism that has the gene but does not have the trait, it would be necessary to interfere with its development so severely that the resulting organism would be abnormal and probably not viable.

There are bodies of scientific literature that defend some version of biological determinism about some human characteristic or other. The sociobiological literature of the 1970s gave the impression that large swaths of human behavior were the expressions of genes specifically selected to produce those behaviors. It conveyed the impression that only the most drastic alterations in other developmental factors could prevent the production of these behaviors. The second-wave sociobiology of the 1990s has switched its focus from human behavior to the psychological mechanisms that produce it. It proposes that human psychology contains “Darwinian algorithms” selected for their fitness-enhancing effects in our ancestral environments. These mechanisms emerge in humans the world over, whatever their upbringing. No environment that produces a functional human psychology can avoid producing them. Proponents of the “language instinct” maintain something similar about the psychological mechanisms that allow us to learn language (Chomsky 1980; Pinker 1994).

The reverse of biological determinism is *environmental* or *social determinism*. Naturally, no one believes that the environment will produce a certain outcome no matter what genes an organism has. No hothousing program will get a chimpanzee into Harvard Law School. Instead, social determinism is the view that biology provides only a broad constraint on the range of outcomes that can be produced by environmental factors. Our genes prevent us from becoming Superman at one end and chimpanzees at the other. Within those constraints, however, only social factors affect what is produced. The striking variation we see in actual human cultures is the result of variation in social environment, and even greater variation is possible—indeed, likely—as novel cultures come into existence. There is no relationship between the variety of human cultures and any genetic variation that may exist in the human species. All actual human cultures, and all the many possible cultures that have not been tried, can be supported by any genome capable of producing a working human being. This view has been expressed by innumerable authors in the social sciences. A typical statement of it occurs in Moira Gatens’s book *Philosophy and Feminism*: “This is not to say that human being is not constrained by . . . rudimentary biological facts but rather that these factors set the outer parameters of possibility only. Within these constraints, if they can be called that, there is a variety of possibilities” (Gatens 1991, 98).

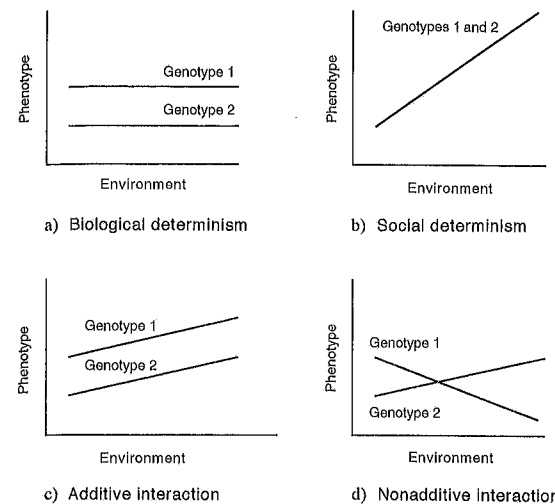


Figure 1.1 Norm of reaction graphs.

The observable features of an organism—its body and behavior—are jointly known as its *phenotype*. If there is one thing all biologists agree on, it is that the phenotype is the product of the *interaction* of genetic and environmental factors (Kitcher, in press). The weakest form of *interactionism* is one that even the strongest proponents of biological and social determinism can accept. The social determinist accepts that a human genome is needed if the environment is to produce a human individual, and the biological determinist accepts that no organism can develop without a suitable environment. A more substantial form of interactionism admits not only that both genetic and environmental factors are needed to produce a finished product, but also that *changes* in either can produce *changes* in the finished product. This is the sort of view often represented in a norm of reaction graph (figure 1.1).

A norm of reaction graph shows the pattern of variation in the kind of organism produced as genetic or environmental factors change (6.2). The two deterministic views just discussed can be seen as very extreme norms of reaction (figures 1.1A and B). Each of these views proposes that a change in one of the variables has no effect on the outcome, except at the extremes, where it has catastrophic effects. Figures 1.1C and D represent increasingly radical forms of interactionism. In the first, the relationship between the two variables is seen as purely *additive* (figure 1.1C). This means that a particular change in one variable has the same sort of effect no matter what value the other variable is set at. If norms of reaction are additive, then a change in a certain developmental factor will always produce a certain sort of difference in outcome. So if we were testing two genetic varieties of wheat, the influence of fertilizer would be additive if a little more fertilizer always produced,

for both varieties, a slightly greater yield. A genetic difference between two organisms would produce the same sort of difference between their phenotypes in any environment that the two share. So one variety of wheat would have a higher yield than the other at each rate of fertilization. This view allows the author of *Male Dominance: The Inevitability of Patriarchy* to argue that, although the effect of the hormone testosterone depends on other factors, assuming that men and women share the same social environment, the fact that men have higher levels of this hormone than women means that they will always be, on average, more aggressive, no matter what social environment we create (Goldberg 1973).

The assumption that interaction is additive also underlies a piece of reasoning often used to dismiss the idea that genes affect human behavior. This argument starts from the premises that there are many radically different forms of human societies and that genetic differences across these societies are minimal. It concludes that the genes have no important role in the production of the features that differ across those societies. The intuitive idea is that difference is explained by difference, so if there are large differences in human behavior but only small genetic differences between cultures, then genetic differences can be playing no significant role. But this argument assumes that interaction is additive. In fact, as Richard Lewontin has argued, gene/environment interactions typically are not additive (Lewontin 1974). So, in the right environment, a small genetic difference can make a large phenotypic difference (figure 1.1D). Jared Diamond has suggested that African American populations have genes that make them vulnerable to hypertension and similar diseases, but that the phenotypic effect of these “salt-thrifty” genes in the very different cultural context of their recent past was very different (Diamond 1991). Some Asian populations have high frequencies of genes that now act to protect their carriers from alcoholism. Their phenotypic expression—if any—in other contexts might have been quite different. So gene differences often contribute to widely varying phenotypes through naturally occurring environmental variation. But even if certain genes are correlated with certain phenotypes in all natural environments, we cannot “bracket off” the environment as a mere constant background factor, playing no important role in producing those phenotypes. For we cannot extrapolate the invariance of that gene/phenotype correlation to new environments. A novel environment may well produce a novel phenotype. Introduce alcohol into the diet, and a wholly new phenotypic effect occurs.

We suspect that dissemination of the idea that genes and other developmental factors may interact with the environment in multifactorial, non-

additive ways to produce outcomes would greatly improve the debate over the role of genetic factors in determining human behavior. It is probably fair to say that many people assume additivity when discussing gene/environment interactions simply because they overlook the full range of the possible. We hope to expand this sense of the possible, particularly in chapters 5–7 and 13–14.

1.5 Biology and the Pre-emption of Social Science

Many biological theories seem to threaten the independence of the social sciences: in Rosenberg’s phrase, biological sciences “pre-empt” the social sciences. Biology offers explanations for the very same characteristics of human beings and human societies that psychology and sociology claim to explain. Are these explanations rivals? Sometimes one explanation does displace another. Clever Hans was a horse believed by his owner to understand simple arithmetic. When given a simple sum (in German), Clever Hans could stamp out the answer with his hoof. It was discovered, though, that his owner had accidentally conditioned Hans to start stamping and continue until cued to stop. The stop signal was an unintentional change in his owner’s body posture when Hans had counted to the right answer. It was his owner’s response that Hans had been conditioned to detect. The explanation of his behavior in terms of reinforcement displaces its explanation in terms of arithmetic understanding. But one good explanation does not always drive out another. An explanation of a riot that appeals to the frustration, poverty, and alienation of the rioters, and an explanation in terms of an igniting incident of police brutality, may be mutually illuminating. So one central question is whether biology and the social sciences offer competing explanations, of which only one can be true, or complementary explanations that mutually illuminate one another (6.1).

Biology seems to have the potential to pre-empt the social sciences in two ways: by constraining the range of admissible social scientific hypotheses, and by displacing those hypotheses. We begin with the idea of constraint. The effect of the group selection debate on social science is typical of the way in which social science seems to be constrained by the findings of biology. In the last few decades there has been a great deal of pressure on social theorists to account for human behavior in terms of individual self-interest. This has given a sort of automatic credibility to some theories and created skepticism about others. According to traditional economic theory, individuals act so as to maximize their individual income, and any cooperative activities are produced as a side effect of this pursuit of self-interest. But in many

situations, common sense suggests that this assumption is flawed. Members of university departments, for example, do not refuse to work unless supplied with financial incentives. Despite the fact that their incentive structure primarily rewards individual research, they are often remarkably concerned about the smooth functioning and relative standing of the teaching units of which they are part. If we are convinced that humans are fundamentally selfish, then we will think up ways to explain this behavior in terms of self-interest. Perhaps a person who volunteers to run a graduate placement scheme in their spare time is trying to please the head of the department. If they do this even when their superiors disapprove, perhaps they are worried about the capacity of the department to attract students in the future and are acting to ensure their job security. Explanations of this sort are produced even when they seem rather forced, because it seems somehow disreputable to suppose that the persons simply values the success of the larger unit of which they are part. But if group selection has been a significant force in human evolution, then there is no reason to rule out this possibility. Group selection would select for individuals whose psychology allows them to sacrifice individual advantages for the good of the group. One obvious mechanism that might be selected would be the capacity to feel emotions such as loyalty, pride, and guilt. A person might experience these emotions in a way that motivates them to act for the good of the group.

The importance of the revival of group selection is not that it proves that mechanisms of this sort exist, but that it removes the assumption that they do not. It allows social scientists to concentrate on how people actually think and behave, rather than being constrained by ideas about how they “must” think and behave. In fact, the findings of social science about human motives may provide just the evidence biology needs to decide whether group selection has been an important force in human evolution. We shall return to this issue in chapter 8.

We now turn to the idea of displacement. A second threat to social scientific explanations seems to come from the suggestion that social and psychological traits are the products of evolution. The social sciences have traditionally assumed that only “human universals”—traits found in all or most human societies—can have evolutionary explanations. Culture is left to explain all those traits, such as clothing, family structure, or aesthetic preferences, that display a pattern of within-group similarity and between-group difference across human populations. This pattern is thought to result from cultural transmission in which individuals pass on mental representations by imitation and inculcation. Since most human characters of interest to social scientists do vary across cultures, this division of territory—biology gets to explain the invariant features, and the social sciences get to explain the

variable ones—suits social scientists just fine. No pre-emption here. But John Tooby and Leda Cosmides have pointed out that evolutionary biology has no reason to cede varying traits to the social sciences. Instead, varying traits may be the result of a disjunctive developmental program that responds to local environmental conditions. Tooby and Cosmides, and the program of evolutionary psychology for which they are standard-bearers, offer evolutionary explanations of many psychological characteristics that are both important and varied: family patterns, mate choice, and much else (Tooby and Cosmides 1992). If an evolutionary explanation of, say, mate choice or the distribution of resources to children really does displace one from the social sciences, then the social sciences are indeed threatened with pre-emption.

However, we have our doubts about the contrast, on which this debate depends, between biologically and socially produced traits. First, evolutionary and cultural explanations may be mutually illuminating rather than inconsistent with one another. One of the founders of the evolutionary analysis of behavior, Niko Tinbergen, distinguished four explanatory projects: (1) the evolutionary history of a behavior; (2) the current use of the behavior in the life of the animal, which may involve a change from (1); (3) the development of the behavior over the life of the organism; and (4) the psychological and other mechanisms used in the control of the behavior (Tinbergen 1963). Given Tinbergen’s distinctions, it’s quite plausible to suspect that evolutionary theorists and social scientists may be engaged in different explanatory projects.

Second, even when we are considering the evolution of human behavior, there is a problem in contrasting biology with culture, for humans have co-evolved with their culture. Humans have had a culture since before they were human. This culture is one of the resources that feeds into both the evolution of human traits over time and individual human development. Social environment must be an essential aspect of both our evolution and our development, so the contrast between the biological and the cultural looks shaky. The cultural plays a deep role within biology, and vice versa. This suspicion is reinforced by the “developmental systems” approach that we discuss in chapter 5. We take up these issues further in chapters 13 and 14.

1.6 What Should Conservationists Conserve?

Ecology refers to both a biological science and the increasingly popular values espoused by the environmental movement. The scientific discipline of ecology is the study of organism/environment interactions. The environmental movement draws on the science of ecology. Moreover, its agenda poses many of the most difficult questions that scientific ecologists are trying

to answer. These questions include the effects of environmental changes on a species, both changes that are the direct result of human action and those that are the result of the invasion or retreat of other species. In the 1960s, ecologists hoped to provide a general theory that could be used to predict the effect on ecosystems of, for example, the introduction of a new species. More recently, critics have stressed the historical nature of ecology. Predicting the fate of an ecosystem may be as difficult as predicting human history: particular facts count for too much and general principles for too little (Kingsland 1985). This issue is explored in chapter 11.

One conceptual issue with major implications for ecology, and for the environmental movement, is the nature of species (9.2). Species are the focus of conservation efforts all over the world. But many of the types of organisms that people try to conserve do not count as species under most scientifically well motivated definitions. New Zealand's black stilt and North America's red wolf are often cited as examples of "mere varieties" that are the subject of expensive conservation programs. Whether this matters depends on the source of concern for the environment. If conservation is seen as a human-centered activity, then we can justify our concern for a favorite color morph on aesthetic grounds. If we want to spend the conservation dollar to preserve biodiversity in some more objective sense, then we will be more concerned with the proper definition of species.

A connected debate concerns the proper measure of biodiversity. Intuitive conceptions of biodiversity seem to be sensitive to two different factors: first, how closely species are related, and second, how different a species is from its closest relatives. Relatedness is relatively easy to measure; divergence is more difficult. The degree of relatedness between two species can be expressed as the number of speciation events between them. This is the evolutionary equivalent of being, successively, sisters, cousins, second cousins, and so forth. A species represents more biodiversity the less closely it is related to its closest living relative. But this measure does not capture the intuitive notion of biodiversity very well. For example, the closest living relative of the Chatham Island black robin is a not too dissimilar robin. The closest living relative of the kakapo is another parrot, either the kea or the kaka, but neither of these is a large, flightless, highly sociable, nocturnal parrot. Many people have an intuitive sense that losing the kakapo would mean losing more biodiversity than losing the robin, even if the number of speciation events separating each species from its nearest relative were the same. This second aspect of biodiversity seems to concern whether a species has evolved into a new and different ecological niche, and whether it has changed physically in important ways. In section 12.3 we take up the idea of physical

divergence; in chapter 11 we ask whether there are really such things as ecological niches, and if so, what they are.

Many conservationists argue for a move away from preserving species and toward preserving whole *ecosystems*. The basic idea behind this change in strategy is that species are not viable as isolated things, but only as parts of a larger whole. No one doubts that ecological communities are very complex, and that each species interacts strongly with many others. But many doubt that these communities are very systemlike. The idea of a system suggests a relatively stable set of relationships, rather than a continual state of change. The popular image of an ecosystem as a rich, diverse community that tends to return to its original state after small perturbations may be as much the result of wishful thinking as of observation. Some ecologists have even claimed to show that diverse ecosystems are less stable, more changeable, than simple ecosystems (although the arguments connecting their data to this exciting conclusion have been criticized: Mikkleson, in press). A major source of the ecosystem concept is undoubtedly the ancient idea of "the balance of nature," an idea that has its roots in the intrinsic order of a universe created by God, but for which it is difficult to find scientific justification (Egerton 1973). We discuss these ideas in chapter 11.

We hope that these short discussions are enough to convince you of both the intrinsic interest of philosophy of biology and its practical importance. On with the show.

The Received View of Evolution

2.1 The Diversity of Life

As we saw in chapter 1, our conception of the living world is important both in itself and in its implications. If we are to understand that living world, evolutionary biology must explain three fundamental phenomena. One is life's variety. The world is rich in living things, yet that richness is limited in important ways. So we need to explain both why there are so many kinds of organisms and why there are not more. A second is adaptation. Organisms typically seem very well suited to their environments; they are *adapted* to their world. A third is development. Organisms "breed true": sparrows give rise only to sparrows, not to eagles. Furthermore, they do so through a long and complicated process of development from an apparently simple egg into a complex, organized, and differentiated adult organism.

In this chapter we introduce the main ideas—the "received view"—of contemporary evolutionary theory and its explanations of adaptation and diversity. Until recently, development played a less central role in evolutionary biology, and hence it is a less central element of the received view of evolution. Many commentators think that this relative neglect of development is itself significant, so we return to this issue in chapters 5 and 10. In the meantime, we focus on variety and adaptation.

Diversity and Its Limits

The world of life as we know it is fabulously diverse. Somewhere between one and a half and two million species have been described and named. There are no very reliable estimates of the number of living species still to be discovered, but one recent estimate is ten million (Minelli 1993, 129). Moreover, the life that now exists is only a fraction—quite likely only a tiny fraction—of the total historical diversity of the tree of life. Perhaps a quarter of

a million fossil species have been described, and they must be only a minuscule sample of all the species that have been and gone.

Yet though life is so diverse, there are gaps in that diversity. To explain the notion of a gap in diversity, we shall hijack Daniel Dennett's metaphor of "design space" (Dennett 1995). Dennett thinks of design space as a vast library containing the exact specifications of all the ways organisms might be—of all the actual and possible creatures. So it includes specifications not just for all the actual dinosaurs, but for all the possible ones as well; not just the formidable enough real *Tyrannosaurus rex*, but also the intelligent, arms-building descendants it might have had.

An appreciation of life's actual diversity is important, for that diversity has generated important controversies in evolutionary theory. It's easy for human beings to overlook much of the actual diversity of life because we tend to think of ourselves as typical of the organic world. But our idea of life's workings should not depend on such unrepresentative exemplars of the living world. We are highly atypical. The vast majority of organisms are not vertebrates like us. Most creatures are single-celled organisms. Probably the most fundamental division in the history of life is within the category of simple single-celled organisms called *prokaryotes*. Prokaryotes have relatively simple genetic systems, and their genetic material is not segregated into a nucleus. They are by far the most numerous of organisms: almost every organism that has ever been alive is a prokaryote. They come in two basic kinds, the *eubacteria* and the *archaeobacteria*, which diverged in the very ancient past (Ford Doolittle and Brown 1995). The archaeobacteria comprise a diverse group of bacteria-like organisms with weird metabolisms. These are the organisms that live in extreme environments and in extraordinary ways; for example, by breaking down sulphur compounds in superheated water from deep ocean hydrothermal vents. The eubacteria are, relatively speaking, the "standard" bacteria—the kind that live in us and in our food. Branching off from one of the prokaryote lineages, probably the eubacteria, are the *eukaryotes*. Eukaryotic cells are complex, with a nucleus containing most of their genetic material and some other molecular machinery separated from the cytoplasm by a nuclear membrane. We and all other multicellular organisms are eukaryotes. We are assemblages of eukaryotic cells. So we are offshoots of an offshoot: we derive from one of the three branches of single-celled life.

So our size and our cells make us atypical. But we are atypical in other respects as well. Plants are physically robust in ways we and most animals are not, often recovering from being mostly eaten or mostly burned. Plant life cycles involve astonishing physical transformations. For example, in many plant lineages, the equivalents of eggs and sperm exist for some time as

complex, independent individuals before producing cells that fuse with those produced by another plant to begin a new life cycle. In particular, in seaweeds and ferns, individual plants exist in two forms. The *sporophyte* form is *diploid*; that is, it has two copies of each chromosome in its cells. It propagates by producing spores. These spores are *haploid*; that is, they contain a single copy of each chromosome, formed by combining genes from the two copies in the sporophyte. If all goes well, these spores germinate and grow into haploid *gametophytes*. A gametophyte can be physically quite different in size and shape from its diploid ancestor. The gametophytes produce haploid gametes, and the fusion of two gametes is the origin of a new diploid sporophyte and a new generation. This complex cycle is known as *alternation of generations*. It is a central feature of the plant reproductive cycle, though the haploid stage is very reduced in seed-bearing plants, and it is only in more ancient lineages that we find both generations living as distinct organisms (Niklas 1997, 157–162).

Alternation of generations is not the only respect in which plant reproductive habits are different from ours. Plants often reproduce *vegetatively* as a chunk or bud grows into a new individual. Even for animals, our life cycles are atypically simple. Many invertebrates undergo great physical transformations across a single life cycle. For example, parasite life cycles often involve an organism traveling through a number of different hosts, in each of which its body form is very different. It's worth tracking through one of these cycles just to show how tame human development is by comparison. The trematode parasite *Dicrocoelium dendriticum* has a life cycle that takes it through three separate hosts. Adult flatworms live in livestock; they lay eggs in the livestock's dung. These eggs are eaten by snails, in which they hatch and in which they reproduce asexually for two generations before forming a mucus-covered larval mass, which the snail excretes. This mass of several hundred parasites is eaten by an ant, the parasites' next host. At this stage one of the larvae invades the ant's nervous system and changes the ant's behavior so that it spends much of its time on grass tips, thus greatly increasing the chances that the ant will be eaten by livestock along with the grass. Should this happen, the brainworm dies, but promotes the completion of the life cycle by the other larvae (Sober and Wilson 1998).

Some colonial organisms also have bizarre life cycles. The Siphonophora—jellyfish-like colonial hydrozoans such as the Portuguese man-of-war—are so integrated that it is hard to say whether they consist of many cooperating organisms or a single organism. The various cells (the *zooids*) within the man-of-war are specialized: there are floatation specialists, propulsion specialists, killer cells, and sex cells. In this respect, the man-of-war

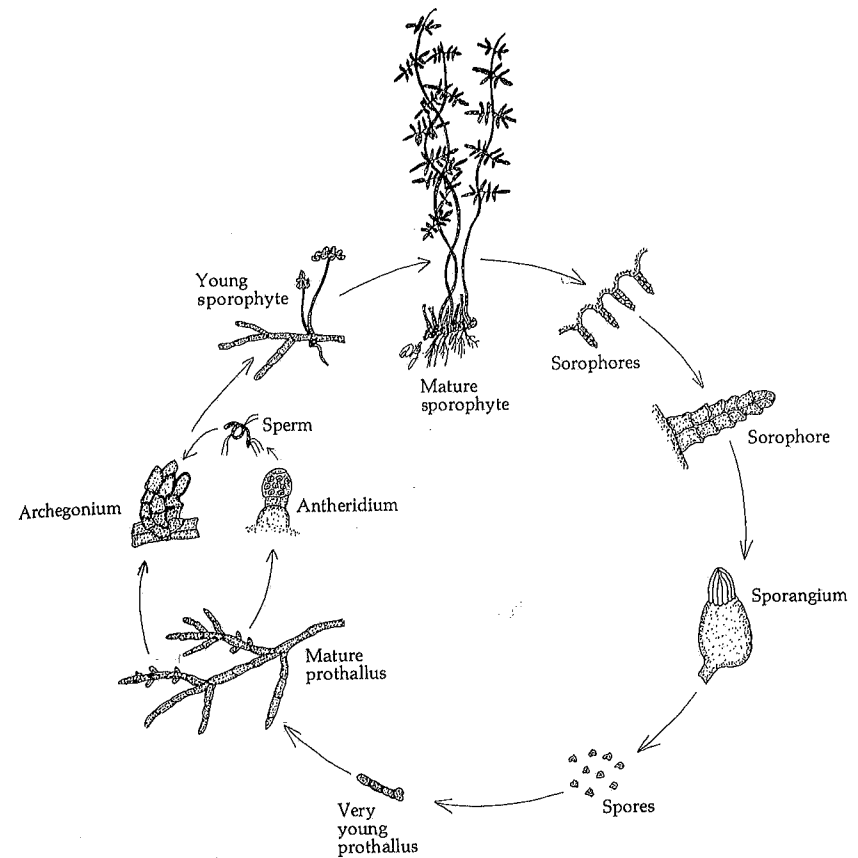


Figure 2.1 The haploid phase of a life cycle need not take the form of short-lived sex cells. The life cycle of *Lygodium*, like that of many other ferns, alternates between a haploid gametophyte (prothallus) and a diploid sporophyte. (From Jones 1987.)

seems to be a single organism. On the other hand, each cell within the colony has an independent origin in a fertilized egg. In contrast to the zooids that jointly form a man-of-war, cellular slime molds spend most of their life as independent cells. But when food runs out, they aggregate into a single body, which develops specialized parts. Some of the cells form a stem, ending in a group of cells that specialize in making spores. So these cells too seem to spend part of their life as individual organisms, and the rest as parts of an organism.

So vertebrates like us are unusually huge and unusually fragile, have relatively simple life cycles, and are built from the least common type of cell.

The fact that we are not the standard mode of life is important to remember, for some think contemporary evolutionary theory is too influenced by the vertebrate paradigm of the organism (see, for example, Dawkins 1982; Gould 1996d); we take up this issue in section 3.4.

The variety of life is the focus of important debates within evolutionary biology. Gould distinguishes between *diversity*—the number of species in existence—and *disparity*—the extent to which evolution has manufactured organisms that are genuinely different in their basic organization (Gould 1991). He argues that evolutionary theory needs to explain not just life's great diversity, but also its disparity—the extent of design space that life occupies. One important aim of evolutionary biology is to explain why some regions of design space are occupied and others are empty. We seek an explanation of the actual richness of the organic world, as well as an explanation of why that richness is not more impressive still.

One group of evolutionary theorists, the *process structuralists*, think that design space is highly constrained, and that many of the organizational features of organisms are explained by intrinsic physical constraints on life's possibilities (Goodwin 1994). There is no doubt that some imagined organisms are not really possible. The constraints of gravity and limitations on the power that can be delivered through standard metabolisms make it unlikely that winged pigs could fly. Other real limitations are less obvious. There may well be constraints on how an organism can grow and work, constraints that make some apparently possible organisms really impossible. Some frogs glide, but there are not, and as far as we know never have been, any flying amphibians. The amphibian metabolism might simply not deliver enough energy for powered flight. If not, there can be no true flying frog. However, even if there are many hidden constraints on design space, many varieties of organisms that are surely possible nevertheless are not to be found. Most possible organisms have never become actual. Though there are plenty of vegetarian lizards, there are no grass-eating snakes. Asexual and two-sex regions of biological space are occupied, but no species has ever required three or more sexes for reproduction. What is so special about two? In some lineages, we find the extremes of sociality known as *eusociality*. In eusocial bees, wasps, ants, aphids, a weird marine crustacean, and the equally weird naked mole rat, some animals have given up reproduction entirely. They live as sterile workers in extended families, and they are often physically quite different from their fertile siblings. African wild dogs are a less extreme example, but here too a single dominant female suppresses reproduction by the other females while herself having large litters. In contrast, while there are plenty of birds that temporarily forgo reproduction to help their parents raise their

siblings, none are irreversibly committed to sterility. So is the lack of eusocial birds living in avian hives a sad accident of history, or is there something about avian genes, avian bodies, or avian lifestyles that makes them unlikely or impossible?

We remarked above that evolutionary theorists seek to explain both the extent of and the limits on life's richness. One fundamental issue is how much of an explanation we should expect. It is no mystery that not all possible species are actual. The space of all the possible organisms there could be is so large that there has not been world enough or time for most of them to evolve. So often the explanation of a missing organism will turn on small accidents of history; no deep principle of biological organization will be involved. We have cheetahs, but no marsupial predators similarly adapted for running. Perhaps there was a marsupial lineage that might have gone down the cheetah path, but the right genetic variation never came together in the right organism at the right time. If so, the fact that there are no cheetahlike marsupials is just an accident of history. Given that many birds do breed cooperatively, it's quite likely that the absence of extreme sociality among the birds is just an accident of history. Eusocial birds didn't happen to evolve, and that is all there is to it.

However, there are other patterns in life's richness that are not likely to be historical accidents. Sex—one, two, but no more—is a good candidate for such a pattern. We shall see others. Gould, for example, has argued that almost no fundamentally new morphological organization has evolved since the Cambrian. The basic body plans all evolved in a short but exuberant burst a bit more than five hundred million years ago (Gould 1989). If this is true, he is surely right in thinking this shutting down of the machine that generated disparity requires explanation. There are also intermediate cases. Richard Francis has pointed out that we might expect many vertebrates to be able to change sex, as some fishes do. In many vertebrate species there is great variation in male reproductive success. Who has not seen documentaries of bull elephant seals fighting for supremacy? The few who succeed and become beachmasters will sire many pups. But most sire none. So if you were a slightly undersized male, or even a beachmaster beginning to feel your scars, surely you would be better off switching to the female role and settling for the modest output of a single pup. In any species in which male success is very uneven, and in which success is not just a lottery, we would expect "likely loser" males to turn female. Yet among vertebrates, only in fishes do we find a capacity to change sex (Francis, personal communication).

G. C. Williams wonders why there are no viviparous turtles (a *viviparous* animal gives birth to live young rather than laying eggs). Any of us who have

seen a turtle's laborious and dangerous struggle up a beach to lay her eggs, the dangers to the clutch, and then the hatchlings' desperate race to the water will agree that a viviparous turtle would make excellent adaptive sense (Williams 1992). Moreover, other reptiles are viviparous. There are plenty of viviparous snakes. Is the missing turtle just an accident, or does she signal an unexpected constraint on the power of evolution to build genuinely different turtles?

There is one fundamental pattern in disparity that is very unlikely to be a historical accident. Organisms come packaged into species. The existence of clusters of similar organisms is an obvious, pervasive, and almost certainly important feature of life as we know it. It is so obvious and so pervasive that it's easy to overlook the need for its explanation. Yet we can certainly imagine life without species. Consider Carnivore Hall, that region of design space where we find dogs, cats, bears, Tasmanian devils, weasels, snakes, and all the various extinct and merely possible carnivores. As it is, Carnivore Hall is occupied in patches. But it's not hard to imagine its denizens varying seamlessly in size. We can certainly imagine a world in which wolves, coyotes, hunting dogs, and the rest vary smoothly from mouse-size poodles to bear-size wolves. On top of this gradation in size, we can add smooth variation in other carnivore characters—for example, from the rather omnivorous bears and foxes to the more meat-specialized cats and snakes; from the runners to the stalkers to the hide-and-wait specialists. So we can imagine a world with carnivores, but no carnivore species. Yet that imagined world is very different from our world.

Thus evolutionary theory must explain why and how life came to be organized into species. Explaining the existence and importance of species might seem a particularly challenging problem for evolutionary theory, for that theory is committed to the idea that one species can be an ancestor of others. All marsupials, for example, are descended from a single ancestral species. Furthermore, in this view, there is no sharp distinction between species and varieties. So there is controversy over whether some population is a species or just a variety: whether, for example, the crimson rosella group of Australian parrots (the crimson, yellow, Adelaide, and green rosellas) is a cluster of very closely related species or a single species with a number of well-defined subspecies. And the varieties within a species—say, the North and South Island subspecies of the New Zealand robin—are themselves potential, incipient species. So the evolutionary theorist has to take on the tough job of defending both the idea that species are important units in the biological world and the idea that they evolve from one another. It has often been argued that evolutionary theory is committed to some version of an

“anti-realist” view of species; that is, to the idea that species only seem to be real objective units to us because of temporal limits on our perspective. That is not our view; we say why in chapter 9.

In sum, the living world presents us with both an array of species and an array of organizations. Life is *diverse*; there are numerous species. Life is *disparate*; those species manifest a considerable variety of adaptive structures and body plans. But though life is disparate, it is not endlessly so. There are adaptive structures and body plans that we might expect to see and do not. Evolutionary biologists diverge over what they take to be most problematic about these phenomena. The received view has focused on explaining how species are made—that is, on explaining the diversity of life. In contrast, some contemporary evolutionists take restrictions on disparity to be the most striking problem posed by life's richness. Mollusks, sponges, bivalves (oysters and the like), arthropods, and many kinds of worms first appear in the fossil record over five hundred million years ago, but the basic layout (the “body plan”) of these organisms remains unchanged. In the eyes of these biologists, this stability in modes of bodily organization over hundreds of millions of years requires explanation (Raff 1996). They think that evolutionary processes have been surprisingly conservative. In their view, we would expect to see more change than we do. A problem with evaluating these ideas is that, despite the intuitive plausibility of the distinction between diversity and disparity, we shall see in sections 9.3 and 12.3 that it faces very serious challenges.

Adaptation

The structured complexity of organisms, and their adaptation to their environment, is every bit as obvious as the diversity of organisms. Perceptual systems are classic examples of such complex, fine-tuned adaptation. One striking example is the extraordinary and interconnected set of mechanisms that jointly compose bat echolocation systems. Echolocating bats have mechanisms that enable them to produce high-energy, high-frequency sound waves. They have mechanisms that protect their ears while they are making such loud sounds. They have elaborately structured facial architectures to maximize their chances of detecting return echoes, together with specialized neural machinery to use the information in those echoes to guide their flight. There are many other equally wonderful examples of adaptation.

Darwin and some other evolutionary biologists have emphasized the *imperfection* of adaptation. Tree kangaroos have many adaptations for life in the trees; their paws, pads, and tails are in many respects unlike those of their

Figure 2.2 Like many other cave dwellers (troglodytes), the salamander *Typhlomolge rathbuni* has vestigial eyes and has lost its pigmentation. (From Barr 1968.)



ground-dwelling relatives. They do surprisingly well. But no biological engineer building a tree-dwelling mammal from scratch would come up with the tree kangaroo. Organisms exhibit design compromises, vestiges, and the accidents of their history. These imperfections, vestiges, and accidents are important to evolutionary biologists because they reveal so much about the organisms' histories. The tree kangaroo is instantly recognizable as a kangaroo because it is carrying so much of its history with it. The different designs of bat and bird wings reflect the separate evolutionary histories of these mechanisms of flight. A famous example of an accident of history is the strange design of the retina in vertebrates like ourselves: light has to go through the cell to the photosensitive pigment at the back. The eyes of squid and octopus, which evolved independently but are in most respects very similar to our eyes, have their photosensitive pigment at the end of the cell nearest the light source. History is perhaps most obvious in vestigial organs. Many cave-dwelling creatures, for example, have vestigial eyes, even though their current environments contain no light with which to use them. Evolutionary theorists are right to point to design compromises and vestiges, but the existence and importance of adaptation is not in serious dispute.

2.2 Evolution and Natural Selection

Darwin and his successors have constructed a "received view" of the pattern of evolution and of the mechanisms that allegedly explain that pattern. One characteristic formulation of this view derives from the work of Ernst Mayr, who has played a triple role as its architect, historian, and philosopher. He sees contemporary evolutionary theory as a complex of five separate elements:

1. The living world in general is not constant; evolutionary change has occurred.
2. Evolutionary change has a branching pattern. The species now alive are descended from one (or a few) remote ancestors.
3. New species form when a population splits and the fragments diverge. More specifically, most new species are formed by the isolation of subpopulations at the periphery of the ancestral species' range.
4. Evolutionary change is gradual. Very few organisms that differ dramatically from their parents survive to found populations.
5. The mechanism of adaptive change is natural selection.

These ideas are related, but they are no package deal. The first two were almost universally accepted in the biological community by the end of the nineteenth century. Darwin, Wallace, and others rapidly convinced the scientific community of the fact of evolution. Mayr's distinctive contribution to the received view is its conception of species and speciation through isolation and divergence. While most accept that there is an important insight in this conception, many think it needs some kind of revision. As the nature of species and speciation remains controversial, 3 is a good deal more controversial than 1 or 2.

In general, claims about the mechanism of evolution have remained controversial since Darwin and Wallace formulated them. In the first decades of the twentieth century, the Darwinian view of natural selection was seen as inconsistent with the developing science of genetics. For it was thought that Darwinism was committed to continuously varying traits, whereas genetics showed that trait differences were fundamentally discrete. It was not until the synthesis of genetics with evolutionary theory by Fisher, Wright, Haldane, and others in the 1930s that there was any consensus about the importance of natural selection in driving evolution. These scientists constructed mathematical models to show that genes inherited according to the patterns discovered by Mendel could replace one another in a population if they were

associated with very small differences in the capacity of organisms to survive and reproduce. Since Mendelian genes and their mutations were known to be real, and the mathematics of the new "population genetics" was demonstrably correct, earlier worries about the power of natural selection were laid to rest. However, more subtle questions about the nature and role of selection persist. While very few deny the importance of selection, its nature and role remain the key controversy in evolutionary theory. So the consensus on the role of selection remains incomplete. But to understand these controversies, we must first explain the received view of selection.

Natural selection has often been presented as the inevitable result of the interaction of three general principles. It is the consequence of

- phenotypic variation
- differential fitness
- heritability

Organisms in a population vary. Some variants will be better suited to dealing with the problems presented by their environment than others. These variants are more likely to survive to reproduce, or to reproduce more fecundly, than their fellows. If the characteristics that promote survival and reproduction are in part heritable, subsequent populations will be biased in favor of these advantageous traits. Thus the distribution of traits in the population will change. It will keep changing if the mechanisms that produce heritable variation add new traits to the evolving population over time.

Imagine the population ancestral to the superbly camouflaged Australasian bittern. Suppose that it too lived in reeds adjacent to wetlands, and sought to escape predation by crouching motionless when a threatening creature was near. It's quite likely that feather patterns varied in this ancestral population. If so, some birds had plumage that made them somewhat harder to see when they froze among the reeds. Those birds were more likely to survive to breed. This advantage need not have been dramatic. Perhaps the advantage held by our proto-camouflaged bittern ancestors was slight. Perhaps it helped only at dusk or dawn, or when a predator was at the very edge of its effective visual range. But a small edge is an edge nonetheless. That marginal advantage would sometimes make the difference between success and failure. So if bittern chicks tended to inherit their parents' plumage patterns, then the plumage patterns of the descendant generation would be somewhat different from those of the ancestor generation. Perhaps, for example, the harder-to-see birds of the ancestor population had more bars and fewer spots on their feathers than the average of their generation. If their chicks tended to be more heavily barred, then the average of their chicks' generation would

Box 2.1 Variation

In discussions of evolutionary theory, variation is often said to be blind, undirected, or even "random," though this last expression is misleading. The forces that give rise to new genetic variation in a population may or may not be deterministic. They are, however, insensitive to the adaptive demands on a population. If a rat population on an island is under extreme hunting pressure from snakes, so that only the very fastest rats have a chance of survival, that fact about the selection pressures on the rat population does not make variation in the direction of high rat speed any more likely. If new mutations arising in the population are relevant to speed at all, they are as likely to produce slower rats as faster ones. Indeed, they are more likely to produce slower rats, for there are more ways of slowing a rat down than of speeding one up. Of course, in such a situation, the slower rats will not be around for very long, but that is a matter of the retention of variation, not of its generation. Natural selection does not require that the mechanisms that generate variation be nondeterministic, or even that they be independent of the adaptive needs of the population. Rather, selection can produce adaptive change in a population even though the mechanisms that produce variation are insensitive to the direction of selection.

be pushed just a little in the direction of bars. The genetic mechanisms in the population responsible for variation would rebuild population variation anew. But not only would the average be edged toward more bars, fewer spots; in all likelihood, so would the limits. The most spotty bird of the chick generation would be less spotty than the spottiest bird of the parent generation. The most barred of the downstream generation would be more barred than any member of the previous generation. Over time, the patterns characteristic of the population would have changed.

In our imagined example we have mentioned only one feature of the plumage: bars versus spots. But color and orientation (and, of course, much else) in the birds' plumage will vary too. So if these traits make a difference in a bird's visibility, and if they tend to be passed on to the chicks, then feather color and the orientation of the spots and bars will change a little in the next generation. The average color will be shifted toward the color of the background vegetation. The average orientation of the bars will line up just a little better with the reed stalks among which the bird crouches. Thus with the color, orientation, and other elements of the feather patterns gradually



Figure 2.3 The Australasian bittern (*Botaurus poiciloptilus*) is superbly camouflaged. (From *Reader's Digest Complete Book of Australian Birds*, 1977.)

shifting, generation by generation, over time, the superbly camouflaged contemporary bittern evolves. Natural selection selects fitter organisms, and the heritability of their traits ensures a changed descendant population. Organisms are selected; populations evolve.

It is very important to see that this change depends on more than just variation, heritability, and fitness differences. The adaptive shift depends on *cumulative selection*. The adaptive shift to good camouflage took place gradually over many generations. Innovation is the result of a long sequence of selective episodes, not just one. For, as creationists endlessly tell us, the chances of a single mutation producing a new adaptation are very low. It is vanishingly unlikely that a single mutation could take us from a poorly camouflaged bittern to a well-camouflaged one. Mutations with large effects are almost always disastrous. If we take any well-functioning mechanism and make large, random alterations—if we double the size of one component, shrink another, and change the shape of a third—we are most likely to produce junk, not an improved machine. For similar reasons, major mutations are almost always lethal.

The extraordinary power of cumulative, as opposed to one-step, selection can be seen in the two ways to open a combination lock. To hit on the

Box 2.2 A Caution on Heritability

Selection works only on traits with some degree of heritability. There is no point selecting parents with good qualities if their offspring will not share those qualities. It is a common mistake to think that high heritability means that a trait is genetically determined—a matter of nature rather than nurture (1:4). In fact, heritability has very little to do with how traits are built in the growing organism. Selection cares about whether your children resemble you, but it doesn't care why. Heritability is purely a measure of how well the state of the parent predicts the state of the offspring.

To measure the heritability of a trait, we need a population of individuals, some of whom have the trait and some of whom lack it. If the only offspring with the trait are those whose parents had it, and all offspring whose parents had the trait also have it, then the trait is perfectly heritable. If the presence of the trait in offspring is unrelated to whether it was present in their parents, then the trait has zero heritability. In between lie the different degrees of heritability.

One way to make a trait highly heritable is to make the environment the same for everyone. By controlling other causes of variation, we can make heritable variation a higher proportion of total variation. For example, IQ scores will be more heritable if we provide equality of educational opportunities. Conversely, genetic uniformity in a population will reduce heritability. In a commercial forest of *Pinus radiata* in which every tree is a clone, most differences in height will be accounted for by differences in microenvironment. Just as it would be a mistake in the first case to infer that intelligence is affected only by genetics, it would be a mistake in the second to conclude that height is affected only by the environment.

combination of the lock in figure 2.4 by chance, you would have to get every wheel in the right place simultaneously. The chances of that are very low. But as every safecracker knows, if you can hear a faint click when each individual wheel falls into the right position, the problem disappears. It will take an average of five random tries to get the first wheel right, and then you can go on to the second. On average, fifty random trials will find the right combination. Natural selection works like the safecracker, by variation and selective retention. Natural selection, of course, does not involve any agent listening for the “clicks.” An organism with “one wheel right” will be the basis for the next set of variations because it will have more offspring than

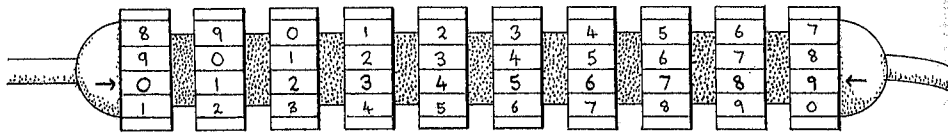


Figure 2.4 Like a safecracker, evolution cheats by solving complex problems one step at a time. (Adapted from Simon 1969.)

organisms with no wheels right. Its offspring with an advantageous mutation will have “two wheels right.” It is this absence of any overseeing agent that makes natural selection natural.

So cumulative selection is the only realistic way in which natural selection can produce adaptive shifts in a population. But for selection to be cumulative, some additional conditions are needed on top of the triad of variation, differential fitness, and heritability. Most obviously, if the direction of selection is not fairly constant over a number of generations, no new adaptive traits will be built. In nature, the direction of selection is not always stable. For example, selection on a certain population of Galápagos finches is not stable; wet and dry seasons select for different beak shapes (Weiner 1994). Another requirement for cumulative selection is a relatively low mutation rate. If the mutation rate is very high relative to the strength of selection, then the mechanisms that generate variation will swamp the effects of selection. But just as too much variation swamps selection, too much selection drives out variation. Intense selection pressure reduces the genetic variation in a population. Since most variation in the physical form or behavior of organisms (so-called *phenotypic variation*) is the result of shuffling of the existing genetic variation, rather than of new genes being created by mutation, reducing genetic variation within the population reduces the differences selection has to work on. Artificial selection by human breeders is typically very intense, as all the organisms with any unwanted character are culled. So artificial selection often produces significant change quickly, then runs out of steam. In the nineteenth century, the experience of animal breeders was sometimes thought to show that there are limits to how much each species can be changed, and hence that evolution by natural selection cannot make a new species. But natural selection operates over a far longer time scale, and so can afford to wait for more mutations to come along.

There is another important restriction on the process of cumulative selection: each intermediate stage must be fitter than its predecessor. Think of an evolutionary change from (say) white herons to streaky dark ones. Suppose, for the sake of argument, that a very dark heron would be fitter, because

better camouflaged, than any other color, but that a slightly dark heron would be easier to see than a wholly white one. If so, natural selection will not drive an evolutionary shift from white to dark herons because slightly darker variants will typically do worse than white ones. In the jargon of the trade, white herons are at a *local optimum*. That is, no small change in their current characteristics (with respect to color) will improve their fitness. Evolutionary theorists illustrate facts like these with geographic images called *adaptive landscapes*. In these diagrams, height represents fitness and the other dimensions represent features of the organisms. In an adaptive landscape, white herons would be represented by a hill, and very dark ones by a higher hill some distance away. Between the two hills would be a valley. Selection cannot drive a population off the top of a hill and down across a valley, even if a much higher hill is in the vicinity.

Thus variation, heritability, differential fitness, and the conditions admitting of cumulative selection result in selection on organisms, and this produces gradual change in populations over time. Such gradual change, continued over long periods of time, results in both adaptation and differentiation as distinct populations become adapted to distinct environments. Populations live in somewhat different local environments and thus face somewhat different challenges. Natural selection enables populations to respond to these different environments, and as they do so, the populations come to be different from one another. Thus one population of herons becomes small and cryptically colored as it becomes adapted to foraging within shallow marshy swamps; another becomes long-legged and white as it becomes adapted to foraging in open estuaries. As populations become increasingly distinct, their members become less able to treat one another as potential mates. Eventually the two populations will be reproductively isolated from one another, and hence speciation will have taken place. The differences between the two populations will have become permanent, leading to new species: to diversity. That diversity reflects both variation in the environment and the reaction of populations under selection to that variation.

In some views, speciation is wholly a by-product of the divergence of populations that have somehow become isolated from one another. In other views, as divergence takes place, there will be selection for reproductive isolation. The idea is that as two populations diverge, any hybrid matings that do occur will be penalized by selection. The issue from these hybrid matings may be sterile, nearly sterile, or suited to neither environment. So selection will start to favor, in both populations, any trait that makes its bearers less likely to accept a mate from the other population. Selection thus entrenches the differences between the two populations. The idea that isolation is criti-

cal to the formation of new species is an important part of the received view. There are, however, differing views on whether selection is important in reinforcing and entrenching isolation or whether new species arise simply as a by-product of isolation (Butlin 1987a,b).

Whatever stand is taken on this question, according to the received view, the two most striking features of life—diversity and adaptation—are both explained by natural selection. Natural selection is a constrained process. It is slow, and it is bounded by both previous history and the availability of variation. Nonetheless, the history of life is the history, essentially, of changes in populations of organisms as a consequence of natural selection.

2.3 The Received View and Its Challenges

Much in contemporary philosophy of biology revolves around the received view and its challenges. It's worth disentangling three strands in these debates. One focuses on the nature of natural selection itself—on what is being selected. A second concerns the place of selection within evolution. A third turns on the role of evolutionary theory within biology.

The Units of Selection

The received view conceives of natural selection as the result of competition between individual organisms in a population. Differences among those organisms result in their differing success, and those differences in success cause generation-by-generation shifts in the character of populations. The received view identifies some very familiar participants in life's history: organisms, populations, and species. In this view, the natural kinds of evolutionary biology are also the kinds identified by common sense. Adherents of the received view see no radical disjunction between our naive folk inventory of the biological world and that world as described by evolutionary biology. That is not always true of science. Color, for example, appears to us to be a simple objective property of material surfaces, but it turns out to be a very complex property. Indeed, perhaps color is not an objective feature of the world at all. The received view faces challenges, and among them are views that see a greater gap between the folk conception of the biological world and that derived from evolutionary theory.

One such challenge comes from the "gene's eye" conception of evolution, introduced by George C. Williams and developed and popularized by Richard Dawkins (Williams 1966; Dawkins 1976, 1982). According to this conception, when we think of the tree of life, we should think not so much

of organisms as of genes. In section 2.2, we emphasized that evolutionary change depends on cumulative selection, and this is the gene selectionists' point of departure. Individual organisms, they say, are unique. When organisms reproduce, their offspring are not copies of either parent. Genes, in contrast, are copied when organisms reproduce. Most of a child's genes are copies of parental genes. In the terminology developed by Dawkins (1982) and Hull (1981), genes are *replicators*. Since organisms cannot be copied, they cannot form chains or lineages in which each link is a copy of the one before it. But since genes can be copied, they can form such lineages: chains of copies, with each link being a copy of its predecessor. Gene lineages can sometimes be many copy-generations deep. They can vary in bushiness, too, for, depending on the number of offspring in each generation, a gene may be copied many times, and the copies may form an increasingly broad lineage as well as a deep one. Alternatively, a gene lineage may be narrow, with only a few copies existing in each generation.

Individuals within a population are typically in competition with one another because resources are limited, and not all will secure enough. In many species of birds, for example, a third or more of the population starves over the winter. The gene selectionist view of evolution takes this notion of competition and applies it to competing gene lineages. Collectives of genes replicate by constructing a *vehicle* or *interactor*—that is, an organism or something like an organism—that mediates both their interaction with the environment and their further replication. So gene replication is typically a very indirect process and thus demands scarce resources. According to this conception, the life or death of an organism has its evolutionary consequences indirectly, by influencing the copying success of the genes within it. Well-built organisms mediate more effective replication of the genes within them, the replicators that help to build them. So selection acts through organisms to target some genes rather than others by virtue of those genes' differential influence on their probability of replication. This differential influence is typically exercised through the gene's organism-building role. Usually genes have high replication capacities because they build effective organisms. So the consequence of selection is the differential growth of lineages of replicators, and hence, indirectly, the differential production of interactors of various kinds. According to this "gene's eye" conception of evolution, the received view is in the grip of the wrong picture of evolution. It fails to make the distinction between replicators and interactors, and to see the fundamental importance of replication in cumulative selection.

As we shall see in the next three chapters, these ideas have generated fierce controversy. Critics of the gene selectionist view think that it requires a very

Box 2.3 Replicators, Interactors, and Lineages

In the gene's eye view, there are three fundamental kinds of entities that play a role in evolution. *Replicators* are copied into the next generation: their pattern survives intact. So they may give rise to a potentially unbounded sequence of descendant copies. However, the materials and energy for construction of those copies must come from somewhere. Replicators must therefore interact with their environment, and they do so with differential success.

One means by which replicators compete is by constructing special-purpose entities. These entities aid replication by mediating the interaction of the replicator with the rest of the world. Hence replicators are usually assumed to carry information that is used in the construction of these entities. These special-purpose entities are *interactors*, or, in Dawkins's roughly equivalent terminology, *vehicles*.

Genes are the paradigm replicator: they are copied across the generations, and are usually thought of as comprising a recipe or a program used in the construction of organisms. Organisms are the paradigm interactor, but perhaps not the only kind. Perhaps, for example, a termite nest is a single interactor, jointly constructed by all the genes in the nest. In any case, the typical replicator codes for characteristics of interactors—organisms, colonies, populations. These interactors reproduce, and their differential reproduction results in the differential copying of replicators. If a particularly aggressive type of ant founds new colonies at a greater rate than others, that differential reproduction will cause a differential replication of the gene(s) that code for that increased aggression. The lineage of copies of the aggression gene will become bushier than those of its more peaceable rivals.

So this picture of evolution recognizes three basic kinds: replicators, which are usually, perhaps always, genes; interactors, which are usually, but perhaps not always, organisms; and lineages, which are chains of copied replicators.

simple relationship between an organism's genes and its traits. They argue that gene selection would occur only if there were something like a one-to-one relationship between genes and traits. Sober, for example, has argued that there is selection for one gene over its rivals only if an organism in the relevant environment is *always* fitter—more likely to survive, reproduce, and replicate its genes—by virtue of carrying that gene (Sober 1984b). In

turn, it seems that the only way a gene could guarantee such a fitness advantage is if it produced a specific trait. So we could think of selection as acting on lineages of bittern camouflage genes if there were particular genes, each of which gave its carriers a distinctive feather pattern. We would then have a cluster of feather pattern genes, and the one responsible for the most cryptic pattern would win out over its rivals coding for different patterns. Sober's interpretation of the debate has the merit of giving the gene selection hypothesis a clear empirical interpretation. But everyone agrees that the relationship between bittern genes and bittern plumage is anything but simple. So the critics conclude that gene selection is fatally flawed, while the advocates of gene selection deny that each competing gene needs to code for a distinctive trait.

A different, and perhaps less radical, challenge to the received view comes from defenders of "hierarchical" conceptions of evolution. They think that the received view has locked onto just one aspect of evolution. Populations of organisms do evolve under natural selection, just as the received view claims. But they argue that organisms are not the only biological entities that form populations. Recall the conditions for evolutionary change under natural selection. If a varied population of entities gives rise to descendants like themselves, and if those entities differ in fitness, selection will generate evolutionary change in that population regardless of the type of entity in question. Suppose, for example, that bat colonies form a population of colonies, in which individual colonies vary one from another. Perhaps some roost in hollow trees and others prefer caves. If colonies found others like themselves, so that daughter colonies tend to share their founders' roosting preferences, and if those colonies differ in fitness (for one type of roosting site may be safer than another), we should expect to see selection change the colony population: the proportion of colonies with the safer roosting preference should rise. Eusocial insect communities, and perhaps many other groups, seem to meet these conditions. In recent work, Wilson and Sober have drawn just this conclusion. They argue that we should regard hives and other cohesive animal societies as subject to selective forces (Wilson and Sober 1989, 1994; D. S. Wilson 1992). We consider these ideas in chapter 8.

Species, too, appear to form populations. Consider, for example, New Zealand's sadly extinct moa species. This group formed a population of closely related species. In the process of speciation, ancestral species give rise to similar descendant species, so we would expect features of species to be heritable. The exact ecological interactions among moa species are unknown, but we can assume that they affected one another and, in doing so, divided the New Zealand habitats of their time among themselves. This

division would have left some species confined to smaller, less productive, or more unstable habitats, and those species would be more likely to face extinction as a result of natural environmental fluctuations. The species would not just vary; they would differ in fitness. So the moa species group seems to meet the conditions that would generate selection among species. Hence we should expect to see natural selection at work in a pool of species.

Just as selection on populations has had its defenders, so too has selection on species. It has been thought to be part of the explanation for the prevalence of sexual reproduction. Sexual reproduction is a major puzzle in evolutionary theory. After all, why waste all that time, energy, and risk on finding a mate when you could reproduce asexually instead? (Sexual reproduction has subtler costs as well.) One answer goes something like this: Sexual reproduction, by mixing organisms' genomes, increases genetic diversity and hence the evolutionary flexibility of a species. Sexual reproduction allows the combination of two independently favorable mutations within a population. If Abu the baboon carries a dominant mutation that makes him more tick resistant, and Belle one that makes her more tolerant of dehydration, and they mate, some of their offspring may benefit twice. Organisms that reproduce by cloning would have to wait for one of the clone lineages to repeat the luck of the other—for example, for one of Abu's descendants lucking upon Belle's mutation. So sexually reproducing species respond better to environmental change. They are more likely to resist extinction if their environment changes in ways that demand that they, too, change. As it happens, there are different, more recent theories of the adaptive advantage of sex to the individual organism. Moreover, sex can act as a brake on evolutionary change. Migration between populations followed by mating can homogenize them, stopping either population from adapting to its specific local conditions. So this particular idea has slipped from favor. But there are other features of the pattern of life that species selection may explain. Lloyd and Gould (1993), for example, have recently argued that variable species are more resistant to extinction than more homogeneous species, and that species selection has acted to preserve variability within species lineages. We return to this issue in section 9.4.

According to the hierarchical view, selection can be operating simultaneously at many levels. An individual organism competes in a population of organisms. If that organism is, say, a wolf, she may be part of a pack competing in a population of packs. It may even be that wolves, coyotes, and dogs form a population of species that are in competition, one with another. Perhaps there are features of the coyote species itself that have enabled it to adapt better to human-altered environments and hence replace the wolf in most of

its American range. When selection operates at different levels at one time, we should expect to see conflicts between the levels at which selection occurs. What's good for General Motors is not necessarily good for GM's office cleaner. Equally, what's good for, say, a baboon troop is not necessarily good for Abu, a baboon currently low on the totem pole in his troop but wanting to rise. Group selection for internal cohesion will push baboon organization one way. Individual selection favoring those who insist on getting a piece of the action will push it another way.

The hierarchical conception of selection does not reject the received view outright. Rather, it proposes that the received view mistakes the most important case for the only case. Those skeptical about hierarchical conceptions of evolution usually do not think it impossible in principle for individuals collectively to form metapopulations that are selected. But they think that, in practice, selection at the level of individual organisms so dominates all super-individual processes that the latter are of no evolutionary significance. We will consider whether they are right in chapters 8 and 9.

Selection and Evolution

So one set of issues within evolutionary biology revolves around the units on which selection acts. But others turn on the effects of selection, and on its role within the total matrix of forces that jointly explain the evolution of life. These issues became prominent in evolutionary theory through the work of Gould and Lewontin (Gould and Lewontin 1978; Lewontin 1985a). Their attack on "adaptationism" initiated a fierce debate on the role of selection within evolution. In this debate, at least four issues are tangled together.

First, does the received view overstate the importance of adaptation? At first glance, it would seem that there is no room here for deep disagreement. No evolutionary theorist denies the existence of complex adaptation, or denies that natural selection plays some important role within evolution. Equally, no one denies the causal importance of other factors in evolution. Selection can operate only on the variation that is available, and history, development, and genetics determine the range of variation. Everyone accepts, for instance, that some genetic changes sweep through a population because they "piggyback" on others. If there is a favorable mutation in a mitochondrial gene, and as a consequence, that mutated gene becomes more frequent in the population, all the other genes in that mitochondrion will share in its good fortune, because all the mitochondrial genes are copied as a whole and are transmitted as a whole. So an advantage to one is an advantage to the whole mitochondrial genome. Moreover, there is no question that

chance is important too. Fitness advantages are propensities; they make one outcome *more likely* than another. Better camouflaged bitterns have a better chance of surviving than less well camouflaged ones. But, especially in a small population, a greater chance of success need not translate into actual success. If a fair coin is tossed four times, we might well get three heads. If it's tossed a thousand times, however, we are extraordinarily unlikely to get 750 heads. So the smaller the population, the more likely it is that the actual success of organisms with some trait will vary from the expected fitness of organisms with that trait. Yet the received view itself—especially Mayr's version of it—suggests that most evolutionary change takes place in small, isolated populations, in which chance—both lucky and unlucky accidents—can play an important role. So the potential importance of both selection and other factors seems accepted on all sides, and there seems room for disagreement only on the mix of factors that explain particular cases.

But the impression that there can be no global disagreement on the importance of selection is misleading. Lewontin and other critics of what they call *adaptationism* claim that those in the grip of the received view pay only lip service to the possibility of evolutionary explanations in which selection plays a secondary role. As Lewontin and his allies read the situation, adaptationist evolutionary biologists, despite conceding the potential importance of chance and history, tacitly assume that virtually every striking feature of an organism somehow contributes to its survival and reproduction, and that that contribution explains why the creature has that feature. In other words, adaptationists suppose that most traits have functions. Bats, for example, often have elaborate facial architectures that play an important role in echolocation. A splendidly bizarre example is the large-eared horseshoe bat *Rhinolophus philippinensis*, which can broadcast directional ultrasound through its elaborately structured nose, so that it can eat and navigate at the same time. To claim that its facial structures function in echolocation is to say that they exist because of their role in the ancestral bat's echolocation. Those ancestral bats got to be ancestors in part because their facial architecture gave them an echolocating edge vis-à-vis their contemporaries. Thus that architecture's role in helping the ancestors of today's horseshoe bats echolocate explains its existence in bats today. This much is uncontroversial. At issue, though, is the role selection must play in this history for these functional claims to be true. Those skeptical about adaptationism think that an adaptive claim about bat facial structure depends on a very strong claim about the role of selection in its evolution. They think that adaptationist hypotheses are committed to an "optimality hypothesis" about bat facial structure: that bat echolocation is the best it could possibly be. As we shall argue in chapter 10, we very much doubt that those who think that the effects of selection



Figure 2.5 The large-eared horseshoe bat (*Rhinolophus philippinensis*), found in Australia and the Philippines, has impressive facial structures that assist echolocation. (From Strahan 1983, 297.)

are pervasive, and who think that most complex traits of organisms have functions, are committed to the idea of the best possible bat.

So the first thread in the adaptationist debate focuses on the importance of selection. The issues are partly empirical and can be addressed only on a case-by-case basis: How much variation do natural populations have? How often are populations small enough for chance events to be important? How often do deleterious genes spread by being physically linked to advantageous ones? But they are also partly conceptual: What role must selection play in the evolution of a trait for that trait to have a function and be an adaptation?

A second thread in the adaptationism debate focuses on the relationship between selection and the other factors that help to explain evolutionary change. How, if at all, can we compare these different factors? In thinking about the evolution of a trait, history matters. Adaptation through natural selection never redesigns from the ground up, but instead tinkers with the results of earlier history. Consider a feral cat hunting in the Australian bush. In semiarid areas of Australia, feral cats are considerably larger than their domestic counterparts, and are light tabbies. Size and color are apparently adaptations of that particular cat population—dark kittens are vulnerable to eagle predation. Some other aspects of their biology are the result, no doubt,

of earlier selective processes that shaped the species. Others are inheritances from their felid, mammalian, and even earlier ancestors. These inheritances constrain the future trajectory of this population of feral cats.

We can make good sense of the idea that the moon has a greater influence on the earth's tides than the sun, for we can sum those effects and compare their relative magnitude. But it is unclear how to make sense of the idea that feral cats' biology is more the result of their history than of selection. History and selection conspire together to drive the evolutionary trajectory of the population. Both are necessary; neither is sufficient. Those skeptical of adaptationism often speak of historical constraints on natural selection as if the history of the cat lineage somehow blocks or prevents the operation of selection. There is something strange about this idea, for it is only the history of previous cat evolution that makes possible the adaptive shifts we now observe. Yet there is something right about this idea too. As we have noted, tree kangaroos, despite their adaptations for arboreal life, are obviously terrestrial mammals jerry-built for or press-ganged into life in the trees. We return to these problems in chapter 10.

A further problem is that some evolutionary patterns seem to be independent of selection. In 1972, Eldredge and Gould put forward the hypothesis of *punctuated equilibrium*. In this view, most species, over most of their life spans, do not change in body or behavior. Evolutionary change and speciation occur in brief—geologically speaking—bursts. Species come into existence quickly, remain phenotypically the same throughout most of their life spans, and then disappear, either through fragmentation into descendant species or extinction. More recently, in his *Wonderful Life* (1989), Gould argued that the standard image of life's history is quite mistaken. We typically think of life as becoming both more diverse and more disparate over time, viewing the history of life as a change from few, simple, and comparatively similar organisms to many, complex, and highly differentiated ones, like the pattern in figure 2.6a. Not so, he argued. Though *diversity* has increased, animal life was maximally *disparate* at the time of the Cambrian explosion, and has become less disparate since then, a pattern more like that in figure 2.6b. This is an idea about macroevolutionary patterns on the grandest possible scale.

How do these ideas about the history of life relate to the received view? While no one now suggests that the hypotheses of punctuated equilibrium or of maximum disparity in the Cambrian are inconsistent with the received view, equally, the thought goes, nothing in the received view predicts them. It is silent about that whereof it should speak. The received view is incomplete: there is at least one important feature of the history of life—the

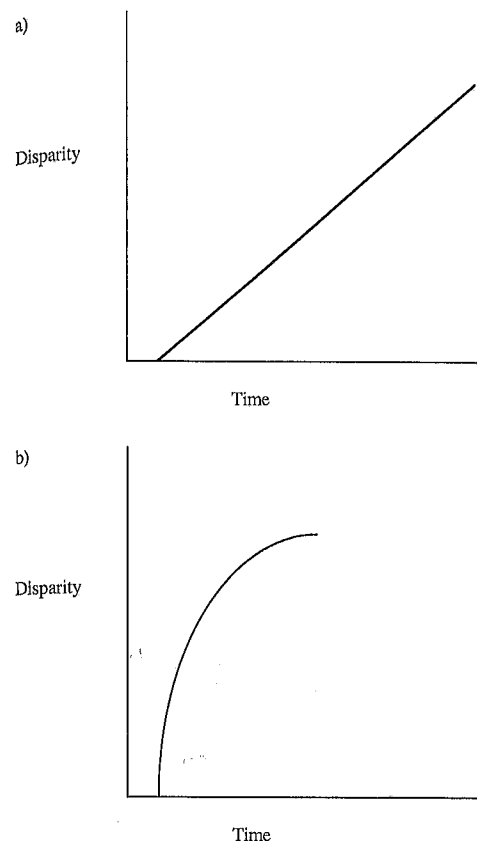


Figure 2.6 (a) The received view would lead us to expect a more or less uniform increase in disparity over time. (b) Gould suggests that disparity reached a plateau early in the history of animal life.

plateau in disparity—that it does not explain. We shall explore these issues in chapter 12.

A third strand in the debate over the role of selection in evolution is methodological. Few will deny that bat echolocation is the product of natural selection. These mechanisms exist because they enable bats to navigate and hunt in the dark. But adaptation is very often less obvious than this. Are psychopaths a “minority strategy” that has been selected during human evolution to take advantage of the relatively benign behavior of most other humans? Is menstruation an adaptation to rid female monkeys of sperm-borne disease organisms? How can we test these ideas? There has been a debate about the strength of evidence needed to establish an adaptationist hypothesis. Gould and Lewontin (1978) refer disparagingly to “just so stories” told by some theorists. A “just so story” is an adaptive scenario, a hypothesis about what a trait's selective history might have been and hence about what

its function may be. Gould and Lewontin think that it is just too easy to think up such adaptive scenarios. Hence we should not accept an adaptive hypothesis just because it sounds plausible. So how do we show that a trait is the product of selection, and how do we show that it was produced by a particular set of selective forces? We deal with this question in chapter 10.

Finally, enmeshed in all these other disputes are questions about the proper scope of evolutionary explanations. One arena in which this issue has surfaced with great bitterness is the debate over evolutionary explanations of human psychological and social organization. In 1975, E. O. Wilson published *Sociobiology*, an adaptationist account of social evolution among animals. In a speculative final chapter, he extended these ideas to humans. This work was followed by many others that were even more speculative, often without emphasizing, or even admitting, their speculative nature. Moreover, they often advanced adaptationist explanations of features of human life that many people wanted to reform: differences in sex roles, xenophobia, rape, and the abuse of stepchildren, to name just a few. The response was often savage, but in the heat, confusion, and rancor, two somewhat different critical strategies emerged.

One response has been to accept that, in principle, evolutionary explanations of important aspects of our psychology and society are possible. According to this line of criticism, evolutionary theories of human nature are potentially promising. But human sociobiology as actually practiced has typically consisted of poor and ill-supported evolutionary hypotheses. Kitcher (1985) typifies this critical response. The second response has been to argue that sociobiological explanations of human social and psychological characteristics are mistaken in principle. Human psychological and social traits are the result of human culture. Evolutionary theory ought to explain how the human lineage evolved the capacities that enable us to be an enculturated species. But ever since we acquired our cultures, it is those cultures that explain the distinctive and interesting features of us and our societies (Levins and Lewontin 1985). We explore these issues in chapters 13 and 14.

Evolution within Biology

Finally, in thinking about the received view, we need to think about the role of evolutionary theory within biology generally. Challenges to the received view can have important ramifications for our conception of the place of evolutionary theory within biology. For instance, they force us to reconsider the relationship between evolutionary biology and ecology. One of the virtues of the received view is the elegance and simplicity of its picture of that relationship. It perceives evolutionary change as driven by the demands

the environment imposes upon organisms. Selection shapes organisms to their environment. Thus evolutionary theory is linked to, and depends on, ecology, because ecology provides a principled analysis of the environment and the selective pressures it generates. Ecology provides this analysis paradigmatically through its depiction of a biological community as a set of interrelated niches. These niches specify the different roles, or ways of making a living, that organisms have in their environments. Since organisms can vary in the degree to which they fit their niche, selection will prefer those that fit their niche well over those that fit it less well. In one of evolutionary biology's most vivid metaphors, one of the architects of the received view, Theodosius Dobzhansky, articulates this view of the relationship of ecology and evolution:

The enormous diversity of organisms may be envisaged as correlated with the immense variety of environments and of ecological niches which exist on earth. But the variety of ecological niches is not only immense, it is also discontinuous. One species of insect may feed on, for example, oak leaves, and another species on pine needles; an insect that would require food intermediate between oak and pine would probably starve to death. Hence, the living world is not a formless mass of randomly combining genes and traits, but a great array of families of related gene combinations, which are clustered on a large but finite number of adaptive peaks. Each living species may be thought of as occupying one of the available peaks in the field of gene combinations. The adaptive valleys are deserted and empty.

Furthermore, the adaptive peaks and valleys are not interspersed at random. Adjacent adaptive peaks are arranged in groups, which may be likened to mountain ranges in which the separate pinnacles are divided by relatively shallow notches. Thus, the ecological niche occupied by the species "lion" is relatively much closer to those occupied by the tiger, puma, and leopard than to those occupied by wolf, coyote, and jackal. The feline adaptive peaks form a group different from the group of canine "peaks." But the feline, canine, ursine, mustelid and certain other groups form together the adaptive "range" of carnivores, which is separated by deep adaptive valleys from the "ranges" of rodents, bats, ungulates, primates, and others. . . . The hierarchical nature of biological classification reflects the objectively ascertainable discontinuity of adaptive niches, in other words the discontinuity of ways and means by which organisms that inhabit the world derive their livelihood from the environment. (Dobzhansky 1951, 9-10)

If the received view is mistaken or incomplete in important ways, especially in its conception of the role of selection in evolution, the relationship between ecology and evolution needs to be rethought. In chapter 11, we sketch out some of the options for this rethinking.

So one problem concerns the relationship between evolution and ecology. But we also need to integrate our picture of evolutionary biology with developments in the other major domains of biology. The "molecular revolution" in biology blasted off after the discovery of the structure of DNA by Crick and Watson in 1953, and it is clear that many thought that our new understanding of the molecular mechanisms of inheritance would make evolutionary biology redundant. E. O. Wilson's autobiography, *Naturalist* (1994), gives a graphic account of the atmosphere of this period, and of the apparent institutional imperialism of molecular biology from the perspective of one who felt threatened by it. (Some will find this ironic, for Wilson, as chief instigator of human sociobiology, is himself suspected of writing redundancy notices for those employed in anthropology, sociology, and psychology departments.)

Tinbergen and Mayr, each in somewhat different ways, showed that it would be a mistake to suppose that a molecular understanding of the mechanism of inheritance would replace an evolutionary one (Tinbergen 1952, 1963; Mayr 1961). As we noted in section 1.5, Tinbergen distinguished four questions we could have in mind in asking why a bittern stands still with its bill pointed directly at the sky. (1) We could be asking for a *proximal* explanation: an explanation of the hormonal and neural mechanisms involved in triggering and controlling this behavior. (2) We could be asking for a *developmental* explanation: an explanation of how this behavior pattern emerges in a young bittern. (3) We could be asking for an *adaptive* explanation: an account, that is, of the role this behavior currently plays in the bittern's life. (4) Finally, we could be asking for an explanation of how and why this behavior pattern evolved in this bittern population or in its ancestors.

The first of these projects is specific to the biology of behavior, but the others apply to any trait. However, as we shall see (especially in section 6.1), identifying different explanatory projects only partially resolves the relations between different domains of biology. For while these projects are distinct, they are not independent. Our views on development, for example, affect our views on evolution, and vice versa. What is developmentally possible influences what is possible in evolution through its effect on the range of variation available to selection. At the same time, developmental mechanisms have themselves evolved. But while no one denies that there are connections between developmental and evolutionary questions, there is a good deal of controversy about the nature of those connections. For there is an influential

line of thought within both developmental and evolutionary biology that suggests that the received view has failed to include developmental biology, and perhaps even is tacitly inconsistent with it. Those who suspect the received view of adaptationism typically think that it greatly understates the importance of developmental constraints in explaining why organisms are the way they are. Perhaps primates have two arms rather than three simply because it is impossible to grow an organism with that asymmetry. Perhaps unsuccessful male elephant seals cannot turn female because it is impossible to make internal changes of such complexity in an organism that must continue to lead a relatively normal life throughout its metamorphosis. Indeed, the only possible counterexample to the claim that the significance of adaptation is universally accepted is the view of the process structuralists, who suggest that the constraints on possible organisms are so severe that natural selection plays only a minor role in evolution (Goodwin and Saunders 1989; Goodwin 1994). We discuss these issues in chapter 5 and in section 10.5.

More generally, as G. C. Williams (1992) notes, evolutionary theory operates on the assumption of mechanism; that is, on the assumption that causal processes in biology involve no occult forces. The mechanisms involved in development, inheritance, selection, and speciation are, or are composed of, standard physical and chemical processes. Inheritance, for example, might be physically or chemically very complex, but it does not involve fundamental processes found only in living matter. The mechanistic hypothesis in biology moves molecular biology onto center stage, for, *prima facie*, molecular biology vindicates mechanism, and perhaps even stronger views about the relationship between biological theories on the one hand and those about physical and chemical processes on the other. These issues are the focus of chapters 6 and 7, where we take up the surprisingly complex problems of saying what a gene is and of describing the relationship between genes as they have been conceived in evolutionary theory and the structures of DNA and the associated cellular components currently being revealed by molecular genetics. In the next part of the book we look at gene selection and the problems it poses.

Further Reading

2.1 The idea of design space is introduced in Dennett 1995; the idea is adapted from Dawkins 1986. For some insights into the extravagance of the actual biological world, see E. O. Wilson 1992. For some sense of the weirdness of organic form, browse in Margulis and Schwartz 1988. Most of the genuinely weird forms are to be found among the invertebrates; one standard survey of these is Brusca and Brusca 1990. Gould's essays exhibit his

wonderful feel for the strange; see Gould 1996e for a very recent celebration of the intricate complexity of parasite lifestyles, and Gould 1996c and 1996a for even more vigorous statements than usual of the dominance of bacteria in the history of life. J. T. Bonner discusses the world of the slime molds in most of his books, most recently in Bonner 1993. For some of the constraints on possible design, see McMahon and Bonner 1983, which discusses the relations between body size and possible body design. Vogel (1988) discusses the effects of differing physical forces on organic design more generally.

2.2 Evolutionary theory is so hotly debated that it's not surprising that there are no uncontroversial introductions to the received view and the controversies it has generated. Perhaps the closest is Depew and Weber 1995, a work with the added advantage of detailed reading guides. But though it is very fair-minded, it is also a very long, detailed historical treatment of the development of Darwinian ideas. Another, less terrifyingly long, historical introduction is Mayr 1991, but it is by a partisan of the received view. Peter Bowler has also produced a number of historically based introductions to evolutionary thought; the one with the broadest scope is Bowler 1989. Cronin (1991) blends historical and contemporary material, concentrating on two problem cases for evolutionary theory: sex and altruism. This is a clear and lively read, but it is very partisan. She writes from the "gene's eye" perspective without making it clear just how controversial that perspective is. Richard Dawkins's introductory books are even more lively, more readable, and more partisan, but they never pretend to be anything else (Dawkins 1986, 1989, 1995, 1996). However, the clarity and vigor of Dawkins's account of the importance of cumulative selection, and of the difference in power between cumulative and single-step selection, is unsurpassed, and this aspect of his thought is not controversial. A more understated account of the same basic picture is Ridley 1985. Defenders of a hierarchical conception of evolution have written plenty of books, but none really intended as general introductions to their views. Perhaps Eldredge 1985a might be the closest. For a very good account of the development and, from his perspective, fall from grace of the received view, see Gould 1983a. Futuyma 1998 and Ridley 1993b are much more technical surveys of evolutionary biology. For good accounts of the critical concepts of the received view, adaptation, fitness, and heritability, see the relevant entries in Keller and Lloyd 1992.

2.3 Suggested reading on these issues will be given at the end of the chapters in which these problems are discussed more fully.



Genes, Molecules, and Organisms