## Chapter

# 10

## **Adaptation, Perfection, Function**

#### 10.1 Adaptation

As we noted in discussing theories of taxonomy (9.3), there are countless ways in which we can describe organisms. Egg laying, a poison spur, and an extraordinary bill are all striking and distinctive traits of the platypus. But the platypus has many other features less likely to be highlighted in natural history documentaries, such as the distance between the eyes divided by the inter-ear distance. That may seem a rather esoteric property, but anatomical descriptions of the platypus in texts on Australian fauna will include many that seem equally obscure: for instance, the length, shape, and weight of its various intestines. *Handbooks to the Birds of Anywhere* always specify the number of various types of wing and tail feathers. So organisms have many characteristics, some of which we routinely measure and describe, and others that languish unstudied. One pressing problem biologists face is making this choice: determining which aspects of an organism are important in its evolution, ecology, and development.

Among the traits biologists study, some are clearly special. As we discussed in section 2.2, some traits are favored by natural selection because they increase the relative fitness of their bearers. In other words, they are *adaptive*. A trait that exists because natural selection has favored it is called an *adaptation*. The eye-blink reflex exists because it protected the eyes of ancestral organisms and so increased their fitness. This reflex is an adaptation "for" protecting the eye. Each adaptation was selected for some effect or effects that influenced the fitness of its bearer.

However, despite the close links between these two concepts, adaptiveness is neither necessary nor sufficient for a trait to be an adaptation (Sober 1993, 84). The human appendix, for example, is an adaptation that is not adaptive. Humans no longer need to digest cellulose, and having this home for symbiotic bacteria that can break down that substance no longer increases our fitness. But the appendix is definitely an adaptation. It evolved through natural selection because it enhanced the fitness of our distant ancestors. So it's an adaptation without being adaptive. The appendix is a *vestigial* trait: a relic of previous selection. Conversely, the ability to read is adaptive without being an adaptation. Literacy is highly adaptive in most modern human societies, as the disadvantages suffered by dyslexic people testify. But the ability to read is probably a side effect of other, more ancient cognitive abilities. The invention of reading was probably much like the invention of computers. The use of computers did not originate in a few people with special new genes for programming. Computer use did not spread through the population because users had more children than nonusers. Our ability to read and use computers almost certainly depends on a set of more general cognitive capacities—capacities that have not changed in the few thousand years in which literacy has spread.

So some traits exist as a consequence of natural selection for one or more of their effects. These are *adaptations*. Some, but not all, of these traits continue to contribute to the fitness of organisms that have them. These traits are *adaptive*. Other traits are mere side effects of evolution, and these include some that happen now to be adaptive. A few Australian parrots have greatly increased in their range and numbers over the last century because they happen to have characteristics that suit them for the new habitat created by agriculture. The female spotted hyena has a hypertrophied clitoris that she uses in greeting ceremonies. But the clitoris is not large and penislike because it is used in such ceremonies. Rather, it is a side effect of selection for aggression and the hormones that drive it (we thank Richard Francis for this striking example). Other traits probably have no effect in themselves on fitness. We doubt that the ratio of inter-eye to inter-ear distance has ever in itself affected platypus life. That ratio is a mere epiphenomenon of the different evolutionary forces that built platypus eyes and ears.

Gould and Vrba have argued for a less obvious distinction among the traits of organisms. Very often a trait comes to play a role in an organism's life quite different from the one it played when it first evolved (Gould and Vrba 1982). The eighteenth-century French philosopher Voltaire accused his contemporaries of believing that the nose exists for holding spectacles in place. No evolutionist would make that mistake, but Gould and Vrba think that biologists are prone to subtler mistakes of the same sort. Feathers are very useful to birds in making wings. The superior efficiency of wings made of feathers may explain why birds rather than bats dominate the skies. But it is unlikely that feathers evolved from reptilian scales *because* they helped the ancestors of birds to fly better. It is thought that they evolved to assist in thermoregulation, and were later found to be useful for flight. Gould and Vrba call this process *exaptation*. A trait is an exaptation if it is an adaptation for one purpose but is now used—often in a modified form—for a different purpose. If the received story of feather evolution is right, feathers are adaptations for thermoregulation and exaptations for flight. Mammal ear bones are converted jaw bones; they are exapted for hearing. In older writings about evolution, this evolutionary pattern is often called *preadaptation:* feathers, for example, are preadaptations for flight. This older terminology is very misleading. The word *preadaptation* suggests that evolution is forward-looking anticipating the future needs of the organism. Evolution by natural selection cannot look forward because it cannot incur costs in anticipation of later benefits: do not ask for credit, as extinction often offends!

Gould and Vrba think that a trait is an adaptation only for the purpose for which it was first selected. But what justifies this special status for the first of many selection pressures? The importance of the concept of adaptation in biology is that it explains the existence of many traits of the organisms we see around us. This explanation is not just a matter of how traits first arose, but of why they persisted and why they are still here today. If we want to understand why there are so many feathers in the world, their later use in flight is as relevant as their earlier use in thermoregulation. Adaptation is a process that happens in stages. Traits arise from new genetic structures. Some of them are adaptive, and hence are spread by natural selection. They become adaptations. They may spread so far that they become "fixed" in the population (possessed by every individual). Alternatively, they may spread to a certain frequency and no further. Later in evolutionary history, the lifestyle of the organism may change, and the trajectory of adaptation may change as well. In New Zealand, where, as far as we know, there were no native mammals except bats before human occupation, flying away from predators ceased to be part of the lifestyle of many birds. Flight ceased to be adaptive, and that had implications for the further evolution of those birds' wings. The wings of the New Zealand weka (a flightless rail) are vestiges of its old adaptations.

But a trait can be retained under changed ecological conditions if it does something else, something new, that is useful. Darwin gave some examples of this phenomenon when he discussed the evolution of emotions (Darwin 1965). He thought that many facial expressions were originally selected for some practical purpose, but were later selected because they had acquired a role in communication between members of the species. He suggested that the baring of the teeth by angry primates may originally have been selected as a preparation for attack or a demonstration of fighting ability. It then acquired a secondary use in signaling anger. That is why it still occurs in humans, who rarely fight with their teeth (see figure 14.1). Since these processes of *secondary adaptation* are probably very common, the adaptation/ exaptation distinction is not very useful except as an indication of the succession of evolutionary events. A trait is an adaptation for *all* the purposes it has served and which help to explain why it still exists. The important distinction is not between the first selection pressure and the others, but between all the selection processes and the processes that are happening today, but have played no role in past evolution. This is the distinction between "being adaptive" and "being an adaptation."

#### **10.2 Function**

The *function* of the heart is to pump blood. The heart also makes noises, but that is not part of its function. The function of the brow-raising response to surprise is to increase the visual field. This response also stretches the skin, but that is not part of its function. Distinctions like these are common in biology, but their equivalents in the physical sciences would seem bizarre. Physics does not tell us what the sun is "for." The sun has all sorts of effects, but there is no distinction between the effects it is "meant" to have and those that are accidental side effects. In an earlier phase of human thought we could have made such distinctions. The sun was created by God to warm the earth, and the fact that it warms Mars, where there are no creatures with souls, is a side effect. But the rise of modern science was marked by the expulsion of explanations in terms of purpose or function in favor of explanations in terms of natural laws. The sun came into existence because the expansion of matter from the Big Bang was not entirely regular, and all its effects, useful or use-less, are equally unintended.

The conventional explanation of this difference between biology and physics is that biology studies the products of natural selection, while physics does not. Talking about functions is just a convenient way of talking about adaptations. If brow raising in surprise is an adaptation for increasing the visual field, then its function is to increase the visual field. Stretching the skin around the eyes has no known connection to reproductive fitness, so brow raising is probably not an adaptation for skin stretching, and skin stretching is not one of its functions. This view of function has been common among biologists for a long time. The architects of the received view even introduced a new name, *teleonomy*, to distance this biological understanding of functions and purposes from more traditional teleological ideas (Pittendrigh 1958). Konrad Lorenz, the co-founder of modern animal behavior studies *(ethology),* describes this perspective very clearly:

If we ask "What does a cat have sharp, curved claws for?" and answer simply "To catch mice with," this does not imply a profession of any mythical teleology, but the plain statement that catching mice is the function whose survival value, by the process of natural selection, has bred cats with this particular form of claw. Unless selection is at work, the question "What for?" cannot receive an answer with any real meaning. (Lorenz 1966, 9)

Philosophers call this the *etiological theory* of biological functions. An etiological theory explains something in terms of its origins, or *etiology*—in this case, its evolutionary origins. The functions of a biological trait are those effects for which it is an adaptation. A distinctive feature of the etiological theory is that a trait can have functions that it is unable to perform. The function of the white coat of a polar bear is to make the bear harder to see. There is no snow in most zoo polar bear enclosures, but it is still correct to point to the white bear on the gray concrete and say that it is white for the purpose of camouflage.

The etiological theory is the orthodox view in philosophy of biology, but it is not universally accepted. One influential criticism of this theory points out that people talked about biological functions long before evolutionary theory was invented. When William Harvey announced in the seventeenth century that the function of the heart is to pump blood, he didn't mean that it had evolved to pump blood—he thought that the heart was created by God. People used the concept of a biological function before having any idea of natural selection, so biological function cannot be about natural selection. This objection depends on the idea that the etiological theory is a conceptual analysis of function—that it is a theory about what people mean by the word function. Ruth Millikan (1989b) has argued that this is a mistake. The etiological theory of function is a scientific theory, not a conceptual analysis. No one objects to the theory that heat is molecular motion on the grounds that people understood the term *heat* long before anyone understood much about molecular motion. We are acquainted with heat, and develop various theories about what it is. One of those theories turns out to be the best. Millikan argues that the etiological theory-functions are effects promoted by natural selection-is the best theory of why organisms have functional traits. Indeed, apart from appeals to theology, it is our only such theory. It is without scientific rivals. Karen Neander makes a similar point (Neander 1991). She agrees that the etiological theory may not capture the definition of *function* ordinary people have in mind. But it may nonetheless capture the current biological conception of function.

The main rival of the etiological theory is the *propensity theory* (Bigelow and Pargetter 1987). According to the propensity theory, the functions of a trait are its *adaptive* effects, rather than the effects for which it is an *adaptation*. Functions are effects that increase an organism's propensity to reproduce. The etiological and propensity theories ask very different questions when trying to determine the function of a trait. Most people are able to learn to read fairly easily because they have typical human brain structures, rather than the slightly different structures found in people who are dyslexic. Is it the function of these structures to promote reading, or is this merely a side effect? The etiological theory asks why the structures evolved. Were they ever selected for producing reading? The propensity theory, on the other hand, asks whether people who can read typically have more offspring now than people who cannot read. If they do have more offspring, then it is the function of these brain structures to support reading.

Many people have been attracted to the propensity theory because it allows creatures with no evolutionary history to have biological functions. This point is often made using bizarre science fiction examples. Suppose a creature identical to you, atom for atom, were to arise through a random coming together of matter. Propensity theorists have a gut feeling that the heart of this creature would have the function of pumping blood and only the side effect of making heart noises. But according to the etiological theory, the creature would have no functions at all, because it would have no history of selection. It is unclear what significance to assign to gut feelings (often dignified with the name intuitions) about bizarre science fiction stories. Fortunately, the same point can be made using examples closer to the real world. Organisms can develop beneficial traits by mutation. If a bacterium incorporates a DNA plasmid from another bacterium that allows its new owner to synthesize a protein conferring resistance to a certain antibiotic for the very first time in the history of life, then according to the etiological theory, this protein has no function. Antibiotic resistance is a mere effect, for it does not explain the existence of the protein via the feedback loop of natural selection. Natural selection has not yet acted, as this variation has only just come into existence. Conferring resistance will become the protein's biological function only when bacteria with it have been favored by selection. According to the propensity theory, however, conferring resistance is the function of the protein from the moment it becomes useful.

Some biologists have also argued for an approach to function that concen-

trates on current adaptiveness rather than evolutionary history. They are not concerned with ordinary intuitions about when something has a function. They want to decouple claims about function from claims about evolutionary history because they have doubts about our ability to reconstruct evolutionary histories accurately. They think that if functional claims are implicitly claims about evolutionary histories, then functional analyses in biology will inherit all the uncertainties of these reconstructions (Reeve and Sherman 1993; Hauser 1996, 82–85). It is obviously desirable that notions like function and adaptation be defined in ways that make it possible to discover a trait's function. These authors' concern about our ability to confirm claims about function and hence adaptation reflects one of the most important debates in recent evolutionary theory—the debate over *adaptationism*—to which we turn in section 10.3.

We should not assume that biology traffics in only one type of function claim. Godfrey-Smith, Amundson, and Lauder all argue that there are two very different senses of function in biology (Godfrey-Smith 1993, 1994b; Amundson and Lauder 1994). Evolutionary biologists often use function in the sense defined by the etiological theory. Anatomists and physiologists, however, are not typically concerned with evolutionary history. They are interested in the activities an organism can perform: flying, digesting food, detecting viruses in its tissues, and the like. They explain how organisms perform these activities by *functional analysis*—by breaking down the overall task into parts that are performed by different parts of the organism. A biomechanical analysis of the knee joint explains how each part of the knee contributes to its ability to flex and bend. These functions of a biological trait are its causal role functions. Sometimes the causal role functions of a trait are the same as its etiological functions. The heart actually does pump blood, and that is what it was selected to do. In other cases the two kinds of function do not coincide. The redness of blood plays an essential causal role function in blushing, but our blood is not red because people who were able to blush had more children than other people.

We can think of the functions defined by the propensity theory as a special case of causal role functions. From a biological point of view, one of the most interesting properties of an organism is its capacity to survive and reproduce. Biological fitness is a measure of this capacity. Like any other capacity, an organism's fitness can be functionally analyzed. Each salient feature of the organism makes particular contributions to its ability to survive and reproduce; these contributions are *components of fitness*. In other words, these contributions are the causal role functions of those features relative to that capacity. They are the effects picked out by the propensity theory as the functions

of those features. So if we concentrate on one particular capacity—the capacity to survive and reproduce—causal role functions and propensity functions coincide. The causal role conception of function is much wider than this, however, because it can be applied to any capacity whatsoever. The biomedical sciences, for example, functionally analyze the body's capacity to fail in various ways.

In this chapter, our primary focus is evolutionary biology. So we will be using the notion of function central in that domain, while recognizing that other branches of biology—biomedical science, physiology, and perhaps others—are often interested in the contribution of a part of a biological system to the activity of the system as a whole, without being concerned with historical questions.

## 10.3 The Attack on Adaptationism

Stephen Jay Gould and Richard Lewontin have compared the idea of biological adaptation to the ideas of Dr. Pangloss in Voltaire's eighteenth-century satire *Candide*. Dr. Pangloss believed that everything in the world was designed by a wise and loving God. Even sexually transmitted diseases like syphilis were really for the best in this best of all possible worlds. Gould and Lewontin accused modern evolutionists of the equally unrealistic belief that if an organism has a trait, then it must be, in evolutionary terms, the best trait the organism is capable of having (Gould and Lewontin 1978; see also Lewontin 1982b, 1985a, 1987). Gould and Lewontin's criticisms had three main components.

## Confusing Adaptiveness with Adaptation

"Adaptationists" conclude that every useful trait exists *because* it is useful. If a bird flies south for the winter, the adaptationist concludes that this must be a behavioral adaptation for avoiding the cold. But what if the bird's ancestors lived in the south, and their habit of flying north each summer was favored by natural selection because of the abundant food resources of the brief northern summer? If all the bird's closest relatives live year-round in the south, then the evolutionary breakthrough is flying north for the summer boom. Then we might question whether flying back is an adaptation for avoiding the cold. Perhaps it is a side effect of flying north for the boom. A properly historical perspective on evolution is necessary in order to see where adaptive explanations are appropriate.

## **Overlooking Nonadaptationist Explanations**

Gould and Lewontin's second criticism is that other kinds of biological explanations are unduly neglected in favor of adaptive explanations. Human arms have two bones rather than one in the forearm. Is this because it is adaptive to have two bones rather than one, or is it because humans are part of a large group of organisms that are designed that way? Within the group Tetrapoda—creatures with a characteristic four-limbed layout—organisms inherit the two-bone design, and they retain it unless there is powerful selection against it.

Part of the issue here is how to divide up an organism into "parts." What features of an organism are its traits? That is, what features of an organism have an evolutionary history to call their own? Mandrills are one of the larger Old World monkeys. Males have electric blue muzzles and a matching blue on their behind and genitals. Should we consider these colors to be part of a single evolving trait, the overall mandrill color scheme, or do the colors of these particularly salient parts of the male monkey have evolutionary histories to call their own? This is no simple question. One aspect of Gould and Lewontin's critique of adaptationism is the charge that adaptationists see organisms as a mosaic of separate parts, each of which has an independent evolutionary explanation. No one doubts that some traits can evolve independently of the rest of the organism. The beaks of the Galápagos finches change under selection without everything else changing. But Gould and Lewontin deny that the picture of the organism as a mosaic of traits is always or usually accurate. They argue, for instance, that the human chin is an inevitable effect of the way the jaw grows, but does not have any particular evolutionary purpose of its own. Seeking to explain the chin as a separate feature is bad biology.

## The Unfalsifiability of the Adaptationist Program

Finally, Gould and Lewontin argue that adaptationism is unscientific because it cannot be disproved by experiment. In their view, adaptationists tell "justso stories" about why a trait was selected in the evolutionary past and regard these stories as scientific explanations. In fact, these stories are only "how possibly explanations." They show that there is at least one way the trait *might have* evolved. This is a useful thing to do, because people are forever alleging that this or that unusual trait refutes the whole idea of natural selection. But it is not the same thing as a testable scientific explanation of how the trait *actually* evolved. Particular adaptive stories can be tested, as we discuss below, but Gould and Lewontin argue that this does not test the idea of adaptationism itself. Whenever a particular adaptive story is discredited, the adaptationist makes up a new story, or just promises to look for one. The possibility that the trait is not an adaptation is never considered.

#### 10.4 What Is Adaptationism?

This critique of adaptationism has provoked a vigorous debate, one that is still very much in progress. But it has become clear that *adaptationism* does not name a single position. To the contrary: Godfrey-Smith (in press-c) argues that three distinct theses have been conflated in the controversies that followed in the wake of Gould and Lewontin's paper. He distinguishes between empirical adaptationism, explanatory adaptationism, and methodological adaptationism.

*Empirical adaptationism* was probably the main target of Gould and Lewontin. It is the idea that natural selection is by far the most powerful factor in evolutionary history, and that most of the biologically significant features of organisms are shaped almost entirely by natural selection. These features exist because of selection for one or more of their effects, and hence are adaptations.

This hypothesis is easily conflated with another, *explanatory adaptationism*. We suggested in section 2.1 that the explanatory agenda of evolutionary theory is dominated by the problems of diversity and adaptation. Explanatory adaptationism takes the existence of adaptation, especially complex adaptation, to be the central problem in evolutionary biology. Because natural selection is the only mechanism that produces complex adaptation, it is indeed the most important factor in evolutionary history. That is not necessarily because of its ubiquity or strength, but because it answers evolutionary biology's \$64,000 question: What explains complex adaptation, even if it is highly constrained, and even if most features of organisms are not adaptations.

Dawkins is an explanatory adaptationist. The first chapter of *The Blind Watchmaker* (Dawkins 1986) is a perfect specimen of that view. But it is not at all obvious that he is an empirical adaptationist. The third chapter of *The Extended Phenotype* (Dawkins 1982) is a careful discussion of constraints on adaptation. Empirical and explanatory adaptationism are independent ideas. As Dawkins (at least in some moods) shows, we can certainly accept explanatory adaptationism without accepting empirical adaptationism. Equally, we can embrace empirical adaptationism without explanatory adaptationism, for as we shall see, explanatory adaptationism has certain presuppositions that the empirical adaptationist may deny. In particular, explanatory adaptationists are committed to an unorthodox definition of adaptation.

Though both are highly contestable, both empirical and explanatory adaptationism make important claims about the natural world. *Methodological adaptationism* makes no such claims. Rather, methodological adaptationists think that the best way to study biological systems is to look for good design. They look at adaptation as a good organizing concept in evolutionary theory.

There is something very plausible about explanatory adaptationism. The intricate, weird, and beautiful adaptations of the living word are genuinely striking. They scream out for explanation. Moreover, there is almost unanimous agreement that natural selection is indeed the only reasonable explanation of platypus electrolocation, bat facial anatomy, the fig tree/fig wasp symbiosis, and the like. Furthermore, this adaptationist idea is important to philosophy. The idea of natural selection has played an important part in refuting theistic arguments from design and in establishing a naturalistic conception of the universe. One of us (Sterelny) is at heart an explanatory adaptationist.

Nevertheless, explanatory adaptationism faces both empirical and conceptual challenges. Ronald Amundson (1998) makes the empirical challenge explicit. He distinguishes constraints on adaptation from constraints on morphology. The conservation of testicle number among the vertebrates, for example, may reflect no constraint on *adaptation*. The environment may not be asking a question that variation in testicle number would answer. Equally, the persistence of basic structural plans in large groups of related but ecologically diverse organisms might be adaptively neutral. Nonetheless, the conservation of these patterns requires explanation, which might be found in developmental and historical constraints on evolution. Constraints can be explanatorily important without being constraints on adaptation. Adaptation, in this view, is one great explanatory challenge that evolutionary biology faces, a challenge that the theory of natural selection meets. But, as Gould has often argued, the persistence of basic structural similarities across such vastly different lifestyles as those of the bats and the whales presents another challenge. The persistence of such similarities over hundreds of millions of years is as striking as the existence of complex adaptations, and it is not explained by natural selection. Natural selection explains adaptation and perhaps even diversity, but not this persistence of type. This challenge, we must mention, is itself controversial. Selection—so-called stabilizing selection—can act to prevent change, so perhaps it might explain the persistence of type

after all. Moreover, persistence may be no more than chance. If change is rare compared with no change, we would expect, simply from chance, all the descendants of a species to manifest some of their ancestor's traits. Nevertheless, Amundson's challenge is clearly powerful.

In addition to this empirical challenge, explanatory adaptationism faces a conceptual one. In section 10.1 we fell in with the standard practice of defining adaptation by appealing to natural selection. Adaptations, by definition, are all, and only, the traits that exist by virtue of selection for their effects, current or past. But explanatory adaptationism does not make sense in this conception of adaptation. We cannot at the same time define adaptation as whatever natural selection causes and promote natural selection on the grounds that it is the explanation of a particularly puzzling phenomenon, namely, adaptation. If the theory of explanatory adaptationism is to mean something substantial, then adaptation, especially complex adaptation, must be characterized independently of its putative explanation, natural selection.

Empirical adaptationism is no less contested. It faces problems of both interpretation and testing. Let's look first at interpretation. Everyone agrees that all evolutionary trajectories depend on many factors. Tree kangaroos have a surprising array of adaptations to arboreal life, and all would agree that the evolution of these characters—for instance, the stiffened, counterweighted tail—depends on selection, history, and chance. Selection could not have made a counterweighted tail without the evolutionary possibilities the previous history of the lineage made available. What, then, does it mean to claim priority for one of these factors? If chance, selection, and history all play crucial roles, how can any one be more important than the others? Once we answer this challenge, we still face the empirical one: How can claims of relative importance be tested?

In the rest of this chapter we focus on empirical adaptationism. In section 10.5 we look in more detail at the biological explanations that are held up as alternatives to adaptationism. In sections 10.6 and 10.7, we return to the problem of formulating and testing adaptationist ideas.

## 10.5 Structuralism and the Bauplan

Gould and Lewontin have revived an old concept from continental European biology: the *bauplan*, or fundamental body plan, of an organism. A trait can be explained by pointing out its position in one of these fundamental body plans rather than by asking what adaptive purpose it serves. The existence of these two different varieties of biological explanation is endorsed by Darwin: It is generally acknowledged that all organic beings have been formed on two great laws—Unity of Type and the Conditions of Existence. By unity of type is meant that fundamental agreement in structure, which we see in organic beings of the same class, and which is quite independent of their habits of life. On my theory, unity of type is explained by unity of descent. The expression of conditions of existence, so often insisted upon by the illustrious Cuvier, is fully embraced by the principle of natural selection. For natural selection acts by either now adapting the varying parts of each being to its organic conditions of life; or by having adapted them in long-past periods of time. (Darwin 1964, 206)

The first of these principles, the unity of type, was central to the advances of nineteenth-century biology that paved the way for The Origin of Species. Georges Cuvier, Richard Owen, and others made great strides in comparative anatomy-the structural comparison of the bodies of organisms of different species. It had been conventional since the eighteenth century to classify living creatures according to a hierarchical "system of nature"-species, genera, families, orders, classes, and phyla. Comparative anatomy demonstrated that the members of a genus or family share similarities that seem quite unrelated to the practical needs of their ecological lifestyles. A lobster shares its segmented body plan with the rest of the arthropods, and shares the distinctive fusing of the first few segments to form a head with the other crustaceans. Neither feature seems to have any particular connection with the lobster's lifestyle. It is as if each class of organisms was designed as a variation on a basic plan common to its order, and each family as a variation on a basic plan common to its class, and so forth down to individual species. Hence, many features of an individual species reflect its position in the system of nature. If we can find evidence that a species fits into a particular part of the system, we can predict that it will have not only the characteristic properties that caused us to place it in that part of the system, but other properties characteristic of the organisms in that part as well.

The law of the unity of type provides an alternative to explanation by adaptation (Darwin's "conditions of life"). We can explain by classifying. Lobsters have fused head segments because they are crustaceans. Pigeons find food by sight and dogs by smell because pigeons are birds and dogs are mammals, and those are the senses those groups typically use. *Explanation by classification* is familiar from the physical sciences. Like the system of nature, the periodic table of elements groups things in ways that predict their properties. We can infer that copper is ductile and conductive *because* it is a metal. Mendelev's discovery of the periodic table was hailed as a great scientific

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achievement because it put a large quantity of information about the properties of different chemicals into a simple pattern, and because new discoveries fitted into roughly the same pattern.

One of Darwin's main achievements in the Origin was to turn contemporary comparative anatomy into an argument for his theory of evolution. The apparently arbitrary resemblances between members of a family or genus make perfect sense if all the species in the family or genus are descended from a single ancestral species. All birds have a furcula, or wishbone, because their common ancestor had one. All vertebrates have their spinal cords on the dorsal side because that's where it was in their common ancestor. With a single stroke, Darwin had turned the life's work of many scientists, including many bitterly opposed to him, into support for his theory. Where does this leave explanation by classification? In one sense, as Darwin says, the law of the unity of type is subordinated to the law of the conditions of existence, or adaptation-that is, to explanations that appeal to natural selection. The "types" or "plans" are themselves the products of earlier evolution. One could argue that explanation by classification simply begs the most interesting question, which is how the characteristics common to the whole group evolved in the ancestral species. The only real explanation is one that traces the origins of these characters by natural selection: "Hence, in fact, the law of the Conditions of Existence is the higher law; as it includes, through the inheritance of former adaptations, that of Unity of Type" (Darwin 1964, 206).

This dismissal of unity of type may be too quick. It might still be true, even after Darwin, that "all organic beings have been formed on two great laws" (Darwin 1964, 206). Amundson and others point out that while the special characters that mark out particular biological taxa may have had their origins in natural selection, they have endured long after their adaptive significance has disappeared. This is the basis of Amundson's challenge to explanatory adaptationism. The independence of many of these highly *conserved* traits from the current adaptive needs of the organism was essential to Darwin's use of comparative anatomy to support his theory. Darwin predicted that current adaptations would exist along with traces from former periods of evolution that create nonadaptive resemblances among living species. These nonadaptive characters are especially problematic for creationists, for they should expect God to suit each organism for its role in life.

Thus two patterns are discernible in nature, one overlaid on the other. The first is the match between organisms and the ecological conditions under which they live. Natural selection accounts for this pattern very well. The second pattern is formed by the highly conserved traits, which cause organisms with common ancestry to resemble one another. Thus mammals, despite their great differences in lifestyle, all have distinctively shaped ear bones. The ecological variety of the mammals suggests (though it does not prove) that mammal ear bone shape serves no distinct function, as function typically depends on distinctive features of an organism's environment. Yet if these traits have no adaptive value, why don't they disappear? There should be mutations that affect these traits, and nothing to select against them. Many other traits do disappear in this way. Flightless birds lose their flight muscles and their wings become smaller. Cave-dwelling species gradually lose their eyes. But traits like the relative positions of the bones in tetrapods and the fused head segments of crustaceans don't disappear in this way.

One obvious way to explain this is to appeal to developmental biology. Perhaps these structural characters play an essential role in the way organisms grow. Mutations that affected them would disrupt the complex process by which tissues and organs find their proper places in the body. Many anti-adaptationist biologists have stressed the importance of such *developmental constraints* in evolutionary explanation. They argue that some traits do not need natural selection to keep them in existence. Their presence in an organism is explained by its place in the system of nature, not by the specific adaptive pressures generated by the specific environment it faces.

The geneticist C. H. Waddington tried to explain the existence of developmental constraints through his concept of *developmental canalization*. Waddington argued that the developmental system is such that any minor perturbation in a developmental input, such as a gene product, will merely cause a different route to be taken to the same developmental outcome. He compared development to a ball rolling through a landscape. He imagined this landscape as a sheet anchored to many points underneath, representing developmental factors such as genes. Changing one of these factors will not usually change the overall shape of the landscape, and the ball will still roll to the same general place. In some cases this canalization might itself be an adaptation, buffering normal development against some disturbances.

The biologists who have placed the most emphasis on developmental constraints are the so-called process structuralists. In the case of the tetrapod limb, for example, process structuralists appeal to a well-known model of tetrapod limb development. This model dictates that all limb structures will begin with a single bone and that there will be no tripartite branchings. The generic forms of the tetrapod limb are hard to escape because they are dictated by very general aspects of the way in which these organisms achieve

Figure 10.1 C. H. Waddington's representation of developmental canalization. (a) The path of the rolling ball, which represents the developmental trajectory of the organism, is determined by a landscape representing the effects of all the developmental inputs to the organism. (b) The shape of this landscape is determined by genes and other developmental inputs, here represented by pegs pulling the landscape into shape with strings, and by their interactions, represented by connections between strings. Canalization is the idea that many changes in developmental inputs will leave the overall shape of the landscape, and hence the trajectory of the ball, unchanged. Other smallchanges in inputs may produce radical change by switching the ball from one valley to another. (From Waddington 1957, 36.)







organized growth. In recent years, process structuralism has drawn on chaos and complexity theory to make its case. In the language of those new disciplines, highly conserved traits are *strong attractors* for development.

One way of interpreting process structuralism is to see its defenders as arguing that the space of possible phenotypes—design space—is much smaller than adaptationists suppose. If, for example, there are no six-legged vertebrates in design space—if such organisms are *not possible*—then we do not need to calculate the relative costs and benefits of extra legs to explain their absence. Natural selection *at most* explains why some of the possible organisms are actual and others are not. The complexity theorist Stuart Kauffinan, whose ideas we consider in section 15.3, is another who thinks that adaptationists overestimate the extent of design space (Kauffinan 1993). Seen in this way, the process structuralists and Kauffinan are challenging explanatory adaptationism. There is a striking fact about life—surprising limitations on the range of the possible—about which natural selection is silent. They may be challenging empirical adaptationism as well: many traits



Figure 10.2 In the model of tetra-

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pod limb development proposed by Oster, Murray, and Maini (1985), three processes combine to create the various forms of the tetrapod limb and to limit the forms that can be created. (a) Focal condensation (F): aggregation of cells forms a tightly packed mass that can grow by recruiting more cells. (b) Bifurcation (B) of the growing condensate. (c) Segmentation (S) into two parts along the length of a limb. (d) The pattern of condensation across the developmental field of a limb growing via these three processes. (e) The role of the three processes F, B, and S in producing one complete form. The graphs above each drawing show the cell density across the transects indicated by the dotted lines in the drawing. (From Goodwin 1994, 152.)

of many organisms may be explained by developmental constraints and limitations on the possible rather than by natural selection.

Process structuralists hope to return to a pre-Darwinian biology in which explanation by classification was the most important sort of explanation. But we can recognize the importance of both selection and developmental constraints. They are two aspects of the same process. William Wimsatt has shown how natural selection could build organisms with highly conserved characters and strong developmental constraints on their future evolution. He calls this process generative entrenchment (Wimsatt and Schank 1988). Wimsatt notes that the key to natural selection is the possibility of incremental design. Very unlikely forms can be produced a piece at a time. Vision starts to evolve as light-sensitive cells appear, then eyeballs, then lenses, then focusing, and so forth. Each stage is selected in its own right because it is better than the last. The improbability of the final design is very large, but the improbability of each stage is quite manageable (2.2). Incremental design has important implications for developmental biology. Each slight modification is generated against the background of the existing developmental system. It makes use of many aspects of what already exists in order to grow correctly. The removal of ancient elements of the developmental system

would be likely to remove things that later modifications have made use of and so to disrupt the growth of those modifications. Elements of the developmental system therefore tend to become increasingly generatively entrenched as more is built on top of them. The existing developmental system of the organism comes to shape the space of possibilities available to the organism in its future evolution.

We have no doubt that generative entrenchment is an important idea, and is part of the explanation of the existence of highly conserved traits over long periods of time. However, it should not be regarded as omnipotent. Rudolf Raff (1996) shows that developmental constraints cannot be the whole explanation of the preservation of the body plan. He gives a series of examples of the preservation of the adult form in lineages in which the developmental trajectory to that form has undergone massive modification. Among sea urchins and amphibians, in particular, *direct development* has evolved in many species—that is, those species have evolved developmental trajectories to the adult form of the organism that bypass the usual intermediate stages.

#### **10.6 Optimality and Falsifiability**

It's important not to let the rhetoric of the adaptationist debate obscure the fact that some specific adaptationist hypotheses are not controversial. There are cases in which we can read the function of a trait from its complexity and the specific role it plays in an organism's life. For example, vultures have traits that are rightly regarded as adaptations for soaring. First, they have a suite of wing and feather features that are well designed, in an engineering sense, for that particular task. Vultures have broad wings, by virtue of which they have a light wing loading, so that relatively weak thermals will support their soaring. Second, soaring is central to these animals' life histories. Finally, this suite of features is not functionally ambiguous. There are no other tasks in which it plays a critical role. Vultures do not, for example, use their broad wings to shade water more effectively so that they can see into it to hunt, as herons do. In cases like this, an argument to the best explanation works. This form of argument claims that if one theory explains the data better than any other, then it is reasonable to accept that theory. Applying it here, we infer that these traits exist because of selection for soaring ability on vultures' ancestors. Equally, no one seriously doubts that the mechanisms that bats now use in echolocation exist because of selection for that function.

However, many other characters are much more problematic. The rapid expansion of brain size in our primate ancestors has been explained as the

effect of an upright stance and the consequent freeing of the hands for complex manual work (Tanner 1981). Alternatively, according to the engaging "aquatic ape" hypothesis, it is the effect of a period when our ancestors were supposedly surviving and foraging in shallow coastal waters (Morgan 1982). The extraordinary "radiator theory" of Falk (1990) suggests that brain expansion is the effect of removing a developmental constraint on the thermoregulation of the brain. Perhaps the most popular current view is that brain expansion is an effect of the social structure of hominid societies. In these social groups, as in chimpanzees today, the ability to form and manipulate personal relationships was the key to success. A person who could form a more complex system of alliances and remembered favors would do well. (For more on this "Machiavellian intelligence" hypothesis, see Byrne and Whiten 1988; Whiten and Byrne 1997.) Like any other science, biology needs a way of testing such competing theories. One way of doing so is to turn these stories into rigorous mathematical models of the evolutionary process and see if they correctly predict the traits that have actually evolved. The other is through integrating adaptationist and phylogenetic hypotheses—through integrating selection and history.

We begin with the idea of testing hypotheses via rigorous quantitative models. These models come in two basic kinds. The simplest ones are known as optimality models. An optimality model analyzes an evolutionary problem the way an engineer would analyze a technological problem. Such a model has four components: a fitness measure, a heritability assumption, a phenotype set, and a set of state equations. The *fitness measure* specifies the currency in which the success of various designs will be measured. The ideal measure would be the number of offspring or grandoffspring an organism produces, but this is rarely practical. If an optimality model was used to examine different leg designs, it might measure the amount of energy needed to cover a distance at a given velocity or set of velocities. The model would assume that the most efficient organisms have the most offspring. The second element of the model, the heritability assumption, specifies the extent to which offspring will inherit a parent's design. An optimality model of leg design might idealize to an asexual population in which every offspring is identical to its single parent. This convenient simplification would be unlikely to distort the results of this particular model. The third element, the phenotype set, states what alternative designs are possible. When looking at short-term evolution, the phenotype set can be restricted to minor variants of types actually observed in the species under study and in related species. Choosing a phenotype set for long-term evolution is more difficult. Developmental constraints of the type mentioned in the last section may rule out many designs. The fourth element, the *state equations*, are the guts of the model. They constitute a theory of the relationship between the organism's phenotype and its environment. In a model of leg design, the equations will come from biomechanics and muscle physiology. The equations determine what result (in terms of the fitness measure) will be produced by each alternative design. When the model is complete, it will show which member of the phenotype set is the optimal design—the one that scores highest on the fitness measure.

Optimality models assume that the fitness of a design depends only on the relationship between the organism and the environment. If hopping is more energy efficient than skipping, it will remain so whether everyone skips or everyone hops. But this assumption is often inappropriate to real-life situations. This problem is addressed by our second variety of quantitative models, called game theoretic models. As we noted in section 3.3, selection can be frequency-dependent. The fitness value of a trait can depend on the frequency of that trait in the population. For example, in sexual species, it can be a good idea (in evolutionary terms) to desert your offspring. The deserting parent can devote its resources to having more offspring somewhere else while the other parent looks after the young. But the more organisms that have this habit, the less likely it is to pay off. It becomes increasingly likely that the young will starve as both their parents try to leave the other holding the baby. We have seen this idea before, in considering sex ratios and the hypothetical evolution of water cricket navigation strategies. Evolutionary game theory models the selection of designs whose value depends on how other organisms are designed. Like optimality models, game theoretic models have a measure of fitness, a heritability assumption, and a phenotype set. The fourth element of these models is a game matrix. The game matrix describes how the value of each design depends on the designs other organisms use. There are also some terminological differences between optimality models and game theoretic models. In game theory, the score that an organism achieves on the fitness measure is known as a payoff, and the different possible phenotypes are usually called *strategies*.

One of the most famous game theoretic models is the "hawk-dove" model. The evolutionary problem it models is how to behave in contests over resources such as food, mates, or nest sites. In the simplest version, the phenotype set contains just two possible strategies: "hawk" and "dove." Hawks fight until one animal is injured. The uninjured animal gets the resource. For simplicity, we assume that every hawk has a 50/50 chance of winning a fight. Doves retreat when a fight threatens and leave the resource to the hawk. If two doves meet, each has a 50/50 chance of getting the

resource after a certain amount of posturing and bluffing (perhaps it depends on who runs first!). We assume that the resource is valuable; winning it is worth, say, 50 fitness units. Time costs something, so there is some cost in losing the game of bluff in dove/dove contests; say, 10 units. But that is much less costly than injury; we will suppose that the loser of hawk/hawk fights loses 100 fitness units. (We borrow these numbers from Skyrms 1996.) Then, assuming a hawk has a 50/50 chance in a fight with another hawk and a dove has a 50/50 chance of bluffing another dove, the payoffs will look like this:

	Hawk	Dove
Hawk	50/2 + -100/2 = -25	50
Dove	0	-10 + 50/2 = 15

Selection in the hawk-dove model is frequency-dependent. When selection is frequency-dependent, it does not make sense to talk of an optimal strategy. Under some conditions one strategy has the highest payoff, but under other conditions another does. Instead of describing the optimal strategy, game theoretic models shows which strategies are *evolutionarily stable*. A strategy is evolutionarily stable (with respect to some set of alternative strategies) if it cannot be *invaded*. A strategy can be invaded if a small number of mutants—would-be invaders using a different strategy—would do better than those organisms using the majority strategy. An evolutionarily stable strategy (ESS) excludes other strategies if it comes to be *fixed*—used by all members of a population.

It is clear that dove is not an evolutionarily stable strategy. The first mutants to follow the hawk strategy in a population of doves would do very well indeed. Hawk is sometimes an ESS. If the value of the resource organisms fight over is greater than the cost of being injured, then even when everyone else is a hawk, it is a bad idea to be a dove. A dove meeting a hawk will get nothing, but if the value of the resource is more than the cost of injury and a hawk wins half its fights, then a hawk will, on average, get a positive payoff. If the value of the resource is less than the cost of injury, however, then hawk is not an ESS. This situation is thought to be common in nature, since for most wild animals any serious injury is fatal. When neither hawk nor dove is an ESS, we expect the evolution of a balanced combination of hawks and doves. The population will be at an evolutionary equilibrium when the average payoff of a hawk is the same as the average payoff of a dove. In this situation, the extra costs hawks bear by fighting other hawks are exactly compensated by the payoffs they get by frightening away doves. The resources doves lose to hawks are exactly compensated by the doves' reduced

chances of injury. The proportion of hawks and doves at equilibrium will depend on the value of the resource and the costs of fighting. Notice that a mix of strategies evolves even though everyone would be better off if the whole population consisted of doves. Given the costs and benefits in the table above, at equilibrium, about one-third of the interactions are hawk/hawk fights, so the average payoff per interaction is just over 6. The successful hawk invasion reduces the average fitness of the population. Even so, once an equilibrium ratio of hawks and doves is achieved, selection will keep it in place. If too many hawks are born in one generation, they will find themselves in more fights, and their fitness will be lowered. If too many doves are born, their fitness will be lowered as hawks take more resources without a struggle.

The two strategies can be maintained in a population at equilibrium proportions in several ways. The population can be made up of hawkish individuals and dovish individuals, or every individual can be a hawk on some occasions and a dove on others. Given the costs of fighting and the benefits of resources in the table above, the equilibrium strategy is to play dove five out of twelve times and play hawk seven out of twelve. We could even get a mix of switch hitters, pure hawks, and pure doves.

Optimality models and game theoretic models are tested by comparing their predictions with the way organisms actually are. If an optimality model of leg design is correct, then the legs of real organisms should match the leg design that has the highest fitness score in the model. If an application of the hawk-dove model is correct, then the observed proportions of hawks and doves should be an ESS, given the estimated value of the resource and the estimated cost of injury. If the model is constrained enough to generate precise, quantitative conclusions, a close match with real data is indeed impressive. If, for example, a model of the evolution of clutch size in kookaburras—taking into account the physiological cost of eggs, the risk of foraging for the chicks, the costs of territory defense, and the trade-off between investing in current versus future reproduction—matched actual kookaburra behavior, the model would be very persuasive.

Yet in a model of kookaburra behavior, physiological costs, foraging risk, and the like can all be estimated independently. We can independently test the ecological and physiological assumptions that feed into the fitness measure of the model. It is much less obvious that the same is true of a quantitative model of human brain size evolution. It is very hard to see how we could construct any kind of principled quantitative model in a case like this, for we have no independent access to the ecological information. The Machiavellian intelligence hypothesis, for example, assumes that human groups gradually became larger (and interacted more complexly). But we have no independent

dent information about human group size. So it is less obvious how persuaded we should be by a match between a model of brain evolution and real data about human brain size.

A match is one possible outcome, a mismatch another. What happens if the model fails to predict reality? Gould and Lewontin's complaint about adaptationism is that the failure of an adaptive model is never taken as a failure of adaptationism. The adaptationist assumes that the problem lies in one of the four elements of the model. Perhaps the predicted optimal result is not really in the phenotype set. Perhaps the heritability assumption is too simple. Perhaps the effect on fitness of some action has been overestimated. Perhaps the trait under study is used for two purposes, and represents an optimal compromise between the best design for one purpose and the best design for the other. The possibility that the phenotype is less than perfectly adapted is not considered.

Some defenders of adaptive models admit that they do not consider this possibility. John Maynard Smith, the inventor of evolutionary game theory, insists that when an adaptive model is tested, the assumption that natural selection will choose the optimal phenotype is never under test. Here we see the conflation of the distinct versions of adaptationism we discussed in section 10.4. If adaptationism is treated as a global hypothesis about the biological world-most characteristics of most organisms are mostly the result of natural selection-then the failure to consider nonadaptive hypotheses is worrying. But Maynard Smith's adaptationism is methodological adaptationism (Maynard Smith 1984, 1987) The optimality model is a heuristic device, designed to reveal otherwise unsuspected constraints on adaptation. This heuristic strategy is premised on the idea that we can best find out about restrictions on heritability, or constraints on the array of possible leg shapes, by comparing the actual leg to the best of all possible legs. Suppose, for example, that there are genetic constraints that prevent a potentially adaptive mutation affecting leg shape from becoming fixed. Perhaps the mutation is linked to, and hence inherited with, a gene that is fit only when it is rare. We will discover that the assumptions about heritability in our model were too simple and will modify the model accordingly. Mismatch, not match, is revealing, because mismatch reveals constraints that we would otherwise not suspect—constraints that are not manifested in phenotypes. So the point of testing is to refine the model, adjusting our phenotype set, our fitness measure, and the like until it does correctly predict the observed phenotype. The constraints on adaptation are not ignored; they are incorporated through the fitness measure and the phenotype set.

So it may well be true that though adaptationists test particular theories

about adaptation using quantitative models, the basic adaptationist idea is never under test. Does this mean that Gould and Lewontin are correct and adaptationism is unfalsifiable and unscientific? Elliott Sober (1993) thinks that it does not. He argues that their critique depends on much too simple a picture of the way scientific theories are tested. He then goes on to develop an indirect test of adaptationism. We think he is right about the oversimplified picture of hypothesis testing, but we have reservations about his indirect test.

Sober begins by pointing out that adaptationism is not a simple scientific claim, like the claim that kiwis are descended from ancestors that could fly. Adaptationism is a research program. The idea of a research program was introduced by Imré Lakatos as a refinement of Karl Popper's falsificationist philosophy of science (Lakatos 1970). Popper's idea is that science makes progress not by proving theories to be true, but by rejecting theories that make false predictions and replacing them with better theories. But simpleminded falsificationism would have been fatal in the history of science. The theory of continental drift suffered from many apparent falsifications-most obviously, its continent-moving mechanism. Darwin's theory clashed with contemporary physicists' calculations of the age of the earth. In the end Darwin was proved right, but to reach this point Darwinians had to tolerate the "anomaly" for eighty years. Faced with examples like these, Lakatos argued that science is organized into research programs. The core ideas of these programs are not tested directly. Instead, scientists spend their time working out how these core ideas can be made to fit the data by elaborating all sorts of extra, detailed theory. This theory comes between the hard core of the research program and the data, just as the four elements of an adaptive model come between the core adaptationist thesis and data about actual organisms. It is only the extra, detailed theory that is tested and perhaps refuted. The core ideas of the research program provide a framework that suggests the detailed hypotheses and makes it possible to test them. If adaptationism is a research program, then one of its core ideas is that natural selection will usually produce optimal phenotypes. This core idea leads to the construction of particular models and also to tests of those models.

Thus, if adaptationism is a research program, it can be tested only indirectly. Lakatos argued that research programs stand or fall on their ability to produce successful detailed results in the long run. A successful research program leads to the discovery of many exciting and unexpected facts. An unsuccessful program spends its time explaining away the continued failure of its detailed research. Orzack and Sober (1994) have discussed how adaptationism could be tested in this global and indirect way. They begin by defining the core of the adaptationist program more precisely. They distinguish three claims about adaptation. The first is that it is *ubiquitous*, meaning that most traits are subject to natural selection. The second is that adaptation is *important*. Adaptation is important if a "censored" model that deliberately left out the effects of natural selection would make seriously mistaken predictions about what sorts of organisms have evolved. Finally, there is the claim that organisms are *optimal*. An organism is optimal if a model censored of all evolutionary mechanisms *except* natural selection could still accurately predict what sorts of organisms have evolved. Orzack and Sober argue that almost all biologists would accept that natural selection is ubiquitous and important. The distinctive feature of adaptationism is its claim that organisms are optimal; that is, that the results of evolution can be predicted reasonably well by models that consider only natural selection.

Orzack and Sober go on to suggest that the real test of adaptationism is whether adaptationist models are successful in predicting how most organisms have evolved. If models censored of all but natural selection correctly predict most of the data, or can be made to predict it with only a few, independently plausible adjustments to their assumptions, then adaptationism is a progressive research program. If such models must be laboriously tinkered with in every case in order to obtain correct predictions, then adaptationism is a degenerate research program and should be abandoned.

## 10.7 Adaptation and the Comparative Method

At the beginning of section 10.6 we mentioned that "arguments to the best explanation" sometimes make particular adaptationist hypotheses very plausible indeed. Friendly treatments of adaptationism often have great confidence in such arguments. They usually identify two kinds: adaptive thinking and reverse engineering (Dennett 1995). Adaptive thinking is the practice of looking at the structure and behavior of an organism in the light of the ecological problems it faces. Adaptive thinking predicts the sorts of features the organism should possess and uses those predictions to guide an investigation of the features it actually possesses. Reverse engineering is a way of working out how things actually evolved. One tries to work out what adaptive forces must have produced the existing form by reflecting on the adaptive utility of that form in either the current environment or a postulated ancestral environment. Reverse engineering infers the adaptive problem from the solution that was adopted; adaptive thinking infers the solution from the adaptive problem. Both forms of adaptationist theory can make use of the modeling techniques described in the last section. Adaptive thinking starts with a model and predicts how organisms will be in reality. Reverse engineering starts with how organisms are and constructs a model to explain this. Both forms of adaptive theorizing assume a strong relationship between adaptive forces and the resulting organism, an idea that adaptationists accept and which Orzack and Sober refer to as the claim of optimality. If this claim is correct, a model of evolution censored of forces other than natural selection should predict with reasonable accuracy the trajectory and destination of organisms in the space of possible designs.

The models described in the last section look at the relationship between an organism and its environment or, in game theory, between an organism, its environment, and other competing organisms. The models predict which design should be most successful in competition with others. It is easy to make the mistake of supposing that these models do not involve any particular assumptions about evolutionary history. They seem to involve only general principles about which traits are most efficient. These principles describe the (causal role) functions that certain designs will perform. The hawk design, for example, will beat the dove design in any single conflict. But in fact, these functional considerations cannot make any predictions about evolution unless we specify the particular historical conditions that make up the selective environment. Thus Orzack and Sober point out that optimality is local, as even censored models must take some account of the background biology of the lineage. For example, the robust beak of the New Zealand takahe, a large flightless bird, is said to be ideally engineered for feeding on alpine tussocks, but if the bird did not evolve living in the Southern Alps (either as a species or as a locally adapted variant), then this engineering excellence would be irrelevant to its evolution (Gray and Craig 1991). So we need a claim about takahe history conjoined with the engineering claim to generate an explanation of takahe beak structure. History also creeps in when we choose the phenotype set. The range of designs presented for selection will depend on the current state of the organisms facing selection. Without knowing what sorts of ancestors an organism had, it is impossible to say which alternatives competed to produce the form we see today. History has yet another role because evolution is a stochastic process. Only in a very large population can we assume that the fittest traits will be successful. In smaller populations, chance plays a larger role. Conventional evolutionary theory says that many important innovations occur when organisms are isolated in small populations. Chance, referred to as evolutionary drift, can be very important in these populations. Taking all these factors into account, the role of particular historical facts in evolution is very large. An adaptive model must make many assumptions of historical fact, although these are often not explicitly mentioned when the model is presented.

Adaptationists have tried to avoid the problem of historical assumptions

**Figure 10.3** The adaptationist abduction. This "argument to the best explanation" is supposed to avoid the need to independently test the historical assumptions built into adaptive scenarios. The fit between the model and the observed data provides an argument in support of the historical assumptions that the model requires.



by thinking of an adaptive explanation as a simultaneous abductive argument for the truth of the historical assumptions it requires (figure 10.3). *Abduction*, or "argument to the best explanation," is an important form of scientific reasoning. As we noted at the beginning of section 10.6, it is the idea that if one theory explains the data better than any other, then it is reasonable to accept that theory. Adaptationists argue that if they make certain historical assumptions, then they can neatly explain the actual trait. Therefore, by argument to the best explanation, we have grounds for accepting these historical assumptions.

But for many of the adaptationist hypotheses central to contemporary evolutionary theory, arguments to the best explanation are too blunt an instrument. Optimality modeling, evolutionary game theory, and the like are powerful engines for generating possible explanations. So in considering the evolution of sex, of sexual dimorphism, of strange sex ratios, of reversed sex roles in some bird species, and the like, there are a number of potentially adequate explanations. Argument to the best explanation is not valid when the "best" explanation is just one of several that are equally good. The problem of choosing between several equally adequate adaptive hypotheses is particularly sharp in those many cases—for example, fire resistance in Australian flora—in which uncertainties about past environments meant that the best we can expect is a qualitative fit between theory and data, or—as in brain size expansion in the hominid lineage—in which quantitative prediction depends on ecological features that are not independently known.

There is no methodological magic bullet that solves all the problems of testing adaptationist hypotheses. Requiring a very precise quantitative fit between adaptationist hypotheses and the traits actually observed does something to reduce the proliferation of hypotheses (Orzack and Sober 1994). But, as we have already noted, we think that this requirement is appropriate for a subset—perhaps only a small subset— of adaptationist hypotheses. We think the *comparative method* is more generally promising. This term refers to a range of techniques that infer how one organism evolved by comparing what evolution produced in that case with what it produced in other cases. The comparative method is one of biology's main windows on the past. We think it has three important applications to the adaptationism debate. First, it enables us to directly test the historical assumptions tacit in adaptationist hypotheses. Second, it enables us to test the proposed link between environmental feature and adapted trait. Third, we can use it to make sense of the adaptationist claim about the explanatory priority of selection.

First, let's consider tests of the historical premises that are built into adaptationist explanations. The simplest comparative tests check the actual sequence of evolutionary changes to see if it is the one presumed by the adaptive hypothesis. Jonathan Coddington (Coddington 1988, 10-11) provides a simple example of this sort of test. Living species of rhinoceroses have either one or two horns. This means that both designs were available to the evolving rhinoceros, so it is natural to invent an adaptive scenario in which both horn conditions are evolutionarily stable strategies (Lewontin 1985a; though see Zahavi and Zahavi 1997, 86-87, for a quirky adaptationist explanation of the two-horn design). If horn configuration is important in mate choice or other social interactions, we might suppose that once a population contains a large proportion of individuals with one number of horns, it cannot be invaded by a mutant with the other number of horns. Victory goes to whichever strategy gets established first in a particular population. Some sexual selection hypotheses fit this picture. If female rhinoceroses developed a preference, however slight, for one design, then males with that design would be at an advantage. In that case, females that lacked the preference for that design would have both less attractive male offspring and female offspring with their mother's unfashionable taste. The small advantage would thus be reinforced by sexual selection until it became a large advantage. Minor but different female preferences might arise by chance in different populations, leading to the evolution of two rhinoceros designs. However, a cladistic analysis (9.3) of the rhinoceratid group shows that the two-horned condition preceded the one-horned condition in the phylogenetic tree. In some population at some time, the two-horn design was successfully invaded by the one-horn design.

Adaptationist hypotheses often concern the relationship between two traits, and often imply that one evolved before the other. This historical presupposition can be independently tested. Mary McKitrick (1993) provides a simple example. It has been suggested that the low birthweight characteristic of the genus *Ursa*—the bears—is the result of an adaptive trade-off. It is the price bears pay for altering their physiology in order to allow hibernation. But a reconstruction of bear phylogeny shows that this cannot be the case. Low birthweight emerges before hibernation, and exists on branches of the phylogenetic tree on which hibernation never originated. Tests of this sort have wide application. The "aquatic ape" hypothesis claims as a particular strength its ability to explain a wide range of human characters: upright posture, bipedalism, hair loss, our layer of subcutaneous fat, our diving reflex, and many more. All these are said to have evolved together as an adaptive complex when our ancestors made a return to a semi-seagoing life. Since the hypothesis suggests that these characters emerged together in a single phase of hominid evolution, we can test it by determining when they appeared on the phylogenetic tree for hominids and their relatives. If the traits appeared at different times, they should be inherited by different chunks of the hominid family tree. If the characters emerge at various different points in the tree—if they did not, in fact, evolve together—then however neatly the hypothesis explains them, it cannot be correct.

A second important role for the comparative method lies in directly testing the idea that adapted traits are responses to particular features of an organism's environment. Adaptationist hypotheses can be supported by finding a correlation between certain traits and habitat factors. Such correlations suggest that the habitat factor has something to do with the evolution of the trait. Suppose we are interested in a group of seabird species, some of which nest in burrows, have plain white eggs, and do not remove the eggshells after hatching. Other species nest on ledges, have patterned eggs (camouflage, we suspect), and remove the eggshells after hatching. We reconstruct the phylogeny of the group and discover that (1) the ancestor species nested in a burrow, (2) it had plain white eggs, and (3) it did not remove eggshells after hatching. In case after case, when a descendant species has changed its nesting habit from burrow to ledge, its eggshell pattern and behavior have changed too. Here the inference of an adaptation to the new nesting condition would be enormously powerful. This example is both simple and ideal: real evolutionary data are unlikely to be as clean and as cooperative as our imagined seabird family. But sometimes we can get close. Again and again, rails-a chunky, rather generalist, and widely dispersed group of birds-have become flightless or nearly flightless on islands to which they have dispersed (Trewick 1997). The firm covariation between island life and flightlessness suggests that on islands something about the costs and benefits of flight changes, and that this alteration in the selective regime explains flightlessness.

Adaptationists have always laid great stress on *convergent evolution*: the phenomenon of the independent evolution of the same trait (or set of related traits) in different species. Perhaps the most frequently used example of convergent evolution is streamlining in large marine hunters. The bottle-nosed dolphin, the ichthyosaur, the blue marlin, and the great white shark all have strikingly similar shapes without inheriting them from their (distant) common ancestor. Convergent evolution has played two roles in adaptationist thinking. Sometimes it is taken to illustrate the overwhelming power of natural selection: it has taken widely separated lineages and remade them in the same mold. This is not a persuasive thought: convergence tells us nothing about the relative power of selection and history unless we can somehow count all the possible convergences that have *not* happened—all the times history "won." More reasonably, convergence has played an evidential role in supporting specific adaptationist hypotheses. What else but natural selection to minimize the energetic cost of high-speed travel through water could explain the similarities among these marine predators? Why else would this trait have evolved repeatedly under these particular environmental demands?

Convergence can indeed serve as evidence for an adaptationist hypothesis. But the systematic study of convergence requires an extensive use of the comparative method. For without a proper phylogenetic tree, it is not even possible to tell whether something is a convergence. Dennett is struck by the fact that "so many creatures-from fish to human beings-are equipped with special-purpose hardware that is wonderfully sensitive to visual patterns exhibiting symmetry around a vertical axis. . . . The provision is so common that it must have a very general utility" (Dennett 1987, 303). He is impressed by the adaptive hypothesis that this piece of neural hardware is a device for detecting other organisms looking straight at the subject, for then they are, from the subject's perspective, vertically symmetrical. But a phylogenetic tree may reveal that this neural hardware evolved just once, in the ancient common ancestor of all the species that display the trait. If so, then the existence of this cognitive trait in many species is no convergence at all. It has not evolved repeatedly in response to some repeated feature of the environment. It could, of course, still be an adaptation. But, equally, having been passed on by descent, it may serve many different adaptive functions in different species, and exist in others merely by "phylogenetic inertia." If so, then seeking an adaptive explanation of why so many organisms are sensitive to vertical symmetry may be as misguided as seeking an adaptive explanation of why humans, birds, and seals all have such similar bones in their forelimbs (the provision is so common that it must have a very general utility!).

The use of the comparative method to test adaptationist claims is widely accepted. We shall conclude this chapter with a more speculative idea. In section 10.3 we discussed the problem of testing empirical adaptationism, but we also noted that it was not an easy idea to interpret. Empirical adaptationists think that selection is the most important force driving evolutionary

history. But how could that be, if the evolution of every trait and every organism depends on many other factors as well? The evolution of streamlining in sharks and ichthyosaurs depends not just on selection, but also on history—on the possibilities created by previous evolution in those lineages. Squids are also marine predators, but are not notably shark-shaped. In our view, the comparative method offers a way of interpreting empirical adaptationism.

In a series of recent papers and a book, Robin Dunbar has argued for a connection between group size and cognitive complexity, using brain size scaled against body weight as a rough index of cognitive complexity (Dunbar 1996, in press; Barton and Dunbar 1997). As group size increases, the demands on memory and other cognitive skills increase, because an agent has to learn and remember more individuals, their characteristics, and their social relations. The agent has to learn not only to recognize individuals, but also to keep track of their friends, relations, and enemies. Because the number of relationships increases faster than the number of individuals—each individual has more than one significant relationship—these extra cognitive demands are quite intense.

So group size selects for intelligence: bigger groups, smarter individuals. But it's clear that Dunbar does not expect this relationship to hold in every group of animals. He obviously does not expect ants that live in huge nests to be smarter than ones that live in small nests. It is not clear whether he expects this relationship to hold among birds. Kookaburras are kingfishers, but unlike most of their relatives, they live in social groups consisting of extended families. Does Dunbar's hypothesis predict that kookaburras are smarter than solitary kingfishers? Selective pressure will produce a particular adaptive shift in a population only if that shift is among the evolutionary possibilities created by the previous history of the lineage.

In section 10.4 we remarked that it is hard to evaluate the idea that selection is more important than history, for every adaptive change in a lineage depends on both the history of that lineage and selection acting on it. But if we think of selection in a comparative context, perhaps we can make sense of claims about its relative importance. For selective hypotheses like Dunbar's can be narrow and shallow, intended to apply to only a small fragment of the tree of life. Or they can be wide and broad, applying not just to fancy primates but to bats and kookaburras as well. For the role of history in the explanation of adaptive change enables us to use phylogeny to specify the scope of adaptationist hypotheses. One way of interpreting Dunbar's hypothesis is to see it as nested high in the primate tree. According to this view, depicted in figure 10.4a, the evolutionary preconditions for an adaptive



**Figure 10.4** Two interpretations of Dunbar's hypothesis. (a) The narrow, shallow-scope interpretation. (b) A deeper, broader interpretation. The heavy box indicates the chunk of the phylogenetic tree in which the preconditions for an adaptive cognitive response to an increase in group size existed.

cognitive response to an increase in group size—getting smarter—have evolved only recently in the primate lineage, in the lineage of the Hominoidea—the lineage of the African and Asian great apes and of our ancestors. Within that small chunk of the primate lineage enclosed by the heavy box, and only there, we predict a correlation between group size and brain size scaled against body weight, for it is only in this clade that the evolutionary preconditions of a cognitive response to group size have arisen.

An alternative, more "history-overriding" version of this adaptationist hypothesis would push the origin of this evolutionary possibility deeper into the tree, and would predict a group size/brain size correlation over more species. So figure 10.4b depicts a less shallow hypothesis. In this version of the hypothesis, the cognitive preconditions for a takeoff in intelligence in response to group size evolved early in the primate lineage, just after the deepest and oldest split in the lineage. In this reading of the hypothesis, we would expect group size and weighted brain size to covary in all primate species except those few survivors of the ancient lemur/loris/bushbaby

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branch. Dunbar himself cites the fact that social bats have larger brains (scaled to body size) than their less social relatives as evidence for his idea, so perhaps he would push the origin of the takeoff point still deeper into the tree, perhaps early in the mammal lineage. Note that this way of interpreting adaptationist hypotheses is insurance against cheating. If social bats with big brains (for bats) count in favor of the hypothesis, then any other social animal with a normal-sized brain in the clade that includes bats and primates counts against the hypothesis.

Seen in this way, empirical adaptationism does not downplay the causal importance of history. Without the developmental and phenotypic possibilities the evolutionary history of a lineage creates, selection for cognitive sophistication would be ineffectual. Rather, adaptationists emphasize (or should emphasize) that the explanatory salience of selection over history depends on the fact that historical factors remain relatively constant, whereas the role of selection changes. We focus on selection in, say, explaining a cognitive change in primate evolution because selection is the *varying factor*  and is primarily responsible (along with drift) for explaining variance of this feature in the primate tree. Were it not for selection (and to a lesser degree, drift), all the primates would be the same. Adaptationists, then, are those who develop and defend deep-scope hypotheses, hypotheses about large chunks of the tree of life. Nesting Dunbar's adaptationist hypothesis deeper in the tree would make it apply to social living bats such as vampires; still deepermuch deeper-and it would apply to social birds like the kookaburra. A defender of deep-scope hypotheses expects many of the historical and developmental constraints on evolutionary change to remain relatively constant over large chunks of the tree of life. Skeptics of adaptationism so understood are those who expect these constraints not just to be important (on this, all are agreed), but to be variable. According to this way of reading adaptationist ideas, Dunbar's hypothesis would be in trouble if the evolutionary possibilities-the range of evolutionarily possible phenotypes-differed significantly from orangutan to chimp to gibbon to siamang. For then, even if group size were important, so too would be the different possibilities of response made available by the evolutionary histories of each of these lineages since their divergence from one another. So there would be no general pattern to capture in the response to selection for behavioral adjustment to living in larger groups.

We see this conclusion as enjoyably ironic. For Gould, in particular, is not just one of the arch-critics of adaptationism. He is also one of the defenders of the idea of stable constraints—of the idea of the conservation of what is evolutionarily possible for a lineage, and what is not, over time. As we see it, he is the defender of the critical empirical presupposition of empirical adaptationism.

#### **Further Reading**

**10.1** As is often the case, Keller and Lloyd 1992 is a good entrée to the literature, with entries on adaptation and teleology. Rose and Lauder 1996 is an impressive recent collection on many of the topics covered in this chapter. Hull and Ruse 1998 has good sections on both adaptation and function; so too does Sober 1994. Many of the important recent papers on function are collected in Allen, Bekoff, and Lauder, 1998, and Buller, in press. A collection of new papers on adaptationism edited by Orzack and Sober (in press) is about to emerge.

There is a voluminous literature on adaptation, adaptive traits, fitness, and related concepts. For accounts of the development of the contemporary concept of adaptation, see Burian 1983, 1992 and Amundson 1996. Belew and Mitchell 1996 has a good selection of early classics on adaptation. The

contemporary concept is discussed by Brandon (1990, 1996) and by West-Eberhard (1992). Gould and Vrba (1982) introduce the adaptation/exaptation distinction, which is criticized by Griffiths (1992), Reeve and Sherman (1993), and Dennett (1995). However, only Reeve and Sherman question the more basic distinction between being an adaptation and being currently adaptive.

The concept of fitness has also been the focus of much interest, as it has evolved from an intuitive notion of "fit" between organism and environment into an array of more precise but more technical concepts. The three essays on fitness in Keller and Lloyd 1992 are probably the best introduction to this difficult topic. The majority view of fitness is to treat it as a reproductive propensity that depends on the other features of an organism. A standard formulation and defense of this view is given by Mills and Beatty (1994). It is criticized by Byerly and Michod (1991). For a good introduction to the different uses of the notion of fitness in evolutionary theory, see Dawkins 1982, chap. 10.

**10.2** The etiological account of function is usually credited to L. Wright (1994). We prefer the more biologically informed and better developed version of the basic idea found in Millikan 1989b, Neander 1991, and Godfrey-Smith 1994b. The propensity view can be found in Bigelow and Pargetter 1987. The causal role view of functions is often credited to Cummins (1994). Godfrey-Smith (1993) and Amundson and Lauder (1994) present very clear and intelligent defenses of the need for distinct function concepts in different areas of biology. The consensus view that functions in evolutionary biology are explained by the etiological theory has recently been called into question by Walsh (1996), Walsh and Ariew (1996), and Schlosser (in press).

**10.3, 10.4** Gould and Lewontin's original attack on adaptationism (1978) is reprinted in Sober 1994. Dupré 1987 is a very important collection on this issue. Godfrey-Smith develops his distinction between different kinds of adaptationism most fully in a forthcoming paper (Godfrey-Smith, in press-c). Amundson 1998 is an insightful exploration of the relationship between adaptationism and developmental constraint. Adaptationism is vigorously defended by Dennett (1983, 1995) and Cronin (1991). In addition to the three lines of criticism we discuss in the text, Lewontin also argues that adaptationism misstates the relationship between organisms and their environments. We discuss this issue in chapter 11, and give references there.

**10.5** Goodwin (1994) offers a very simple introduction to process structuralist research. Kauffman (1993) has written a very important but *extremely* 

difficult book on the role of complexity in evolution. The best introduction to Kauffman's work is Depew and Weber 1995; their introduction to structuralism is also very helpful. Kauffman provides his own introduction in Kauffman 1995a,b. Smith (1992), Dennett (1995), and Griffiths (1996a) all argue for the compatibility of these ideas with conventional Darwinism. Wimsatt is another important but difficult author; his ideas are most accessibly presented in Wimsatt and Schank 1988. Gould's views on the relationship between development and form are explored most fully in his *Ontogeny and Phylogeny* (1977), a most impressive combination of history and theory. His views have continued to develop since that work, and we discuss them extensively in chapter 12. The empirical literature on vestiges is surveyed by Fong, Kane, and Culver (1995). There has been some debate on whether there is a real conflict between developmental and selectionist explanations of a trait; see Sherman 1988, 1989; Jamieson 1989; Mitchell 1992; Sterelny 1996a.

**10.6** Maynard Smith 1982 is a fairly accessible introduction to evolutionary game theory, but an even better introduction is Sigmund 1993. Maynard Smith's take on the philosophical issues can be found in Maynard Smith 1984, 1987. For a recent review of issues on optimality, see Seger and Stubblefield 1996. The idea of a global test of adaptationism is defended by Sober (1993) and by Orzack and Sober (1994). Brandon and Rausher (1996) present a critical response, arguing that Orzack and Sober's suggestion is biased toward adaptationism. They reply in Orzack and Sober 1996. Gray (1987) and Pierce and Ollason (1987) present detailed critiques of optimality theory.

**10.7** The significance of the comparative method for the study of adaptation is discussed by Taylor (1987), Horan (1989), Griffiths (1994, 1996b), and Sterelny (1997b). There are two very good book-length surveys of the modern comparative method and its application: Brooks and McLennan 1991 and Harvey and Pagel 1991. Eggleton and Vane-Wright 1994 is an important recent collection on the use of phylogenetic methods to study adaptation; the first four papers are general discussions of the issues discussed in this section. Lauder, Armand, and Rose (1993) discuss the limitations of these methods. Finally, for a wonderful parody of all these debates, see Ellstrand 1983. In a similar vein, see Shykoff and Widmer 1998 for the application of the comparative method to the vexed question of the temporal order of eggs and chickens.