

5

PEAKS AND VALLEYS

Consider this sequence of words: “rat,” “rut,” “rum,” and “sum.” Each word differs by one letter from the word before it, and each is correctly spelled and means something. Yet the last word differs from the first at every position. If you think this game is easy to play, try beginning with a longer phrase, such as “brain of a rat.” It no longer works to change “rat” into “rut,” because “brain of a rut” doesn’t mean anything. We could change “rat” into “bat,” but there are not many such possibilities. There is no way I can find to produce a new phrase that differs at every position. This difficulty reflects the fact that we began with a longer phrase. The longer the word or phrase, the harder it is to transform.

Michael Denton suggests that this, in microcosm, is the problem of evolving complex adaptations [34, Chapter 4]. The more complex the adaptation, the less likely it is to be useful in an incomplete form. And unless it is useful, it cannot spread by natural selection. There are, of course, complex adaptations within every species, so Denton argues that each species is trapped on an “island of function.” Evolution can move a species around on its island but cannot move it to another island. From time to time, mutant individuals that lie between islands may arise. Such individuals would have a mixture of features that work poorly together. They would therefore be eliminated by natural selection. For this reason, Denton argues that selection can make minor adjustments to existing adaptations but cannot create complex adaptations from scratch.

This argument hinges on the idea (introduced in Chapter 3) that intermediate forms may be maladaptive. This idea has a long history, going back to Georges Cuvier [24, p. 11], who opposed evolution decades before Darwin, and extending to authors such as Michael Behe [7], who oppose evolution today.

Evolutionists have responded to such arguments in several ways. One response points to complex adaptations such as the vertebrate eye. As discussed

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in Chapter 4, the eye seems to have evolved by a series of small changes, each of which was advantageous. This example refutes Denton's claim that complex adaptations *cannot* evolve without passing through maladaptive intermediate stages.

It is tempting to stop here. Denton's central claim is false, so what more is there to say? In fact, there is rather a lot. Many evolutionists would *agree* with Denton's central point—that the evolution of complex adaptations often requires passing through maladaptive intermediate stages. It seems dishonest to pretend that the whole idea is merely silly. Denton has raised a good question (several really), so this chapter will explore what evolutionists have had to say.

Like Denton, evolutionists are concerned with the relationship between the characteristics of an organism and its fitness. To be concrete, let us talk about the length and depth of beaks within some hypothetical species of bird. Presumably, some combinations of length and depth are better than others, and this will affect the birds' fitnesses. In this context, a length/depth combination with high fitness is one that allows birds to leave lots of descendants.

Imagine making a graph, with beak length on the horizontal axis and beak depth on the vertical axis. Each combination of length and depth corresponds to a point on the graph. To represent fitness, we might draw contour lines as on a topographic map. Alternatively, we can use a perspective drawing, as in Figure 5.1. Either way, the graph represents what is called a *fitness surface*. The horizontal position on the graph refers to beak dimensions, and the vertical position to fitness. Combinations of beak length and depth with high fitness will graph as high points on the fitness surface.

The surface in Figure 5.1 has two peaks, one for beaks that are short and deep, the other for those that are long and shallow. Recall that among medium ground finches, short deep beaks were best for cracking hard seeds and long, shallow ones for probing in cracks. Something of this sort presumably accounts for the two peaks in our hypothetical surface.

So far, I have talked about this surface as though it described the fitnesses of individual birds, and that is certainly one way to think of it. But there is also another way, which is often more useful. In this second interpretation, each point on the surface refers to an entire population. The horizontal axes refer not to the beak dimensions of individual birds, but to the mean values of these dimensions. For example, a population in which the average bird has a short deep beak would plot near the lower of the two peaks in the figure. One in which the average beak was long and shallow would plot near the higher peak.

This second interpretation is useful because it gives us a way to think about evolutionary change. Natural selection always pushes populations uphill on

Mean Fitness

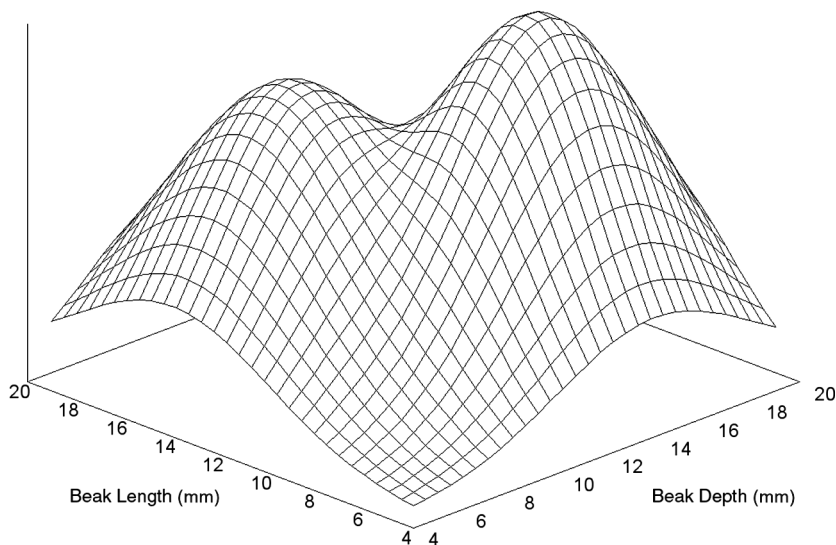


Figure 5.1: Hypothetical fitness surface.

the fitness surface.¹ In other words, it favors the character values that increase mean fitness. The finches of Daphne Major provide a good example. During the drought, selection reshaped their beaks. The result was a population with members that were better able to eat the remaining food and thus had higher Darwinian fitness. We picture this as an uphill movement on the fitness surface that prevailed during the drought. This uphill trajectory is both the blessing and the curse of natural selection.

It is a blessing because it is the engine of adaptive evolution. Without it, evolution would not improve the fit between organisms and environments. It could never have produced anything as complex as a bacterium, let alone a mammal. But it is also a curse. To see why, imagine that a population starts somewhere on the left half of Figure 5.1 and then climbs uphill. It is likely to reach the peak on the left—the lower of the two. Once it reaches that peak, it

¹Although selection always pushes straight uphill, this may not be the direction in which the population moves. For one thing, the population is jostled about by random forces. The smaller the population, the larger are these random shocks. Even in large populations, the movement may not be straight uphill because populations are easier to push in some directions than others. Just as a wagon is easiest to push in the direction that the wheels roll, populations are easiest to push in the direction with most genetic variance [4]. Nonetheless, they still move generally uphill.

will stop. It cannot then reach the higher peak without crossing a valley. But this would involve going downhill *against* the force of natural selection. So the population will stay there, stuck on the lower fitness peak, for a very long time. This is the curse of adaptive evolution.

The lack of foresight here is spectacular. Populations get stuck on inferior fitness peaks even when a superior peak is (so to speak) in plain view. This is not some defect in the theory of evolution. It is just how evolution works. Natural selection is an engine that improves adaptation, but it does not promise perfection. If populations evolve on a rugged fitness surface—one with lots of peaks and valleys—then adaptations should often be imperfect. But how do we know that the fitness surface *is* rugged? It is time to look at evidence.

Poor engineering

As we have seen, natural selection is a pretty stupid engineer. It simply walks uphill on the fitness surface. If that surface has lots of small peaks, selection is likely to get stuck on one. This will look to us like poor engineering. On the other hand, if the fitness surface were relatively smooth, poor engineering should be hard to find. This does not seem to be the case, however, for nature provides many examples of bad engineering.

Consider the gardener in Figure 5.2, who has run out of hose. For natural selection, this is an old story. As our ancestors evolved from fish into amphibians, reptiles, and mammals, their bodies changed enormously in size and shape. This required corresponding changes in the various tubes and wires—arteries, veins, nerves, and so on—that run throughout our bodies. In many cases these tubes became stretched around some obstacle, confronting selection with a dilemma like that of the gardener in the figure. All too often, it failed to do the sensible thing. Rather than walking back around the tree, selection got another length of hose.

One such example involves the vas deferens, the tube that carries sperm from testicle to penis [123]. In cold-blooded animals such as fish, the testes lie deep within the body cavity, not far from the heart. (Not a bad place, when you think of it, for an organ so delicate and so crucial to its owner's reproductive success.) Each testicle is a factory for making sperm. The process takes about five weeks (in humans) and is surprisingly sensitive to temperature. It works well in the body cavity of a shark but would work poorly at the higher temperatures that prevail inside our own bodies. As the bodies of our ancestors got warmer, it must have gotten harder and harder to make sperm. Selection would have favored individuals with testes a little closer to the skin, where things

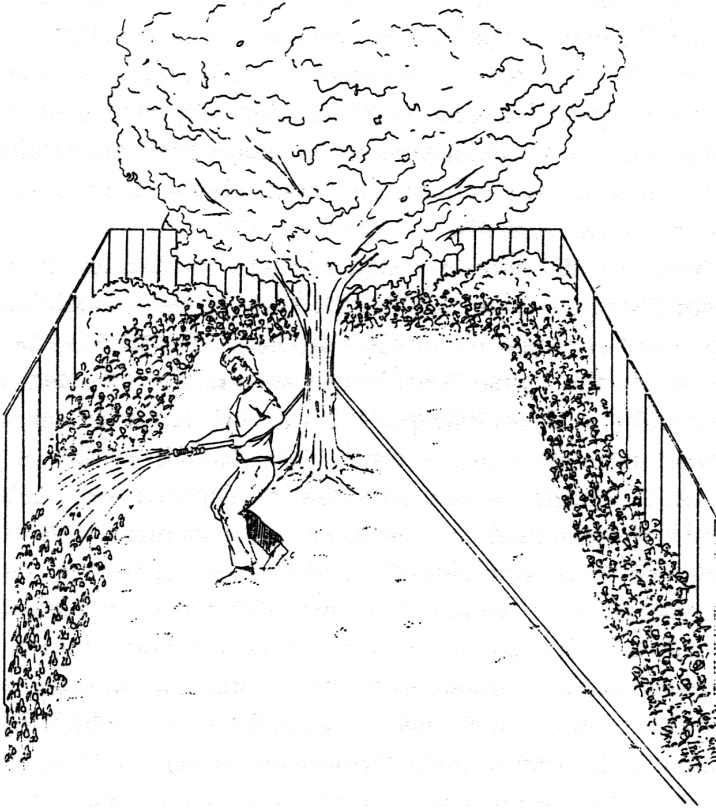


Figure 5.2: The gardener has run out of hose. What would you do: (A) go back around the tree, or (B) add another length of hose? Natural selection chose option B. Copyright © 1996, 1998, George C. Williams. Reprinted from G.C. Williams, *Plan and Purpose in Nature*, by permission of Weidenfeld & Nicolson, an imprint of The Orion Publishing Group, London, and from reference by permission of Basic Books, a member of the Perseus Books Group [124].

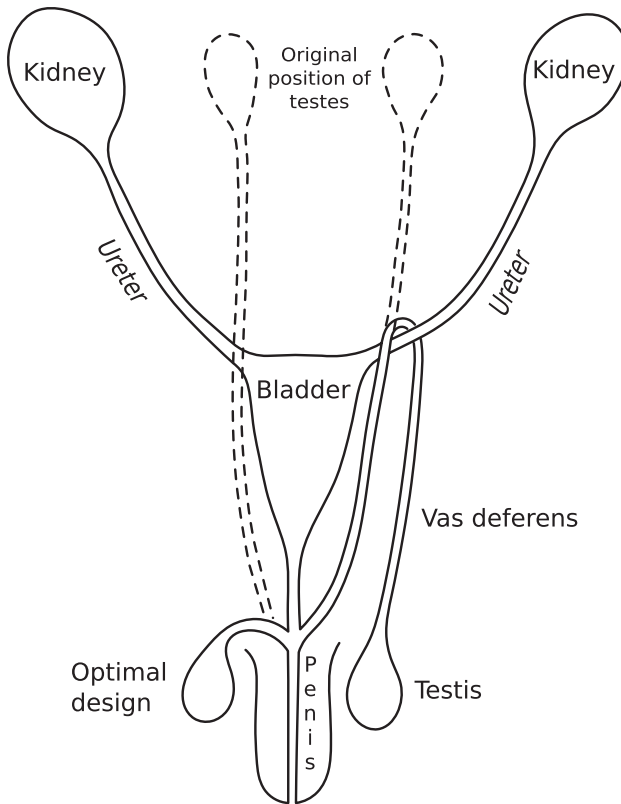


Figure 5.3: In human males, the vas deferens follows a circuitous route around the ureter, as shown on the right, instead of the direct route shown on the left [123, p. 142]. Redrawn from reference [123, p. 365].

were a little cooler. Over time, the testes migrated out of the body cavity and into the little pouch—the scrotum—that hangs between the legs of every male mammal. Along the way, however, the testes took a false turn. This took them the wrong way past the ureter, the tube that carries urine from kidney to bladder. The vas deferens got hooked there, just as the gardener’s water hose is hooked around the tree. But rather than unhook the vas deferens, selection increased its length. The result is shown on the right side of Figure 5.3. It works, but it is not something an engineer would be proud of.

Other waterhose problems can be found among the nerves of the head and neck. In fish, the layout is sensible. Each gill arch is supplied by its own artery

and its own nerve. These arteries and nerves all branch from a larger artery and a larger nerve, which run lengthwise down the fish. There is nothing in this arrangement to make an engineer wince.

These nerves and arteries can be traced back into the fish embryo, where the four gill arches are just wrinkles (called *pharyngeal arches*) at the base of the blob that will become the fish's head. At that stage, most vertebrate embryos have similar pharyngeal arches. The resemblance is more than superficial, for the arches develop into similar structures in adult animals. For example, your first arch develops into a jaw, whether you are a shark or a human. Even where mammalian anatomy is vastly modified, it is sometimes possible to trace the changes in the fossil record. For example, there is a clear sequence of fossils connecting the rear-most bones of a reptile's jaw to two tiny bones (the malleus and incus) in the human ear [100].

The structures that develop from each arch are fed by nerves and arteries that originate in that arch. In the nerves of a fish, this leads to a simple wiring diagram. In ours, it leads to a tangle that generations of anatomy students have learned to dread. The best example is the recurrent laryngeal nerve, which enervates the voice box and thus enables us to speak. It starts in the head, travels down to the chest where it loops around an artery, and then travels back up to the throat. In humans, it ends up only a few inches from where it started. This is another waterhose story. In fish, the nerve and artery both feed the rear-most gill arch. Over time, the artery descended into the chest, and the nerve went with it [33]. In giraffes, the nerve is 20 feet long, yet the direct route is only a foot. Engineers get fired for this sort of thing.

One can also find poor engineering in the retina of the vertebrate eye, which appears to have been installed backwards. The light-sensitive portion of the retina faces away from the light, but this in itself does not appear to be a problem [65]. It is unfortunate, however, that the nerves, arteries, and blood vessels that serve each photocell are attached at the front rather than the back. They run across the surface of the retina, obscuring the view. To provide a route for this wiring, nature has poked a hole in the retina, which causes a substantial blind spot in each eye. You don't notice these because your brain patches the image up, but that fix is only cosmetic. You still can't see any object in the blind spot, even if it is an incoming rock. Retinas don't *have* to be attached this way: those of cephalopods are attached more sensibly, with the wiring at the back.

These examples are hard to reconcile with the notion that each species was carefully designed by a deity. They remind me more of the plumbing system in an old house that has been repeatedly remodeled by a succession of plumbers, none of whom thought much about the house as a whole. In my old house, this has led to a plumbing system in which everything works, but nothing works as

well as it might. There are toilets that stop up, faucets with too little pressure, and faucets where one must wait a long time for the hot water. When you take a wall apart, you find pipes that lead nowhere and pipes that reach their destinations by improbable routes. It looks a lot like the plumbing of the human body.

The paragraphs above describe several examples in which evolution arrived at a suboptimal design. Why does evolution not fix them? Because doing so by gradual steps would require evolving through intermediate forms that were even worse. It would require, in other words, evolving through adaptive valleys. For example, to unhook the vas deferens from the ureter, the testes would have to travel back into the interior of the body, across the ureter, and back out again. Along most of this route, the testes would be too warm to produce sperm efficiently. The individuals involved would have low fertility and would be selected against. This is just another way of saying that this evolutionary path goes across a valley in the fitness surface. We are stuck with design flaws because such adaptive valleys are hard to cross.

From this, we can draw two conclusions. First, it seems clear that organisms evolved. Had they been specially created by a deity, we would not expect design flaws. Yet flaws make perfect sense under the hypothesis of evolution. These design flaws also justify a second conclusion—that the fitness surface has lots of peaks and valleys. If the fitness surface were less rugged, there would not be so many places to get stuck.

Adaptive valleys may be hard to cross, yet it would be rash to conclude that evolution never crosses them. After all, some may be easier to cross than others. Let us look at a few examples.

Crossing adaptive valleys

One example involves snails of the South Pacific. If you hold a snail shell with the point toward your eye, the shell will spiral away from you. The shell is “right-handed” if these spirals are clockwise but “left-handed” if they are counter-clockwise. Right-handed and left-handed shells work equally well, but there is trouble when the two types try to mate. They often cannot bring their genital slits into contact. Neither snail is fertilized and neither reproduces. This problem is especially acute in species with wide, round shells [46]. For this reason, it is good to have a shell that coils in the same direction as those of the other snails around you. In a population of right-handers, a left-handed snail is a lonely snail: unable to mate and with low Darwinian fitness. Selection favors the common type, whichever type that is.

Because of this disadvantage, new mutations that change the direction of coiling are unlikely to spread. Every mutation is initially rare, and while rare it suffers a handicap. Thus, populations of right-handed snails tend to stay right-handed, and vice versa. In this sense, right-handers and left-handers constitute separate peaks on a fitness surface. Selection tends to prevent populations of snails from switching peaks.

Yet somehow, they occasionally manage to do so. In one case, we got a glimpse of the process in action. The island of Moorea lies just northwest of Tahiti in the south Pacific. Thirty years ago (before they were all driven extinct), it was home to several endemic land snails of the genus *Partula*. Most of these species were right-handed, but a few were left-handed. Since these species were all closely related, some species must have switched their coil fairly recently. But how? Bryan Clarke and James Murray found a clue in the distribution of one species, which had individuals of both coils [19]. *Partula suturalis* was left-handed in the west of its range but right-handed in the east. These regions were separated by a narrow transitional zone, about a kilometer wide, that contained both types. Clarke and Murray noticed an interesting coincidence: *suturalis* was right-handed only in that portion of its range that it shared with a closely related snail, *P. mooreana*. This second species happened to be left-handed. Where the two types coexisted, left-handed *suturalis* wasted time and resources in fruitless hybrid matings with *mooreana*. Because of these fruitless matings, left-handed *suturalis* individuals were at a real disadvantage. They had low fertility in regions dominated by *mooreana*. Clarke and Murray suggest that this may explain, at least in part, why this population switched from one adaptive peak to another—from left-handed to right-handed.

This seems plausible, but it is probably not the whole story. After all, rare left-handers would *still* have had trouble finding mates. The need to avoid hybrid matings might have made the valley shallower, but it would not have eliminated the valley altogether. Another factor may have made it shallower still. In these snails, the direction of coil is governed by an unusual genetic system. A snail's coil is determined not by its own genotype but by that of its mother. The very first right-handed mutant would have had a left-handed shell and would thus have had no trouble finding mates. Right-handed snails would begin to appear only when the daughters of this initial mutant had offspring of their own. These would still have been rare, but they would not have been unique. They could have mated with each other.

Both factors would have tended to make the adaptive valley shallower. Nonetheless, most experts think there was still an adaptive valley to cross. If so, these snails provide the best example from nature of an adaptive peak shift. However, we cannot be certain that the adaptive valley was really a valley.

Perhaps the strange genetics and the need to avoid hybrid matings gave right-handers an absolute advantage over left-handers. If so, then the snails could have shifted state without crossing any adaptive valley. No one is really sure. There are other examples of probable peak shifts in natural populations, but none of them is entirely convincing. All can be challenged in one way or another [22]. To find a really convincing case, we need to go to the laboratory.

As we saw in Chapter 2, it is hard to do laboratory experiments on the formation of new species. The trouble is that new species arise only rarely. You need to study a large population for many generations, and you are not likely to succeed in this if you study elephants. Thus, scientists have concentrated on species that have short generations and can be raised in large numbers. The same considerations also apply to the problem of crossing adaptive valleys. Christina Burch and Lin Chao decided to attack that problem using what is surely the smallest and fastest-breeding species that one can study [12]. They studied a virus that infects bacteria. Such viruses are called “bacteriophages,” or more briefly “phages.”

Their experiment had two phases. The first phase involved a series of “bottlenecks,” or reductions in population size. In each bottleneck, the phage population was reduced to a single individual and then allowed to recover. (This didn’t take long: in five generations there were several billion phage.) This process was repeated again and again: bottleneck, then recovery, then bottleneck again, and so on. Severe bottlenecks such as these cause large random changes in gene frequencies. These random shocks were so severe that they overwhelmed the much smaller changes made by selection. In this environment, selection cannot be effective. Within a few dozen repetitions, a harmful mutation had arisen and spread through the population. All the phage carried it, and it greatly reduced their fitness.

At that point, Burch and Chao shifted to the second phase of the experiment. The second phase was a lot like the first, except that the recoveries did not start from single phage. They started from large numbers, so that the population never passed through any narrow bottleneck in population size. Gene frequencies no longer bounced around at random, and selection was far more effective. It eliminated any harmful mutations that arose, and it encouraged the helpful ones. Gradually, the population regained its original fitness.

Although the loss of fitness happened in a single large step, the gain involved several smaller steps. This shows that the beneficial mutations did not simply reverse the mutation that caused the original damage. (Had they done so, fitness would have been restored just as it was lost—in a single step.) This implies that the phage population had a different genotype at the beginning of the experiment than at the end. Both of these genotypes had high fitness,

although the route from one to the other involved intermediates with low fitness. In other words, Burch and Chao had watched their population evolve across an adaptive valley.

This experiment shows that no miracle is needed to push a population across an adaptive valley. Burch and Chao did it by repeatedly reducing the size of their population. There is nothing miraculous in that. Natural populations often suffer through harsh conditions that greatly reduce their numbers. These natural bottlenecks have effects analogous to those in the experiment, causing gene frequencies to bounce around at random. If these random shocks are large, they can overwhelm the effect of selection and push the population into an adaptive valley.

Nonetheless, there are reasons to be skeptical that peak shifts are important in nature. The bottlenecks of Burch and Chao were *very* severe, reducing the population size to a single individual. When this happens in nature, the population seldom survives. For more realistic population sizes, it can take a very long time to cross an adaptive valley [22]. On the other hand, the whole process speeds up if the fitness surface wobbles a little [119], or if some populations are more isolated than others [83], or if the population is continuously distributed in space [5], or if the population's size varies [118]. Do these factors speed things up enough to make peak shifts a plausible engine of adaptive evolution? Maybe, but no one knows for sure.

Where does this leave us? The many examples of poor engineering in nature imply that species *do* get stuck on suboptimal adaptive peaks. This shows that the adaptive landscape is rugged, with lots of peaks and valleys. It is also clear that evolution *can* cross adaptive valleys, at least in the laboratory. It is not clear whether this ever happens in nature. There are a few plausible cases, but only a few, and none of these is beyond challenge.

For these reasons, evolutionists disagree about the importance of peak shifts in adaptive evolution. Some argue that peak shifts play no central role in adaptive evolution. As Richard Dawkins puts it, “there can be no going downhill—species can’t get worse as a prelude to getting better” [32, p. 91]. Others are not so sure. This is an open question in evolutionary biology.

Conclusion

This chapter began with Denton’s argument that natural selection cannot build complex adaptations because doing so would require crossing adaptive valleys. This (according to Denton) would require a miracle; it is something that evolution cannot do. We are at last in a position to evaluate that argument.

First, let us agree that Denton was right about one thing: the adaptive landscape is rugged, with lots of peaks and valleys. There is no other way to interpret the extensive evidence of poor design in nature. It does not follow however that adaptive evolution requires crossing valleys. We saw in Chapter 4 that complex adaptations can evolve via a series of small, individually advantageous changes. No valley need be involved. Many evolutionists would argue that this is the whole story—that all adaptations evolve in this way. If this view is correct, then the adaptations that exist are simply the ones that could be reached *without* crossing valleys.

On the other hand, we need not appeal to miracles even if evolution does cross valleys. Denton was wrong about this too. In small populations, gene frequencies are buffeted by a variety of random forces, and these can push populations across valleys. We understand the mechanisms involved, and we have seen them operate in the laboratory. Evolutionists may argue about how often they happen in nature, but one thing is clear: there is no plausible basis for the argument that adaptive evolution requires miracles.