There is an old joke that goes something like this:

**Question:** Why does it take millions of sperm to fertilize one egg?

**Answer:** They won’t stop to ask for directions.

What makes this joke funny of course is its allusion to the conventional wisdom that among the foibles of the male members of our species is a reluctance to admit they are lost, especially when they are in the company of women. Moreover, the joke implies that given the same circumstances, a woman would have no such inhibitions. The fact that putative sex differences such as this are so often the subject of jokes speaks to their inherent interest to so many of us. So it is not surprising that scientific investigations of human sex differences feature prominently in the popular media. Just last week I awoke one morning to the news on my clock radio informing me that scientists had discovered the neural basis for another sex difference that has inspired many jokes: the “fact” that women remember the details of past arguments much better than men. It seems that modern brain imaging techniques revealed that the “emotional centers” of the brain “light up” during arguments to a greater extent in women than they do in men. This finding, coupled with the fact that the more emotional salience a memory has the better it is remembered, apparently explains women’s elephantine memory for verbal slights.

Fun stuff. But even if you take these putative human psychological sex differences unsalted, it is not obvious that they require an evolutionary explanation. Nature abounds with robust sex differences compared with which the sex differences we are talking about here are piddling and inconsequential from an evolutionary perspective. Take songbirds, for example. In most species, males do most if not all of the singing. Moreover, we know that male songbirds sing in order to attract mates and ward off male competitors, clearly evolutionarily relevant functions. Then there are the fishes known as wrasses. In more than one wrasse species, male and female members look so different, even to the trained eyes of professional ichthyologists, that they were originally classified as separate species. Now that’s a sex difference! It is one we should bear in mind in considering the claims of human sex differ-
ence enthusiasts, such as evolutionary psychologists, who, without going so far as to embrace the popular doctrine that human males and females had separate interplanetary origins, certainly tend to treat each sex as a distinct species of humanoid.

The tendency of evolutionary psychologists to overinterpret human psychological sex differences stems directly from the fact that they have embraced with unprecedented fervor a particular evolutionary perspective known as adaptationism. Adaptationists are distinctive among natural scientists in the way they query nature; they use “why-questions”—not just generic why-questions, as in “why is the sky blue,” but why-questions of a particular sort. Here are a few examples of their why-questions that we will examine in this book: Why does the male mockingbird mimic the songs of other bird species? Why do female spotted hyenas have male-like phalluses? Why do women have orgasms? And yes, why won’t men ask for directions?

What these why-questions have in common is that they require answers of a particular form; answers that refer to ends as opposed to means and to effects as opposed to causes. Answers of this sort are often referred to as reasons, functions, intentions, or purposes, all of which fall into a category known as “teleological.” Teleological thinking is the norm in our everyday interactions with each other, but in the realm of science its status is controversial. Indeed, teleology is steadfastly eschewed in most of the natural sciences, including most of biology. But evolutionary biologists of the adaptationist persuasion rely heavily on teleological thinking and increasingly flaunt it. I will argue that despite its undeniable heuristic value, teleology is a distorting lens through which to view the evolutionary process. I will further argue that questions such as “Why won’t men ask for directions?” are often the wrong questions to be asking.

Such questions seem so natural, however, that many people find it difficult if not impossible to resist asking them. They seem so natural because all of us, scientists and nonscientists alike, are teleologists at the outset. As children, we found it most natural to explain things by connecting them to the intentions, purposes, and goals of some agent analogous to ourselves. Hence, our curiosity is expressed in the form of teleological why-questions. Among the why-questions posed to me by my 10-year-old son of late are: “Why are there mosquitoes?” “Why do mockingbirds sing at night?” and “Why do I have to go to bed now?” Each of these questions is a request for a teleological explanation, an explanation that explains by identifying intentions, purposes, reasons, or goals. It is only gradually that he will learn to differentiate those questions for which the teleological perspective is appropriate, such as why he must go to bed now, from those for which the teleological perspective is misguided, such as why there are mosquitoes. Learning when the teleological perspective is warranted and when it isn’t is an
important part of normal cognitive development. In part, this learning entails knowing when teleological why-questions should be resisted and replaced by questions of a different sort, “how-questions,” for example. How-questions, as a child learns, are requests for a quite different sort of explanation: what the cause is; or how it came to be.

This transition is not easy; it takes a certain kind of discipline. Many adults, in fact, never learn how to resist looking for teleological explanations. I have been asked more than once by adult acquaintances why mosquitoes exist. This question was motivated less by my perceived biological expertise than by the teleological perspective of my interlocutors. They presumed that, as a biologist, I could explain the benefic mosquitoes provide in the grand scheme of nature, their purpose. God, or Mother Nature, must have had a reason for creating mosquitoes; they must be doing something useful. My attempts to answer this question from outside the teleological perspective—for example, that mosquitoes exist because they are good at what they do—were not well received. My answers seemed lame, the equivalent of “these things happen.”

Though we all pass through a teleological stage, most of us come to recognize that at some point the teleological perspective can become problematic; in fact, excessive teleology is an important aspect of the pathology known as paranoia. The paranoid is convinced, in a visceral way, that everything happens for a reason of the sort requested by “why” questions. The paranoid’s reasoning is deemed unreasonable not just because it reflects a sense of persecution, nor because it is so ego-centered, but because of the assumption that behind every occurrence there are intentions, a purpose, a design.

You don’t need to be paranoid to have a paranoiac mindset. Wherever the teleological perspective is used to devalue causal explanations, wherever it is believed that the answers to teleological why-questions trump all others, you will find evidence of the paranoiac explanatory style, and its characteristic distortions. Most religions, for example, foster the paranoiac mindset in their insistence on teleological “ultimate explanations.” But scientists, on the whole, are especially careful to guard against these teleology-induced distortions; indeed, scientists tend to be the least paranoiac citizens among us. By the time a child becomes a scientist, he or she has usually abandoned the teleological perspective, at least for the purposes of doing science. The glaring exception is evolutionary biology; in that field, some adaptationists rely heavily on teleology in their own search for ultimate explanations. For them this “teleological” quest for ultimate explanations seems to follow from Darwin’s principle of natural selection. As we will see, however, you can whole-heartedly embrace Darwin’s principle of natural selection without embracing teleology. In fact, there are some distinct ad-
vantages to nonteleological Darwinism, not least in avoiding the paranoiac pitfalls to which all teleologists are prone. These pitfalls are especially obvious in the Grandfather of Darwinian teleology, Bishop William Paley.

**From Paley to Darwin**

It is at least ironic that the teleological perspective of the staunch creationist William Paley continues to exert so much influence on Darwinians. Paley was one of the most important advocates of a particular theological tradition known as Natural Theology. What distinguished Natural Theology from other theological traditions was its attempt to accommodate and assimilate science, and more broadly, reason, by way of promoting a religious agenda to an educated audience. Perhaps the central problem for Natural Theology was to reconcile God’s presumed benevolence with his omnipotence. By the middle of the eighteenth century, European intellectuals were increasingly vexed by the so-called problem of evil: how it was that a God who is assumed to be both benevolent and omnipotent could allow so much that is evil to exist. One popular solution to this problem was the view that evil is only apparent and that ours is, in fact, the best of all possible worlds. One way of demonstrating such, popular among English theologians, was to provide evidence for the “fit” between animals and their environments. William Paley was perhaps the most famous of these naturalist-theologians who took to the English countryside in order to demonstrate God’s beneficent design.

Paley everywhere found signs of God’s beneficence; his was an ecstatic view of nature: “It is a happy world after all. The air, the earth, the water, teem with delighted existence. In a spring noon, or a summer evening, on whichever side I turn my eyes, myriads of happy beings crowd upon my view.”

Paley was not at all perplexed by the abundant evidence of discomfort and suffering, nor did he believe that we must defer until death any reward for our suffering. According to Paley, our suffering is more than compensated for by the heightened pleasure we experience during the interludes, a pleasure which “few enjoyments exceed.” Paley would have no problem with the “why are there mosquitoes?” question. For Paley, mosquitoes exist because mosquito bites are actually blessings, without which we would be denied the pleasure of the relief that comes from scratching them. Paley could also use this strategy to effectively deal with much deeper sorts of suffering, including his own. When he wrote those words, he was slowly dying a painful death from intestinal cancer.

It seems odd that a man like Paley, given his agenda, could be so loudly
exalted by such an outspokenly atheistic Darwinian as Richard Dawkins, and could inspire another neo-Darwinian, John Maynard-Smith, to proclaim that “The main task of any evolutionary theory is to explain adaptive complexity, that is, to explain the same facts that Paley used as evidence of a creator.” Surely, Maynard-Smith is not seeking to explain all of the “facts” that Paley used as evidence of a creator; nor does it seem likely that Dawkins’s notoriously dark view of life is compatible, no matter how far we stretch it, with Paley’s conviction that “it is a happy world after all.” No, there is something else about Paley that makes him attractive to these neo-Darwinians: his teleological adaptationism, his conviction that every feature of living things reflects the imprint of a designing or design-like force, and that this is most evident in the way that living things are adapted to their environment. This form of adaptationism comes straight out of Paley’s creationism.

In this approval of Paley, Maynard-Smith and Dawkins can legitimately say that they are following in Darwin’s own footsteps. Though Darwin rejected Paley’s creationism, he largely accepted Paley’s adaptationist teleology, a fact he quite openly acknowledged: “I was not able to annul the influence of my former belief, then almost universal, that each species had been purposely created; and this led to my tacit assumption that every detail of structure, excepting rudiments, was of some special, though unrecognized, service.”

This premise of “some special, though unrecognized, service” is Darwin’s explicit recognition of the teleological mindset he acquired by virtue of his indoctrination in Natural Theology. Darwin, however, because of his conflicts with advocates of Natural Theology over the issue of evolution (descent with modification), was much more aware of the pitfalls in the teleological perspective than are modern Darwinians such as Dawkins and Maynard-Smith. Nature’s imperfections provided him some of his best evidence for descent with modification, because this was the hardest evidence for Natural Theology to assimilate. It was because of their preoccupation with demonstrating evolution that early Darwinians were concerned to disassociate themselves from the idea of design in nature.

As the fact of evolution became more apparent to one and all, save those who chose to ignore the evidence, the original conflict between Darwinians and Natural Theologians over descent with modification largely receded to the background and a greater emphasis was placed on the assumption common to both—though increasingly unacknowledged as such—about the centrality of adaptation. Many of those evolutionists who are self-consciously “Darwinian” have become increasingly prone to design thinking and much more sympathetic toward Paley than Darwin ever was. For these “adaptationists,” Mother Nature has replaced God as the guarantor of suit-
ability or adaptation, through her omnipotence as a natural selector. Nature could still be interpreted as if designed, not all at once, but over time—“designed on the installment plan,” to use Dewey’s droll phrase.7

Obviously, a lot rides on how closely natural selection approximates Paley’s God in its powers of design. If the approximation is close, the teleological perspective is quite powerful; if it is not close, the teleological perspective will mislead. Throughout this book, I will argue that those neo-Darwinians who describe themselves as adaptationists tend to exaggerate the similarities between natural selection and Paley’s beneficent God.

Some adaptationists are more prone to paranoia than others, of course, depending on their attitude toward teleology. For some, it is merely of heuristic value, sometimes useful, sometimes not; for others, however, the neo-Paleyans, teleology is embraced much less consciously. The great danger of teleology, even for those who use it primarily as a heuristic, is that it tends to take over one’s mental landscape. Kenneth Weiss has aptly likened teleology to kudzu, that rampant vegetational scourge of the southeastern United States, which rapidly comes to dominate the landscape unless it is diligently beaten back.8 It is these kudzu-like properties of teleology that lead to paranoiac regression. This pitfall has always been more apparent in those adaptationists who study behavior—behavioral ecologists and sociobiologists—than in those who study anatomy and physiology. Sexual behavior, in particular, has proved a wellspring for some of the most paranoiac thinking ever to pass itself off as science, the apotheosis of which is a new adaptationist discipline called “evolutionary psychology.” On the premise that, given the obvious link between reproduction and evolutionary fitness, every detail of sexual behavior must reflect design, evolutionary psychologists have provided teleological explanations of all manner of sexual phenomena ranging from wet dreams to rape.

Fortunately, there are effective ways to control the kudzu-like tendencies of adaptationist teleology; one of the most effective was devised by George Williams. According to Williams, we should view adaptation as an onerous concept, one that carries with it the burden of proof, not the presumption of truth. In order to be confident that a trait is an adaptation, we need strong evidence of natural selection for that trait, evidence that the trait exists because bearers of that trait experience a competitive advantage over those who lack that trait. If we lack compelling evidence to this effect, Williams advises us to assume that this trait is not an adaptation but a mere “effect”—or to use the term I prefer, a byproduct—of some other processes and hence requires a different sort of explanation, a how-explanation.9

Most adaptationists at least pay lip service to Williams’s distinction between adaptations and byproducts, but many fewer take it to heart, evolutionary psychologists least of all. Instead, they are guided by another distinction, this one guaranteed to promote a kudzu-like proliferation of adapta-
tionist teleology. This distinction, which we owe to Ernst Mayr, is very much in the spirit of Paley.

**Causes and Agendas in Modern Biology**

Mayr proposed that there are actually two radically distinct explanatory agendas within biology; one for evolutionary biologists, who ask “Why?” and seek teleological answers to these why-questions, and another agenda altogether for the physiologists, morphologists, geneticists, and developmental biologists who ask “how?” and use material and causal conditions as their explanatory resources. We can call the biology of teleological explanations “why-biology” and the rest of biology with its material/causal considerations, “how-biology.” Mayr referred to the material/causal explanations of how-biology as “proximate explanations” and to the teleological explanations of why-biology as “ultimate explanations.”

The terms *proximate* and *ultimate* reveal Mayr’s teleological bias and his allegiance to Paley. In his estimation, asking “why” gets you to the end of the explanatory line; proximate explanations are just mileposts along the way. Mayr further proposed that in fulfilling the teleological why-agenda we can jump to the end of the line and bypass the proximate material/causal how-biology considerations altogether. Put another way, why-biology’s teleological explanations trump all how-biology’s material/causal explanations.

At best, on this view, how-biology can help us flesh out the teleological explanations of why-biology. There is no question of adaptations versus by-products here; rather, how-biology can only complement the teleological accounts of adaptations provided by why-biology. This would be true if we lived in a perfectly Paleyan universe; in that case, teleological explanations would indeed trump any how-biology considerations. We do not live in such a universe, however, or anything approximating it. And in the non-Paleyan universe in which we find ourselves, there are three possible outcomes when why-biology meets how-biology. First, sometimes the material/causal explanations from how-biology do indeed complement and support the why-biology explanations. In such cases, something like Mayr’s proximate/ultimate distinction is appropriate. In other cases, however, the how-biology considerations fundamentally alter the explanation provided by why-biology. And finally, in still other cases, how-biology explanations should be viewed as outright replacements for teleological explanations; this outcome is implicit in Williams’s distinction between adaptations and by-products. In these latter two cases, Mayr’s proximate/ultimate distinction is not at all germane; rather it constitutes a barrier to a better understanding of the evolutionary process.

It is only by bringing how-biology considerations to the foreground that
we can remove the dead hand of Paley from evolutionary biology, and hence Darwinian paranoia. This process will require a reintegration of Mayr's two biologies, an increasing trend within evolutionary biology in any case. For example, the most dynamic and rapidly expanding area of evolutionary biology as a whole, evolutionary developmental biology (known as evo-devo) sits squarely at the intersection of Mayr's two biologies. And so, too, does my own area of special interest, evolutionary neurobiology (or evo-neuro, by way of analogous shorthand). For both evo-devo and evo-neuro, the how-biology is paramount, in contrast to evolutionary psychology (evo-psycho?), which lightly skips over these considerations in favor of pure teleology.

The value of the view of evolution informed by how-biology goes well beyond this negative program of correcting teleological excesses within Darwinism. In fact, the real payoff of this approach comes from connecting this how-biology to evolutionary history, or phylogeny, as represented in the tree of life. A picture of evolution quite different from that of the neo-Paleyans then emerges, one that places more emphasis on the contingent historical or genealogical connections within this tree and less emphasis on the ecological conditions in which each species on that tree finds itself. All living things are connected through a branching genealogy (or phylogeny); as a result, all living things share traits with even their most distant ancestors. This genealogical-based resemblance increases, of course, as we move from more distant to more immediate ancestors, no matter what environment a given species inhabits or what sort of natural selection it is subject to. On this view, natural selection does not at all resemble a divine engineer, but rather a tinkerer who must work with the materials at hand and who is fundamentally limited with respect to how deeply his tinkering can penetrate. Because genealogy limits the capacity for natural selection to adaptively modify an organism, it is often viewed as a constraint on adaptation. Biologists who emphasize the role of genealogy in evolution point to the predictive power of taxonomy, as reflected in the hierarchical branching of the "tree of life," rather than to ecological factors in explaining the traits of living things. They tend to emphasize similarities within branches rather than selection-induced dissimilarities.

Recognizing a role for genealogy in evolution is only a first step in developing an alternative to unrelieved adaptationism. The next step is to identify the particular biological properties that are conserved within particular branches, or lineages, that constitute the tree of life, and this is where the how-biology comes in. In multicellular organisms such as ourselves, these properties are often subsumed under the category of "development." Any evolutionary alteration of a given species requires an alteration in an existing highly integrated developmental process inherited from the species' ancestors; this requirement greatly limits the set of viable adaptive responses to
any environment because any deep modification is overwhelmingly likely to mess things up. This fact has given rise to the notion of “developmental constraints” and development-based alternatives to adaptationist explanations. But it is important to remember that developmental constraints are how-biology imperatives born of genealogical connections.

In this book, I focus on only one branch of the tree of life—that of the vertebrate animals—because, frankly, I know more about this branch than any others. I will further confine myself to sexual phenomena, broadly construed. The how-biology of sex is not confined to the gonads and their secretions; it also includes the neural and the hormonal systems, both of which function to integrate and coordinate the body’s activities and behavior. At a finer scale, it includes biochemicals called hormones and other biochemicals called neurotransmitters, by means of which the endocrine and neural systems affect and are affected by events elsewhere in the body; it also includes other biochemicals called genes, which serve in the production of hormones, neurotransmitters, and other biochemicals.

We will find that once we incorporate even the most basic considerations about how brains and gonads work, how they interact, and how genes and hormones act and interact, we will have a different view of the evolution of sex differences and the other subjects of this book. But let us begin, not with a sex difference, but with what, from an adaptationist perspective, seems like a problematic similarity in human males and females.