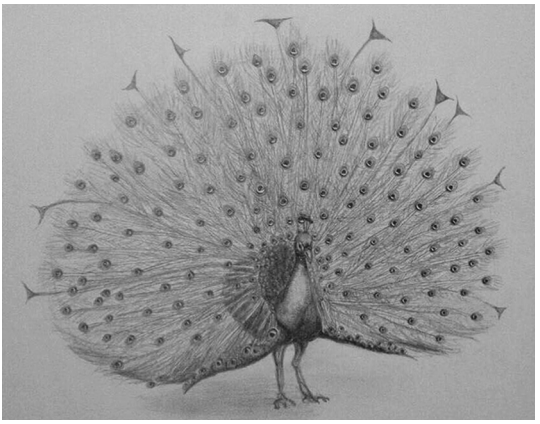
ONE

Why All the Fuss about Sex?

The sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick! —*Charles Darwin*



Nature usually gets down to business. Let's think about sleep. When I go to bed, I pull back the sheets, put my head on the pillow, and I'm in dreamland. I do not have a sleeping ritual, I don't dance, sing, chant, or perfume myself. I just go to sleep. So do most animals. Eating is the same way. When a howler monkey finds an edible leaf, she plucks it and eats it; a heron just throws back his head and swallows the fish he speared out of the water; and a cheetah doesn't do a celebratory dance before she starts to devour the gazelle she just brought down, even though she sprinted at her personal best of 75 mph to do so. Granted, in our own species we can sometimes make a bigger deal out of eating, especially when a meal coincides with a special event. But for the most part, we are little different from the howler, the heron, and the cheetah. Take a bite, give it a good chew, and gulp it down. Much of life for most animals is like that— the job is to just get it done.

Sex is different: a just-get-it-done policy won't get it done. In humans and most other animals, extensive courtship rituals precede the sex act. Most of our sexual rituals are laden with accessories, including candles and music, poems and flowers, and even special wardrobes. The list goes on, but it is no less diverse for animals. Animals sing and dance, they perfume themselves, they show off their colors and even light themselves up, all in the hope of attracting a mate. Although we distinguish ourselves in the language and technology we deploy in courtship, all animals have evolved spectacular, even obscene, morphologies and behaviors as both sexual lures and strategies for consummation. The colors of butterflies and fishes, the songs of insects and birds, the sexual odors of moths and mammals all evolved in the service of sex. The same is true for many of the traits in our own species that make women sigh and men gasp when someone of striking beauty crosses their paths. These aspects of sexual beauty evolved not because they make their bearers live longer but because they enable them to mate more and thus pass on more offspring and genes to the next generation.

Sexual beauty is everywhere, woven through the fabric of all sexually reproducing animals. We humans strive for beauty; we pay for it; we judge whether others have it; and if they do, we treat them better. Animals and humans both go to extreme lengths to appear beautiful to those who judge them. Peacocks evolve magnificent tails that cause peahens to sway, fishes sport bright colors that catch the eye of the other sex, crickets chirp endearingly to their mates, and spiders dance and vibrate their webs to show off. We humans take a more active role in engineering our beauty than do most other animals. Perfumes, fashion, cars, and music have all been employed in the service of sexual beauty, as have the surgeon's knife and a pharmacopeia of drugs. But to enhance one's beauty, either through the painstakingly slow process of evolution or the more immediate gratification of beauty-engineering, one must have some notion of what is beautiful.

This book is about sexual beauty, where it comes from and what it is for. Of course, many have been inspired to write in appreciation of natural beauty and the enchanting mating behaviors that occur in wild animals. Their emphasis is usually on the details of beautiful male traits: How does having such a long tail benefit the peacock? How many carotenoids does the male guppy need to eat to be so brilliantly orange?

How many syllables can a songbird pack into his complex vocal repertoire to make him even more sexy to females? These are interesting questions, but they represent only one-half of the equation of sexual beauty, because they ignore what is going on inside the head of those who actually judge beauty. Such studies often assume that the female brain must evolve tools to figure out what is beautiful. But instead, the converse is often true. The brain has a long evolutionary history that biases how it assesses the entire world around it, not just the world of sex; and it functions within the framework of numerous neurobiological and computational constraints. I argue that instead of the brain having to evolve to detect beauty, the brain determines what is beautiful, and all of its constraints and contingencies give rise to a breathtaking diversity of sexual aesthetics throughout the animal kingdom. In this book, I will show that to understand what beauty is, we need to understand the brain that perceives it.

I will expand our understanding of sexual beauty by asking how the details of an animal's brain give rise to its sexual aesthetics, which, in turn, drive the evolution of beauty in that species. Specifically, I argue that beauty only exists because it pleases the eyes, ears, or noses of the beholder; more generally, that *beauty is in the brain of the beholder*. Some of the brain's neural circuitry has evolved to sense and respond to sexual beauty so that animals can find a good mate. But the brain also has other things on its mind besides sex. Other adaptations of the brain, such as those that help an animal find food, avoid becoming food, or recognize the difference between its mother and its father, can have unintended but important consequences on how that brain defines beauty. Only when we understand the biological basis of sexual aesthetics can we understand how sexual aesthetics drive the evolution of sexual beauty.

I have a unique perspective to offer on these issues as I have spent the past forty years studying the sexual behavior of a tiny, bumpy frog in Central America.[1] This work has opened my eyes and mind to both the diversity of sexual behavior in the animal kingdom and a core unifying theory that I have developed called *sensory exploitation*. The key idea is simple: features of the female's brain that find certain notes of the males' mating call attractive existed long before those attractive notes evolved. Thus, females are the biological puppeteers, making the males sing exactly what their brains desire. Beauty is indeed in the brain of the

beholder, and in most cases, that means the female's brain, although I will review numerous cases where males judge female beauty and where there is mutual display and assessment of beauty by both sexes. This simple idea contributed to a paradigm shift in the study of sexual selection, one in which the importance of the sexual brain as a driver of evolution finally was acknowledged.

In this chapter, I will give some background on how scientists have come to understand the evolution of beauty and also explain which sex usually evolves this beauty and why. In the next one, I'll focus on the bumpy frog that has been the focus of much of my scientific brain power, to show how scientists actually go about learning how the brain relates to mating behavior. Chapter 3 delves into how the brain defines beauty by discussing the evolution of sensory systems and the cognitive processing of sensory information. Chapters 4 through 6 describe what is known about visual, acoustic, and olfactory beauty throughout the animal kingdom. Chapter 7 describes some biological underpinnings to the claim that percepts of beauty are sometimes fickle. And in chapter 8, I describe how some percepts of beauty lie masked and unknown until just the right individual appears to elicit attraction. This logic is extended to provide an evolutionary understanding of how various human enterprises, from the fashion industry to pornography, have been able to exploit these hidden preferences. In the epilogue, I close the book with some comments about the biological basis of beauty.

In our search for answers about beauty, we will explore nature and journey to where scientists have studied some of the world's most stunningly beautiful animals. We will probe the basic premises of why sexual beauty had to evolve and delve into new findings from neuroscience that provide insights into how the brain perceives beauty. The analogies between animals and humans might cause us to rethink our own sexual aesthetics. As with much of biology, the best place to start thinking about sexual beauty is with Charles Darwin. Where I will depart from Darwin is within an arena that he knew little about: the brain.

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It is hard to overestimate the impact of Charles Darwin's theory of evolution by natural selection on our view of humanity's place in the universe. It is one of the crowning intellectual achievements of humankind,

ranking right up there with Copernicus's theory of celestial motion, Newton's laws of physics, and Einstein's theory of relativity. His book, *On the Origin of Species*, sold out in a few days; subsequent editions continued to sell out for decades; and it is still one of the most widely cited books in the world.[2]

The most amazing thing about natural selection is its brilliant simplicity, which can be unpacked into three ideas or principles. The first, which comes from Thomas Malthus's *Essay on the Principle of Population*, is that the rate of reproduction outstrips the available resources to support it—not all offspring survive to reproduce.[3] Consider a pair of house flies that sneak into your dwelling through a small tear in the window screen. This couple is capable of producing five hundred offspring during their short lifetime of one month. If all of their offspring and their future progeny survived to reproduce, six months later you would be inundated by about two trillion flies with a combined weight of more than 2,500 tons, whose body mass would cover more than one thousand square miles, an area close to the size of Luxembourg. Luckily, this doesn't happen, as most of these flies die, and only a handful survive.

The second principle is that differential survival is not always random. Some survivors are just lucky—for example, those who happen not to be around as your fly swatter comes bearing down. But others survive because they are "better"; they have adaptations that allow them to avoid your swat and live to reproduce. Perhaps they are more sensitive to the wind displacements caused by the fly swatter, or they have faster flight muscles that allow escape before they get splat. But they are survivors, and they get to stay on the island, or at least in your house.

The third principle is that if variation in survival traits has a genetic component, these traits will be differentially passed down to the next generation. If the surviving flies have genes for faster flight muscles, for example, so will their offspring. These offspring will constitute a new generation of flies that fly faster, live longer, and reproduce more. This is how natural selection causes the evolution of survival traits. Time to fix that tear in your window screen.

When Darwin, along with Alfred Wallace, formulated the theory of natural selection, he never suggested it explained everything—he never thought that every aspect of every individual was an adaptation for survival.[4] He was aware of the power of culture, in animals as well as

humans. Darwin also understood random variation, which occurs when alternative forms of the same trait can become fixed in small populations. But one thing he did not understand, at least not immediately, was the peacock's tail. It caused him such consternation, he wrote to the botanist Asa Gray, that it made him sick. We know that Darwin was often sick, and a hypochondriac to boot, but such malaise in response to something so magnificent seems a bit extreme.[5] The peacock's tail is the mascot for scientific studies of animal beauty, but for Darwin it was a stark reminder of what his theory did not explain, and it motivated him to find a new theory to complement that of natural selection. He called it *sexual selection*.[6]

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The peacock is a majestic and beautiful beast. He initiates courtship with a female by erecting his feathers to form a fan that spreads out more than 180 degrees. He has two hundred feathers up to four feet long that are adorned with eyelike spots and have an iridescent sheen that causes them to sparkle brilliantly in the sunlight. Once they are erect, he shakes, rattles, and rolls his feathers, causing them to hum like an engine and the eyespots to vibrate hypnotically. All of this beauty evolved in the service of sex. Peahens get to choose their mates, and peacocks evolved their beauty to better compete in the sexual marketplace, where only the beautiful get chosen to pass their genes forward.

A peacock displaying in all his splendor is a majestic sight to us and to peahens alike. But have you ever seen a peacock run or fly? It's pathetic! Dragging his tail behind him, he can't outrun a child let alone a fox, and he can barely fly. If Darwin was correct that natural selection causes adaptations for survival by weeding out the weak, where did this monstrosity come from, and why wasn't it culled out long ago? This is why a mere feather was so distressing to one of science's greatest minds. But it was mental, not physical, duress that caused this particular malady. The peacock's tail offered a major challenge to Darwin's theory of natural selection, so he went to work on another theory to explain how it could evolve.

The peacock's tail was not the only challenge to Darwin's calculus of survival evolution; it was just the tip of the iceberg. In his second-most famous book, *The Descent of Man and Selection in Relation to Sex*,

published twelve years after *On the Origin of Species*, Darwin noted that many animals, not just peacocks, harbored traits that seemed at odds with the process of natural selection. Many of these traits also appear beautiful to us and seem superfluous to the animal's survival. Fireflies light up when they glide across a nocturnal meadow; crickets spend hours chirping during the summer nights; coral reef fishes sport colors that focus our gaze; frog choruses announce the coming of spring; canaries sing arias that have charmed their mates for millennia and humans for centuries; bowerbirds decorate and paint their bowers with such creativity that one researcher invoked a comparison to Matisse;[7] and Irish elk carried around eighty-eight-pound antlers with such high calcium demands that this might have eventually led to their extinction.[8] We are no more restrained with our sexual beauty, as we invest billions of dollars each year to paint, perfume, and trim parts of our bodies that make us more sexually attractive. None of this has anything to do with improved survival.

These nonsurvival traits share other commonalities. Most of them are more developed in males than females; they are usually employed in courtship or in battle for mates; and, as first haunted Darwin, many of these traits are detrimental to survival. Darwin called these *secondary sexual characters* because they differed between the sexes and were associated with reproduction, although not crucial for it. How they evolved required some additional theorizing.

Artificial selection provides some instructive examples of how these showy sexual characters might evolve. It might be one of the most important human inventions since the control of fire, and Darwin used artificial selection as an analogy to natural selection. In artificial selection, humans are the agents of selection. We decide which traits, as the targets of selection, will evolve to meet our predetermined goals. We often selectively breed organisms for utilitarian purposes, such as disease resistance in crops and greater meat yield in cattle. But we also breed animals to please our aesthetic senses. Fish hobbyists breed aquarium fishes with spectacular colors and even implant foreign genes to make some fish glow in the dark, and we are all familiar with breeds of domestic dogs that humans have engineered because they are cute rather than functional.

Based on his intuitions derived from artificial selection, Darwin reasoned that if female animals also had their own aesthetics, their own

standards of beauty, they too could exert selection to enhance their species' beauty. If female canaries were attracted to more variable male song, males with more variable song would produce more offspring, and canary song would evolve to be highly variable over time. If female peacocks found longer feathers to be sexually beautiful, they would choose to mate with males that have longer feathers, and consequently those males would have more offspring. Longer tails would come to flourish in future generations, even if these tails increased the male's predation risk. A short-feathered peacock that cannot convince females to mate will not pass his genes along to any offspring, even if he is fast enough to outrun any fox and lives to a ripe old age. Darwin's realizations about these issues allowed him to develop the theory of sexual selection using the same logic he employed for natural selection.

Survival is secondary to sex, merely an adaptation to keep animals alive so they can have a shot in the sexual marketplace. The essence of sexual selection is that traits of beauty that enhance an animal's mating success will evolve even if they somewhat hinder survival, as long as they are not too burdensome, as long as the costs they impose on survival do not outweigh the benefits they deliver for sex. Although most species have about the same number of males and females, not everyone gets to mate. In many species, some males get more than their fair share of matings, while most males die as virgins. An individual's mating success is influenced by how sexually attractive he is perceived to be by potential mates. The peacock with the longer tail, the frog with a more variable call, and the fruit fly with sexier odors are more sexually attractive and chosen by more females as mates. As with traits for survival, when sexual beauty has a genetic basis, it is passed down from generation to generation as males evolve more seductive ornaments.

When Darwin put together his two great theories, natural selection and sexual selection, he went a long way toward explaining the diversity of life. Many unique traits evolve because they attract more mates. Of course, being attractive enough to be chosen by females is not the only way to enhance mating opportunities. Fighting off the competition is also effective. This book focuses on how sexual selection leads to the evolution of sexual beauty, but I should mention that sexual selection can also lead to the evolution of sexual weaponry to fight off competition for mating. This other side of the sexual selection coin has been

covered in great detail by Doug Emlen in his book *Animal Weapons: The Evolution of Battle*.[9] But now let's travel to the cloud forests of Central America to return to the topic at hand, sexual beauty, and specifically to think about how the two sexes contribute to this phenomenon.

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Consider what has been called the world's most beautiful bird. Birders from all over the world travel to the cloud forests of Central America to see the Resplendent Quetzal, or at least the male quetzal. The first time I saw one in the mountains of western Panama, my hands shook as I steadied the binoculars to peer at him through the fog in the forest's canopy. He had a light green body marked by a bright red chest, the blue iridescent patch on his head added to his collage of colors, and what made me shake was the sight of his sparkling two-foot tail. Perching above us in the towering forest, he seemed more like a Mexican piñata than a real animal. I also saw a female quetzal, but no matter. She lacked all of the male's fancy embellishments, and I hardly gave her a second look.

Although the difference in plumage between the male and female quetzal can hardly be more striking, the difference between them is more fundamental than their feather-deep beauty. It resides deep inside their bodies—in their gametes, cells that contain copies of all of the animal's DNA and can be fused with a mate's gametes to form new individuals and continue the cycle of life. The male's gametes, his sperm, are the smallest cells in his body, and there are lots of them. Meanwhile the female's gametes, her eggs, are the largest cells in her body, and there are fewer of them. This difference in gamete size defines the sexes, male and female, for all animals—everything else is secondary—even the external sex organs.

In humans and other animals, you can often correctly identify an individual's biological sex by the sex organs. Males, with small gametes, often have penises, and females, with large gametes, often have vaginas. But human sexual identity depends both on cultural and biological factors, such as brain development. An individual with female gametes, for example, could have a masculinized brain. In humans, there is a difference between sex and gender, the latter being a culturally created construct. Only humans have gender identities, a topic I will return to later.

But even for the rest of the animal kingdom, sex organs do not always correctly indicate an individual's sex, thus making the focus on gametes critical to determining biological sex.

One example in which the sex organs can give a misleading indication of sex occurs in some lice. Bark lice are small insects, about the size of a flea, often found scavenging algae and lichen under barks. Others, sometimes called book lice, feed on the paste that is used to bind books. A most bizarre group of species are less well known and cloistered away in some caves in Brazil, where they survive by feeding on bat guano. But it is not their diet that makes them so interesting. These females have a penis and, correspondingly, the males a vagina.[10]

The female bark lice use their penis as most penises were intended to be used, to insert into the opposite sex's vagina when mating. But unlike a typical male's penis, the female's penis does not deposit sperm. It telescopes to penetrate deep inside the male, where it then expands, anchoring the barbs on the penis to the male's vaginal wall, effecting a copulation that can last more than forty hours. The barbs provide such strong purchase inside the male that when a researcher tried to separate a mated pair, the male was torn in two. During the marathon copulation, the penis sucks up large volumes of sperm into the female's body, where they eventually reach and fertilize her eggs. Despite this role reversal in their sex organs, there is no confusion about their sex. By definition, the males are males because they have the smaller gametes, and the females are females because they have larger gametes. When it comes to sexual identification in nonhuman animals, it all comes down to sperm and eggs, and their difference in size is at the root of all the other differences between the sexes and the reason why there is sexual selection. To understand the evolution of sex differences, including sexual beauty, we need to understand why this difference in gamete size matters so much.

Let's unpack this idea of how gamete size is tied to the evolution of sexual beauty. The human egg has a volume one hundred thousand times greater than a sperm.[11] If your gametes are smaller, you can make more of them; a woman produces only about 450 mature eggs during her lifetime, while a man makes about 500 billion sperm during his. Since fertilization requires only one sperm and one egg, eggs are a limiting resource. In addition, once a female has her eggs fertilized, it can take weeks to months to get another batch ready. Males, on the other

hand, can replenish their sperm supply within hours. In many species, once a female's eggs are fertilized, she is out of the mating game while she nurtures her inner embryo—a month for a guppy, nine months for a human, and almost two years for an elephant. While a female is tied up with her embryo, a male can go on mating. As with the sex-reversed bark lice, there are exceptions to the patterns in sexual selection. Male seahorses, for example, become pregnant, and a tropical male wading bird, the jacana, tends the nest while the female is mating with more males, "feathering" their nests with more eggs. But these examples tend to be not only exceptions to the general rule, but as we will discuss later, the exceptions that prove the general rule. And the general rule is that in most mating systems there is an excess of males ready to mate at any one point in time. This imbalance results in a sexual marketplace where many males compete for fewer females, a marketplace that features an abundance of courters and a limited number of choosers. All of this because sperm are smaller than eggs. So what can a male do to increase the chances of his sperm fertilizing her eggs? How can he compete in the sexual marketplace?

In some cases, males can control a resource that females want and need, which in turn makes a male more attractive. Males can control areas with food, nesting sites, and refugia from predators, all of which are important to a female with mating on her mind. Females can then shop and compare resources among males and mate with the most attractive choice. Of course, these resources are not free, as males have to fight for them, and sometimes rather fiercely. The weapons males use in these battles are varied and include larger size as well as assorted fangs, claws, horns, and antlers. The resources they defend can also vary, but all of them, in one way or another, are crucial to reproduction. For example, male damselflies defend areas of water with floating vegetation that females need to deposit their eggs; male fiddler crabs defend burrows that are used as refugia from predators as well as for mating; and men of the Kipsigis people in Kenya, as well as many other societies, accumulate wealth in various forms to recruit females for mating. And to the winner goes the spoils: the males with superior resources are more likely to be chosen to mate.

Although resource defense is one means by which an animal can enhance its sexual attractiveness, most of the interest in sexual selection

centers on the beauty of the individual itself. The stunning male peacock is just the beginning. I have already discussed the quetzal's tail and the canary's song, and throughout this book we will look closely at an incredible diversity of traits that have evolved in the name of sexual beauty.

Thus far I've explained how natural selection and sexual selection came to exist as scientific theories, why sexual selection usually acts on males, and how sexual selection can result in the evolution of beauty. I have argued that to understand beauty we must understand the brain of those who behold beauty, but I have yet to illustrate how we can explore this relationship between beauty and the brain. Now I will focus on one species, the one that provided me an entrée into this field and led me to begin to explore the neural underpinnings of sexual aesthetics. This compelling example of sexual selection favoring the evolution of acoustic beauty comes from a frog most unassuming in his looks but quite audacious in his voice. In the next chapter, we will have a detailed look at how the sexual aesthetics of a female can drive the evolution of a distinctly beautiful, although somewhat dangerous, male voice. We will delve into her brain's function as well as its evolutionary history to uncover why she has judged this male voice to be so beautiful.