

8

Resolving the Problem of Sexual Beauty

Michael J. Ryan

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

CHARLES DARWIN, LETTER TO ASA GRAY, 1860¹

CHARLES DARWIN PENNED THIS COMPLAINT, in a letter to the famed North American botanist Asa Gray, in 1860. Darwin was physically sick much of his adult life, but this ailment was psychological, most likely a result of cognitive dissonance.² The resolution of this revulsion toward the peacock's tail serves as a compelling metaphor for Darwin's theory of sexual selection.

The peacock's tail is a stunning ornament and somewhat of an icon for the sexual beauty that surrounds us in nature (Figure 8.1). Melodious songs of birds, sparkling colors of fishes and butterflies, overpowering choruses of frogs and crickets, the musky odor of deer, and all the cultural accouterments of courtship in our own species are only some examples. Darwin had a profound understanding and appreciation of the natural world, including its ubiquitous sexual beauty. So why did this particular form of beauty bother him so much?



FIGURE 8.1. A male peacock displaying his tail to a female peahen. (iStock by Getty)

This work is celebrating the 150th anniversary of *The Descent of Man*, but that is not the full title of the work, which reads: *The Descent of Man, and Selection in Relation to Sex*. Part 2 of the book lays out the theory of sexual selection and then surveys several animal groups, to which Darwin applies this theory to explain the evolution of traits akin to the peacock's tail. In the final chapters of the book, he applies sexual selection to humans, especially asking how sexual selection might be important in generating population variation in morphology and behavior within our own species. The purpose of this chapter is to give an overview of sexual selection, Darwin's second great theory.

Natural Selection Is Not Sexual Selection, or at Least It Wasn't to Darwin

In order to understand sexual selection and all the fuss that surrounded it, we first need to have a clear understanding of natural selection, the main topic of Darwin's 1859 book, *On the Origin of Species*.

—1
—0
—+1

Darwin's main premise of that book can be summed up in three words, "descent with modification." He argued that all organisms at some point in their history share a common ancestor, and when they diverged from that ancestor, over time, many of their traits were modified to enhance their survivorship. Take the finches Darwin discovered on the Galápagos Islands as an example.³ They all shared a common ancestor, a finch species of the mainland of Central or South America that first arrived on the Galápagos Islands about 2.3 million years ago. The descendants of these migrant finches subsequently invaded the different islands of the archipelago, where they diverged from one another in a number of characteristics. Most notably, beaks evolved in response to natural selection to exploit different local food sources. Beaks can vary in size and shape, and there are specific genes responsible for this variation.⁴ Selection will favor those variants that enhance foraging performance in the local environment. On some islands, selection favored large beaks that were good for cracking seeds and nuts; on other islands, selection favored long, pointed beaks that allowed the birds to extract insects from their hiding places; and in still other cases, selection favored the evolution of medium-size beaks that were adapted for catching insects on the wing (Figure 8.2). As the birds diverged from one another in morphology, they also diverged in their behavior, their songs, and their genes. These differences, in combination with the fact that the populations on different islands were separated by ocean, inhibited mating between the populations and ultimately resulted in populations becoming different species.

Charles Darwin and Alfred Russel Wallace were codiscoverers of the theory of evolution by natural selection. Their joint paper was read at a meeting of the Linnean Society of London on July 1, 1858, and was published in the society's journal later that year. A year later Darwin published a more detailed account of this theory in *On the Origin of Species*.⁵ Despite the book's title, his main emphasis was on the role of natural selection in the evolution of adaptations.

There are three factors that need to conspire for an adaptation to evolve. The first is an insight that Darwin gleaned from his readings of Thomas Malthus's *An Essay on the Principle of Population*: the rate of

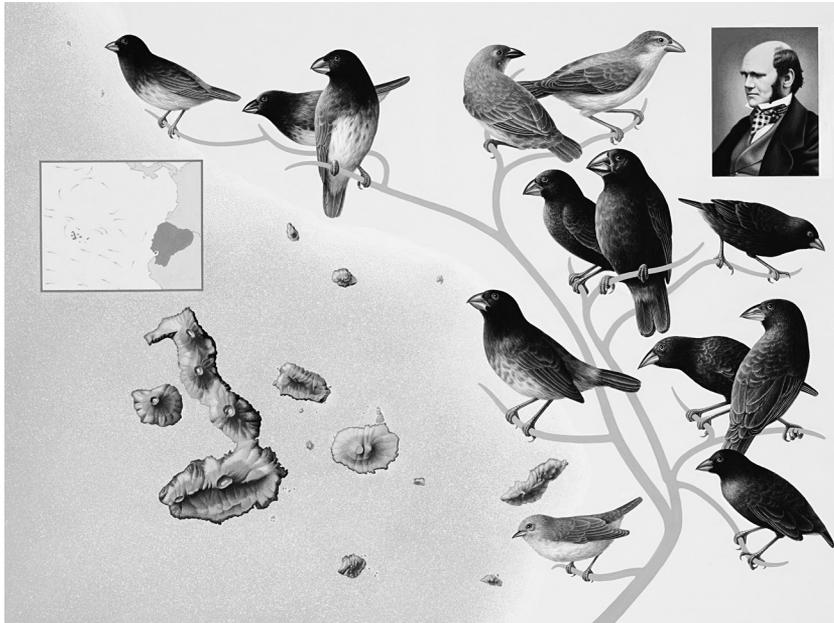


FIGURE 8.2. Diversity of beaks in Galápagos finches. (© National Geographic)

reproduction of the population will often far exceed the resources in nature that can support it.⁶ Thus, not all of the individuals that are born into a population survive to reproduce. The second part of this theory is that survival is not random. Certain individuals survive because they have traits that enhance their survivorship. These are the traits that are favored by natural selection. But selection does not lead to evolution unless those favored traits have a genetic component. This is the third piece of this puzzle. When traits favored by natural selection can be inherited, genes associated with these traits increase in subsequent generations, in turn causing an increase in the frequency of these traits that enhance survivorship. Of course, Darwin did not know about genes; Mendelian genetics (the principles of inheritance Gregor Mendel formulated in 1865) was a few years off, but the notion of heredity was central to animal and plant breeding at the time and well known to Darwin and most other scientists. This third piece is how adaptations evolve; it is why Galápagos finches have those exquisite beaks that are so good at what they do.

—1
—0
—+1

The power of the theory of natural selection is in its brilliant simplicity and the fact that it generates predictions that have been scientifically verified over the ages. Evolution by natural selection is one of the most well-established facts in all of science.⁷

In 1860, Darwin was well recognized for explaining how organisms' adaptations evolved for survival. But when he gazed at the peacock's tail, it stared back at him as a stark challenge to this theory of natural selection. It was obvious, at least to Darwin, if not to Wallace, that the peacock's tail was not an adaptation for survival, more likely hindering survival than promoting it. As the male is signaling his presence to potential mates, he is also being eyed as a potential meal by a variety of predators from tigers to mongooses. His tail makes him more attractive as a mate but more conspicuous as a meal. If the peacock's tail was a single aberrant glitch in the workings of natural selection it might not have been such a focus of Darwin's consternation. Darwin acknowledged, however, that these types of traits, those that seem maladaptive for survival, are ubiquitous in the animal kingdom. Long tails, bright colors, elegant courtship dances, and elaborate vocalizations all seem to invite death, not to circumvent it. How could this be explained?

There were some immediate hints. These types of traits were usually more developed in males than in females; in fact, they were often absent in females. Peahens (female peafowl) have tails, but they are dwarfed by the size of the males' tails. Also, males usually employed these traits in the breeding season, and many of these traits were part of the animal's courtship display.

Darwin's theory of sexual selection was his explanation for the peacock's tail and other courtship traits that were partners in the crime of seemingly reducing survivorship. This theory followed a three-step road map, similar to natural selection. First, unless there is perfect monogamy, there are often more males trying to mate than there are females willing to mate. Second, mating success is not random; the successful males have traits that enhance their ability to gain direct access either to females or to resources needed by females, or the males have traits that enhance their beauty, making them more attractive as mates. Third, these traits have a genetic component, resulting in traits that enhance

mating success being disproportionately promulgated in subsequent generations.

It was not difficult to resolve the conflict between natural selection and sexual selection. Traits evolve only if they are passed on to the next generation through mating, but animals can mate only if they survive. Thus, a male peacock with an abnormally short tail might survive quite well but never mate, while a male with an abnormally long tail might be quite attractive to females but likely would not live long enough to try out his tail. Thus, in many cases, there is a conflict between natural selection and sexual selection, and the traits that evolve strike some balance between survivorship and mating success.

Sexual Selection Is Borne out of Sexual Conflict

Why is there a sex bias in sexually selected traits? Why is it typically the males that have to compete for females and not vice versa? Of course, there is a lot of variation in mating systems; in seahorses and pipefish the sex roles are reversed, and females compete for males; and in a larger number of species, such as sticklebacks and humans, there is mutual mate choice. But why are these mating systems the exception rather than the rule?

The answer is as fundamental as can be imagined. Many of the differences between males and females, in almost all the species known to reproduce sexually, result from differences in gamete size. In humans and in most other animals, a female's eggs are the largest cells in her body, while a male's sperm are the smallest cells in his body. Females invest much more in their gametes than do males, even though males produce many more gametes. In humans, females have a few hundred eggs, while a male will produce a few billion sperm during his life.

Gamete size is the fundamental character that defines an animal's sex. Many would think that an individual's genitals might be diagnostic of its sex, but those many would be wrong. As a case in point, there is a species of lice that lives in caves in Brazil and feeds on bat guano. This is a typical sexually reproducing species, in that there are males and there are females. But atypically, the females have "penises" and the

—1
—0
—+1

males have “vaginas.” A female inserts her penis into the male’s vagina and sucks up the sperm from the inside of his body into her body, where his sperm fertilize her eggs.⁸ It is not a very typical mating strategy, but these lice are quite typical in that the females have the large gametes and the males have the small gametes.

The difference in gamete size mirrors the difference in reproductive investment by the sexes. In a landmark paper, published in 1972, that revitalized interest in sexual selection theory, Robert Trivers pointed out that this difference in reproductive investment results in different mating strategies between the sexes that, in turn, results in a conflict of interests when it comes to how males and females maximize their reproductive success.⁹ In shorthand, we refer to this as sexual conflict.

One offspring arises out of one sperm fertilizing one egg. Thus, there are many sperm competing for access to a few eggs, which translates to many males competing for fewer females. This simple fact has caused many evolutionary biologists to question why males even exist, a conundrum referred to as the “cost of males.”¹⁰ If females reproduced clonally, with no genetic input from males, all of their offspring, all of which would be daughters, would bear offspring. If females in a similar population reproduced sexually, only half of their offspring would be female, only their daughters but not their sons would bear offspring, and the sexual population would grow at a much slower rate than the asexual population. The short answer explaining the existence of males is that sexual reproduction provides a means for creating genetic variation among offspring, even though it slows the rate of population growth.¹¹

Selection favors both males and females to produce as many offspring as possible, but the difference in the size of gametes can result in two different mating strategies for the sexes. Males are selected to mate often, while females are selected to mate carefully. A famous experiment with fruit flies produced in 1948 by Angus Bateman illustrates this dichotomy.¹² Male and female flies were allowed to mate between one and four times. The number of offspring for each fly was counted. The more often a male mated, the more offspring he produced, while mating with more males had little effect on the female’s reproductive success.

Bateman's study has generated some controversy as well as some additional support. The controversy comes from the interpretation that we should always expect males to mate promiscuously and females to choose mates carefully. This controversy is especially heated when applied to our own species, sometimes being used to justify promiscuity in men while enforcing monogamy in women.¹³ Genetic markers, however, have now revealed that in some species females can be promiscuous and that additional matings can influence her reproductive success. On the other hand, it does seem that in many if not most animal mating systems, the number of matings has a greater effect on male reproductive success than it does on female reproductive success, and the exceptions to this pattern actually lend support to Bateman's theory.¹⁴ Also, in many species almost all of the females will reproduce about the same number of times, while many males will go unmated and a smaller proportion of males will garner a greater proportion of matings. Thus there is more variation in mating success among males than there is among females. Since selection acts on variation, sexual selection will be more intense on males than on females.¹⁵

Competition between males for females is also heightened by what is called the operational sex ratio.¹⁶ Even if the sex ratio of a population is balanced, the number of males and females ready to mate at any point in time is often biased toward males. Again, this has to do, in part, with the differences in gamete size. Once a female's eggs are fertilized, she must nurture them to gestation if there is internal fertilization or begin to develop a new set of eggs if fertilization is external. Thus, once a female mates, she is out of the mating game for a while, but in most species males do not have the same constraints and are able to continue mating. Consider our own species: once a woman conceives, she cannot do so again for another nine months, while her mate could continue to fertilize other women almost immediately. If a woman had sexual intercourse 100 times during gestation, she would still probably birth only one child. A man with similar sexual proclivities might have sired a small village in that time. Thus, the ratio of reproductively ready males to reproductively ready females (i.e., the operational sex ratio) results in

—-1
—0
—+1

many more males competing for many fewer females. How does this competition play out?

How to Get a Mate

In general, there are two ways males can get mates. One is competition. Males might compete for direct access to females. For example, in a baboon troop, dominant males aggressively prevent copulations by lower-ranked males when females are ovulating. Males might also compete by defending resources critical to females. For example, male red deer defend areas where females congregate for grazing. The evolution of animal weapons is most often in response to sexual selection for fighting with other males to get mates.¹⁷

The peacock's tail and other traits of sexual beauty can hardly be considered weapons. These traits arose from another form of sexual selection—female mate choice. In these mating systems, females are in the driver's seat when it comes to deciding who gets to mate. Males evolve traits that make them more sexually attractive to females. These are the traits that constitute much of the sexual beauty that we see in nature. Most of these elaborate traits, such as the peacock's tail, evolved in the service of sex. Female mate choice based on elaborate male traits is especially important in mating systems in which males do not offer resources to females or have the opportunity to gain access to females directly. These mating systems, often referred to as lek-like, are characterized by males gathering together to advertise for females and females surveying the males and then freely exercising their choice for a mate. In sage-grouse, for example, sometimes hundreds of males congregate in a breeding ground, or lek, in the sagebrush plains of North America from March until May. Females visit the leks, often congregating in the territories of just a few males, where they select mates. It is not uncommon for fewer than 10 percent of the males to be responsible for more than 75 percent of all the matings.¹⁸ Although true lek systems are usually restricted to birds, this type of mating system, in which females reign supreme, can occur in almost any type of animal.

Nature is diverse and especially so when it comes to the mating game. In some species females compete for males, and males choose their mates. This is often referred to as sex role reversal, and a classic example is that of seahorses and pipefish. In these species, males become “pregnant” in that they carry around the developing embryo in their pouch, during which time they usually do not mate. Once a female deposits her eggs in a male’s pouch, however, she is then free from the responsibility of maternal care and can seek out other males for mating.

Another exception to the strict male competition–female choice paradigm is that of mutual choice. Our own species might be one of the best examples. In some societies, men compete for the attention of women during courtship, and women are often able to choose the men with whom they pair, but men also will choose among females as potential partners. Sometimes men and women base their choice on similar characteristics. Other times, however, they use quite different criteria; for example, some studies have proposed that men tend to weight a partner’s age and physical beauty more heavily, while women are more attendant to the resources of a potential mate.¹⁹

There are also exceptions to the two tactics, direct competition and advertising, that males can employ to gain matings. Some mating systems are characterized by alternative mating tactics. Take freshwater sunfish as an example. Some large colorful males defend areas that are ideal for mating.²⁰ These fish have external fertilization, and as females release their eggs into the water column, males simultaneously release their sperm, and fertilization takes place when the gametes of the two sexes happen to make contact with one another. Some males, however, resemble females, and this allows them to loiter near these territorial males. When the territorial male and his female start to shed their gametes, the male who is impersonating a female begins to broadcast his sperm. In addition, so-called sneaker males, who are small and inconspicuous, will dart past a mating couple while broadcasting his sperm, hoping to steal a fertilization. In some cases, alternative mating strategies have a strong genetic component, such that courting males father courting sons while sneaker males father sneaker sons. In other cases, males are making the best of a bad situation, and genes

—-1
—0
—+1

might have nothing to do with these mating strategies, which instead arise from environmental influences. If a male has limited access to resources during development, for example, he might mature at a small size. A small courting male would probably be less attractive to a female than a large courting male, and consequently the small male adopts the alternative mating strategy of sneaking.

There are many exceptions to the “typical” mating systems in which males compete for females and females choose their mates. But all the exceptions prove the rule of Darwinian sexual selection theory rather than challenge it. Then why, we must ask, has sexual selection by female choice always been shrouded in controversy?

Darwin versus Wallace and the Controversy of Female Mate Choice

There were two main criticisms of Darwin’s theory of sexual selection by female choice. The first cited the lack of compelling evidence that females choose mates. The second criticism was that even if it were to occur, Darwin could not explain why females have these preferences.

Darwin and Wallace did not part ways after their codiscovery of natural selection theory. They became lifelong friends and scientific confidants and mostly agreed in their interpretation of how natural selection shapes the world around us. But the same cannot be said when it came to Darwin’s second great theory, sexual selection. As Wallace noted:

Two or three considerations appear fatal to the theory [of sexual selection]. . . . In the first place, it seems quite incredible, without direct evidence on the point, that a large majority of the females of any species, over the whole area of its range and for many successive generations, should agree in being pleased by the same particular kind of variation.²¹

Wallace was not the only one of Darwin’s contemporaries to reject his theory of sexual selection. For many, the idea of males competing “red in tooth and claw”²² for access to females seemed a proper exten-

sion of the theory of natural selection. The notion, however, that females had strong preferences for males based on the details of their courtship behavior and morphology, details that seem only to hasten the male's demise, was a real stretch. The Victorian notion that male mate choice reigned supreme in our own species made it seem improbable that in other species it was the females who wielded similar powers. It is notable that, contrary to these Victorian biases, Darwin implicitly, and sometimes even explicitly, endowed female animals of many species with superior power in the mating game. But at the same time it is confounding that, like a typical Victorian, he viewed women as inferior and devoid of such power, as is clearly documented in the next chapter by Holly Dunsworth.

Wallace too was a Victorian, so how did he explain these traits of sexual beauty, such as the sexual dimorphism in plumage coloration in birds? Rejecting Darwin's idea that sexual selection favored males with bright colors, Wallace suggested that natural selection favored females with dull colors because of the advantage being camouflaged afforded them.

The second criticism of sexual selection by female choice was that Darwin did not offer a cogent explanation for why females would have such preferences for males. His suggestion that females had an aesthetic sense much like our own seemed to be kicking the can down the road. It led only to the question of why the females would have a taste for the beautiful. When Wallace did give female choice some credence, he suggested that females were assessing traits that indicated a male was vigorous not beautiful. This difference of opinion between Darwin and Wallace, which they never resolved, is wonderfully documented in a recent book by Evelleen Richards.²³ This disagreement that started between the two Victorians continues until this day.

The Evolution of Female Mate Choice

There is now no controversy about the existence of female mate choice.²⁴ Hundreds of studies have shown, through natural observation and experimental manipulation, that females of many taxa, including

—-1
—0
—+1

crickets, fish, frogs, and birds, show preferences for the traits that are more elaborately developed in males and play some obvious role in courtship behavior. Numerous studies show that females prefer brighter colors, faster dances, longer tails, louder calls, more complex songs, and stronger odors.

The Darwin-Wallace controversy as to why females have such preferences is sometimes so heated it is forgotten that in many cases there is no controversy. To explore some of these arguments, I will borrow from an example in my recent book *A Taste for the Beautiful: The Evolution of Attraction*.²⁵

Now that it is well documented that females exhibit preferences for sexually selected traits, the next challenge is understanding why females show these preferences. There are three main processes that can bring about the evolution of mate choice. One, females can evolve preferences for traits of males who will deliver immediate benefits to the female, such as mating with the male who will fertilize more eggs. Two, traits and preferences can become genetically linked, such that male courtship traits evolve because they are favored by females, and the female preference evolves only because it is genetically linked to the traits under selection. Three, traits can evolve if they exploit hidden preferences; these are preferences harbored by the female but not expressed, as the traits that elicit them have yet to evolve. I will review these different processes in turn.

For the sake of argument, we will assume that there are genes influencing both female preferences and male traits, and that males and females contain both preference and trait genes but only females exhibit preferences and only males exhibit the sexually selected traits.

To explore these different scenarios for the evolution of female preferences we will consider the red-winged blackbird. Males perch on top of vegetation, quite often cattails, in early spring, singing as they flash bright red epaulets, or patches on their wings, in an exhaustive effort to advertise themselves to females. Why do males have these flashy colors, and why are females attracted to them?

Imagine that a closely related species, the yellow-headed blackbird, begins to nest in the same marsh as the red-winged blackbird, some-

thing that can happen in nature. As with most matings that take place between different species (i.e., heterospecifics), if a female red-winged mates with a male yellow-headed blackbird, her eggs will not be fertilized. Thus, there is a premium on females being able to recognize their own species and discriminate against other species. The easiest way for a female red-winged to identify a male of her species is through the red epaulets. Imagine there are two types of females, those that are more attracted to males with the red epaulets and those who do not discriminate and instead mate randomly with red-winged and yellow-headed males. Females with the preference for red wing patches will sire offspring, and if there is a genetic basis to their preference for red, this preference will be passed on to the next generation. Females that mate with yellow-headed blackbirds will not produce offspring, as her eggs will not develop, and her genes will never swim in the next generation's gene pool. Eventually, through time, all the female red-winged blackbirds preferentially mate with their own species over the yellow-headed blackbirds. Female preference for males of their own species is the most common form of mate choice and the best example of its utilitarian benefits.²⁶

Imagine another visitor now invades the marsh, but it is not another species of bird—it is feather lice. These lice have a variety of ill effects on the birds' health, and they also influence the brightness of the birds' plumage. Females already prefer males with red epaulets, because this preference delivers mates of the same species, but now selection will also favor females that prefer brighter red epaulets, because these females will avoid contracting sexually transmitted parasites. Females who don't discriminate based on the intensity of the red coloration are more likely to become infected with lice themselves and will suffer a decrement in their reproductive success—sick females do not lay as many eggs as healthy ones. Those females who prefer both the red-winged males and the brighter red-winged males garner two types of direct benefits from their mate choice: they mate with the correct species and the healthier males of their own species. These are called direct benefits because they directly influence the number of offspring a female produces.

—1
—0
—+1

Females can also garner indirect benefits through mate choice. Indirect benefits influence not the number of a female's offspring but instead the quality of her offspring. We know from many studies that some animals can be more parasite-resistant than other animals, and there can be a genetic component to this parasite resistance. Females who prefer more brightly colored males will produce offspring, both sons and daughters, who will be more resistant to parasites. Selection favors the evolution of these parasite-resistance genes in birds because individuals with these genes survive longer. The female preference genes, those genes underlying the preference for redder males, now end up in offspring that also have the parasite-resistance genes. The female preference genes, in this case, increase in frequency not because they are directly favored by selection but because they are in the bodies of individuals with parasite-resistance genes that are under direct selection. This is how a female preference for a male's "good genes"—genes that enhance survivorship—can evolve. The female preference genes hitchhike a ride into the next generation along with the good genes for survivorship. Studies of peacocks and frogs document how good genes preferences operate in nature.²⁷

Another case in which female preferences can evolve through genetic hitchhiking is called runaway sexual selection or the "sexy son" hypothesis. In this scenario, the males who are bright versus dull red do not differ in their survival abilities. Even though most females are mating at random relative to plumage brightness, some of the females mate only with the redder males; therefore, these males will increase in subsequent generations. Offspring of these matings will have genes for redder coloration and the preference for redder coloration. As noted above, the sons express only the trait, while the females express only the preference. The genes for brighter wings will evolve because they are favored by female choice, and the genes for this female preference will evolve through genetic hitchhiking because they are present in these more attractive males, the sexy sons. This has been a difficult hypothesis to test empirically, but studies of stalk-eyed flies bear out the major predictions of runaway sexual selection.²⁸ Thus, both good-genes preferences and runaway sexual selection can result in the evolution of female preferences through genetic hitchhiking.

We will consider one final scenario that can bring about the evolution of elaborate courtship traits and preferences for those traits. In this case, males evolve traits to tap into hidden preferences in the female; these are “preferences” that might have evolved for other tasks, such as foraging, but then become co-opted by mate choice. Again, we will consider the blackbird example but further back in time, before males evolved the red epaulets. In this scenario there is no benefit to a mutation that causes red epaulets, but there is a cost, as predators are more likely to spot these birds. If there is all cost and no benefit, these mutations quickly go extinct, as the bearers of this mutation quickly become meals for predators instead of mates for females. Now, let’s imagine that a new food source appears, brightly colored red worms that are much more nutritious than the brown ones common in this environment. Selection will now favor both males and females who are preferentially attracted to the red worms. Now that females have the sensory/cognitive bias for red, when males evolve red epaulets, the females are already tuned in to seeing this color. Thus, while the females are searching for a mate, they spot these more conspicuous males with this mutation more quickly than the less conspicuous males, and even though this mutation might still exact a cost from predation, it is also generating benefits to the male because of increased matings. This is sensory exploitation, because when the males evolve the trait, there is already a hidden bias for that trait, in this case for the color red. This scenario has played out in the evolution of courtship displays in guppies.²⁹

We have reviewed a handful of scenarios that can explain the evolution of female preferences: females get direct benefits from their mates that increase their number of offspring; females get indirect benefits from their mates by passing on “good” survivorship genes to their offspring; females get indirect benefits from their mates by producing sexy sons; and perceptual biases harbored by females are recruited into mate preferences when they are exploited by male traits. To make matters more complicated, these are not mutually exclusive scenarios, and they can all interact with one another.³⁰ Whereas Wallace and other critics of Darwin thought there were not plausible explanations for why females should show preferences for elaborate male traits, today there are

—1
—0
—+1

a plethora of plausible explanations. The current controversy is over which of these hypotheses are more important in which species.

The Neural and Cognitive Bases of Mate Choice

Today, 150 years after Darwin's presentation of sexual selection theory and 50 years after Trivers's seminal paper that resurrected this theory, there is no question about the ubiquity of female mate choice in nature. In addition, the emphasis of much of the work in animal sexual selection has shifted from an understanding of the forces that can lead to the evolution of female mate choice to an understanding of the neural and cognitive bases of this behavior. Many of these studies have been quite successful in documenting the biological bases of aesthetic sexual preferences in animals.

Jacob von Uexküll introduced the concept of the *Umwelt*,³¹ the main idea of which is that different types of animals reside in different sensory worlds. For example, unlike many birds, we cannot see in the ultraviolet; unlike bats, we cannot hear their ultrasonic echolocation calls; and unlike dogs, we have only very restrictive access to most of the odors around us. These sensory biases play an important role in the details of male sexual traits that females find attractive.³² For example, the colors to which the eyes of surfperch are most sensitive have evolved to enhance prey detection in the kelp forests where these fish reside. These sensory biases were then targeted by the details of the courtship displays that males evolved to attract females.³³ Similarly, the túngara frog has evolved additional syllables, called chucks, to adorn its basic mating call, a whine, which stimulate an inner ear organ that had yet to be recruited for use, in communication among close relatives.³⁴ This added stimulation of the ear has two results: it leads to enhanced stimulation of the auditory centers in the brain, and female túngara frogs find whines with chucks more attractive than a simple whine.³⁵ Sensory biases are key components of the aesthetic preferences of females.

Biases in how we perceive the world are not restricted to sensory end organs—eyes, ears, and noses. There are also a number of cognitive biases that can influence an animal's taste for the beautiful. Many human

psychophysical perceptions follow a power function known as Weber's law.³⁶ Our perception of the difference in the magnitude of two stimuli, for example, decreases as the absolute magnitude of the stimuli increases. We can more readily detect the small difference between a one-kilogram and a two-kilogram weight than we can detect that same difference between a twenty-five-kilogram and a twenty-six-kilogram weight. Weber's law also influences how animals weight the attractiveness between different stimuli. The túngara frogs mentioned above can add from one to seven chucks to their mating call. Females prefer whines followed by more chucks over whines followed by fewer chucks, but the strength of preference depends on the total number of chucks added to the call. The strength of preference between whines followed by two versus one chucks is much stronger than the preference between five versus four chucks.³⁷

Weber's law also influences our perception of the attractiveness of human faces in at least a couple of populations of undergraduates in the United States. Gassen et al. morphed a series of faces from pairs of what were previously judged as an unattractive face and an attractive face.³⁸ The difference in perceived attraction between pairs of faces that differed morphometrically by 10 percent was much greater for two unattractive faces than it was for two attractive faces. These studies of frogs and humans indicate that the aesthetics of these two species does not vary linearly with the traits they are judging. These results have important implications for the tempo and mode of the evolution of beauty.

In animal studies, we often think aesthetic preferences are fixed for an individual's lifetime, while in humans, on the other hand, percepts of attractiveness of both men and women are often thought to be notoriously fickle. Pennebaker et al. showed that human perceptions of the attractiveness of the opposite sex vary as a function of "closing time."³⁹ Patrons at a bar were asked to rate the attractiveness of same- and opposite-sex patrons early in the evening and then again as closing time approached. Men and women both perceived opposite-sex patrons as more attractive later in the evening. When this study was repeated, and alcohol blood levels were measured and statistically controlled for, the same closing time effects were found.⁴⁰ One interpretation of these

—-1
—0
—+1

results is that to avoid cognitive dissonance, individuals change their perception of the attractiveness of individuals they would like to meet as the time available for social interactions decreases.

Animals face their own closing times. Female túngara frogs visit a chorus of males only on the night they are going to mate. If they do not choose a mate by the end of the night they still ovulate, expelling all of their eggs into the pond. It then takes the females another six weeks to develop a new set of eggs ready for fertilization. Lynch et al. tested females early in the evening with synthetic calls that had previously been shown to be unattractive to the females; these calls rarely elicited a response from the females—that is, movement to the speaker broadcasting the call.⁴¹ The exact same calls, however, were very attractive to the same frogs later in the night, when the females were becoming desperate to find a mate. Both humans and female frogs are broadening their tastes for the beautiful as closing time approaches.

Peer pressure is another factor that can lead to unstable percepts of attraction. A simple experiment with a fish (a molly) showed that peer pressure is not restricted to humans. A female fish was placed inside a test tank with one male on each side of the tank. The males were separated from the focal female by a pane of glass, but the female could approach the males and be courted by them. When females were tested, they preferred courting with the larger of the two males. The female was then constrained to the middle of the aquarium in a glass cylinder, from which she observed the previously un-preferred male being courted by a female selected as the “model female.” The model female was then removed, and the female-choice test was repeated; now the female switched her preference to the previously un-preferred male. The interpretation is that she was copying the mate choice of the model female.⁴² Furthermore, the more attractive the model female, the greater her influence on mate-choice copying by the focal female.⁴³

A number of studies have examined mate-choice copying or, more specifically, context-dependent attractiveness in humans. Typically, individuals rate a photograph of a person pictured with a member of the opposite sex as more attractive than a photograph of the same person alone. Recently, Gouda-Vossos et al. conducted a meta-analysis and

showed there was strong evidence for this phenomenon in women but not in men.⁴⁴ Street et al. also demonstrated female mate-choice copying based on facial attractiveness, but they showed that the degree of copying was no different when analogous experiments were conducted in other domains, such as evaluation of art.⁴⁵ Their interpretation is that, at least in this instance, mate-choice copying is one expression of social facilitation and is not necessarily a psychological adaptation for mate choice. This does not lessen the influence of mate-choice copying in the evaluation of facial attractiveness and is yet another example of how cognitive biases in an individual's sexual aesthetics can have origins in domains outside of mate choice. Furthermore, these studies illustrate one role of social context in evaluating sexual beauty and suggest the importance of evaluating such phenomena across the breadth of cultural variation that is the hallmark of our species.

Summary

Darwin proposed his theory of sexual selection to explain how elaborate, sexually dimorphic traits used in courtship could evolve, despite being maladaptive for survival. Although sexual selection by male-male competition was readily accepted, the same was not true for sexual selection by female choice. The theory's strongest critic was Alfred Russel Wallace, the codiscoverer of the theory of natural selection. Initially, Wallace was skeptical of female choice in general, doubting that females would base consistent mate preferences on nuances of male courtship behavior and morphology. When he did grant some credence to female choice, he suggested choice was based on traits that indicated male vigor. Darwin, on the other hand, suggested that female animals have a "taste for the beautiful,"⁴⁶ that they possess sexual aesthetics not all that different from ours. His theory lay dormant for 100 years and was resurrected in the 1970s, primarily by Trivers's theory of parental investment. Since then, there have been hundreds of studies to demonstrate clearly the efficacy of female mate choice, thus validating Darwin's primary prediction about sexual selection. Disagreements still exist as to what causes the evolution of female mate choice, echoing the fundamental

—-1
—0
—+1

disagreement between Darwin and Wallace. There are now a number of studies supporting Wallace's utilitarian view that females acquire direct and indirect benefits from their mate choice. Other studies support Darwin's notion of sexual aesthetics by documenting the sensory, neural, and cognitive biases that underlie female mate preferences. The recent trend in the field has been to delve deeper into mechanisms of mate preference to further document the female's taste for the beautiful.

-1—
0—
+1—

29. Alondra Nelson, *The Social Life of DNA: Race, Reparations, and Reconciliation after the Genome* (Boston: Beacon Press, 2016); Dorothy Roberts, *Fatal Invention: How Science, Politics, and Big Business Re-Crete Race in the Twenty-First Century* (New York: The New Press, 2012); Saini, *Superior*.
30. Graves, “Nonexistence of Biological Races,” 1474–95; Marks, Ten Facts, 265–276; Nelson, *Social Life of DNA*; Roberts, *Fatal Invention*; Saini, *Superior*.
31. Fuentes, *Race, and Other Lies*; Clarence C. Gravlee, Amy Non and Connie Mulligan, “Genetic Ancestry, Social Classification, and Racial Inequalities in Blood Pressure in Southeastern Puerto Rico,” *PLoS One* 4, no. 9 (2009): e6821; Jacklyn Quinlan et al., “Genetic Loci and Novel Discrimination Measures Associated with Blood Pressure Variation in African Americans Living in Tallahassee,” *PLoS One* 11, no. 12 (2016): e0167700; Nancy Krieger, “Measures of Racism, Sexism, Heterosexism, and Gender Binarism for Health Equity Research: From Structural Injustice to Embodied Harm—an Ecosocial Analysis,” *Annual Review of Public Health* 41 (2020): 1–26.
32. For example, Nicholas Wade, *A Troublesome Inheritance: Genes, Race and Human History* (New York: Penguin Press, 2014); Richard J. Herrnstein and Charles Murray, *The Bell Curve: Intelligence and Class Structure in American Life* (New York: Free Press, 1994); Charles Murray, *Human Diversity: The Biology of Gender, Race, and Class* (New York: Twelve, 2020).
33. Darwin, *Descent*, 1st ed., 1:249.
34. Steven Rose, “Darwin, Race and Gender,” *European Molecular Biology Organization Reports* 10, no. 4 (2009): 297–298.
35. Adrian Desmond and James Moore, *Darwin’s Sacred Cause: How a Hatred of Slavery Shaped Darwin’s Views on Human Evolution* (Boston & New York: Houghton Mifflin Harcourt, 2009).
36. Fuentes, *Race, and Other Lies*; Agustín Fuentes, *Why We Believe: Evolution and the Human Way of Being* (New Haven, CT: Yale University Press, 2019).

Chapter 8: Resolving the Problem of Sexual Beauty

1. Darwin to Asa Gray, April 3, 1860, Darwin Correspondence Project, letter no. 2743, <https://www.darwinproject.ac.uk/letter/DCP-LETT-2743.xml>.
2. Fabienne Smith, “Charles Darwin’s Ill Health,” *Journal of the History of Biology* 23 (1990): 443–59.
3. Peter R. Grant and B. Rosemary Grant, *How and Why Species Multiply: The Radiation of Darwin’s Finches* (Princeton, NJ: Princeton University Press, 2011).
4. Arhat Abzhanov et al., “Bmp4 and Morphological Variation of Beaks in Darwin’s Finches,” *Science* 305 (2004): 1462; Arhat Abzhanov et al., “The Calmodulin Pathway and Evolution of Elongated Beak Morphology in Darwin’s Finches,” *Nature* 442 (2006): 563–67.
5. Charles Darwin, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, 1st ed. (London: John Murray, 1859).
6. Thomas R. Malthus, *An Essay on the Principle of Population; or, a View of Its Past and Present Effects on Human Happiness* (London: Reeves & Turner, 1888).
7. See, for example, John A. Endler, *Natural Selection in the Wild* (Princeton, NJ: Princeton University Press, 1986).

8. Kazunori Yoshizawa, Rodrigo Ferreira, Yoshitaka Kamimura, and Charles Lienhard, “Female Penis, Male Vagina, and Their Correlated Evolution in a Cave Insect,” *Current Biology* 24 (2014): 1006–10.
9. Robert L. Trivers, “Parental Investment and Sexual Selection,” in *Sexual Selection and the Descent of Man*, ed. Bernard G. Campbell (Chicago: Aldine, 1972), 136–79.
10. John Maynard Smith, *The Evolution of Sex* (Cambridge: Cambridge University Press, 1978).
11. Ibid.
12. Angus J. Bateman, “Intrasexual Selection in *Drosophila*,” *Heredity* 2 (1948): 349–68.
13. Zuleyma Tang-Martínez, “Rethinking Bateman’s Principles: Challenging Persistent Myths of Sexually Reluctant Females and Promiscuous Males,” *Journal of Sex Research* 53 (2016): 532–59; Angela Saini, *Inferior: How Science Got Women Wrong—and the New Research That’s Rewriting the Story* (Boston: Beacon Press, 2017).
14. Adam G. Jones et al., “The Bateman Gradient and the Cause of Sexual Selection in a Sex-Role-Reversed Pipefish,” *Proceedings of the Royal Society of London, ser. B: Biological Sciences* 267 (2000): 677–80.
15. Michael J. Wade and Stephen M. Shuster, “Don’t Throw Bateman Out with the Bathwater!,” *Integrative and Comparative Biology* 45 (2005): 945–51.
16. Stephen T. Emlen and Lewis W. Oring, “Ecology, Sexual Selection, and the Evolution of Mating Strategies,” *Science* 197 (1977): 215–23.
17. Douglas J. Emlen, *Animal Weapons: The Evolution of Battle* (New York: Henry Holt, 2014).
18. R. Haven Wiley, “Territoriality and Non-Random Mating in Sage Grouse, *Centrocercus urophasianus*,” *Animal Behaviour Monographs* 6 (1973): 85–169.
19. David M. Buss, *The Evolution of Desire* (New York: Basic Books, 1994).
20. Mart R. Gross, “Sunfish, Salmon, and the Evolution of Alternative Reproductive Strategies and Tactics in Fishes,” *Fish Reproduction* (1984): 55–75.
21. Alfred R. Wallace, “Lessons from Nature, as Manifested in Mind and Matter,” *Academy* 562 (1876).
22. Alfred Tennyson, *In Memoriam AHH* (Los Angeles: Hardpress Publishing, 2012 [1850]).
23. Evelleen Richards, *Darwin and the Making of Sexual Selection* (Chicago: University of Chicago Press, 2017).
24. Malte Andersson, *Sexual Selection* (Princeton, NJ: Princeton University Press, 1994); Richard O. Prum, *The Evolution of Beauty: How Darwin’s Forgotten Theory of Mate Choice Shapes the Animal World—and Us* (New York: Doubleday, 2017); Gil G. Rosenthal, *Mate Choice: The Evolution of Sexual Decision Making from Microbes to Humans* (Princeton, NJ: Princeton University Press, 2017); Michael J. Ryan, *A Taste for the Beautiful: The Evolution of Attraction* (Princeton, NJ: Princeton University Press, 2018).
25. Ryan, *A Taste for the Beautiful*.
26. Rosenthal, *Mate Choice*; Jerry A. Coyne and H. Allen Orr, *Speciation* (Sunderland, MA: Sinauer, 2004).
27. Marion Petrie, “Improved Growth and Survival of Offspring of Peacocks with More Elaborate Trains,” *Nature* 371 (1994): 598–99; Allison M. Welch, Raymond D. Semlitsch and H.

Carl Gerhardt, "Call Duration as an Indicator of Genetic Quality in Male Gray Tree Frogs," *Science* 280 (1998): 1928–30.

28. Gerald S. Wilkinson and Paul R. Reillo, "Female Choice Response to Artificial Selection on an Exaggerated Male Trait in a Stalk-Eyed Fly," *Proceedings of the Royal Society of London, ser. B: Biological Sciences* 255 (1994): 1–6.

29. F. Helen Rodd, Kimberly A. Hughes, and Trevor E. Pitcher, "Sex, Color and Mate Choice in Guppies," *Reviews in Fish Biology and Fisheries* 9 (1999): 203–7.

30. Rosenthal, *Mate Choice*; Hanna Kokko, Robert Brooks, Michael D. Jennions, and Josephine Morley, "The Evolution of Mate Choice and Mating Biases," *Proceedings of the Royal Society of London, ser. B: Biological Sciences* 270 (2003): 653–64.

31. Reviewed in Thomas A. Sebeok, *The Sign and Its Masters* (Austin: University of Texas Press, 1979).

32. Michael J. Ryan and Molly E. Cummings, "Perceptual Biases and Mate Choice," *Annual Review of Ecology, Evolution, and Systematics* 44 (2013): 437–59.

33. Molly E. Cummings, "Sensory Trade-Offs Predict Signal Divergence in Surfperch," *Evolution* 61 (2007): 530–45.

34. Walter Wilczynski, Ann Keddy-Hector, and Michael J. Ryan, "Patterns and Basilar Papilla Tuning in Cricket Frogs, I. Differences among Populations and between Sexes," *Brain, Behavior & Evolution* 39 (1992): 229–37.

35. Kim L. Hoke et al., "Functional Mapping of the Auditory Midbrain during Mate Call Reception," *Journal of Neuroscience* 24 (2004): 11264–72; Michael J. Ryan, *The Túngara Frog: A Study in Sexual Selection and Communication* (Chicago: University of Chicago Press, 1985).

36. Roger N. Shepard, "Toward a Universal Law of Generalization for Psychological Science," *Science* 237 (1987): 1317–23.

37. Karin L. Akre et al., "Signal Perception in Frogs and Bats and the Evolution of Mating Signals," *Science* 333 (2011): 751–52.

38. Jeffrey Gassen et al., "Beauty Is in the Psychophysics of the Beholder: Facial Attractiveness, Sexual Selection, and Weber's Law," (unpublished manuscript, 2018).

39. James W. Pennebaker et al., "Don't the Girls Get Prettier at Closing Time: A Country and Western Application to Psychology," *Personality and Social Psychology Bulletin* 5 (1979): 122.

40. Carly Johnco, Ladd Wheeler, and Alan J. Taylor, "They Do Get Prettier at Closing Time: A Repeated Measures Study of the Closing-Time Effect and Alcohol," *Social Influence* 5 (2010): 261–71.

41. Kathleen S. Lynch, A. Stanley Rand, Michael J. Ryan, and Walter Wilczynski, "Reproductive State Influences Female Plasticity in Mate Choice," *Animal Behaviour* 69 (2005): 689–99.

42. Ingo Schlupp, Catherine A. Marler, and Michael J. Ryan, "Benefit to Male Sailfin Mollies of Mating with Heterospecific Females," *Science* 263 (1994): 373–74.

43. Sarah E. Hill and Michael J. Ryan, "The Role of Model Female Quality in the Mate Choice Copying Behaviour of Sailfin Mollies," *Biology Letters* 2 (2006): 203–5.

44. Amany Gouda-Vossos, Shinichi Nakagawa, Barnaby J. W. Dixson, and Robert C. Brooks, "Mate Choice Copying in Humans: A Systematic Review and Meta-Analysis," *Adaptive Human Behavior and Physiology* 4 (2018): 364–86.

-1—
0—
+1—

45. Sally E. Street et al., “Human Mate-Choice Copying Is Domain-General Social Learning,” *Scientific Reports* 8 (2018): 1715.
46. Charles Darwin, *The Descent of Man, and Selection in Relation to Sex*, 1st ed. (London: John Murray, 1871), 1:64.

Chapter 9: This View of Wife

1. Charles Darwin, *The Descent of Man, and Selection in Relation to Sex*, 1st ed. (London: John Murray, 1871), 2:316.
2. Charles Darwin, *The Descent of Man and Selection in Relation to Sex*, 2nd ed. (London: John Murray, 1874), 563. In the first edition, the phrase “in securing wives” is used instead of “in their contests for wives.”
3. Darwin, *Descent*, 1st ed., 2:326–27.
4. *Ibid.*, 329.
5. *Ibid.*, 385.
6. Darwin, *Descent*, 2nd ed., 556.
7. *Ibid.*, 558–59.
8. Nina Jablonski, “Skin Color,” in *The International Encyclopedia of Biological Anthropology*, ed. Wenda Trevathan (New York: Wiley & Sons, 2018), 1430–34.
9. Nina Jablonski and George Chaplin, “The Evolution of Human Skin Coloration,” *Journal of Human Evolution* 39 (2000): 57–106.
10. Jablonski, “Skin Color.”
11. Ellen Quillen et al., “Shades of Complexity: New Perspectives on the Evolution and Genetic Architecture of Human Skin,” *American Journal of Physical Anthropology* 168 (2018): 4.
12. Tina Lasisi and Mark D. Shriver, “Focus on African Diversity Confirms Complexity of Skin Pigmentation Genetics,” *Genome Biology* 19 (2018): 13.
13. Jablonski, “Skin Color,” 1433.
14. Paolo U. Giacomoni, Thomas Mammone, and Matthew Teri, “Gender-Linked Differences in Human Skin,” *Journal of Dermatological Science* 55 (2009): 144–49.
15. Lorena Madrigal and William Kelly, “Human Skin-Color Sexual Dimorphism: A Test of the Sexual Selection Hypothesis,” *American Journal of Physical Anthropology* 132 (2007): 470–82.
16. Smith (2016) referred to this logical trap as “current utility versus historical role” in his review of this and related issues in the science of paleoanthropology. See Richard J. Smith, “Explanations for Adaptations, Just-so Stories, and Limitations on Evidence in Evolutionary Biology,” *Evolutionary Anthropology* 25 (2016): 276–87.
17. Darwin, *Descent*, 2nd ed., 563.
18. Holly M. Dunsworth, “Expanding the Evolutionary Explanations for Sex Differences in the Human Skeleton,” *Evolutionary Anthropology*, May 2, 2020, <https://doi.org/10.1002/evan.21834>.
19. Giacomoni, “Gender-Linked Differences,” 144–49.
20. Sue T. Parker and Karen E. Jaffe, *Darwin’s Legacy: Scenarios in Human Evolution* (Plymouth, UK: Altamira, 2008).