REVIEW SUMMARY

SEXUAL SELECTION

Sexual selection and the ascent of women: Mate choice research since Darwin

Gil G. Rosenthal* and Michael J. Ryan*

BACKGROUND: Charles Darwin's *Descent of Man, and Selection in Relation to Sex* tackled the two main controversies arising from the *Origin of Species:* the evolution of humans from animal ancestors and the evolution of sexual ornaments. Most of the book focuses on the latter, Darwin's theory of sexual selection. Research since supports his conjecture that songs, perfumes, and intricate dances evolve because they help secure mating partners. Evidence is overwhelming for a primary role of both male and female mate choice in sexual selection—not only through premating courtship but also through intimate interactions during and long after mating.

But what makes one prospective mate more enticing than another? Darwin, shaped by misogyny and sexual prudery, invoked a "taste for the beautiful" without speculating on the origin of the "taste." How to explain when the "final marriage ceremony" is between two rams? What of oral sex in bats, cloacal rubbing in bonobos, or the sexual spectrum in humans, all observable in Darwin's time? By explaining desire through the lens of those male traits that caught his eyes and those of his gender and culture, Darwin elided these data in his theory of sexual evolution.

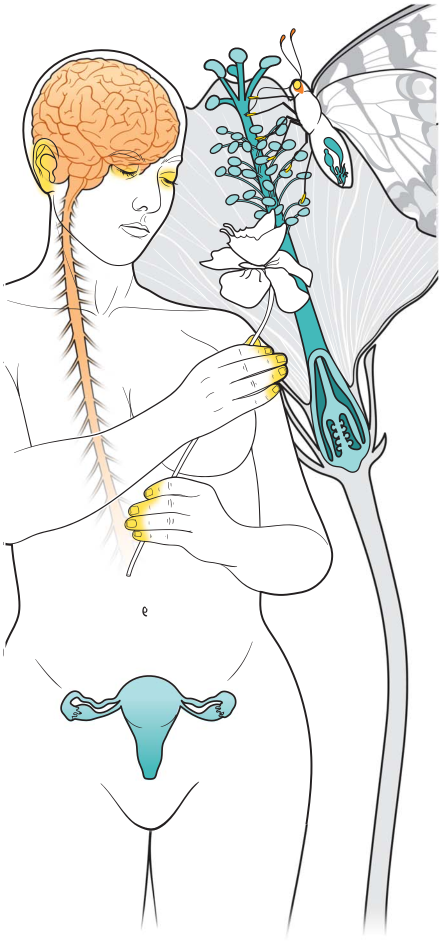
Work since Darwin has focused on how traits and preferences coevolve. Preferences can evolve even if attractive signals only predict offspring attractiveness, but most attention has gone to the intuitive but tenuous premise that mating with gorgeous partners yields vigorous offspring.

By focusing on those aspects of mating preferences that coevolve with male traits, many of Darwin's influential followers have followed the same narrow path. The sexual selection debate in the 1980s was framed as "good genes versus runaway": Do preferences coevolve with traits because traits predict genetic benefits, or simply because they are beautiful? To the broader world this is still the conversation.

ADVANCES: Even as they evolve toward ever-more-beautiful signals and healthier offspring, mate-choice mechanisms and courter traits are locked in an arms race of coercion and resistance, persuasion and skepticism. Traits favored by sexual selection often do so at the expense of chooser fitness, creating sexual conflict. Choosers then evolve preferences in response to the costs imposed by courters.

Often, though, the current traits of courters tell us little about how preferences arise. Sensory systems are often tuned to nonsexual cues like food, favoring mating signals resembling those cues. And preferences can emerge simply from selection on choosing conspecifics. Sexual selection can therefore arise from chooser biases that have nothing to do with ornaments.

Choice may occur before mating, as Darwin emphasized, but individuals mate multiple times and bias fertilization and offspring care toward favored partners. Mate choice can thus occur in myriad ways after mating, through behavioral, morphological, and physiological mechanisms.



Mate choice mechanisms across domains of life. Sensory periphery for stimulus detection (yellow), brain for perceptual integration and evaluation (orange), and reproductive structures for postmating choice among pollen or sperm (teal).

ILLUSTRATION: KELLIE HOLOSKI/*SCIENCE*

Like other biological traits, mating preferences vary among individuals and species along multiple dimensions. Some of this is likely adaptive, as different individuals will have different optimal mates. Indeed, mate choice may be more about choosing compatible partners than picking the "best" mate in the absolute sense. Compatibility-based choice can drive or reinforce genetic divergence and lead to speciation.

The mechanisms underlying the "taste for the beautiful" determine whether mate choice accelerates or inhibits reproductive isolation. If preferences are learned from parents, or covary with ecological differences like the sensory environment, then choice can promote genetic divergence. If everyone shares preferences for attractive ornaments, then choice promotes gene flow between lineages.

OUTLOOK: Two major trends continue to shift the emphasis away from male "beauty" and toward how and why individuals make sexual choices. The first integrates neuroscience, genomics, and physiology. We need not limit ourselves to the feathers and dances that dazzled Darwin, which gives us a vastly richer picture of mate choice. The second is that despite persistent structural inequities in academia, a broader range of people study a broader range of questions.

This new focus confirms Darwin's insight that mate choice makes a primary contribution to sexual selection, but suggests that sexual selection is often tangential to mate choice. This conclusion challenges a persistent belief with sinister roots, whereby mate choice is all about male ornaments. Under this view, females evolve to prefer handsome males who provide healthy offspring, or alternatively, to express flighty whims for arbitrary traits. But mate-choice mechanisms also evolve for a host of other reasons

Understanding mate choice mechanisms is key to understanding how sexual decisions underlie speciation and adaptation to environmental change. New theory and technology allow us to explicitly connect decision-making mechanisms with their evolutionary consequences. A century and a half after Darwin, we can shift our focus to females and males as choosers, rather than the gaudy by-products of mate choice. ■

The list of author affiliations is available in the full article online.
*Corresponding author. Email: gil.rosenthal@unipd.it (G.G.R.); mryan@utexas.edu (M.J.R.)

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REVIEW

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Sexual selection and the ascent of women: Mate choice research since Darwin

Gil G. Rosenthal[1,2]* **and Michael J. Ryan**[3,4]*

Darwin's theory of sexual selection fundamentally changed how we think about sex and evolution. The struggle over mating and fertilization is a powerful driver of diversification within and among species. Contemporaries dismissed Darwin's conjecture of a "taste for the beautiful" as favoring particular mates over others, but there is now overwhelming evidence for a primary role of both male and female mate choice in sexual selection. Darwin's misogyny precluded much analysis of the "taste"; an increasing focus on mate choice mechanisms before, during, and after mating reveals that these often evolve in response to selection pressures that have little to do with sexual selection on chosen traits. Where traits and preferences do coevolve, they can do so whether fitness effects on choosers are positive, neutral, or negative. The spectrum of selection on traits and preferences, and how traits and preferences respond to social effects, determine how sexual selection and mate choice influence broader-scale processes like reproductive isolation and population responses to environmental change.

One hundred and fifty years ago, Charles Darwin published his second great book, *The Descent of Man, and Selection in Relation to Sex* (*1*). Darwin's book on sexual selection is traditionally viewed as a supplement to *On the Origin of Species*, tackling two distinct topics from his theory that were steeped in controversy. The societal influence of *The Descent of Man, and Selection in Relation to Sex* has perhaps been as far-reaching as Darwin's natural selection book. Although our descent from a nonhuman ancestor is settled science, sexual selection—specifically through mate choice—continues to fascinate (*2*) and frustrate (*3*).

Mate choice: The fuzzy center of Darwin's theory

This sesquicentennial offers an appropriate time to reevaluate "Darwin's really dangerous idea" (*4*). Darwin's evolutionary science and abolitionist politics (*5*) were animated by the "contingent fact" of human equality (*6*). Published on the heels of the US war to abolish slavery, *The Descent of Man, and Selection in Relation to Sex* (*The Descent*) is perhaps the best anyone could have done on this score given that Darwin was steeped in the structural racism of his time, tribe, and place. Darwin believed in the manifest superiority of white Anglo-Saxon Protestants and the inferiority of "savages" like the Fuegians. Critically, however, Darwin emphasizes that this superiority stems from factors that are (largely) not immutable, but rather dependent on culture and environment. He cites his personal experiences with Orundellico ("Jemmy Button") and John Edmonstone—"civilized" men from savages and slaves—to reinforce his point that heritable differences existed between ethnic groups but were largely due to the caprices of sexual selection acting on human populations.

As detailed in Richards (*7*), Darwin's sexual selection was a revolutionary tool to take on both the theological racism of polygenist creationists like Louis Agassiz, who posited separate-and-unequal Creations on each continent, along with the pseudoscientific racism of his white scientific contemporaries, who argued for the essential inferiority of Black and Brown people. In the first third of *The Descent*, Darwin argues that we all share a recent common ancestor and that our mental and moral differences are largely the product of culture and environment. In two chapters near the end, he argues that our physical differences—skin color, hair, and so forth—are just superficial by-products of sexual selection. These two parts of *The Descent* add up to a scientific case for, if not equality among humans, enough brotherhood among men to put chattel slavery beyond the moral pale even in a forthrightly white-supremacist society (*7*).

There is a lively debate over the nature and extent of Darwin's racism (*8*). By contrast, Darwin's essentialist misogyny—his belief that women were immutably inferior to men—is unambiguous. Here, Darwin argues for sexual selection not as a force driving superficial differences among groups, but rather as the driving force for the biological supremacy of males: "hence man has ultimately become superior to woman" [(*1*), p. 565]. As we detail below, Darwin's dismissal of female agency (*9*) and promiscuity (*10*) continues to shadow the field of sexual selection. Yet the broad logic of Darwin's theory stands today:

> Sexual selection depends on the success of certain individuals over others of the same sex, in relation to the propagation of the species, whereas natural selection depends on the success of both sexes, at all ages, in relation to the general conditions of life. The sexual struggle is of two kinds; it is between the individuals of the same sex, generally the males, to drive away or kill their rivals, the females remaining passive—while it is also the struggle between individuals of the same sex, to excite or charm those of the opposite sex, generally the females, which no longer remain passive, but select the more agreeable partners. [(*1*), p. 630]

In the quote above, Darwin makes it clear that through mate choice, females become active agents of sexual selection rather than mere passive participants. As we note below, however, this empowerment of females was not extended to his own species. As Richards (*7*) explains, Darwin naturalized female choice among animals and normalized male choice among humans.

Sexual selection was revealed to Darwin in the form of sexual dimorphism, and it is sexual dimorphism that continues to fuel our inquiries. Just as Darwin invokes sexual selection to explain human differences, he spends 10 chapters—three on birds alone—on an encyclopedic analysis of differences between the sexes across the animal kingdom. Throughout, his focus is on the color, song, and morphology of males. How could these sexually dimorphic traits evolve when they seemed to decrease the survivorship of the sex that bore them? The answer was simple: These traits were favored because they increased the likelihood of mating, either by prevailing over rivals for access to reproductive opportunities or by wooing prospective partners.

Much of what we know about sexual selection is well-documented and relatively intuitive—traits that make males more successful are favored by selection. If selection takes the form of intrasexual competition, males evolve weapons that make it easier to fight, as well as ornaments and behaviors used in aggressive signaling (*11*). Conventional signaling theory, whereby communication systems evolve to minimize costs for both signalers and receivers, provides a well-supported framework for the evolution of sexually dimorphic traits through male-male competition. These traits are typically "honest"; that is, variation in sexually dimorphic signals predicts variation in signalers' fighting ability (*12*).

We also know that if traits "excite or charm" potential mates, they will give a reproductive

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[1] Department of Biology, University of Padova, Padova, Italy. [2] Centro de Investigaciones Científicas de las Huastecas "Aguazarca," Calnali, Hidalgo, Mexico. [3] Department of Integrative Biology, University of Texas, Austin, TX, USA. [4] Smithsonian Tropical Research Institute, Balboa, Republic of Panama.
***Corresponding author. Email: gil.rosenthal@unipd.it (G.G.R.); mryan@utexas.edu (M.J.R.)**

advantage to courters with those traits, which is in line with the broad strokes of what Darwin proposed. It is this advantage that favored the evolution of the elaborate, gaudy, and conspicuous traits that are often used in mate attraction—traits that are not necessarily always "honest" because they do not always convey information about inherent survival attributes of males (*2*, *3*, *9*). Although Darwin's interest in sexual selection was piqued by a certain kind of dimorphism, greater expression of both armaments and ornaments in males, we now know that these Darwinian sex roles are often reversed, with females battling it out for access to males and also being subject to the vicissitudes of male mate choice (*13*, *14*).

Ears, brain, clitoris: The unwhisperable substrates of Darwin's theory

Darwin's radical hypothesis assigned females a pivotal role in mate choice. His contemporaries scoffed at his assertion that females actively decided what is sexually attractive and thus which males got to mate (*7*). Tellingly, Darwin did not suggest the same agency in female humans (*15*) and generally expressed deeply misogynistic views on women's roles in the mating endeavor. Throughout *The Descent*, he views women's intellectual inferiority as a manifest fact of nature [(*1*), p. 565].

Darwin's reflexive misogyny makes for an uncharacteristically euphemistic, muddled view of mate-choice mechanisms. Whether human, bird, or butterfly, Darwin's females are allowed neither strategy nor lust: They are charmed or dazzled by beauty, ingénues entranced by cameos of eligible Lords on display at the Victoria and Albert. Darwin observes above the waistline and at a distance, with a chaste focus on "beautiful" plumage and song; he is squeamish about sex and particularly about female sexual desire. Even in butterflies, courtship culminates not in copulation but in a "final marriage ceremony." What little there is about the "messier" aspects of sex, such as rubbing and licking and sniffing and secreting, is cloaked in euphemism or in Latin, and some things are actively avoided, unwhisperable in any language: homosexuality, ejaculate mixing, female orgasm. Darwin ignored multiple mating and therefore all of postmating sexual selection, including sperm competition and cryptic female choice.

Darwin may have had little choice in adopting his prudishness in such a socially charged environment: Even 26 years later, when Havelock Ellis tackled such topics in his *Psychology of Sex*, a bookseller was charged with distributing obscene material (*16*). Such public outrage also greeted Kinsey (*17*, *18*) in the USA a half century later.

Darwin set up another major hurdle that had little to do with prurience or misogyny and indeed ironically contradicted his dismissal of the females of his own species: the requirement for sophisticated "mental faculties" to exercise choice. Certainly, the brain shapes mating outcomes in species that have one, but a brain is not required for choice. Indeed, the oldest and most universal forms of sexual selection take the form of interactions among gametes and within the reproductive tract (Fig. 1, areas in blue).

What Darwin couldn't see: Postmating sexual selection, variation among females, and male choice

Postmating sexual selection—sperm competition among males, fertilization bias by females, and allocation bias by both sexes—was beyond the pale for Darwin, yet such mate choice after mating is often a stronger agent of sexual selection than the premating "taste for the beautiful" (*19*). Yet postmating sexual selection is only one of several avenues where Darwin's denial of women's intelligence, agency, or promiscuity led him astray on mate choice in humans and nonhumans alike: not only ignoring multiple mating, but ignoring variation among choosers across scales, and the mutual nature of mate choice and its consequences.

Although Darwin was quite interested in variation among males, he treated females and their preferences as uniform, rather than as distinct individuals. Kinsey, whose earlier career as an entomologist endowed him with an appreciation for individual variation (*6*), was an early pioneer in quantifying variation in sexual proclivities across genders. But much research on mate choice continues to follow Darwin's lead in ignoring preference variation. Preferences can be diametrically opposed in sister species, choosers from the same population with different experiences, and even the same chooser over the course of ontogeny. For example, older satin bowerbird females respond positively to high-intensity male courtship displays, whereas their younger sisters are startled away (*20*). A host of variables, from the developmental trajectory of sensory systems (*21*) to diet (*22*), predation risk (*23*), pathogen infection (*24*), and maternal hormone

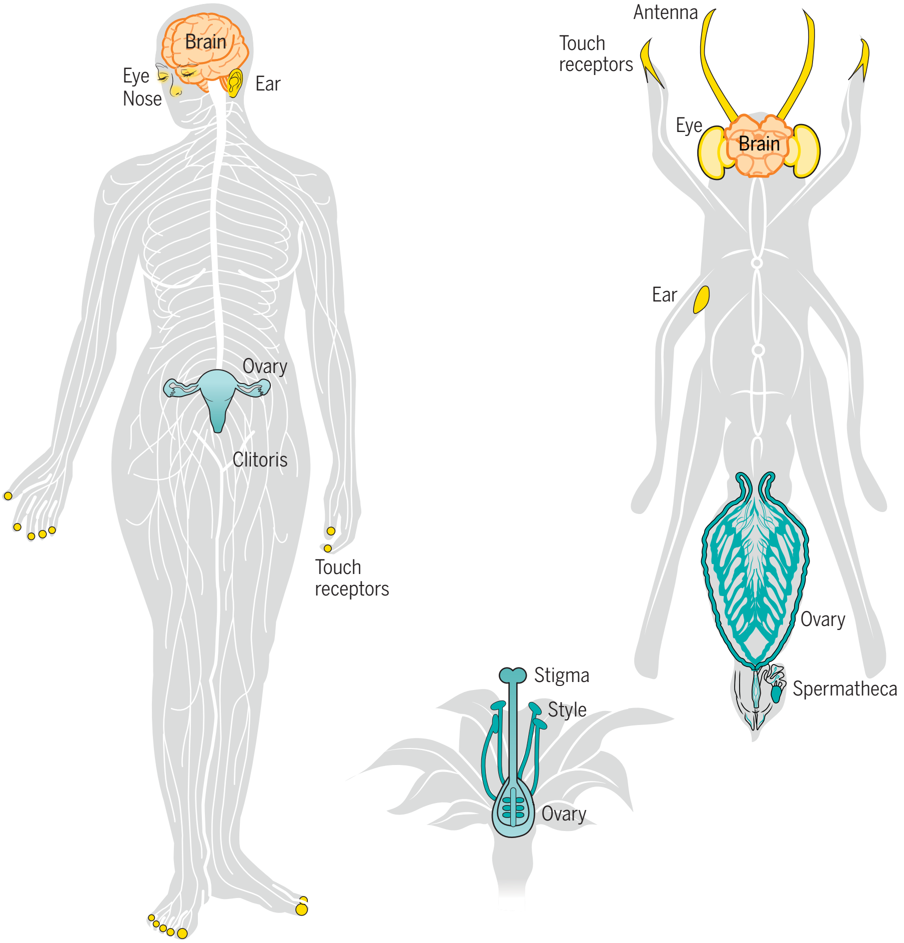

Fig. 1. Analogous mate-choice mechanisms in a flowering plant, an insect, and a mammal. Sensory periphery for stimulus detection (yellow), brain for perceptual integration and evaluation (orange), and reproductive structures for postmating choice among pollen or sperm (teal).

transfer (*25*), can have marked effects on how preferences vary [reviewed in (*3*), chapters 9 to 12]. Female spadefoot toads take preference modulation to the logical extreme, flipping their mate preferences for conspecifics versus heterospecifics depending on climatic conditions (*26*). Despite such notable examples, a recent meta-analysis (*27*) suggests that such adaptive plasticity in mate choice may be an exception: Environmental context effects on mate choice are small and inconsistent.

Darwin's treatment of females as uniform might have contributed to his failure to appreciate the importance of male mate choice in nonhumans: If females are all the same, then there is no variation to choose upon. Male mate choice is most pronounced in species where males are a limited resource for females, like male-pregnant pipefishes; in these cases, females compete aggressively with each other and for the attentions of males. Even in highly polygynous systems where males compete for females, males devote more courtship effort to more-fecund females and females they haven't mated previously. A recent surge of interest in male mate choice also expands the importance of females in sexual selection theory (*14*).

Without variation in females, there is no male mate choice; and without male mate choice, it's a one-way process. Darwin recognized, in passing, that mate choice can be a reciprocal process, with incompatible mates exhibiting "mutual repugnance to pairing" [(*1*), p. 182]. Yet throughout the renaissance of sexual selection a century later, studies emphasized mate choice interactions as unilateral, with information and stimulation flowing in only one direction, usually between the male courter and the female chooser. This was despite the fact that contemporaneous studies of reproductive physiology emphasized the importance of interactions between individuals during courtship (*28*).

Perhaps Darwin would have arrived at a broader understanding of mate choice if he had diverted his fascination with birds to a wider array of systems. Despite *The Descent*'s extensive survey of sexual dimorphism in display traits, Darwin swept behavior under the rug, focusing on animals that seemed to conform to traditional Victorian sex roles. He did not give much thought to sexual behavior outside the context of heterosexual reproduction, nor did he address hermaphroditism. Whereas terrestrial vertebrates and arthropods have only one functional sex over a lifetime, sequential and simultaneous hermaphroditism are widespread in fishes, flowering plants, and mollusks, among others. With simultaneous hermaphrodites, there is of course no sexual dimorphism, and postmating interactions play a primary role in sexual selection (*29*). With sequential hermaphroditism, sexual selection theory has provided the framework to understand when individuals should change sex and in what direction (*30*), and how social dynamics shift the timing of sex change from individual optima (*31*).

The fields of animal behavior, neuroscience, and genetics have given us the tools we need to elucidate mechanisms of sexual selection, measure their consequences, and build quantitative theory. Perhaps more notably, much of the latter-day progress on mate choice and sexual selection occurred because we are less afraid to talk about mate-choice mechanisms and mating outcomes. Using value-neutral, gender-neutral terms—multiple mating rather than promiscuity, arousal thresholds rather than coyness and eagerness—helps us avoid some of Darwin's pitfalls.

Sexual selection research is also no longer a Victorian patriarch's club. The resurgence of the study of sexual selection in the 1970s saw queer and women scientists at the center of the field (*32*–*36*), and studies increasingly engage their entanglement with implicit bias and public views on sexuality (*37*). Although this piece comes from yet two more straight cisgender men, our intellectual world is nevertheless shaped by perspectives that were missing in Darwin's time.

Feminism and changing sexual mores have eased the misogyny and prudery that clouded Darwin's thinking on the "taste for the beautiful." Yet like Darwin, we mostly remain charmed by beautiful males, rather than by the biological mechanisms that made them beautiful (*38*) (Fig. 1). Nevertheless, we are starting to learn much by focusing on the basics of choice and preference (*38*). Below, we focus on three key aspects of mate choice that Darwin approached but that have taken 150 years to begin unraveling. We concentrate first on the "taste for the beautiful": the mechanisms that are the evolving agents of sexual selection. We then discuss how "tastes" are shaped by the social environment, which in turn constrains how preferences are realized into choices. Finally, we address how preferences come to be and return to Darwin's original impetus for *The Descent*—namely, sexual selection as an agent of diversification among populations and species. Research since Darwin reveals that whereas mate choice is a fundamental agent of sexual selection, sexual selection may not be that important to mate choice.

What have we learned about sexual selection since Darwin?

Mate choice can occur before, during, and after mating. Almost any aspect of a chooser's biology can potentially bias matings and therefore serve as an agent of sexual selection. Even a comprehensive account of more than 600 pages (*3*) could not encompass everything from membrane-bound chemoreceptors to the muscles surrounding the vaginal wall to the cortical circuits integrating third-party social information with a hedonically labeled representation of a potential mate. The fact that nearly anything can be a mate-choice mechanism is important first because each of these mate-choice mechanisms have different histories of selection in sexual and nonsexual contexts, and different ways of covarying—or not—with traits under selection. Second, so-called "mental faculties" are simply the most complex of countless factors that influence mate choice. Yet third, mental faculties—the brain—are the key to understanding mating outcomes in most animals (*39*).

The 20th-century rise of animal communication as a field of study (*40*) provided a profitable framework for studying mating decisions and their consequences. Although communication theory provides a framework for incorporating mutual feedback and two way-interactions (*28*), the simplest case is where a courter emits a signal and the signal is transmitted through the environment. The chooser detects and analyzes that signal, compares it to other signals, and makes a mating decision. We begin by offering an overview of how mate-choice mechanisms vary among species and individuals at each of these stages—sensory transduction, perceptual integration, and evaluation.

The sensory periphery

The first steps in responding to a stimulus constitute important mate-choice mechanisms. Any communication signal must be detected in its environment, and choosers are more likely to favor signals that result in easier detectability and greater sensory stimulation (*41*, *42*). Signals tend to match the tuning of peripheral end organs, be these correlations between signal colors and photopigments, sounds and inner-ear tuning, or odors and odorant receptors. How does this match come to be? Phylogenetic analyses across the animal kingdom suggest that whereas signal-receiver properties (i.e., the properties of the signal and the preferences for them) sometimes coevolve tightly, courter traits often evolve in response to preexisting biases, a process known as sensory exploitation (*43*, *44*). Some of these biases may be ancient and tightly constrained. For example, habituation and release from habituation, starting at the sensory periphery and cascading through the brain, are universal properties of neural networks (*45*). Choosers often have preferences for signals of greater magnitude and/or more complex signals. These preferences might have nothing to do with what these signals mean or do not mean or how costly they are or are not to signalers, but rather how they grasp and hold the receiver's attention. Alerting signals are a good example, as they seem to function in attracting the receiver's attention and little else (*46*).

Of course, the cost of the signal to a signaler will shape the evolution of that signal even if it means little to the receiver.

Biases that are involved in mate choice need not have evolved for mate choice. Often they arise in response to ecological selection on sensory tuning and other preference mechanisms—not because of mating decisions but because these mechanisms function in another context (*47*, *48*). For example, in the haplochromine cichlids of Lake Victoria, the ambient light environment influences evolution of photopigment tuning, which in turn influences female preference for male color and, consequently, the evolution of the color itself (*49*). Nevertheless, there are sense organs that have evolved purely in the service of sex (*2*, *3*). Membrane-bound odorant receptor molecules, for example, often respond narrowly to conspecific pheromones. In fact, replacing a *Drosophila* antennal receptor gene with the moth gene that recognizes a moth sex pheromone makes female flies attracted to moth pheromones (*50*).

Perceptual integration

Detection is only the first step in responding to a stimulus. Choosers must both pay attention to courters and integrate complex streams of sensory information within or across modalities. It is pertinent to remind ourselves that just as there are colors, sounds, and smells that are important to other animals but imperceptible to us, so too is our perception of complex signals shaped by our own biases regarding what's salient and what's attractive. A male's "beauty" to humans tells us little about what his target audience cares about. During courtship, for example, female peahens spend more time gazing at a male's comparatively drab lower feathers rather than the colorful tail feathers prized by humans (*51*). The same study suggested that these ocelli serve a rather prosaic function, to elicit a female's attention at a distance rather than influencing the female's assessment of the male in close encounters. All else being equal, a signal that elicits more initial attention is favored by sexual selection (*46*).

But all else is not equal. Different signals often interact with each other in ways not predicted by the conspicuousness or attractiveness of individual components. Perfumes and curries are enticing because of emergent olfactory percepts that are different from their individual components. Túngara frogs are a well-studied example of perceptual integration along multiple axes. First, females go beyond just attending to a particular acoustic frequency; they are consistently choosy about the temporal structure of the male's "whine" call, imposing strong stabilizing sexual selection. Neurons in the female's auditory mid-brain exhibit greater activity in response to the mating call's downward frequency sweep compared to other stimuli (*52*). As choosy as they are about the whine, they are permissive about acoustic accoutrements to the whine. Given that a male makes the appropriate whine, additional novel call components that stimulate the female's auditory system make him more attractive (*53*). Finally, these complex calls come with a complex visual stimulus: inflation of a conspicuous pigmented vocal sac. A silently inflating vocal sac is ignored by females, but adding it to a call makes the multimodal display more attractive and perhaps easier to find (*54*). How receivers integrate different components of signals is key to how mate choice operates as an agent of selection.

Just as signal detection is constrained by ecological selection, so too is perception. The olfactory system in fruit flies is involved in two important functions: feeding and mating. The olfactory receptor neurons that are involved in feeding project to the mushroom body, and those involved in mating project to the lateral horn. Males are more likely to court in the presence of rotting fruit, which is where females lay eggs. A specialized olfactory receptor neuron that responds to volatiles of rotting fruit enhances the male's motivation to court when stimulated. This neuron, unlike others that detect rotting fruit, projects to the fly's mating brain, the lateral horn, rather than the mushroom body (*55*). Thus, not only is the function of a food detection neuron co-opted for mating decisions, so is its neuroanatomical position in the brain. Understanding how and where in the brain mating decisions are made is a major area of investigation in sexual selection and mate choice.

Just as sensory biases can favor certain signals, so too can perceptual biases that arise from integrating sensory information within or across modalities (*44*). The complex courtship structures of the greater bowerbird provide a spectacular example. Males arrange objects around the bower to create a forced perspective to make themselves appear larger to females (Fig. 2) (*56*). Such illusions occur often in courtship (*57*).

Evaluation and hedonic marking

Sensory and perceptual biases of receivers can have important influences on the evolution of mating signals, but they are certainly not the whole story. A courter's signal may be processed similarly by two choosers who come to opposite conclusions about its attractiveness (*58*, *59*). Both social (see below) and environmental effects can easily cause choosers to lose, intensify, or reverse their preferences—even as most aspects of stimulus processing are conserved. Recent studies of guppies (*60*) and spadefoot toads (*61*), for example, have shown that neural responses in brain areas that process sensory stimuli need not predict responses in areas of the brain involved in decision-making. In some cases, gatekeepers in the brain differentially influence how sensory information is transferred to areas where behavioral responses are generated (*62*, *63*).

Not only do neural mechanisms act to filter out unappealing stimuli, they can readily label them "good" or "bad" (*58*, *59*). In insects, structural changes to a single gene are sufficient to cause a "flip" in axon targeting responsible for attraction versus avoidance of intersexual pheromone cues (*64*). Small genetic or environmental changes can thus potentially have disjunct effects on the strength and direction of sexual selection.

Mate choice after the brain

Observations of nature would have shown Darwin that there is no "final marriage ceremony"; he was probably too mortified to write it down. Mate choice is mutual partly because not only males but also females mate multiply in many species. Genetic paternity assignments have uncovered multiple mating throughout the animal kingdom, and this is arguably the greatest contribution of the molecular revolution to animal behavior. Across over 500 studies in socially monogamous birds, for example, fully a third of broods contain at least one offspring from outside the pair bond (*65*). Getting to mate is, thus, simply the end of the beginning. In species with internal fertilization, sexual selection continues to occur during and long after mating. Parker's insight that sperm from different males compete with each other (*66*) was followed by Eberhard's work on cryptic female choice (*67*). Mechanical, chemosensory, and somatosensory structures within the reproductive tract serve as mate-choice mechanisms as much as brains and head-bound sense organs do (*10*). For example, the ancestral state in mammals is that stimulation of the clitoris—and the resultant somatosensory input to the brain—is required to trigger ovulation (*68*).

Biasing fertilization is only one example of how mate choice can occur during and after mating. Australian redback spiders provide a stark example, where the male's courtship finale positions him between his mate's jaws; males eaten by a female fertilize a greater share of her eggs (*69*). In birds, females will often spend more time feeding the offspring of attractive males than unattractive males. This effect persists when attractive males are experimentally rendered unattractive (*70*). Any time that an individual mates with multiple partners over the course of its lifetime, there is the potential for postmating sexual selection.

Mate choice is a social process

A chooser's "taste for the beautiful" does not develop in a vacuum, and the way that taste is expressed depends on a chooser's internal

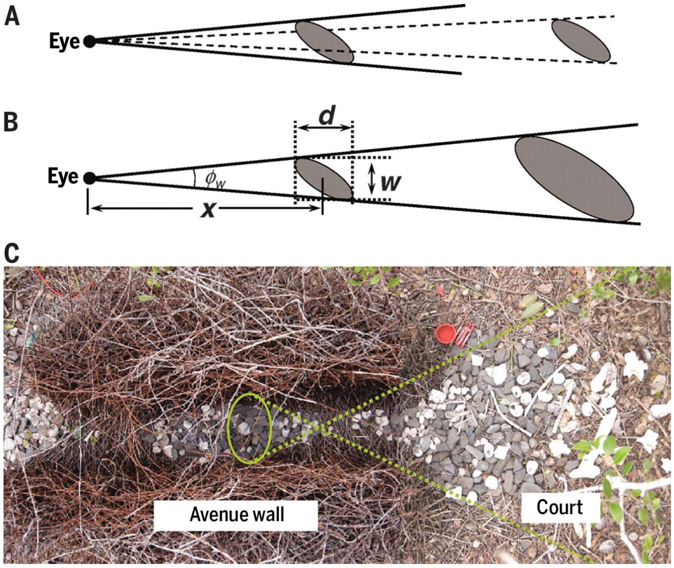

Fig. 2. Forced perspective and mate choice in bowerbirds. (**A**) When two objects are the same size but different distances from the viewer, the more distant object subtends a smaller angle on the eye. (**B**) In forced perspective, as long as the width (*w*) and depth (*d*) of the larger object increase with distance from the viewer (*x*), the larger object will subtend the same visual angle as the smaller one (ϕ_w is the visible angle). (**C**) This top view of a bower shows where the female is positioned in the avenue (oval) when she observes the courting male in his court. The female moves her head between the walls, leading to a predetermined field of view (dotted line). [Reprinted from (*56*) with permission]

state and external inputs. The physical environment and ecological community can have big effects on how preferences are organized and expressed, and the same is true of social interactions.

The social environment—conspecific individuals and groups of individuals interacting with a focal actor—shapes preferences and choices at all scales, from maternal effects when the brain starts to develop to audience effects at the time of mating. Third parties can influence mating outcomes long before choosers reach maturity and can act to reverse mating decisions in the moment. These social effects play a determining role in how preferences are shaped and, in turn, how those preferences are realized in the individual choices that together generate sexual selection. We can divide these influences broadly into two general categories: those that shape preferences before they are expressed and those that shape how preferences map onto choices when choosers are comparing potential mates.

Imprinting and social exposure

We know little about how cellular epigenetics shape mate choice (*71*), but epigenetic modification in the broader sense is ubiquitous. Parents and siblings frequently influence adult preferences when choosers are still in a nest or with a parent. Cultural imprinting on a genetic parent acts to powerfully couple variation in traits and variation in preferences (*72*). These effects can be irreversibly specified during early development, or they can be the flexible consequences of short-term exposure (*73*). Choosers often favor mere familiarity or, conversely, mere novelty in courters; these biases act to make sexual selection positively or negatively frequency-dependent, respectively. A special and extreme case of preference for familiarity is pair bonding in socially monogamous vertebrates (*74*).

Sexual imprinting and pair bonding are domain-specific and circumscribed to species with particular life histories. A more universal if underappreciated driver of preference variation, and therefore of sexual selection, may be associative learning. Pairing sexual reward with an arbitrary object elicits fetishes in rats and quail, whereby a piece of cloth, for example, becomes required for sexual arousal (*75*, *76*). Just as positive interactions with a mate can positively reinforce associations with an arbitrary stimulus, it is reasonable to suppose that negative interactions with a phenotype should lead to sexual avoidance. Notably, different receivers may label the same courter trait arousing or aversive (*59*). As previously mentioned, young female bowerbirds flee from the high-intensity courtship displays that entice their more experienced elders (*77*).

Genotype-by-environment interactions are as pervasive for social effects as for everything else and are yet another factor that biases stimulus preferences (*78*); learning biases are no exception. Marler's "instinct to learn" (*79*) means that structural differences among species, sexes, and/or individuals act to bias the effects of experience on mate choice. For example, female sheepshead swordtails prefer familiar male phenotypes, whereas their sister species, highland swordtails, are repelled by familiarity (*80*).

Mate sampling and decision-making

Numerous studies suggest adaptive flexibility in preferences, whereby choosers become more permissive as mates become scarce, risks increase (*81*, *82*), and time becomes short. Human standards of beauty broaden over the course of a social evening as closing time at bars approaches (*83*), just as do preferences in some female fishes in the days before death (*84*).

Mate assessment involves comparing potential mates, and the strength of sexual selection depends critically on how many mates an individual samples and how these individuals are remembered and compared. Sounds are ephemeral, and in most cases an auditory memory is required to compare them. This is especially true in choruses of insects and frogs in which bouts of singing are interrupted by periods of silence. Auditory memory can be flexible; studies of two frog species show that addition of call syllables (*85*) or a visual cue (*86*) instantiates sufficient memory to exceed intercall bout intervals.

Mating outcomes thus depend on whether a chooser is remembering individual courters or simply mating with anyone above a threshold. Often, however, experience with multiple courters can affect both the stringency of the threshold and the attractiveness of courters relative to one another. This can produce nonlinearities that complicate sexual selection. Rational choice theory posits that the relative attraction between A and B should be independent of the presence of an alternative, C. We know that this assumption is violated quite often in humans and other animals, and some recent studies show an effect of such competitive decoys on mate choice (*87*, *88*).

Finally, the decisions of individual choosers depend on other choosers. For example, males in internally fertilizing species tend to avoid females with previous mates because of increased sperm competition. Male Atlantic mollies are more likely to court unattractive females when other males are nearby (*89*). In females, by contrast, mate choice copying is ubiquitous and powerful, at least in experimental settings. Dozens of studies show that a preference for a typically more attractive versus unattractive male can be reversed if a female sees the unattractive male being courted by another female (*90*, *91*). Mate choice copying can also be influenced by the phenotype of the model female (*92*).

In females, copying may often be favored as long as popular males have abundant sperm and few sexually transmitted diseases. But there has been little success in uncovering its fitness benefits (*90*). This might be because mate choice copying need not have evolved for mate choice, but instead might be a special case of domain-general social facilitation that evolved in another social context (*93*). For example, a recent study in humans shows that copying the decision of others has the same magnitude of effect when they evaluate facial attraction or attraction of hands, as well as abstract art (94). Similar across-domain comparisons in nonhuman animals would be worthwhile.

Mate choice has consequences for choosers, not just courters

We saw above that preferences frequently arise outside the context of mating decisions. These effects of pleiotropy (95), sensory drive (47), sensory exploitation (96), and sensory traps (34) have notably changed the way we think of mate choice. The brain is an important sex organ but, for females at least, mainly has other things on its mind (Fig. 3A).

It is only once there are choices to be made among partners that preference mechanisms become subject to selection in the context of mate choice (Fig. 3B). We can ask three primary questions about the fitness consequences of mating decisions. First, are they good, neutral, or bad for a given measure of fitness (Fig. 3, B and C)? Second, are those fitness costs (like sexually transmitted diseases) or benefits (like protein-rich spermatophores) directly experienced by a chooser or their offspring (Fig. 3B), or are preference mechanisms under indirect selection because they are genetically correlated with courtship traits that are under direct selection, and thus preferences evolve through genetic hitchhiking (Fig. 3C)? Finally, are fitness consequences additive, meaning that costs and benefits from a courter are independent of who the chooser is, or are they complementary, depending on the interaction between courter and chooser (Fig. 3D)?

Direct selection as a result of mating outcomes plays a major role in the evolution of sexual and social phenotypes. There are some systems where direct benefits are evident as tangible resources, such as food, protection, and parental care, but every sexual interaction carries costs and benefits. Even broadcast spawners and wind pollinators synchronize the timing of gamete release and express mate choice through sperm-egg interactions (97). And there is always a downside risk to making mistakes, such as initiating the acrosome reaction in response to a nonviable sperm or other foreign object.

Direct selection therefore has a powerful influence on mate-choice mechanisms at the gamete level, but direct benefits and costs apply to mating decisions even when gametes are not involved. It is useful to think about sexual selection as a special case of social selection (34, 35). In complex organisms, sexual behavior is about more than exchanging gametes, and it can have fitness consequences that go beyond reproducing with a partner. Consider same-sex interactions between gull parents, or as a mediator of social hierarchies in bonobos (3). Nonreproductive sexual behavior carries similar downside risks of trauma and pathogen transmissions as reproductive sex.

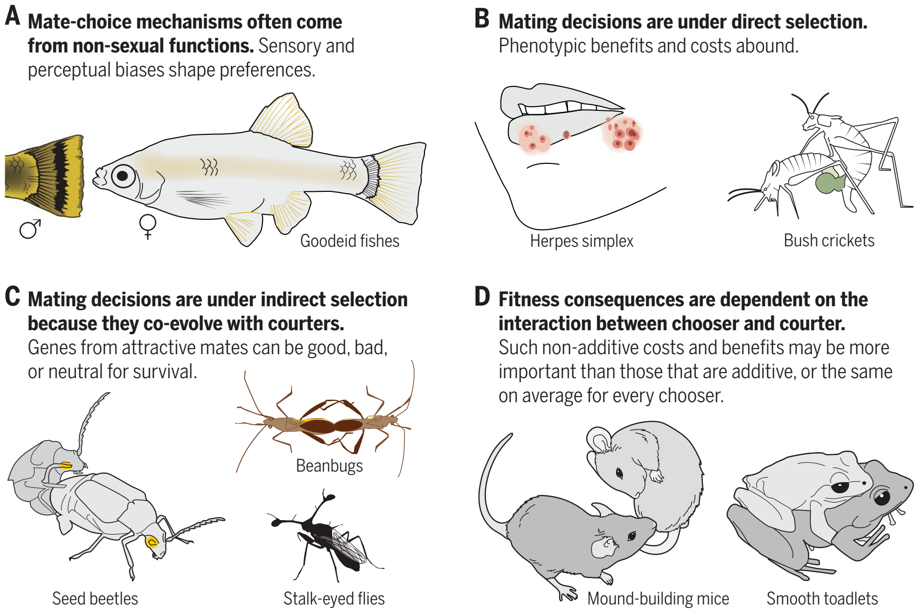

Fig. 3. Origin and evolution of mating preferences. (**A**) Mating preferences can emerge from nonsexual biases like foraging (goodeid fish) (107). (**B**) Once preferences are expressed as such, they are under direct selection (herpes sore in human, spermatophore transfer in bush crickets) (142). (**C**) Traits and preferences coevolve; attractive courters can have good genes (bean bugs) (143), bad genes (seed beetles) (144), or neutral genes (stalk-eyed flies) (145) with respect to offspring viability. (**D**) Consequences of mate choice are often complementary; *Uperoleia laevigata* frogs drown if their mate is too big (115); mound-building mouse pairs start breeding faster if they have matching personalities (146).

An overlooked cost of mate choice is that associated with cognitive processing. Making decisions takes time, energy, and neural hardware. Animals can suffer cognitive overload, especially when there is information being delivered in multiple sensory modalities (98). There may be hedonic rewards to decreasing neural computational costs—pleasure from fluency of processing (99). In a percid fish, females prefer male visual signals that are easier to parse (100).

Like any other trait, mate-choice mechanisms evolve in response to direct selection on both their sexual and nonsexual function. Those mechanisms in turn drive the evolution of sexual signals. The coevolutionary dynamics between mating signals and mating preferences depend not only on the direct costs and benefits associated with mating decisions but also on the indirect genetic benefits of mating outcomes. Attention has centered on the genetic benefits of mating decisions (Fig. 3C), specifically the additive genetic benefits (Fig. 3D). These benefits (and costs) are usually partitioned into viability—offspring vigor and health—and offspring attractiveness.

A preference that successfully predicts offspring viability is favored by a so-called "good genes" process. Preferences are favored because attractive courters sire offspring that thrive. But preferences are also favored simply because attractive mates produce attractive offspring: the Fisher-Lande-Kirkpatrick process of genetic hitchhiking (101). In both cases, a preference evolves not because it is under direct selection but instead because preference genes become statistically associated with the good genes for survival or with the genes for attractive traits (102). These mechanisms are likely episodic but ubiquitous and may play an important role in hindering or facilitating adaptation to new environments. Hitchhiking happens automatically if there is genetic variance in both sexually dimorphic traits and preferences, whereas good genes require that traits predict offspring viability. Although there are few studies on preferences, meta-analyses suggest ample genetic variance in traits (103), whereas genetic effects on offspring viability ("good genes") are generally small and likely to have only a small effect on preference evolution (101, 104). Sex chromosomes provide interesting dynamics in sexual selection: Y chromosomes that make males more attractive, for example, can accumulate "bad genes" that delay maturity or reduce viability, whereas selfish W chromosomes can select for traits that harm males but favor daughters [(105); see also (106)].

Sexual cooperation and sexual conflict

The coevolutionary scenarios discussed so far return us to Darwin's emphasis on mate-choice mechanisms as agents of selection. In the simplest evolutionary scenario for sexual selection through mate choice, only one thing need evolve:

a display trait that elicits a latent "taste for the beautiful" in choosers, whether or not that "taste" has any heritable variation. This is the case for the terminal yellow band of male goodeid fishes, which evolved to elicit female attention to a similar-looking insect larva.

The terminal yellow band was advantageous for males, but costly for females, who lost weight chasing after male tails rather than food (Fig. 3A). In goodeid lineages with yellow bands, females evolved greater sophistication, decoupling the feeding response to insects from the sexual response to males (*107*, *108*). The coevolution of the preference and trait here is an example of sexual conflict. Males gain fitness by increasing their mating success at the expense of female foraging success. Females, in turn, increase their foraging success while making it more difficult to mate.

Sexual conflict always occurs when partners have divergent interests in a mating interaction. This is the flip side of sexual reproduction as cooperation, where producing and/or rearing offspring is to each partner's mutual benefit. In the extreme case of lifetime genetic monogamy, there is no sexual conflict; your partner's lifetime reproductive success is your own. If both males and females mate multiply, sexual conflict is extreme. In *Drosophila*, experimentally enforcing monogamy, and therefore arresting sexual selection and sexual conflict, eliminates genetic load by relaxing selection on male seminal fluid proteins, which are toxic to females, and on female resistance to toxicity, which reduces male fertilization success (*109*).

Sexual conflict can take two forms. The first is intralocus sexual conflict. Here, an allele that is favored in males is disadvantaged in females, or vice versa. A single locus, RXFP2, is associated with much of the variation in horn size in male Soay sheep. One allele makes horns larger, giving males an advantage in male-male competition. An alternative allele makes smaller horns but is associated with increased offspring viability. Similarly, male seed beetles that succeed in sperm competition sire daughters that are less likely to survive (*110*).

In both cases, females are saddled with "bad genes" when they mate with competitively successful males; their offspring are less likely to thrive, even if those sons that survive to maturity have a competitive advantage. Preferences for traits that confer "bad genes" can only persist if those "bad genes" are limited to courters. In two species of poeciliid fish, some of the variance in male attractiveness comes from genes on the Y chromosome. Haplotypes that make males more attractive accumulate mutations that reduce survival, such that females face a trade-off: Either mate with unattractive males who produce sons more likely to survive but less likely to reproduce if they do, or attractive sons who will have higher fitness if they make it to maturity (*111*–*113*). Also, if males but not females suffer reduced survivorship, and females are the heterogametic sex, then preference for more attractive males can be favored by selection even if they have breeding value for lower variability (*105*, *106*).

In contrast to intralocus sexual conflict, interlocus sexual conflict follows more conventional dynamics analogous to predator–prey coevolution. Sexual cannibalism provides perhaps more than an analogy. Where mates are scarce, males and females cooperate; if a male and a female mate once, sacrifice increases the fitness of both partners. In systems where mates are dense and males encounter multiple females, they may endeavor to mate with a female but deprive her of a meal as they search for their next partner. Finally, if females encounter multiple males, they may choose to eat a male but eschew his sperm. When male and female interests over mating diverge, the stage is set for antagonistic coevolution.

Most of the evolutionary dynamics discussed so far are additive (Fig. 3): A courter's effect on a chooser or her offspring is independent of that chooser. But one individual's ideal mate is often another's nightmare. Such nonindependent or complementary processes constitute major, underappreciated sources of selection on mate choice, if not sexual selection (*114*).

Phenotypic compatibility, assortative mating by body size (*115*) or personality (*116*), or synchronization of reproductive state (*7*, *8*) are all major outcomes of mate choice. In any sexually reproducing system, compatibility is a fundamental, yet underappreciated, force in mate-choice evolution. Choosers benefit by choosing partners with compatible genes (*117*) such as conspecifics or individuals with complementary immune genes (*118*, *119*).

Conspecific pollen precedence and conspecific sperm precedence are examples of selection favoring a preference for a compatible genotype—in this case, a conspecific. Self-incompatibility in plants (*120*) is, at the other extreme, also a preference for a compatible genotype.

Sexual selection and gene flow

A clearly complementary outcome is when choosers decide between conspecifics and heterospecifics. Where do conspecific mate preferences come from, and why do choosers prefer heterospecifics? When populations stop exchanging genes, they can develop incompatibilities in sexual communication, as a special case of genetic incompatibilities among divergent regions in the genome (*121*). Traits and preferences coevolve along different trajectories in different populations. This can happen because of stochastic processes like mutation-order effects (*122*) and genetic hitchhiking (*123*) and can be accelerated by ecological divergence (*121*) or antagonistic coevolution due to sexual conflict (*124*). Sexual selection can thus accelerate divergence in allopatry, when external barriers prevent gene flow. Darwin's intuition for differences among human groups—that sexual selection could lead to morphological diversification—is theoretically sound and has received ample support in animals.

Darwin sought to explain recent divergence among isolated populations within the same species—humans. But what happens when two different but closely related species come into secondary contact? Here, selection for compatible genes favors reinforcement, i.e., divergence of traits and preferences in sympatry. Selection against hybridization in different locations can lead to signal-receiver divergence among conspecific populations, also known as cascade reinforcement (*125*).

When there is gene flow among populations, sexual selection plays an even more interesting role. Environmental and social effects on individual mating decisions, described above, can modulate hybridization between species (*126*). If traits evolve purely because they are attractive, theory suggest that sexual selection homogenizes populations, because choosers will mate with genetically divergent courters bearing a preferred trait (*127*). By contrast, if display traits and/or mating biases are subject to divergent ecological selection, theory suggests they can reinforce reproductive isolation and divergence in sympatry (*128*). "Magic traits" (*129*), which are defined as traits that are involved in both reproductive isolation and ecological divergence such as visual sensitivity in Lake Victoria cichlids (*49*, *130*), link divergent ecological selection for different color sensitivity to assortative mating by color. Perhaps counterintuitively, preference-trait combinations can contribute most easily to reproductive isolation if preferences are learned from genetic parents (*131*). In poison frogs, imprinting on maternal phenotypes could maintain coexistence of distinct color morphs in sympatry through the congruent actions of the two main mechanisms of sexual selection. Females mate with males with their mother's color pattern, promoting assortative mating by color morph. Males attack rival males with the same pattern, giving rare color morphs an advantage (*132*).

Finally, sexual selection is just beginning to be reconciled with an emerging view of macroevolution as a reticulate process heavily influenced by gene flow among divergent lineages. Hybridization was accepted in Darwin's time as an important force in the evolution of plants and microorganisms but was largely dismissed as an aberration in animals, the "grossest blunder in sexual preference," according to Fisher [(*133*), p. 150]. A love of racist typology perhaps hindered the field's appreciation of the importance of hybridization, which we now understand to play an important role in adaptation (*134*) and speciation (*135*). Environmental modulation of individual mating decisions may play a key role in macroevolutionary processes (*126*), including the evolution of *Homo*; for example, how did mate choice, sexual coercion, and sexual combat modulate gene flow between Neanderthals and humans?

The ascent of choice: Sexual decisions as a linchpin of evolution

In the broadest strokes, Darwin's theory of sexual selection is one of the best documented and most important contributions in evolutionary biology (*7*). Darwin's specific idea of sexual selection by mate choice redefined females as not merely passive actors over which males raise combat, but instead as the arbiters who wield the sword of selection separating those males who do and do not reproduce. Yet Darwin's idea of female empowerment evaporated when applied to his own species. Darwin's misogyny infiltrated his understanding of human mating patterns and polluted his general notion of the value of women in society. His elisions on female desire and agency contributed to a caricature of Darwinian evolution that has compromised and fragmented the way we study sexuality. Variation among humans, the explicandum for Darwin's long argument about sexual selection and human equality, has become the almost exclusive province of the social sciences, whereas evolutionary psychology searches for human universals (*3*).

Mate choice mechanisms matter

Knowing the nature of the "taste for the beautiful" lets us make predictions about how sexual selection should facilitate or hinder gene flow between species. For example, an early model of sympatric speciation through mate choice (*136*) was discredited because it posited discrete flips in preference or antipathy for courter traits. As argued above, however, empirical studies of evaluative mechanisms suggest that such flips may occur. Similarly, recent theoretical models have shown that learning from genetic parents facilitates assortative mating and therefore genetic divergence (*137*, *138*). The mechanisms underlying signal-receiver congruence, and the fitness consequences of mate choice, are crucial to predicting whether sexual selection acts to promote or inhibit genetic exchange.

Mate-choice evolution is not chained to sexual selection

The obsession over "good genes" and the "evolution of beauty" hinges on genetic variation in preferences. In a chooser-centric view, this means heritable variation in preference mechanisms. Such variation remains elusive, notably in female vertebrates. This is foremost limited by the low repeatability of mating preferences, with a modal repeatability of zero in vertebrate studies (*3*). At the other end of the spectrum, preference mechanisms under strong stabilizing selection may be stable over decades (*139*), perhaps showing little opportunity for selection. Even if we could measure stable preference phenotypes in individuals, individual social experience and life history add an incredible amount of variation to genotypic effects, some of which may be adaptive. The effect of this nongenetic variation will generally be to reduce the heritability of preference and therefore the opportunity for genetic coevolution between traits and preferences. In people as in fruit flies, it is impossible to understand sexual selection without considering how genes interact with their environment, especially their sociocultural environment.

Darwin's observation that mutual attraction and mutual repugnance shape mating outcomes deserves renewed focus now that we understand the importance of multiple mating and mating decisions by both males and females. Understanding mate choice as a dynamic process involving choices by at least two actors has the potential to overturn intuitive predictions about the evolution of choices and sex roles. An instructive example is lekking topi antelope females, who aggressively compete for access to a preferred male. The preferred male, sperm limited and in demand, prefers unmated females. Being the most preferred male topi antelope is unambiguously good for male fitness, but being the most preferred female fruit fly is not. Being chosen can be costly as well. Attractive female fruit flies suffer reduced fecundity as a result of constant harassment by males (*77*).

Understanding multiway interactions in their social and ecological context is needed to tackle Darwin's original focus with *The Descent*, the nature of diversity among humans. Human diversity has become close to a taboo subject in the biological study of sexual selection, with the notable exception of a growing body of work on the neuroendocrinology and genetics of same-sex attraction (*37*). The broader sexual spectrum deserves study, as does Darwin's primary conjecture that sexual selection generated differences in appearance among human populations.

We need to better understand conflict and cooperation dynamics in sexual interactions before we can generalize about whether sexual selection is on the whole good or bad for populations. Does it reinforce purifying and ecological selection for "good genes," those that increase viability, or do "bad genes," those that decrease viability, hitchhike along with attractiveness (*129*)? A recent model (*140*) suggests that sexual conflict over reproductive investment can stabilize into cooperation over a broad range of conditions.

Indeed, removing the opportunity for mate choice often results in reduced population fitness (*141*), but studies seldom disentangle the effects of choosing compatible mates from those of selecting the best-adapted mates. We need more empirical data to disambiguate the consequences of mate choice from those of sexual competition. In particular, we need to distinguish consequences that are additive from those that are complementary. Numerous studies show a benefit of premating choice to chooser fitness, but these conflate additive "good genes"—choosers all picking only the best mates—with complementary outcomes where choosers get to pick their preferred individual partner. Complementarity of genotypes—whether whole conspecific genomes or at discrete loci like the major histocompatibility complex (*118*, *119*)—compatibility of reproductive physiological states (*28*), and compatibility of behavior (*129*) are of primary importance to the evolution of mate-choice mechanisms.

So where are we 150 years after Darwin suggested a sex-based theory to explain natural flamboyance and human diversity? Natural selection theory had its predecessors, such as Darwin's grandfather Erasmus, as well as other scientists who focused on the same explanation, as did Alfred Russel Wallace. But sexual selection theory seems to have been birthed purely by Darwin without historical precedents and also without contemporary support (*7*). Sexual selection theory is almost purely Darwinian, and the controversy it generated 150 years ago might be different in the details but certainly not in the societal discontent it continues to breed, especially in some corners of the social sciences. The Victorian prejudices that infiltrated Darwin's science have evolved somewhat but not gone extinct. Our focus continues to be shaped by the flamboyant ornaments and displays that caught Darwin's eye. Directional sexual selection on courter traits may well emerge as a "spandrel" from perceptual biases, avoidance of downside risk, and selection of the right partner.

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Science

Sexual selection and the ascent of women: Mate choice research since Darwin

Gil G. RosenthalMichael J. Ryan

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The power of choice
In his book *The Descent of Man, and Selection in Relation to Sex*, Darwin proposed the concept of sexual selection, specifically that the vagaries of choice during reproduction could also shape patterns of adaptation—and thus evolution. Despite this groundbreaking thinking, his Victorian ideas about women affected his ability to see just how influential mate choice, especially from the female side, could be. Rosenthal and Ryan review progress that has been made in this area in the 150 years since Darwin first proposed sexual selection, paying special attention to how more equitable thinking has led to significant scientific advances in our understanding. —SNV

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