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FEATURE

How Beauty Is Making Scientists Rethink Evolution

The extravagant splendor of the animal kingdom can't be explained by natural selection alone — so how did it come to be?

By Ferris Jabr

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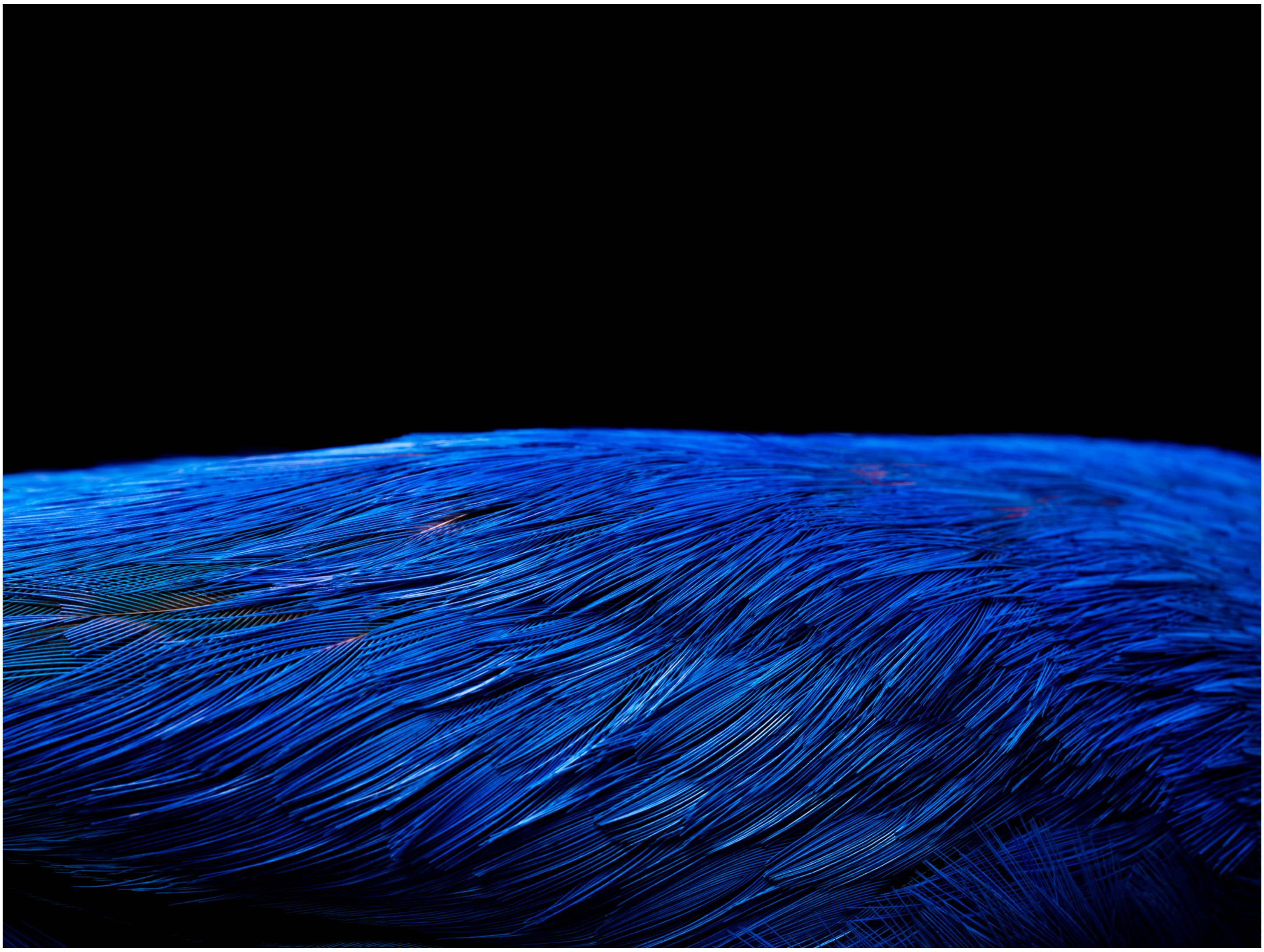
A male flame bowerbird is a creature of incandescent beauty. The hue of his plumage transitions seamlessly from molten red to sunshine yellow. But that radiance is not enough to attract a mate. When males of most bowerbird species are ready to begin courting, they set about building the structure for which they are named: an assemblage of twigs shaped into a spire, corridor or hut. They decorate their bowers with scores of colorful objects, like flowers, berries, snail shells or, if they are near an urban area, bottle caps and plastic cutlery. Some bowerbirds even arrange the items in their collection from smallest to largest, forming a walkway that makes themselves and their trinkets all the more striking to a female — an optical illusion known as forced perspective that humans did not perfect until the 15th century.

Yet even this remarkable exhibition is not sufficient to satisfy a female flame bowerbird. Should a female show initial interest, the male must react immediately. Staring at the female, his pupils swelling and shrinking like a heartbeat, he begins a dance best described as psychotically sultry. He bobs, flutters, puffs his chest. He crouches low and rises slowly, brandishing one wing in front of his head like a magician's cape. Suddenly his whole body convulses like a windup alarm clock. If the female approves, she will copulate with him for two or three seconds. They will never meet again.

The bowerbird defies traditional assumptions about animal behavior. Here is a creature that spends hours meticulously curating a cabinet of wonder, grouping his treasures by color and likeness. Here is a creature that single-beakedly builds something far more sophisticated than many celebrated examples of animal toolmaking; the stripped twigs that chimpanzees use to fish termites from their mounds pale in comparison. The bowerbird's bower, as at least one scientist has argued, is nothing less than art. When you consider every element of his courtship — the costumes, dance and sculpture — it evokes a concept beloved by the German composer Richard Wagner: *Gesamtkunstwerk*, a total work of art, one that blends many different forms and stimulates all the senses.

This extravagance is also an affront to the rules of natural selection. Adaptations are meant to be useful — that's the whole point — and the most successful creatures should be the ones best adapted to their particular environments. So what is the evolutionary justification for the bowerbird's ostentatious display? Not only do the bowerbird's colorful feathers and elaborate constructions lack obvious value outside courtship, but they also hinder his survival and general well-being, draining precious calories and making him much more noticeable to predators.



A male plum-throated cotinga. Kenji Aoki for The New York Times

Numerous species have conspicuous, metabolically costly and physically burdensome sexual ornaments, as biologists call them. Think of the bright elastic throats of anole lizards, the Fabergé abdomens of peacock spiders and the curling, iridescent, ludicrously long feathers of birds-of-paradise. To reconcile such splendor with a utilitarian view of evolution, biologists have favored the idea that beauty in the animal kingdom is not mere decoration — it's a code. According to this theory, ornaments evolved as indicators of a potential mate's advantageous qualities: its overall health, intelligence and survival skills, plus the fact that it will pass down the genes underlying these traits to its children. A bowerbird with especially bright plumage might have a robust immune system, for example, while one that finds rare and distinctive trinkets might be a superb forager. Beauty, therefore, would not confound natural selection — it would be very much a part of it.

Charles Darwin himself disagreed with this theory. Although he co-discovered natural selection and devoted much of his life to demonstrating its importance, he never claimed that it could explain everything. Ornaments, Darwin proposed, evolved through a separate process he called sexual selection: Females choose the most appealing males "according to their standard of beauty" and, as a result, males evolve toward that standard, despite the costs. Darwin did not think it was necessary to link aesthetics and survival. Animals, he believed, could appreciate beauty for its own sake. Many of Darwin's peers and successors ridiculed his proposal. To them, the idea that animals had such cognitive sophistication — and that the preferences of "capricious" females could shape entire species — was nonsense. Although never completely forgotten, Darwin's theory of beauty was largely abandoned.

Now, nearly 150 years later, a new generation of biologists is reviving Darwin's neglected brainchild. Beauty, they say, does not have to be a proxy for health or advantageous genes. Sometimes beauty is the glorious but meaningless flowering of arbitrary preference. Animals simply find certain features — a blush of red, a feathered flourish — to be appealing. And that innate sense of beauty itself can become an engine of evolution, pushing animals toward aesthetic extremes. In other cases, certain environmental or physiological constraints steer an animal toward an aesthetic preference that has nothing to do with survival whatsoever.

These biologists are not only rewriting the standard explanation for how beauty evolves; they are also changing the way we think about evolution itself. For decades, natural selection — the fact that creatures with the most advantageous traits have the best chance of surviving and multiplying — has been considered the unequivocal centerpiece of evolutionary theory. But these biologists believe that there are other forces at work, modes of evolution that are much more mischievous and discursive than natural selection. It's not enough to consider how an animal's habitat and lifestyle determine the size and keenness of its eyes or the number and complexity of its neural circuits; we must also question how an animal's eyes and brain shape its perceptions of reality and how its unique way of experiencing the world can, over time, profoundly alter both its physical form and its behavior. There are really two environments governing the evolution of sentient creatures: an external one, which they inhabit, and an internal one, which they construct. To solve the enigma of beauty, to fully understand evolution, we must uncover the hidden links between those two worlds.

A male lesser bird-of-paradise. Kenji Aoki for The New York Times

Perhaps no living scientist is as enthusiastic — or doctrinaire — a champion of Darwinian sexual selection as Richard Prum, an evolutionary ornithologist at Yale University. In May 2017, he published a book, "The Evolution of Beauty," that lucidly and passionately explains his personal theory of aesthetic evolution. It was nominated for the Pulitzer Prize for general nonfiction, but within the scientific community, Prum's ideas have not been as warmly received. Again and again, he told me, he has asked other researchers for feedback and received either excuses of busyness or no reply at all. Some have been openly critical. In an academic review of Prum's book, Gerald Borgia, one of the world's foremost experts on bowerbirds, and the ethologist Gregory Ball described the historical sections as "revisionist" and said Prum failed to advance a credible case for his thesis. Once, over a lunch of burritos, Prum explained his theory to a visiting colleague, who pronounced it "nihilism."

Last April, Prum and I drove 20 miles east of New Haven to Hammonasset Beach State Park, a 900-acre patchwork of shoreline, marsh, woodland and meadow on Long Island Sound, with the hope of finding a hooded warbler. Birders had recently seen the small but striking migratory species in the area. Before he even parked, Prum was calling out the names of birds he glimpsed or heard through the car window: osprey, purple martin, red-winged blackbird. I asked him how he was able to recognize birds so quickly and, sometimes, at such a great distance. He said it was just as effortless as recognizing a portrait of Abraham Lincoln. In Prum's mind, every bird is famous.

Binoculars in hand, we walked along the park's winding trails, slowly making our way toward a large stand of trees. Prum wore jeans, a quilted jacket and a beige hat. His thick eyebrows, round spectacles and sprays of white and gray hair give his face a vaguely owlish appearance. In the course of the day, we would see grazing mallards with emerald heads, tree swallows with iridescent turquoise capes and several sparrow species, each distinguished by a unique ornament: swoops of yellow around the eye, a delicate pink beak, a copper crown. On a wooded path, we encountered a lively bird flinging leaf litter into the air. Prum was immediately transfixed. This was a brown thrasher, he told me, describing its attributes with a mix of precision and fondness — "rufous brown, speckled on the breast, yellow eye, curved beak, long tail." Then he reprimanded me for trying to take a picture instead of observing with my "binos."

About two hours into our walk, Prum, who is a fast and fluid talker, interrupted himself midsentence: "Right there! Right there!" he said. "There's the hooded! Right up against the tree!" Something gold flashed across the path. I raised my binoculars to my eyes and scanned the branches to our right. When I found him, I gasped. He was almost mythological in his beauty: moss-green wings, a luminescent yellow body and face and a perfectly tailored black hood that made his countenance even brighter by contrast. For several minutes we stood and watched the bird as it hopped about, occasionally fanning white tail feathers in our direction. Eventually he flew off. I told Prum how thrilling it was to see such a creature up close. "That's it," Prum said. "That moment is what bird-watching is about."

As a child growing up in a small rural town in southern Vermont, Prum was, in his words, "amorphously nerdy" — keen on reading and memorizing stats from "The Guinness Book of World Records" but not obsessed with anything in particular. Then, in fourth grade, he got glasses. The world came into focus. He chanced upon a field guide to birds in a bookstore, which encouraged him to get outdoors. Soon he was birding in the ample fields and woods around his home. He wore the grooves off two records of bird calls. He befriended local naturalists, routinely going on outings with a group of mostly middle-aged women (conveniently, they had driver's licenses). By the time Prum was in seventh grade, he was leading bird walks at the local state park.

In college, Prum wasted no time in availing himself of Harvard University's substantial ornithological resources. The first week of his freshman year, he got a set of keys to the Museum of Comparative Zoology, home to the largest university-based ornithological collection in the world, which today has nearly 400,000 bird specimens. "I've been associated with a world-class collection of birds every moment of my adult life," he says. "I joke with my students — and it's really true — I have to have at least 100,000 dead birds across the hallway to function intellectually." (He is now the head curator of vertebrate zoology at Yale's Peabody Museum of Natural History.) He wrote a senior thesis on the phylogeny and biogeography of toucans and barbets, working on a desk beneath the skeleton of a moa, an extinct emu-like bird that stood 12 feet tall and weighed 500 pounds.

After graduating from Harvard in 1982, Prum traveled to Suriname to study manakins, a family of intensely colored birds that compete for mates with high-pitched songs and gymnastic dance routines. In 1984, he began graduate studies in biology at the University of Michigan, Ann Arbor, where he planned to reconstruct the evolutionary history of manakins through careful comparisons of anatomy and behavior. In the process, a colleague introduced him to some research papers on sexual selection, piquing his interest in the history of this fascinating yet seemingly neglected idea.

Yellow plumes from a male lesser bird-of-paradise. Kenji Aoki for The New York Times

Darwin was contemplating how animals perceived one another's beauty as early as his 30s: "How does Hen determine which most beautiful cock, which best singer?" he scribbled in a note to himself sometime between 1838 and 1840. In "The Descent of Man," published in 1871, he devoted hundreds of pages to sexual selection, which he thought could explain two of the animal kingdom's most conspicuous and puzzling features: weaponry and adornment. Sometimes, males competing fiercely for females would enter a sort of evolutionary arms race, developing ever greater weapons — tusks, horns, antlers — as the best-endowed males of each successive generation reproduced at the expense of their weaker peers. In parallel, among species whose females choose the most attractive males based on their subjective tastes, males would evolve outlandish sexual ornaments. (It's now well known that all sexes exert numerous different evolutionary pressures on one another and that in some species males choose ornamented females, but to this day, many of the best-studied examples are of female preference and male display.)

Unlike natural selection, which preserved traits that were useful "in the struggle for life," Darwin saw sexual selection as exclusively concerned with reproductive success, often resulting in features that jeopardized an animal's well-being. The peacock's many-eyed aureole, mesmerizing yet cumbersome, was a prime example and remains the mascot of sexual selection today. "A great number of male animals," Darwin wrote, "as all our most gorgeous birds, some fishes, reptiles and mammals, and a host of magnificently colored butterflies have been rendered beautiful for beauty's sake."

Darwin's peers embraced the idea of well-armed males dueling for sexual dominance, but many scorned the concept of animal aesthetics, in part because it was grounded in animal consciousness and female desire. In one critique, the English biologist St. George Mivart stressed "the fundamental difference which exists between the mental powers of man and brutes" and the inability of "vicious feminine caprice" to create enduring colors and patterns. The English naturalist Alfred Russel Wallace, who independently formed many of the same ideas about evolution as Darwin, was also deeply critical. Wallace was particularly tormented by Darwin's suggestion of beauty without utility. "The only way in which we can account for the observed facts is by the supposition that color and ornament are strictly correlated with health, vigor and general fitness to survive," Wallace wrote. In other words, ornamentation could be explained only as a heuristic that animals use to judge a potential mate's fitness — a view that came to dominate.

In the early 1980s, while researching the history of sexual selection, Prum read a seminal 1915 paper and a 1930 book on the subject by the English biologist and statistician Ronald Fisher, who buttressed Darwin's original idea with a more sophisticated understanding of heredity. At first, Fisher argued, females might evolve preferences for certain valueless traits, like bright plumage, that just happened to correspond with health and vigor. Their children would tend to inherit the genes underlying both their mother's preference and their father's trait. Over time, this genetic correlation would reach a tipping point, creating a runaway cycle that would greatly exaggerate both preference and trait, glorifying beauty at the expense of the male's survival. In the early 1980s, the American evolutionary biologists Russell Lande and Mark Kirkpatrick gave Fisher's theory a formal mathematical girding, demonstrating quantitatively that runaway sexual selection could happen in nature and that the ornaments involved could be completely arbitrary, conveying no useful information whatsoever.

Although Fisherian selection was certainly not ignored, it was ultimately overshadowed by a series of hypotheses that seemed to rescue beauty from purposelessness. First, the Israeli biologist Amotz Zahavi proposed a counterintuitive idea called the handicap principle, which put a new spin on Wallace's utilitarian explanation for sexual ornaments. Extravagant ornaments, Zahavi argued, were not merely indicators of advantageous traits as Wallace had said — they were a kind of test. If an animal thrived despite the burden of an unwieldy or metabolically expensive ornament, then that animal had effectively demonstrated its vigor and proved itself worthy of a mate. Similarly, in 1982, the evolutionary biologists W.D. Hamilton and Marlene Zuk proposed that some ornaments, in particular bright plumage, signaled that a male was resilient against parasites and would grant his children the same protection. Many scientists began to think of sexual selection as a type of natural selection. Scores of researchers joined the hunt for measurable benefits of choosing an attractive mate: both direct benefits, like better parenting or more desirable territory, and indirect benefits, namely some evidence that more alluring males really did have "good genes" underlying various desirable qualities, like disease resistance or higher-than-average intelligence.

A male Guianan cock-of-the-rock. Kenji Aoki for The New York Times

After more than 30 years of searching, most biologists agree that although these benefits exist, their prevalence and importance is uncertain. A few compelling studies of frogs, fish and birds have shown that females who choose more attractive males typically have children with more robust immune systems and a greater chance of survival. On the whole, however, the evidence has not equaled the enthusiasm. A 2012 meta-analysis of 90 studies on 55 species found only "equivocal" support for the good-genes hypothesis.

Prum thinks the evidence for the heritable benefits of choosing a beautiful mate is scant because such benefits are themselves rare, whereas arbitrary beauty is "nearly ubiquitous." Over the years, the more he contemplated runaway selection, the more convinced he became that it was a far more powerful and creative evolutionary force than natural selection, which he regards as overhyped and boring. “Animals are agents in their own evolution,” he told me during one conversation. “Birds are beautiful because they are beautiful to themselves.”

In the summer of 1985, around the same time that biologists were rekindling their interest in sexual selection, Prum and the nature documentarian Ann Johnson (who would later choose him as her husband) traveled to Ecuador to continue studying manakins. The first morning, while hiking through a cloud forest, Prum heard odd bell-like notes, which he took to be the murmurings of parrots. Later that day, on the same trail, he heard the strange sounds again and followed them into the forest. He was astonished to find that the source was a male club-winged manakin, a small cinnamon-bodied species with a red cap and black-and-white mottled wings. The manakin was jumping around in a showy manner that suggested he was courting females. Instead of singing with his throat, he repeatedly lifted his wings behind his back and vibrated his feathers furiously against one another, producing two electronic blips followed by a shrill buzzing ring — a sound Prum transcribes as “Bip-Bip-WANNGG!”

At the time, Prum had not fully developed his evolutionary theory of beauty, but he immediately suspected that the club-winged manakin was emblematic of nature’s capacity for pushing creatures to aesthetic extremes. The bird’s singular vibrato haunted him for years. In the early 2000s, when Prum had become a professor of biology at the University of Kansas, he and his graduate student Kimberly Bostwick revealed that the demands of courtship had drastically altered the bird’s anatomy, turning it into a living violin. Male club-winged manakins had feathers with contorted shafts that rubbed against each other 100 times a second — faster than a hummingbird beats its wings. Whereas a vast majority of birds have light, hollow bones in service of flight, Bostwick has recently shown via CT scans that male club-winged manakins have solid ulnas — wing bones — which they need to withstand the intense quivering. Female manakins have inherited related anomalies as well.

Although there are no published studies of the club-winged manakin’s aeronautics, Prum says it’s obvious from observation that the birds fly awkwardly — even the females. The self-perpetuating pressure to be beautiful, Prum argues, has impeded the survival of the entire species. Because the females do not court males, there can be no possible advantage to their warped bones and feathers. “Some of the evolutionary consequences of sexual desire and choice in nature are not adaptive,” Prum writes in his recent book. “Some outcomes are truly decadent.”

In the following decade, as Prum’s hearing declined, he withdrew from field research and birding, but he still managed to make a series of groundbreaking scientific discoveries: He helped confirm that feathers evolved in dinosaurs long before the emergence of birds, and he became one of the first scientists to deduce the colors of a dinosaur’s plumage by examining pigment molecules preserved in fossilized feathers. All the while, he never stopped thinking about sexual selection. Prum formally presented his theory of aesthetic evolution in a series of scientific papers published between 1997 and 2015, proposing that all sexual ornaments and preferences should be regarded as arbitrary until proven useful.

Despite his recent Pulitzer nomination, Prum still stings from the perceived scorn of his academic peers. But after speaking with numerous researchers in the field of sexual selection, I learned that all of Prum's peers are well aware of his work and that many already accept some of the core tenets of his argument: namely that natural and sexual selection are distinct processes and that, in at least some cases, beauty reveals nothing about an individual's health or vigor. At the same time, nearly every researcher I spoke to said that Prum inflates the importance of arbitrary preferences and Fisherian selection to the point of eclipsing all other possibilities. In conversation, Prum's brilliance is obvious, but he has a tendency to be dogmatic, sometimes interrupting to dismiss an argument that does not agree with his own. Although he admits that certain forms of beauty may be linked to survival advantages, he does not seem particularly interested in engaging with the considerable research on this topic. When I asked him which studies he thought offered the strongest support of "good genes" and other benefits, he paused for a while before finally responding that it was not his job to review the literature.

A male painted bunting. Kenji Aoki for The New York Times

Like Darwin, Prum is so enchanted by the outcomes of aesthetic preferences that he mostly ignores their origins. Toward the end of our bird walk at Hammonasset Beach State Park, we got to talking about club-winged manakins. I asked him about their evolutionary history. Prum thinks that long ago, an earlier version of the bird's courtship dance incidentally produced a feathery susurration. Over time, this sound became highly attractive to females, which pressured males to evolve adaptations that made their rustling feathers louder and more noticeable, culminating in a quick-winged strumming. But why, I asked Prum, would females be attracted to those particular sounds in the first place?

To Prum, it was a question without an answer — and thus a question not worth contemplating. "Not everything," he said, "has this explicit causal explanation."

Prum's indifference to the ultimate source of aesthetic taste leaves a conspicuous gap in his grand theory. Even if we were to accept that most beauty blooms from arbitrary preferences, we would still need to explain why such preferences exist at all. It's entirely conceivable that an animal might be inherently partial to, say, a warbling mating call or bright yellow feathers, and that these predilections would have nothing to do with advantageous genes. Yet such inclinations are inarguably the product of an animal's neurobiology, which is itself the result of a long evolutionary history that has adapted the animal's brain and sensory organs to specific environmental conditions. In the past two decades, a cohort of biologists have dedicated themselves to studying how an animal's "sensory bias" — its ecological niche and its particular way of experiencing the world — sculpts its appearance, behavior and desires. Like Prum, they don't think beauty has to be adaptive. But where Prum celebrates caprice, they seek causality.

Molly Cummings, a professor of integrative biology at the University of Texas at Austin, is a leading researcher in the field of sensory ecology. When I visited her last spring, she drove us to one of her field laboratories: a grassy clearing populated with several large concrete basins. The surface of one basin was so packed with woolly algae and pink-flowered water lilies that we could hardly see the water. Cummings began pushing some of the vegetation out of the way, forming shady recesses that permitted our gaze at the right angle. "Let me see if I can find a big, beautiful boy," she said.

A paper-clip-size fish swam toward us. I leaned in for a closer look. His silver body was decorated with a single black dot and a stripe of iridescent blue; his lengthy tail, shaped like a knight's blade, was streaked with yellow. "Oh, yeah, there's a guy courting," Cummings said. "He's coming up to that female, trying to impress her." The fish, a male swordtail, seemed almost manic in his effort to be noticed. He darted back and forth in front of the female, shimmying as he went, his scales reflecting whatever light managed to breach the murk.

A little while later, we drove the few miles back to her campus laboratory, where shelves of fish tanks lined several rooms and Ernst Haeckel's resplendent illustrations of jellyfish undulated across the walls. As we toured the facilities, Cummings told me about the arc of her career. While an undergraduate at Stanford University, she spent a summer scuba diving in the giant kelp forests at Hopkins Marine Station, adjacent to the world-renowned Monterey Bay Aquarium. After college, she moved to James Cook University in Townsville, Australia, where she studied marine ecology and discovered the work of the biologists John Lythgoe and John Endler, both of whom were interested in how the type of light in an animal's environment shaped its visual system.

Cummings thought about the fish she had observed in California and Australia. She was astounded by the dynamic beauty of surfperch in the kelp forest: the way they communicate through the color and brightness of their skin, flashing blue, silver and orange to attract mates. Equally impressive was the diversity of their aquatic habitats. Some patches of water were sparkling and clear; others were cloudy with algal muck. In Australia, sunlight bathed the many vibrant species of reef fish almost constantly, but they lived against a kaleidoscopic backdrop of coral. How did fish evolve effective and reliable sexual ornaments if the lighting and scenery in their homes were so variable?

The tips of the outer tail feathers of a male king bird-of-paradise. Kenji Aoki for The New York Times

After earning a postgraduate degree in Australia in 1993, Cummings began a Ph.D. at the University of California, Santa Barbara. For several years, she studied various species of surfperch, repeatedly diving in the kelp forests with a Plexiglas-protected spectrometer to quantify and characterize the light in different habitats. At night, she would use powerful diving lights to stun surfperch and take them back to the lab, evading the hungry seals that routinely trailed her in hopes of making a meal of the startled fish. After hundreds of dives and careful measurements, Cummings discovered that water itself had guided the evolution of piscine beauty. A female's preference for a blaze of silver or blue was not arbitrary; it was a consequence of the particular wavelengths of light that traveled farthest through her underwater niche. Whichever males happened to have scales that best reflected these wavelengths were more likely to catch the eye of females.

In her studies, Cummings showed that surfperch living in dim or murky waters generally preferred shiny ornaments, while surfperch inhabiting zones of mercurial brightness favored bold colors. Later, Cummings found that Mexican swordtails occupying the upper layers of rivers, where the clear water strongly polarized incoming sunlight, had ornaments that were specialized to reflect polarized light — like a stripe of iridescent blue. These findings parallel similar studies suggesting that female guppies in Trinidad prefer males with orange patches because they first evolved a taste for nutritious orange tree fruits that occasionally fell into the water. "Some people think female preferences just somehow emerge," Cummings says, "but what has been overlooked is that in many cases, it's a result of environmental constraints. It's not always random."

What a creature finds attractive depends on more than the unique qualities of its environment, however; attraction is also defined by which of those qualities cross the threshold of awareness. Consider the difference between what we see when we look at a flower and what a bumblebee sees. Like us, insects have color vision. Unlike us, insects can also perceive ultraviolet light. Many plants have evolved flower parts that absorb or reflect ultraviolet light, forming patterns like rings, bull's-eyes and starbursts. Most creatures are oblivious to these ornaments, but to the eyes of many pollinators, they are unmistakable beacons. There is an entire dimension of floral beauty invisible to us, not because we are not exposed to ultraviolet light, but because we do not have the proper biological hardware to perceive it.

Michael Ryan, a professor of zoology whose lab and office are just a few floors below Cummings', has spent more than 30 years investigating how the quirks of an animal's anatomy determine its aesthetic preferences — a career he details in his recent book, "A Taste for the Beautiful." Since 1978, Ryan has been traveling to Panama to study a mud-colored frog called the túngara. Like the club-winged manakin, the túngara has a unique form of beauty that is not visual but aural. At dusk, male túngara frogs gather at the edges of puddles and sing to seduce females. Their mating call has two elements: The main part, dubbed the whine, sounds precisely like a miniaturized laser gun; sometimes this is followed by one or more brief barks, known as chucks. A long and complex mating call is risky: It attracts frog-eating bats. Yet there is a high payoff. Ryan has shown that whines followed by chucks are up to five times as appealing to females as whines alone. But why?

According to the adaptive model of beauty, the chucks must convey something about the males' fitness. As it happens, larger males, which produce the deepest and sexiest chucks, are also the most adept at mating, because they are closer in size to females. (Frog sex is a slippery affair, and a diminutive male is more likely to miss his target.) Moreover, the túngara frog has an inner organ tuned to 2,200 hertz, which is close to the dominant frequency of a chuck. Together, these facts seem to indicate that the túngara's puddle-side serenade is an example of adaptive mate choice: Females evolved ears tuned to chucks because they indicate the biggest and most sexually skilled males.

Ryan's research revealed a stranger story. When he examined the túngara frog's family tree, he discovered that eight frog species closely related to the túngara also have inner ear organs sensitive to frequencies of about 2,200 hertz, yet none of them produce chucks in their mating call. Ryan thinks that eons ago, the ancestor of all these species probably evolved an inner ear tuned to roughly 2,200 hertz for some long-abandoned purpose. The túngara later revived this neglected auditory channel, probably by happenstance. Male frogs that happened to burp out a few extra notes after whining were automatically favored by females — not because they were more suitable mates, but simply because they were more noticeable.

Like the glistening scales on the surfperch and swordtails that Cummings studied, the túngara's costly mating call did not evolve to convey any pragmatic information about health or fitness. But that doesn't mean that these traits were arbitrary. They were the result of specific, discernible aspects of the animals' environments, anatomy and evolutionary legacy.

“I took a real beating when I suggested this idea in 1990,” Ryan says. “It was very widely criticized. But now sensory bias is considered an important part of the evolution of these preferences.”

During our walk at Hammonasset, while admiring seabirds from shore-side cliffs, I asked Prum about sensory bias. He said it could not possibly explain the staggering diversity and idiosyncrasy of sexual ornaments — the fact that every closely related sparrow species has a unique embellishment, for example. Prum sees sensory bias as just another way to maintain the predominant “adaptive paradigm” that refuses to acknowledge his theory of aesthetic evolution. Tellingly, Prum and Ryan do not discuss each other’s work in their recent books.

A male king bird-of-paradise. Kenji Aoki for The New York Times

While mulling over the similarities and discrepancies between Prum's ideas and those of his peers, I kept returning to a passage in his book. In 2010, Prum and his colleagues revealed that a crow-size dinosaur called Anchiornis huxleyi was beautifully adorned: gray body plumage, an auburn mohawk and long white limb feathers with black spangles. Why dinosaurs originally evolved feathers has long perplexed scientists. At first, layers of fuzzy filaments, similar to a chick's down, most likely helped dinosaurs repel water and regulate body temperature. But what explains the development of broad, flat feathers like those found on Anchiornis? Flight is the intuitive answer, but the first planar feathers were probably too primitive for flight or gliding, lacking the distinct asymmetry that makes birds' feathers aerodynamic. In his book, Prum advocates for an alternative hypothesis that has been gaining support: Large feathers evolved to be beautiful.

The aesthetic possibilities of fuzzy down are limited. "The innovative planar feather vane, however, creates a well-defined, two-dimensional surface on which it is possible to create a whole new world of complex color patterns within every feather," Prum writes. Only later did birds co-opt their big, glamorous plumes for flight, which is probably a key reason that some of them survived mass extinction 66 million years ago. Birds transformed what was once mere frippery into some of the most enviable adaptations on the planet, from the ocean-spanning breadth of an albatross to the torpedoed silhouette of a plunging falcon. Yet they never abandoned their sense of style, using feathers as a medium for peerless pageantry. A feather, then, cannot be labeled the sole product of either natural or sexual selection. A feather, with its reciprocal structure, embodies the confluence of two powerful and equally important evolutionary forces: utility and beauty.

Most of the scientists I spoke with said that the old dichotomy between adaptive adornment and arbitrary beauty, between "good genes" and Fisherian selection, is being replaced with a modern conceptual synthesis that emphasizes multiplicity. "Beauty is something that arises from a host of different mechanisms," says Gil Rosenthal, an evolutionary biologist at Texas A&M University and the author of the new scholarly tome "Mate Choice." "It's an incredibly multilayered process."

The environment constrains a creature's anatomy, which determines how it experiences the world, which generates adaptive and arbitrary preferences, which loop back to alter its biology, sometimes in maladaptive ways. Beauty reveals that evolution is neither an iterative chiseling of living organisms by a domineering landscape nor a frenzied collision of chance events. Rather, evolution is an intricate clockwork of physics, biology and perception in which every moving part influences another in both subtle and profound ways. Its gears are so innumerable and dynamic — so susceptible to serendipity and mishap — that even a single outcome of its ceaseless ticking can confound science for centuries.

On my last day in Austin, while walking through a park, I encountered a common grackle hunting for insects in the grass. His plumage appeared black as charcoal at first, but as he moved, it shimmered with all the colors of an oil slick. Every now and then, he stopped in place, inflated his chest and made a sound like a rusty swing set. Perhaps dissatisfied with the local fare, or uncomfortable with my presence, he flew off.

In his absence, my attention immediately shifted to something his presence had obscured — a golden columbine bush. From a distance, its flowers resembled medieval illustrations of comets, big and bold with long, trailing streamers. Up close, I was struck by the complexity of a single blossom: a large yellow star wreathed a cluster of five tubular petals, shaped like angel's trumpets and pooled with nectar. A tuft of pollen-tipped filaments fizzed through the very center. Viewed from above, the flowers looked like huddles of tiny birds with their beaks pressed together and wings flared. The name "columbine" comes from the Latin for "dovelike."

Why are flowers beautiful? Or, more precisely: Why are flowers beautiful to *us*? The more I thought about this question, the more it seemed to speak to the nature of beauty itself. Philosophers, scientists and writers have tried to define the essence of beauty for thousands of years. The plurality of their efforts illustrates the immense difficulty of this task. Beauty, they have said, is: harmony; goodness; a manifestation of divine perfection; a type of pleasure; that which causes love and longing; and M = O/C (where M is aesthetic value, O is order and C is complexity).

Evolutionary psychologists, eagerly applying adaptive logic to every facet of behavior and cognition, have speculated that the human perception of beauty emerges from a set of ancient adaptations: Perhaps men like women with large breasts and narrow waists because those features signal high fertility; symmetrical faces may correlate with overall health; maybe babies are irresistibly cute because their juvenile features activate the caregiving circuits in our brains. Such claims sometimes verge on the ludicrous: The philosopher Denis Dutton has argued that people around the world have an intrinsic appreciation for a certain type of landscape — a grassy field with copses of trees, water and wildlife — because it resembles the Pleistocene savannas where humans evolved. In a TED Talk, Dutton explains that postcards, calendars and paintings depicting this universally beloved landscape usually include trees that fork near the ground because our ancestors relied on their conveniently low branches to scramble away from predators.

Of course, it is undeniable that we, like all animals, are products of evolution. Our brains and sensory organs are just as biased as any other creature's. Our inherited anatomy, physiology and instincts have undoubtedly shaped our perception of beauty. In their recent books, Richard Prum and Michael Ryan synthesize research on animals and people, exploring possible evolutionary explanations for our own aesthetic tastes. Ryan is particularly interested in the innate sensitivities and biases of our neural architecture: He describes how our visual system, for example, may be wired to notice symmetry. Prum stresses his conviction that in humans, as in birds, many types of physical beauty and sexual desire have arbitrarily co-evolved without reference to health or fertility. What complicates their respective arguments is the overwhelming power of human culture. As a species, we are so thoroughly saturated with symbolism, ritual and art — so swayed by rapidly changing fashions — that it is more or less impossible to determine just how much an aesthetic preference owes to evolutionary history as opposed to cultural influence.

A male Mandarin duck. Kenji Aoki for The New York Times

Perhaps more than any other object of aesthetic obsession, flowers expose the futility of trying to contain beauty in a single theoretical framework. Consider how flowers came to be and how we grew to love them: 150 million years ago many pollen-producing plants depended on the wind to spread their pollen and reproduce. But certain insects, perhaps beetles and flies, began to eat those protein-rich pollen grains, inadvertently transporting them from one plant to another. This proved to be a much more efficient means of fertilization than capricious air currents. Plants with the richest and most obvious sources of pollen were especially successful. Likewise, insects that were particularly adept at finding pollen had an advantage over their peers.

Through a long process of co-evolution, plants and pollinators transformed one another. Some plants began to modify their leaves into proto-flowers: little flags that marked the location of their pollen. Bold colors and distinctive shapes helped them stand out in a tangle of green. Strong aromas and ultraviolet beacons played upon pollinators' senses. Nectar sweetened the deal. Insects, birds and mammals began competing for access, evolving wings, tongues and brains better suited to the quest for floral sustenance. As the pressure from both parties intensified, plants and their pollinators formed increasingly specific relationships, hurtling each other toward aesthetic and adaptive extremes — a bird that hums and hovers like an insect, an orchid that mimics the appearance and scent of a female bee.

Many millions of years later, flowers enchanted yet another species. Perhaps the initial attraction was purely utilitarian: the promise of fruit or grain. Maybe we were captivated by their consonance of color, form and aroma. Whatever the case, we adopted numerous flowering plants into an expanding circle of domesticated species. We brought them into greenhouses and laboratories, magnifying their inherent beauty, creating new hybrids and tailoring their features to our individual tastes. We contracted orchid delirium and tulip mania, and we have never fully recovered. The flower began as a plea and became a phenomenon.

If there is a universal truth about beauty — some concise and elegant concept that encompasses every variety of charm and grace in existence — we do not yet understand enough about nature to articulate it. What we call beauty is not simply one thing or another, neither wholly purposeful nor entirely random, neither merely a property nor a feeling. Beauty is a dialogue between perceiver and perceived. Beauty is the world's answer to the audacity of a flower. It is the way a bee spills across the lip of a yawning buttercup; it is the care with which a satin bowerbird selects a hibiscus bloom; it is the impulse to recreate water lilies with oil and canvas; it is the need to place roses on a grave.

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