As if on a catwalk, this male ruff appears to display his plumage. But appearance alone doesn't impress anyone. While other males fight, this one simply waits and seizes the first opportunity to mate.

PHOTO: MICHAEL GERBER

LOOKS AREN'T EVERYTHING

TEXT: CLAUDIA DOYLE

Males flaunt bright colors and elaborate plumage – but in the end, female zebra finches and ruffs choose a partner not for their beauty, but for their superior display or clever mating strategy. Wolfgang Forstmeier and Clemens Küpper of the Max Planck Institute for Biological Intelligence in Seewiesen study mate-choice preferences in birds.

The courtship of some bird species is a feast for the eyes and ears: males try to win over females with heart-stirring songs, dazzling colors, and elaborate dance performances. Much of it seems almost human. "Because birds use their appearance and song to charm a potential mate, you might think they find the same traits attractive as we do," says Wolfgang Forstmeier, a researcher at the Max Planck Institute for Biological Intelligence in Seewiesen. But is that really how it works? Forstmeier has spent much of his career testing this widespread assumption – and getting surprising results. But let's start at the beginning.

"We humans are convinced that, even in the animal kingdom, mate choice is mainly about beauty."

WOLFGANG FORSTMEIER

At the Max Planck Institute in Seewiesen, a male zebra finch perches on a wooden bar in his aviary, waiting. Will he find his life partner today? The small gray-and-white bird, with its bright red beak and orange cheek patch, tilts its head to the side. A female flies in and settles opposite him. Now it begins: the male starts to sing with gusto – though "chirp" is a more accurate description of the finches' rather unmelodious sounds. The lady listens and makes her choice.

Wolfgang Forstmeier recorded and analyzed over 75,000 such encounters on video. He also weighed the males, cataloged their beak color, and measured their cheek patches – all to determine which traits the females preferred. The result was unexpected: "It became clear to us that there can't be a single factor that makes certain males attractive, because the females completely disagree on which ones they like," Forstmeier summarizes. "Humans are convinced that mate choice in the animal kingdom is primarily about beauty. At least for zebra finches, that doesn't seem to be the case," explains the ornithologist from Bart Kempenaers' department. Instead, the behavior of a potential partner may play a crucial role, in addition to his song. "True likes and dislikes seem to develop between the birds," says Forstmeier. Whereas visual traits, in his view, serve no particular function and may just be signals of sex and species identity. So where does the widespread belief that visual traits are important in mate choice come from? Wolfgang Forstmeier suspects a "publication bias" – that is, studies supporting this assumption are more likely to be published, while negative results gather dust in a researcher's filing cabinet.

For Forstmeier, the central role of song is undisputed. He was able to show that female zebra finches have a preference for specific song "dialects". Two groups, kept separately at the Institute over the years, developed distinct dialects. These dialects appear to influence attractiveness: females clearly prefer the familiar dialect over the unfamiliar one.

Forstmeier has since turned his attention to another species: the ruff. These magpie-sized birds inhabit wetlands in northwestern Europe and Russia, and some are kept in spacious aviaries at the institute in Seewiesen. During courtship, the birds put on an impressive display: from vain posturing to wild pecking. The males try to attract as many females as possible to their display arenas. To do so, they raise their impressive, individually colored neck collars and leap into the air, flapping their wings. The females watch the spectacle from a safe distance at first.

And just like with the zebra finches, appearance is not the decisive factor in ruffs either. "Even though the males display their magnificent plumage during courtship, it doesn't influence the females' choice," explains Forstmeier. There are not only males with striking neck collars, but also less conspicuous ones, some even resembling females. "If all females preferred a specific aesthetic, the other variants would have long since disappeared." Plainly, that hasn't happened. Forstmeier therefore assumes that the diversity of neck collars is used for the purposes of individual recognition.

It is strength, more than anything else, that impresses the females. Dominance seems to be particularly attractive to some females. This is likely why constant fighting occurs in the display arenas: the birds flutter a few centimeters into the air, strike at their rivals with their feet, and peck at each other with their beaks. This continuous struggle to defend or improve one's position is exhausting, but it pays off – the alpha male gets far more opportunities to

SUMMARY

For zebra finches and ruffs, reproductive success is determined not by the most striking plumage but by song, strength, and behavior. External traits – contrary to common belief – play only a minor role.

Male ruffs exist in three genetically determined types – fighters, satellites, and faeders – which differ in appearance, behavior, and hormone regulation. A supergene on chromosome 11, which arose millions of years ago, shapes this diversity and maintains it despite unequal reproductive opportunities.

Traits that humans perceive as "beautiful" are typically thought to serve an aesthetic function in courtship. Yet, in zebra finches, mate choice is about behavioral compatibility rather than beautiful colors.

mate and pass on his genes. "More than half of all matings go to the dominant male. Lower-ranking males rarely get a chance or end up with nothing at all," explains Clemens Küpper, who leads the Behavioral Genetics and Evolutionary Ecology research group at the Max Planck Institute for Biological Intelligence in Seewiesen.

Satellites and Sneakers

Küpper has been studying these birds for more than ten years, investigating how diversity within a species arises and persists over long periods. The ruff is an ideal subject for this research, as the birds have taken the principle of diversity to the extreme. Besides the dominant, conspicuous "fighters," there are two other types of males: 15 percent are slightly smaller than the fighters and their courtship plumage is more striking – the feather collar is usually white rather than dark. But the most remarkable trait of these so-called "satellites" is their behavior. They show no aggression; instead, they join a fighter and willingly submit to his dominance. Through this peaceful behavior, they get close to females and shamelessly seize every opportunity to mate whenever their partner is engaged in a fight.

Even stranger is the third type, the "faeder" (Old Frisian: Father) resembling a slightly oversized female. Well camouflaged, it sneaks unnoticed through the display arena, waiting for a female to crouch and signal that she is ready to mate. The faeder confuses other males by imitating the female's position and behavior. It exploits this confusion to be the first to mate with the female. About one percent of males belong to this type.

Through genome analysis, Clemens Küpper discovered whilst doing postdoctoral research at the University of Sheffield (2012–2015) that the three male types differ from each other at a single location in the genome. The researchers were even able to estimate when this →

PHOTO: AXEL GRIESCH

The plumage of male zebra finches (left) is full of color. Yet colorful feathers are unimportant when it comes to choosing their mate. For the females, the personality of the suitor is what matters most.

PHOTO: AXEL GRIESCH

At the Seewiesen Institute, ruffs are kept in large aviaries. In the photo, Veronika Rohr and Clemens Küpper test a young bird's ability to fly. Once it can fly over the water basin in front of it, it is considered fledged – a key stage in life, as it means the bird will be better able to escape its predators in the wild.

change occurred: about four million years ago, a segment of roughly 125 genes on chromosome 11 was excised and reinserted in the opposite orientation. This group of genes, known as a supergene, was thereafter isolated from the rest of the genome and evolved independently. "Inversions occur quite frequently in nature," explains Küpper. For example, they are found in fruit flies, ants, and even humans. Hemophilia, for instance, is caused by a small inversion on the X chromosome. Ruff males with both copies of chromosome 11 altered in this way are not viable. If only one copy is mutated, the animals develop normally, even if their appearance and behavior differ from their conspecifics.

A few thousand years ago, the satellites evolved from the faeders. In this process, the satellites regained intact copies of genes in several locations of the supergene whose functions had previously been lost. As a result, these individuals inherited back the impressive neck feathers of the fighters – now in white instead of black. Their behavior also signals their readiness to mate – even though, like the faeders, they completely lack aggression. Clemens Küpper and his team are investigating which genes are responsible for all these changes. A key factor in the differing aggressiveness among fighters, satellites, and faeders is their testosterone levels. As expected, fighters have high testosterone in their blood during the mating season. Faeders and satellites, by contrast, have almost none. Initially, Küpper suspected that the hormone production in these latter types might be impaired. But this theory

"More than half of all matings are achieved by the dominant male."

CLEMENS KÜPPER

Male ruffs come in three forms: peaceful satellites (left), *faeders* that resemble females (center), and aggressive fighters (right). They each use different strategies to reproduce successfully.

turned out to be wrong. "In fact, the faeders and satellites actually produce even more testosterone in their testes than the fighters. However, they break it down immediately in the bloodstream," he explains. The gene responsible is called HSD17B2. It provides the blueprint for an enzyme that converts testosterone into the much weaker androstenedione. Due to a mutation, this enzyme gained a sort of "superpower": it is now produced in greater amounts and works much more efficiently. Almost all the testosterone that enters the bloodstream is immediately converted back into androstenedione.

Female birds can also carry the *faeder* or satellite mutations. *Faeder* females are noticeably smaller, while satellite females hardly differ in appearance from non-mutated birds. The differences in testosterone and androstenedione are similar to those in males, although females naturally produce much lower amounts of these hormones. Küpper's team is currently investigating whether female sex hormones are also affected. Additionally, the researchers want to understand what advantages or disadvantages these gene variants confer on female birds. Over several years, his team counted and weighed the eggs of ruff females living in aviaries. Their measurements showed that the biological fitness of *faeder* females is severely compromised by the mutation: they lay fewer and smaller eggs, and both the embryos inside the eggs and the hatched chicks have a lower chance of survival. As a result, *faeder* females produce eight times fewer offspring than fighter females. So why hasn't this gene variant been eliminated by evolution, given the severe disadvantages for females? "It can only persist because *faeder* males gain a disproportionate number of benefits from it," the ornithologist explains. "In a display arena, where most fighter males never get a chance, pursuing an alternative strategy pays off," Küpper adds. However, this only works if there aren't too many *faeder* males. If they become too common, they are more easily recognized by other males and driven out of the mating arena.

Beauty is Individual

Beauty, then, is not a decisive factor in mate choice for either ruffs or zebra finches. Song, strength, and behavior are at least as important. Beauty alone has little appeal. True attractiveness often emerges from the interplay of many different traits in a potential partner. A male can be "beautiful" by singing in the right dialect, showing courage in a fight, or behaving appropriately toward others. Each species has its own concept of beauty – and, as the rather unmelodious song of zebra finches shows, it does not always align with human notions of attractiveness.

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