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# She's gotta have it

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A FEMALE barn swallow patrols the skies, searching for a mate. She's picky and isn't going to settle for just any male. Suddenly, she notices a brilliant flash of colour—a proudly parading suitor. She is instantly drawn to him. With that stunning red throat pouch, she just can't resist him.

It seems that the brashest, most brightly coloured males always get the girls. A flashy yellow wing tip or radiant red tail feathers are sure to attract attention. And it's not just birds who dress to impress. Throughout the animal kingdom, there are males who show off through their wardrobe.

There can be no doubt that colours are status symbols, but what exactly do they symbolise? And why do females fall for them? After all, a patch of red is not going to help a male cope with life's essentials, such as catching food. On the contrary, bright colours attract predators as well as partners, making them a disadvantage in the battle for survival.

This conundrum has been bothering evolutionary biologists since Darwin's time. Now they are beginning to lift the lid on this enigma. The key, it seems, is understanding the high price of putting on such colourful displays.

It's 130 years since Darwin coined the term sexual selection to describe the central role that sex plays in evolution. Sexual selection works in one of two ways. Either males compete with one another for potential mates, with the winner taking the spoils, or females take the initiative and choose their partner. Where males compete directly, it is usually easy to see how sexual signals work. Large antlers on a stag, for example, not only warn rivals that he is no Bambi; they can also be used as weapons. But the dandy yellow suits worn by canaries or yellowhammers aren't as handy in a scrap.

Over the past century or so, it has become increasingly clear that most bird species—and many other animals, including fish, reptiles and mammals—use the second strategy. Those that do are among the most strikingly coloured animals alive. But biologists have struggled to understand exactly how bright colours signal a male's worth. Explanations haven't got much further than the Darwinian notion that impressively adorned males must be the fittest of their kind, capable of investing more energy in their sexual signals than their rivals.

Such fumblings are underpinned by some important theory, though. For a start, a signal between individuals usually contains reliable information about the sender. Otherwise, like the boy who cried wolf, it will soon be ignored and become meaningless. For a signal to be reliable, or honest, it is essential that it cannot be faked by scrawny males.

Amotz Zahavi of Tel Aviv University realised that an honest signal must be costly to produce and called this the handicap principle. In other words, the cost of producing a signal will be too high for low-quality males—just as forking out for a flashy sports car will hit the pocket of someone with a low income much harder than that of a millionaire—ensuring that only the best males can invest in bright signals.

But just what do we mean when we talk of low-quality or high-quality males? In 1982, evolutionary biologists William Hamilton and Marlene Zuk proposed a new handicap hypothesis that forged a link between the quality of individuals and their sexual signals. They argued that disease resistance is crucial in the evolution of sexually selected characteristics. In essence, only males with genes for, say, parasite resistance would be in prime condition and thus able to express the best sexual signals. The flip side of the theory is that sick males will look drab in comparison with healthier rivals. "I think Hamilton and Zuk deserve a lot of credit for having started this," says Anders Møller of the Pierre and Marie Curie University in Paris.

Hamilton and Zuk's idea sparked a rush to find evidence to back the theory. "It's a damn difficult idea to test," says Ian Owens of the University of Queensland in Brisbane, Australia. And what followed was a mishmash of equivocal results. Early evidence showing a relationship between levels of parasites in the blood and plumage brightness turned out to be biased, because the assessment of colour intensity was subjective and did not take into account the fact that birds and humans have very different colour vision.

Once colour scoring was standardised, the correlation seemed to disappear. More recently, conflicting evidence has come from studies of birds, fishes and lizards that looked at the levels of blood parasites or more general measures of immune function, such as the concentration of white blood cells, or the size of the spleen or other immune organs.

To find a way through the confusion, Møller and his colleagues Philippe Christie and Elena Lux used a statistical technique known as meta-analysis to merge the results of around 50 studies. These yielded 69 separate comparisons of relationships between the expression of secondary sexual characters such as colour and either parasite load or immune response. Last year, they reported that parasite load is not strongly linked to the expression of sexual signals. But immune function is.

"Most of the early tests of the Hamilton-Zuk hypothesis based on parasite data are pure misunderstandings, because they do not address the question of resistance to debilitating parasites," says Møller. Animals are often affected by a range of parasites. But because most of the experiments focused on single parasites, it is likely that they were looking at relatively harmless organisms, Møller says. "What Hamilton and Zuk were really talking about is resistance, and using parasite abundance as a measure is an extremely indirect way of addressing the question. Rather than looking at parasites we should look at immune defence mechanisms."

But how could immunity be linked to sexual signals such as colour? One idea, proposed in the early 1990s by Ivar Folstad of the University of Tromsø in Norway and his colleague Andrew Karter, suggested that the key was testosterone. In many vertebrates, the hormone is essential for the full expression of male sexual characteristics, but it also suppresses the immune system. Folstad and Karter described testosterone as a double-edged sword. Their immunocompetence handicap theory predicted that only males with the best immune systems could afford to have their immunity hindered by the development of extravagant ornaments. The idea gained some support, but it is difficult to prove, and was soon eclipsed by a more promising line of inquiry.

In the 1990s, interest was growing in a large family of natural pigments known as carotenoids. Animals can produce colours in several ways, such as using structures like butterfly wing scales to reflect various wavelengths of light, or by exploiting combinations of melanin pigments. But carotenoids form an important part of the colourful signals used by many animals. The pigments, which can be stored in a variety of tissues, are made mainly by plants and algae, and are acquired either directly from them or by eating insects. Most carotenoids are either red, orange or yellow, but purples, greens and blues can be produced by binding proteins to the pigments.

Studies of house finches, guppies and stickleback fish have shown that females prefer males with a brighter, carotenoid-based colouration. But for carotenoid-based signals to be an honest reflection of a male's status, they must be costly. Last year, Owens and his colleague Valérie Olson described three ways in which this cost might be incurred. Carotenoids, they said, would be costly if they are either risky, rare or required. They dubbed these the three Rs.

Carotenoids would be risky if they have detrimental effects on the body. "This [suggestion] is based largely on a few cases in the medical literature where carotenoid supplementation led to a higher than expected rate of cancer," says Owens. Many researchers have looked for such an effect in fish and poultry, yet there is no evidence to back such claims except in humans, says Møller. Olson agrees that "risky carotenoids" cannot explain wonderfully coloured sexual ornaments.

The conventional view is that carotenoids are costly because they are rare. Healthier males can forage for more of the pigments than their inferior counterparts. To some extent, this is true. "The question," says Owens, "is whether this is the full story, and even whether it is the most important part of the story."

Indeed, evidence is piling up in favour of the third mechanism—that carotenoids are required, in particular by the immune system and in the detoxification processes that neutralise free radicals. In rodents and other mammals, researchers have found that the pigments help stimulate the proliferation of the T and B-lymphocytes that fight invading pathogens. Carotenoids are also involved in the production of cytokines and interleukins, essential molecules in the inflammatory response to injury. What's more, carotenoids are antioxidants that help mop up free radicals before they damage DNA, lipids and proteins.

**More than skin-deep**

These pigments look like the missing link in Hamilton and Zuk's original handicap theory. They explain how the colourful calling cards of males reflect their status: males can either use scarce carotenoids for immune defence and detoxification, or for attracting females. Males that are more susceptible to disease and parasites will have to use their carotenoids to boost their immune systems, says Møller, whereas males that are genetically resistant will use fewer carotenoids for fighting disease—and advertise this by using the pigments for flashy displays instead.

Until recently, this idea was simply speculation. "At the moment there is a big, big difference between the evidence and the theory," says Owens. "We need to know whether organisms really can shift the allocation of their carotenoids between their immune system and their ornament." Møller set out to answer this question, and some of his early findings happened almost by accident during research at Chernobyl.

Working with Italian colleagues, including Nicola Saino of the University of Milan, Møller investigated the health of male barn swallows that have been forced to live with debilitating background radiation since 1986. "I was trying to measure mutation rates because of the unnaturally high levels of radioactivity," he says. But blood samples revealed something more. The types of white blood cells indicated, as expected, that the birds were under stress, yet their immune response was down. Chernobyl swallows were also uniformly pale in colour—even males with long tail feathers, a sexual signal normally accompanied by bright colouration. Møller believes that the high background radiation forces the birds to neglect their disease-fighting capabilities and shift carotenoids from sexual signalling to countering their unnaturally high levels of free radicals.

Research on chickens also supports the idea that carotenoids can be co-opted to fight disease. Infection by a single blood parasite can reduce an individual's carotenoid levels by as much as 80 per cent in a week. "The turnover can be dramatic in association with disease," says Møller.

In a recent study, Møller, Saino and their colleagues again looked at barn swallows, this time in a normal environment outside Milan. These small, graceful birds have several types of sexual signals to attract females, including their long tail feathers and bright red throat patch. The birds with the longest tails also have the brightest patches. Møller and his colleagues found that males with dull signals had higher levels of immunoglobins, indicating they were more frequently infected by pathogens. They also had lower levels of carotenoids in their blood than brightly coloured rivals, who didn't need to use up the pigments in fighting disease. "I love the idea of individuals facing a trade-off between using carotenoids to make sexual ornaments or using them for their immune systems," says Owens. "It's a beautifully elegant explanation for a lot of puzzling facts."

However, much work remains to be done to find out how important the phenomenon is, and exactly how the payoffs between carotenoid-based sexual signalling and immune function pan out. Møller has some ideas about how the work might proceed. "One could genetically engineer individuals to change their production of immune substances, or explicitly change the amount of free radicals that have to be neutralised by the detoxification system," he says.

But such manipulations will be no substitute for studies of animals in the wild. That is why Møller is planning to return to Chernobyl, where the washed out male barn swallows cannot help advertising their plight, and the females can't afford to be so picky about the colour of their mate.

**Best for baby**

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