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Figure 1 | The hummingbird _Florisuga mellivora_. Females of this species exist in two forms of differing colours. Around 20% of females have the same colouring as the males (blue and white plumage). Falk _et al._[3] offer an evolutionary explanation for why some females mimic male colouring.

Evolution

Female birds disguised as males get extra food

Tim Caro

Around 20% of female hummingbirds have plumage that is characteristic of the males of the species. Evidence for why this happens offers a surprising perspective on how evolution helps to maintain colour variations.

The breathtaking palette of colours seen in nature is the fuel that drives many of us to become biologists, and is the reason why some researchers try to understand the biological basis of animal and plant coloration[1]. Normally, the drivers of such evolutionary processes can be bracketed into categories that result in colour for protection, signalling or physiological reasons[2]. Writing in _Proceedings of the Royal Society B_, Falk _et al._[3] propose an evolutionary driver with a new twist.

Variation in coloration occurs between species but also within them — leopards (_Panthera pardus_), for example, can have a black or mottled tawny coat, and the flowers of _Iris lutescens_ can be purple or yellow. These colour differences are variations in form called polymorphisms. For some scientists, it is sufficient to know that such colour polymorphisms exist, but for others, the underlying genetics of such variation must be understood. Formally, a polymorphism is "the occurrence together in the same habitat of two or more distinct forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation"[4]. In other words, for the rare forms to be present, a new mutation doesn't have to occur each time.

Polymorphisms evolve for several reasons. Historically, the mechanism that has received most attention is 'negative frequency-dependent selection', in which predators overlook rare prey types and therefore the fitness of each form (morph) is inversely related to its frequency in the population. Negative frequency-dependent selection can also occur through sexual selection if one sex favours novel or rare members of the opposite sex.

Other examples of colour polymorphisms occur when individuals match different environmental backgrounds or mimic different unpalatable species. Light conditions can have a role in the evolution of colour polymorphisms; for example, the hunting success of colour morphs of the barn owl _Tyto alba_ depends on whether the night is moonlit or dark. Or more simply, local colour polymorphisms might be evident if individuals from different coloured populations disperse into each other's area. Lastly, and perhaps less likely in nature, two colour forms might be maintained if their underlying genes are linked to other genes that have higher fitness when carried as heterozygotes (individuals having two differing copies of a relevant gene)[5–8].

Now comes a twist, but one related to a

frequency-dependent phenomenon. To explain within-sex colour polymorphism in hummingbirds, Falk and colleagues borrow an intriguing idea — long suspected, but currently languishing in the mimicry literature — that species mimic each other to gain access to resources. The authors reframe this hypothesis as an example of within-species variation. This long-standing idea is that a convergence in form between different species is used to gain access to resources through competitive mimicry, such that smaller and less-competitive species mimic the appearance of larger, more-dominant species[9]. For example, a smaller species of woodpecker or toucan resembles the appearance of another larger woodpecker or toucan living in the same area to get priority access to food sources. This constitutes a different sort of dishonest mimicry signalling from the textbook examples of a palatable prey resembling an unpalatable organism (Batesian mimicry) or two unpalatable prey types resembling each other (Müllerian mimicry).

Falk and colleagues' research focused on *Florisuga mellivora* (Fig. 1), a hummingbird in which all males and around 20% of females sport an iridescent blue head and a white neck and tail (called androchromic), whereas 80% of females are non-ornamented (termed heterochromic) with green plumage, a speckled throat and dark tail. Androchromes (of unknown sex) initiate more chases than their peers such that members of the same species and other hummingbird species avoid them[10]. This might give androchrome females better access to food compared with heterochromic females.

Although this suggests that some females are mimicking males, another explanation is possible. It could be that androchrome males and females are simply more aggressive and territorial and that they signal this through gaudy plumage, whereas heterochrome females are not territorial. Such examples of aggression are seen in lizards and fish. However, after taking a variety of measurements (morphometric and standardized colour data) for adult hummingbirds at a field site in Panama, Falk *et al.* found that birds' power bursts (weights lifted in flights under controlled conditions), wing load (mass in flight by wing area), wing shape and body size did not differ between androchrome and heterochrome females. By contrast, males had greater physical strength and agility (greater burst power, lower wing loads and larger wing lengths, widths, area and tapering) than was the case for both types of female.

Falk *et al.* also assessed feeding strategies by putting out a grid of sugar feeders, and followed the movements of individual birds using a tracking method (PIT tags and a radio-frequency identification system). Both types of female bird increased their use of space (number of feeders visited) as their feeding frequency rose, whereas males reduced their feeder-space use as their feeding frequency increased, implicating territoriality. In conjunction with a previous study[10] indicating that androchrome females were subject to less aggression than heterochrome females were, the findings by Falk and colleagues suggest that androchrome females can fool members of their own species about their ability to defend food resources.

Mimicry in just one sex is not unusual in nature, but it usually manifests as males mimicking females to get between courting partners, as is the case, for example, in Atlantic salmon (*Salmo salar*)[11]. But for hummingbirds, and perhaps several other species, female mimicry of males is maintained because of extra access to resources. In classic Batesian mimicry, deception is frequency dependent because mimics gain more when they are rare. Similarly, if androchrome females became common, they might be challenged by heterochrome females so often that the flamboyant plumage, which probably incurs some developmental costs, would be unprofitable.

This study adds to a growing list of unexpected explanations for the evolution of coloration that have come to light because of current intense research in this area. These examples include using iridescence as camouflage[12], ultra-black scales that make deep-sea fish seem invisible[13] and contrasting wing surfaces that reduce in-flight collisions of large birds[14]. Falk and colleagues' work also provides an alternative explanation for the sex-linked deceptive mimicry in swallowtail butterflies[15] highlighted by the naturalist Alfred Russel Wallace (who, alongside Charles Darwin, proposed natural selection). Females of some of these species, but not males, are polymorphic to mimic different species that have an unpleasant taste to predators. Wallace would have surely loved this parallel explanation from birds.

Tim Caro is in the School of Biological Sciences, University of Bristol, Bristol BS8 1TQ, UK, and at the Center for Population Biology, University of California, Davis, USA.
e-mail: tmcaro@ucdavis.edu

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