other planetary systems to favour one model in particular, we must keep all alternatives in mind as we pursue our understanding of planet formation. ■

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Evolutionary biology

Seeing red in speciation

Michael J. Ryan

Mating patterns in sticklebacks have been investigated for over fifty years. The latest studies show how a complex interplay between males, females and the environment can contribute to the formation of new species.

Speciation and sexual selection are central processes in evolution. Speciation occurs when divergence between organisms becomes such that they cannot produce viable offspring, and so constitute different species. Sexual selection results from female preferences for certain male attributes in choosing a mate, and promotes the evolution of extreme male appearance and behaviour during courtship.

How might these processes interact? On page 944 of this issue[1], Janette Boughman describes how she has addressed the question by studying sticklebacks in Canadian lakes. She shows how sexual selection can drive speciation through the complex interplay between ambient light levels in different parts of the lakes, male coloration, and female sensitivity to light in different parts of the spectrum.

Mate preference is important in both speciation and sexual selection[2], but it gained wide recognition only with the appearance of papers by West-Eberhard[3] and Lande[4] some 20 years ago. These papers suggested that sexual selection can cause divergence of mating preferences among populations so that individuals from nearby populations perceive one another as 'different' rather than 'the same'. If so, sexual selection could generate the reproductive isolation that contributes to bringing about new species. When viewed by one another as different, individuals don't reproduce; this is reproductive isolation.

ERNIE COOPER

Figure 1 **Courting couple — a male stickleback in red mating livery makes a pass at a female. Inset: a male with black mating coloration.**

Why would populations come to differ in their mate preferences? One possibility is 'sensory drive'[5], a change in the female perception system that could initially be unrelated to mate choice but could have an effect on it. Although sexual selection generally promotes the evolution of conspicuous male traits, 'conspicuous' is defined by the female's perceptual system and the context in which she perceives it. We know that differences among habitats can influence signal efficacy, one example being the way in which ambient light influences the conspicuousness of visual signals[6].

In the case of the sticklebacks studied by Boughman[1], the signal sent from male to female is throat colour (usually red), which becomes more intense during the mating season. This feature has made sticklebacks the subject of numerous studies in behavioural ecology[7] and evolution[8], ever since Tinbergen[9] observed that their response to red is so strong that a stickleback in an aquarium will swim at red postal trucks driving past on the road outside.

For her study, Boughman predicted the following: first, that male signals are transmitted in a habitat-specific way; in this case the red throat is more conspicuous in some parts of a lake than others because of the ambient light. Second, she predicted that the female's perceptual sensitivity adapts to local conditions, and third, that male signals match female sensitivity. If these three conditions are met, the idea is that mate preferences are then likely to diverge in different populations and that divergence will contribute to the reproductive isolation of those populations.

To test her predictions, Boughman studied six populations of sticklebacks from four lakes in British Columbia. In these populations, male mating coloration varied from red to black (Fig. 1). She found that males appeared redder, at least to her, in habitats with less red light. (This is one of the drawbacks of the study. More quantitative measures of the area and reflectance of red coloration would have allowed direct quantification of its conspicuousness to females; see, for instance, ref. 10. Subjective rankings of colour are based on reflectance as filtered by a human visual system, presumably under very different light conditions to those experienced by sticklebacks.)

To measure the sensitivity of female sticklebacks to wavelength, Boughman used experiments in which the intensity of monochromatic light is varied to determine the threshold at which a fish ceases to follow rotating black and white stripes. She found that females in areas with less red light, such as where the water is 'tea-stained' in colour rather than clear, are more sensitive to red light, and that male signals are matched to female sensitivity. So there is the predicted three-way correlation between sensitivity, light and colour.

Cause and effect, though, are not clear. As Boughman says, male coloration could have evolved to match female spectral sensitivity, as suggested by one hypothesis (the 'sensory exploitation' hypothesis[11]). Or both colour and sensitivity could have evolved independently to match ambient light levels. A final possibility, which Boughman does not mention, is that the contrasting colours could initially have evolved in the males, with females then developing their spectral sensitivity to match the signal. Only an analysis of evolutionary relationships could distinguish between these possibilities.

Does divergence in male traits and female preferences contribute to reproductive isolation? In this case it does. Boughman found that females that are more sensitive to red also prefer redder males within their population, and that the probability of spawning between populations is related to the degree of divergence in male redness and female preference for red. Unlike in some other studies of sticklebacks[10], however, we do not know whether the mate preferences between populations are due to overall brightness, to true colour alone, or to the contrast of colour with the background or with other body parts.

Much of the study of speciation can be distilled into trying to understand how reproductive isolation happens[12]. As Boughman has shown, her approach can provide detailed knowledge of how reproductive isolation comes about in sticklebacks. Future studies might tackle the intriguing subject of the neural and genetic mechanisms underlying the changes in spectral sensitivity that mediate this female preference. Is preference determined by the absorption spectrum of the photopigment that is sensitive to long wavelengths[13]? If so, one might be able to identify changes in the structure of the pigment molecules that account for such differences, and thus be able to identify one of the genes that contribute to speciation in sticklebacks (as has been claimed for the fruitfly *Drosophila*[14]).

Alternatively, the differences in female preference could be related to the number of long-wavelength-sensitive cones in the retina, or to the proportion of spectrally opponent neurons in the visual system. Furthermore, mathematical models of how visual scenes are analysed, some of which have been applied to sticklebacks[10], could offer further insights into why not all females see red in the same way. All in all, sticklebacks may be outstanding subjects for investigating the biology of speciation in general. ■

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Condensed-matter physics

Nickel probes superconductivity

Michael E. Flatté

Magnetism usually destroys superconductivity, but a magnetic nickel atom inserted into a high-temperature superconductor has surprisingly little effect on its local environment.

The unusual properties of superconductors arise from the coherent behaviour of electrons when they flow together in pairs. Two key properties for electrons in a superconductor are their negative charge, which normally keeps them apart, and their spin, which can be thought of as a tiny bar magnet, pointing either up or down. If electrons of opposite spin overcome their mutual repulsion they can form Cooper pairs and flow without resistance — the essence of superconductivity. One useful way of exploring the properties of a superconductor is to alter this pairing coherence.

Applying a magnetic field disrupts the pairing of electrons, and as a result, diminishes the energy required to break Cooper pairs, thereby reducing the 'transition temperature' at which the material becomes superconducting. A sufficiently large magnetic field can even disrupt pairing to the point where the material ceases to be superconducting. Adding a single magnetic atom to a superconductor creates a similar effect, although the perturbation to the superconductor is localized near the magnetic atom. On page 920 of this issue, Hudson *et al.*[1] describe the effect of adding a magnetic nickel atom to a high-temperature superconductor. Nickel weakly perturbs its local environment in the superconductor, suggesting that this impurity could be used as a non-invasive probe of superconducting behaviour on the nanoscale.

In a superconductor, pairing coherence occurs when a free electron 'grabs' an electron of opposite spin, forming a Cooper pair and leaving behind a positively charged 'hole' in the electron sea of the superconduc-

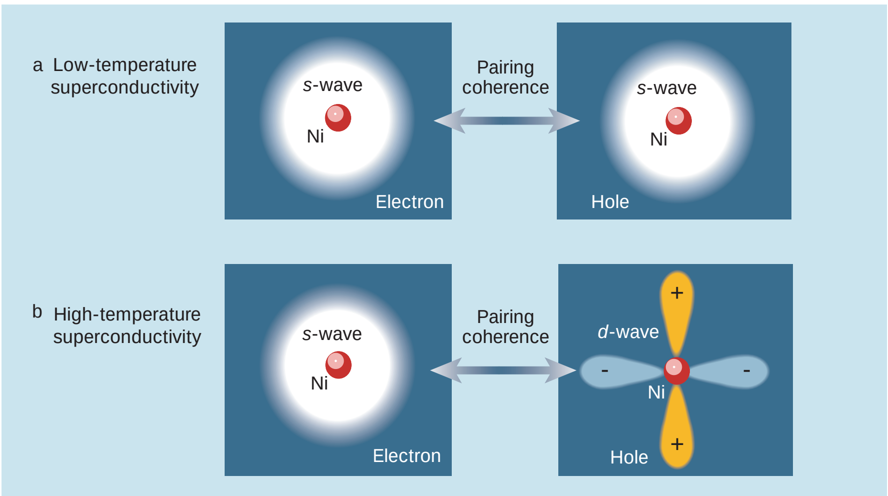

Figure 1 **Quasiparticles in a superconductor. An electron bound to an impurity atom, such as nickel (Ni), mixes with a hole, to form a low-energy Bogoliubov quasiparticle.** a, **In a conventional superconductor, like niobium, the symmetry of the wavefunction of the electron component and of the hole component are identical. They both have *s*-wave (spherical) symmetry.** b, **In a high-temperature superconductor, like the one studied by Hudson *et al.*[1], the electrons that form the Cooper pairs rapidly revolve around each other, to keep their distance and lower their mutual repulsion. The *d*-wave nature of their angular momentum is reflected in the *d*-wave symmetry of the hole component of the associated quasiparticle.**