Seeing red by accident?

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Lars Chittka has found that chance processes could, in part, govern the colour vision of island bees and ultimately aid evolutionary adaptation.

For some reason, scientists abhor chance. Einstein, for example, was uncomfortable with Heisenberg's uncertainty principle, countering that 'God does not play dice'. Likewise, biologists often assume that evolving organisms only rarely stray from a linear path towards evolutionary optimisation and that evolutionary chance processes play little or no role in how the behaviour and sensory systems of animals evolve.

There is an awe-inspiring diversity in animal sensory systems. Take an insect's sensitivity to ultraviolet and polarised light, or the ultrasonic hearing abilities of bats, or the magnetic compass of birds, or the infrared sensitivity of fire beetles. The list goes on and on. Undoubtedly, these are all spectacular adaptations to these animals' particular modes of operation. But nature does not guide adaptation like an almighty creator. Even if God doesn't play dice, evolution does so extensively. When and where mutations occur in the genome, the particular genes you have been allocated from your parents and which genes spread in a population, all depend to some extent on chance.

In terms of sensory systems, some examples for the importance of chance processes are well known for human vision. On the tiny Micronesian island, Pingelap, 75 of the 700 inhabitants are totally colour-blind: they entirely lack the cones required to see the world in colour, and have only rods, the types of receptors that other humans use in dim light. This is the result of a classic bottleneck effect. In 1775, the island had almost 1000 inhabitants. It was struck by a typhoon, which reduced the population of the island to only 20 survivors, one of whom was the king. After a few generations, the population was almost back to its pre-typhoon level. Unfortunately, the king was a carrier of the gene responsible for colour blindness and he was particularly fecund. Now one-third of the population carries the recessive gene that is responsible for this defect, and more than 10 percent of the population is fully colour blind. In other human populations, the frequency of this defect is about 1 in 30,000.

But it's not only the harmful mutations that spread with a higher probability in small populations. The likelihood of any mutation spreading and ultimately becoming established in all individuals, is inversely related to population size. Even an advantageous evolutionary innovation is likely to be lost by chance if it occurs in a very large population. So, small populations (especially those on islands) could actually function as a resource for evolutionary innovation, if it weren't for the complication that new variation is also less likely to be generated in a small population. However, perhaps combining the advantages of small populations in spreading new mutations with those of large populations in generating them, could be possible in species that are large as a whole, but are broken up into several smaller populations with limited gene flow between them.

With this in mind, we studied the colour vision system of a common old world bumblebee species, *Bombus terrestris*. This species not only occurs in most locations of continental Europe, but also on all large Mediterranean islands. These various island populations are so distinct in coat colour that they can be mistaken for different species, yet they are entirely

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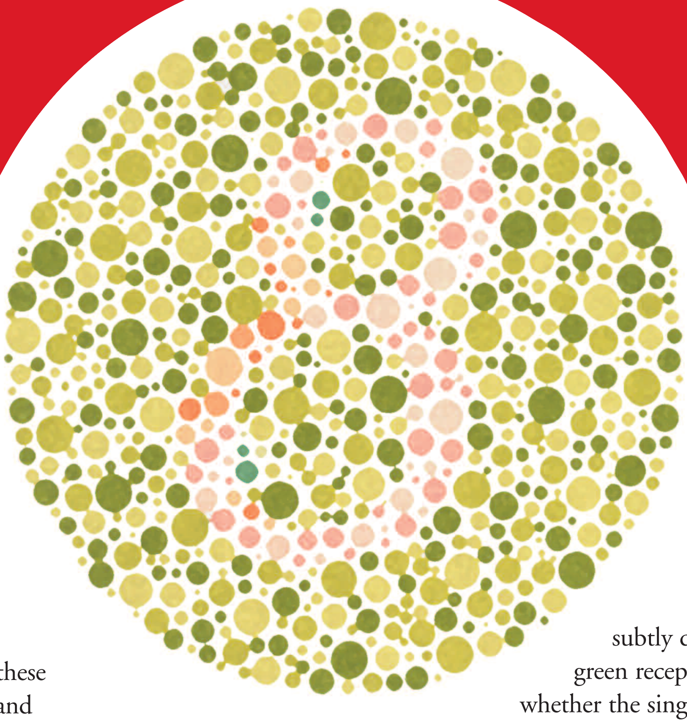

compatible with their mainland cousins.

When studying the innate floral colour preferences of these populations, we were excited to find that some of these island bees, notably those from Sardinia, showed a strong preference for the colour red, a colour that by many textbook accounts, bees should be entirely blind to. Could it be that these Sardinian bees had 'invented' a red receptor that is not shared by any other social bees possessing only ultraviolet (UV), blue and green receptors? Such a red receptor could give bees a fundamental evolutionary edge over nectar-foraging competitors, given that many flowers reflect strongly in the red domain of the electromagnetic spectrum.

There is molecular-genetic evidence that some of these island populations have been exposed to repeated bottlenecks, presumably through drought. In such populations, genetic drift (random changes over generations determine how common certain genes are in a population) may temporarily outcompete selection, so that new genes may spread even if they are adaptively neutral (or even deleterious). An upshot of this could be a degree of tuning of the bee's visual receptors along the electromagnetic spectrum, even if this must be based on several adaptively neutral mutational steps.

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We decided to measure the spectral sensitivity of the photoreceptor cells in the eyes of these island bees and compare them with those from a similar but continental environment (Turkey). Scientists can do this by inserting a microelectrode into a single photoreceptor cell – no small feat when you consider that these cells are about five micrometers in diameter. We illuminated the eye with light of various wavelengths and measured the resulting voltage signal produced by the cell. The results show both populations to have only UV, blue and green receptors, and no specialised red receptors. We did, however, find a small but significant red-shift of the green receptor sensitivity in the island bees. The spectral peak sensitivity in this receptor was shifted by 5 nanometres from 533nm (Turkish bees) to 538nm (Sardinian bees). Being such a small change, we cannot yet be sure whether the gene responsible for the green sensitivity in these receptors has been duplicated, so that there are now two subtly different green receptors, or whether the single green receptor pigment has been slightly shifted to longer wavelengths.

While the population difference in colour preference and the tuning of the green receptor are probably entirely the result of evolutionary chance – as a consequence of small population size or bottlenecks: the range of flower colours visited by different populations of *Bombus terrestris* does not appear to differ and the change in spectral sensitivity might be too small to be of any adaptive significance. The island bees have not yet 'invented' a new colour vision system, but they have perhaps made a first step in that direction.

We need data on the colour vision systems of more populations, and molecular data to examine the numbers and sequences of genes that code for visual pigments, to better understand whether island populations could serve as a resource for sensory innovation. There is a particular urgency to start this research soon: there is a severe danger that the behavioural and sensory differences between bumblebee populations may soon vanish because of the large-scale movement of bumblebees for commercial pollination, with very little concern for preserving fragile island pollination systems. We might not only lose the diversity itself, but also a very valuable natural laboratory for evolutionary biologists interested in how sensory systems and behaviour evolve. ❖

Lars Chittka is Professor for Sensory and Behavioural Ecology at the School of Biological & Chemical Sciences, Queen Mary College, University of London. Email: l.chittka@qmul.ac.uk

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