

can cause mating preferences to evolve as a side effect. One example of this is what is called the good-genes hypothesis. In this model, for example, versions of genes that boost the immune system lead to better health, which enables the males that carry these versions to be more brightly coloured. The females that have mating preferences for the brightest males will pass these good genes, which improve survival, to their offspring, along with the versions of genes for a mating preference for bright males. As selection causes these beneficial immune-system genes to spread, they also drag along the genes that drive the preference for brighter males. This hypothesis is popular among behavioural ecologists, but the evidence in support of it is mixed⁴.

The hypothesis put forward by Muralidhar to explain the evolution of female mating preferences is also based on indirect selection. This model hinges on sexually antagonistic selection — the situation in which a version of a gene that is beneficial when present in one sex is harmful when present in the other sex. Among evolutionary geneticists, there is a growing appreciation of the prevalence of sexually antagonistic selection and its myriad consequences⁵. Imagine a genetic mutation that causes an increase in the redness of both male and female plumage. This mutation might increase male fitness by increasing mating success, but it would decrease female fitness by increasing predation. Therefore, genes that cause females to prefer to mate with redder males will cause their sons from such matings to have high fitness, whereas their daughters would have low fitness. Those two opposing effects on fitness at the population level would offset each other, and, on balance, mating preferences for redder males would be selected neither for nor against.

But could there be an exception to this logic if genes that affect mating preference are inherited in an unusual way? Consider what might happen if such genes are on sex chromosomes.

In mammals and fruit flies, males have two different sex chromosomes (X and Y), whereas females have two X chromosomes. Organisms such as birds and butterflies⁶ have sex chromosomes called Z and W, and the opposite arrangement exists — the males have two of the same type of sex chromosome (Z chromosome), whereas the females have one Z and one W chromosome. A gene that affects mating preference and is located on a W chromosome exists only in females, and never in males. Therefore, a female that has a version of a gene on the W chromosome that causes a mating preference for a trait that decreases male survival will pass that version only to her daughters. If those daughters also receive from their fathers the versions of genes for a trait that is beneficial to females, the daughters will have high fitness, and this W chromosome will spread. These nefarious chromosomes can be described as selfish — they spread regardless of their effect on male fitness.

Muralidhar's mathematical analysis shows

that genes affecting mating preference that are carried by other types of sex chromosome (X, Y and Z) also have evolutionary dynamics that differ from those of genes that affect mating preference but are carried on non-sex chromosomes. But of the four types of sex chromosome, Muralidhar found that it is the W chromosome that has the greatest potential to favour the spread of versions of genes that increase female mating preferences for exaggerated (and harmful) male traits.

Models show what is possible, but only data can reveal whether the possible is a reality. Is there evidence that sex chromosomes harbour genes that affect mating preferences? Muralidhar reviewed the genetics of mating preferences that have been reported for 36 species. In more than half of these species, there is indeed evidence that genes that affect mating preferences are carried on the sex chromosomes. Disappointingly, none of these preferences is linked to the W chromosome, but the number of existing studies available for this analysis is small.

A second opportunity to bring data to bear on this model relates to its prediction that species that have ZW chromosomes should be more prone to evolve female mating preferences for sexually antagonistic traits than those with XY chromosomes. Indeed, some researchers have concluded that species that have ZW sex chromosomes tend to have exaggerated sexual displays more often than do those with XY chromosomes⁷. Muralidhar's work provides a call for more comparative data on the inheritance of mating preferences and the connections between sex-determination systems and sexual ornamentation.

Could this selfish-sex-chromosome

hypothesis explain female mating preferences for vibrant colours, as is the case for the brilliantly coloured male flame bowerbirds (*Sericulus aureus*), which are preferred by the dull-coloured females of that species (Fig. 1)? Perhaps not. Genes that affect colour (and most other traits) tend to have similar effects on both sexes. Thus, females that choose dull-coloured males will have dull-coloured daughters that will survive well. If genes that affect mating preferences are carried on the W chromosome, this would favour the evolution of preferences for dull males.

It seems that some other explanation might be needed for cases such as that of the flame bowerbird. It could well turn out that preferences for different types of male trait evolve by different evolutionary pathways. If so, the decades-old debates over which hypotheses best explain how mating preferences evolve² might ultimately transform into discussions of which mechanisms operate most commonly in certain contexts. ■

Mark Kirkpatrick is in the Department of Integrative Biology, University of Texas, Austin, Texas 78712, USA.
e-mail: kirkp@mail.utexas.edu

1. Muralidhar, P. *Nature* **570**, 376–379 (2019).
2. Kirkpatrick, M. & Ryan, M. J. *Nature* **350**, 33–38 (1991).
3. Basolo, A. L. *Proc. R. Soc. B* **259**, 307–311 (1995).
4. Prokop, Z. M., Michalczyk, Ł., Drobniak, S. M., Herdegen, M. & Radwan, J. *Evolution* **66**, 2665–2673 (2012).
5. Rowe, L., Chenoweth, S. F. & Agrawal, A. F. *Am. Nat.* **192**, 274–286 (2018).
6. Bachtrog, D. et al. *PLoS Biol.* **12**, e1001899 (2014).
7. Reeve, H. K. & Pfennig, D. W. *Proc. Natl Acad. Sci. USA* **100**, 1089–1094 (2003).

This article was published online on 5 June 2019.

MATERIALS SCIENCE

Crazy colour

The formation of microscopic pores and fibrils in polymers under stress — a process called crazing — often preludes material failure. Controlled crazing has now been used to produce an array of colours in polymer films. [SEE LETTER P.363](#)

SEUNG HWAN KO

When a typical transparent, glassy polymer is bent or stretched, partial whitening of the material often occurs just before it cracks or fractures¹. This unpredictable phenomenon is called crazing, and has generally been seen as something to be avoided. But on page 363, Ito *et al.*² report that crazing can be fully controlled, and can be used to endow transparent polymers with colour. Controlled crazing could therefore be developed as the basis of an inkless, high-resolution method for printing colour on various flexible and transparent polymer materials.

Transparent polymers have conventionally been colored by mixing them with pigments, or by printing pigment-containing ink on polymer surfaces. However, transparent polymers can also be colored by producing microscopic structures within the materials — an effect known as structural coloration. Structural colours are frequently observed in nature, for example in butterfly wings³. Ito and co-workers use crazing as the basis for structural colour.

Crazing patterns in polymers form in a direction perpendicular to the applied stress, and consist of interpenetrating, micrometre-scale voids bridged by highly oriented polymer

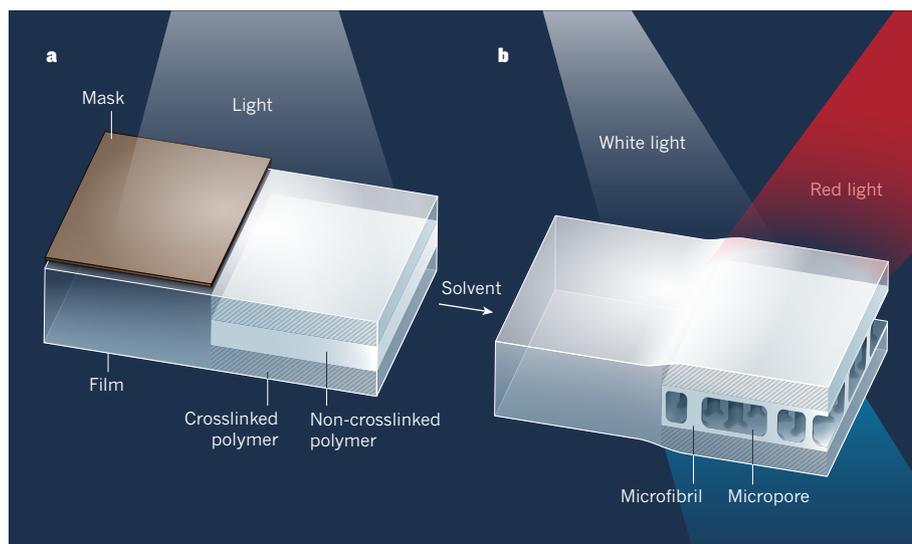


Figure 1 | Inkless colour printing in polymers. **a**, Ito *et al.*² have produced colour images in transparent polymers by shining standing waves of light through masks on polymer films. The light generates alternating layers of crosslinked and non-crosslinked polymers, which causes stress to build in the non-crosslinked layers. **b**, When treated with solvent, the non-crosslinked layers undergo crazing — microscopic pores and fibrils form, releasing the stress. This produces alternating dense and porous polymer layers, which cause the refractive index of the film to vary periodically. White light striking the layered parts of the film therefore reflects in such a way that a particular colour is produced. In principle, any colour can be generated.

microfibrils. The microvoids and microfibrils in uncontrolled crazes vary widely in size, and reflect a broad range of wavelengths of light — which explains why crazes usually look white. Ito and colleagues have demonstrated that, if crazing is controlled to generate porous layers that alternate with compact, non-porous layers, this can reinforce interference of the light reflected from the different layers, thereby producing specific colours.

The authors take advantage of a phenomenon⁴ that controls a polymer's stress field (the distribution of forces within it that balances external forces), and so controls craze generation. When a 'standing wave' light pattern is formed in a light-sensitive polymer film, crosslinks between the polymer molecules form selectively in layers, which are separated by other layers in which no crosslinking has occurred (Fig. 1); this causes tensile stress to build across the non-crosslinked layers. The authors exposed such layered films to a solvent, which releases the stress by causing crazes to form in the non-crosslinked layers. The resulting films therefore contained alternating dense and porous layers, generating periodic variations in the refractive index of the material. Light shining on the films is reflected at successive craze layers, leading to interference effects that cause structural coloration.

Ito *et al.* carried out a series of experiments to investigate the physical mechanism of, and the optimum conditions for, periodic craze formation in various transparent polymer films. The microvoids in crazes are, effectively, tiny cracks, and the authors conclude that the formation of the cracks must be controlled to control the crazing process. Their method is therefore a

real triumph: crack-formation processes are much more complex and difficult to manage in amorphous materials⁵ (such as polymer films) than in crystalline ones⁶, because the microscopic structures of amorphous materials are more random.

The authors report the production of only a few colours in their work, but a wide range should, in principle, be generated by carefully adjusting the spacing of the alternating layers. The spacing can, in turn, be controlled by

“This simple, inexpensive coloration method is based on a phenomenon that was previously regarded as useless.”

altering several factors: the wavelength of light used to produce the layers and the amount of time used to irradiate the films; the type and molecular weight of the polymer; the initial thickness of the film; the type and temperature of the solvent used to produce crazing; and the period of time for which the film is immersed in the solvent.

The authors are not the first to observe this kind of structural coloration in a multi-layered transparent film. However, most research in this area has involved complex and expensive methods in which alternating layers of films are deposited on a substrate in a vacuum (see ref. 7, for example). By contrast, Ito and co-workers have developed a simple, inexpensive method based on a phenomenon that was previously regarded as useless. Indeed, previous studies of crazing have concentrated mostly on finding ways to inhibit or

prevent it^{8,9}, rather than to control it.

The authors demonstrate that craze control can be used for inkless colour printing at incredibly high resolution (up to 14,000 dots per inch). The resolution of conventional colour-printing methods, such as inkjet printing, is generally just 600–1,200 dots per inch because of limitations associated with the size of the ink droplets that can be generated and the effects of ink spreading. Another advantage of Ito and colleagues' technique is that the printing time will not depend strongly on the size of the substrate, because it is a parallel process (the whole pattern is printed into the film at the same time), whereas conventional inkjet printing is a serial writing process that takes considerably longer to print large areas.

The impact of this work is not limited to the coloration of transparent polymer materials — it will also enhance our understanding of crazing more generally. For example, the crazing described by Ito *et al.* occurs in the out-of-plane direction (the layers stack up in the direction of the film's thickness), rather than in the plane of the film, as is normally observed in polymers under stress. It is thus an intriguing phenomenon that deserves further study. It will also be interesting to explore the mechanical and electrical properties of controlled crazing.

The surprisingly simple nature of the authors' method means that it could easily be adapted for use by currently available technology for colorizing polymers. However, as with any new technology, several hurdles will need to be overcome. The authors' process is largely limited to a narrow set of operating conditions and certain material combinations, so its general applicability to other materials remains to be seen. Further work exploring the physical mechanism involved in detail might reveal how the method could be applied to any polymer material. In the meantime, craze control will probably find exciting applications beyond inkless colour printing in a transparent polymer, such as in electronic devices and sensors. ■

Seung Hwan Ko is in the Department of Mechanical Engineering, Seoul National University, Gwanak-gu, Seoul 08826, South Korea.

e-mail: maxko@snu.ac.kr

- Swallowe, G. M. *Mechanical Properties and Testing of Polymers* (Springer, 2010).
- Ito, M. M. *et al. Nature* **570**, 363–367 (2019).
- Vukusic, P., Sambles, J. R., Lawrence, C. R. & Wootton, R. J. *Proc. R. Soc. Lond. B* **266**, 1403–1411 (1999).
- Henderson, C. in *Encyclopedia of Microfluidics and Nanofluidics* (ed. Li, D.) 2073–2079 (Springer, 2008).
- Kim, M., Ha, H. & Kim, T. *Nature Commun.* **6**, 6247 (2015).
- Nam, K. H., Park, I. H. & Ko, S. H. *Nature* **485**, 221–224 (2012).
- Kolle, M. *et al. Nature Nanotechnol.* **5**, 511–515 (2010).
- Kim, S. Y., Kim, S. H., Pak, S. Y. & Youn, J. R. *J. Appl. Polym. Sci.* **125**, 3029–3037 (2012).
- Tervoort, T. A. & Govaert, L. E. *J. Polym. Sci. B* **42**, 2066–2073 (2004).