Commentary

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# False colour photography reveals the complexity of flower signalling. A Commentary on: 'A bee's eye view of remarkable floral colour patterns in the Southwest Australian biodiversity hotspot revealed by false colour photography'

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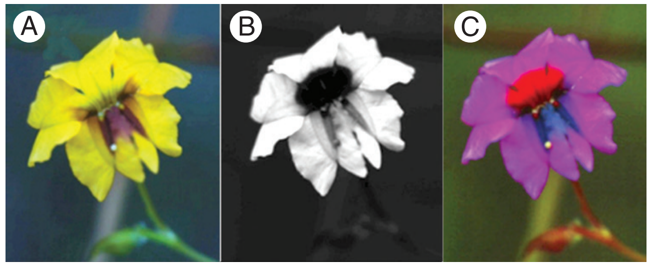


FIG. 1. Digital photographic images showing the various spectral components of the pattern displayed by the flowers of *Velleia trinervis* (typical collora length 9–13 mm) using the method given by Lunau *et al.* (2021). (A) Digital, red, green and blue (RGB) image as perceived by human colour vision. (B) UV reflectance component of the same flower when imaged through a specialized UV-transmitting filter. (C) False colour representation integrating the UV-, BLUE- and GREEN-component channels of images B and A, respectively.

One of the joys of botanists, gardeners, photographers and the general public is that flower displays can present a dizzying array of patterned colours. Whilst such displays are often enthralling to human observers with our blue-, green- and red-sensitive trichromatic vision (Fig. 1A), humans are not the biological agent that promoted the evolution of such colour complexity (Dyer *et al.*, 2021), and thus flowers may have very different colours and patterns when considering pollinator vision (Fig. 1B, C). In the past two decades, botanists have thus shifted from describing floral colours based on human visual comparisons of samples using reference colour charts, to embrace the use of spectrometers to obtain an observer-independent spectral signature describing colour information (van der Kooi *et al.*, 2019). These techniques have shed light on the complexities of plant community assembly by considering competition or facilitation to attract animal visitors as they perceive the world (Kemp *et al.*, 2019; Garcia *et al.*, 2020). Whilst spectrometers remain the gold standard for the precise quantitative appraisal of flower colours, this method remains limited to point measurements of small areas. This limitation makes it challenging to obtain a holistic view of the complex flower patterns that an animal observer might perceive when foraging.

In this issue of *Annals of Botany*, Lunau *et al.* (2021) embraced this challenge by employing digital false-colour imaging to map flower colours from Western Australia. Australia is an important comparative study site for understanding flower evolution due to its geological isolation as an island continent, and well-documented evidence that flower colours are signals that have evolved due to biotic pollination (Dyer *et al.*, 2012; Dalrymple *et al.*, 2020). Furthermore, its native plants frequently reflect UV patterns to enhance signalling to bees (Dyer, 1996). In their new study, Lunau *et al.* (2021) employed a specially modified UV-sensitive digital camera fitted with a fused-quartz lens to capture two-dimensional information reflected from the entire flower surface. They then used digital false-colour imaging techniques to translate the spectral signals as might be seen by a pollinator into a biologically useful visual representation that we can interpret. This method employed waveband-specific light filtering and enabled the translation of the UV-, BLUE- and GREEN-component camera channels that allow bee vision to be displayed as a mixture of blue, green and red colours as perceived by typical human trichromatic vision.

Lunau *et al.* (2021) surveyed 55 species from four plant communities and 16 families, frequently observing complex floral signals in terms of colour patterns, floral guides, stamens, and pollen- and stamen-mimicking structures. The striking images show that colour information is often far more complex than the story told by just considering the primary petal colour of a flower, or a typical colour photograph taken in the field. One of the best known UV floral patterns is a bullseye effect in which the outer petals reflect significant amounts of UV whilst the inner flower parts absorb UV and create a salient target for landing bees (fig. 1A–C in Lunau *et al.*, 2021). Several but not all yellow flowers in the Lunau *et al.* (2021) survey had such bullseye patterns, showing that a human colour such as 'yellow' might actually appear as completely different colours to biologically relevant pollinators.

In their paper, Lunau *et al.* (2021) show the amazing floral guides of *Labichea lanceolata* (their fig. 2D), *Lotus subiflorus* (fig. 3A), or the floral patterning of bird-pollinated *Kennedia rubicunda* (fig. 5D) and *K. prostrata* (fig. 5F). The false colour photographs produced by Lunau *et al.* (2021) reveal much additional information not available in conventional photographs, showing us that floral colour patterning is often more salient for pollinators. This is important as many insect pollinators such as bees are known to be attracted to colourful edges, and floral nectar guides are a key feature in interpreting how bees interact with flowers (Lunau, 1992). The technique for surveying flowers with false colour imaging thus has potential value for both taxonomic classification, as well as informing functional and behavioural studies of how various flower traits may have evolved as potential signals.

Perhaps due to the difficulty of objectively quantifying the spatial component of flower patterns from point samples, the role of patterning in visual communication between plants and animals remains understudied. Birds with high-resolution vision are likely to be capable of discriminating complex flower patterns made up of different elements (Caves *et al.*, 2018), information that they can potentially use to drive decisions in natural environments (Spottiswoode and Stevens, 2010). The presence of markings on the petals of bird-pollinated flowers in Lunau *et al.* (2021) such as *K. prostrata* (their fig. 5F) suggests that these pattern elements may play a role in visual communication. Likewise, by improving our understanding of flower patterns using false-colour imaging, it may be possible to reformulate and test new hypotheses regarding the effect of the multiple spatial elements of flowers on the behaviour of pollinators. An additional advantage of the use of photographic images is the potential to obtain two-dimensional arrays of calibrated spectral information (Garcia *et al.*, 2013) and assess how understudied factors such as flower pigment density influence colour signals and pollinator behaviour in complex environments (Garcia *et al.*, 2014, 2020; van der Kooi *et al.*, 2019). Exploring the world as experienced by pollinators via new photographic techniques thus promises to open up new avenues of research to improve our understanding of flower pollination, and the success of angiosperms.

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