Commentary

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Selective attraction in bird-pollinated flowers. A commentary on: 'Red flowers differ in shades between pollination systems and across continents'

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Signals from flowers attract pollinators, usually with a mutualistic relationship giving reciprocal benefits. However, this relationship carries with it many pitfalls, including various kinds of deception in flowers and illegitimate visits of flower visitors or flower antagonists (van der Kooi *et al.*, 2019). Flowers do not benefit from attracting as many flower visitors as possible, but select among potential flower visitors, since visual, tactile and olfactory floral cues can selectively allure pollinators and distract floral antagonists including pollen thieves, nectar robbers and florivores. That the exclusion of antagonistic flower visitors is not a local phenomenon of a few species is shown by Chen *et al.* (2020), who provide evidence that the exclusion of bees from bird-pollinated flowers via a private colour channel is a global phenomenon.

The predominance of red flowers among bird-pollinated flowers has puzzled researchers over decades (Lunau *et al.*, 2011). The first attempts to solve this puzzle were focused on the pollinators, i.e. the response of birds to the red flowers. However, spontaneous choice experiments with hummingbirds were unable to demonstrate innate preferences for red flower colours. The need of migratory hummingbirds to find reliable nectar sources on their migratory routes seemed to explain the advantage of only one single identification cue, whereby migrating hummingbirds may rely on previous experience with red flowers.

More recent studies provide evidence that antagonistic flower visitors also drive the evolution of specific flower traits if acting as floral filters based on floral morphological, chemical and visual cues. In the case of red coloration of bird-pollinated flowers, bees as less effective pollinators are thought to be the main driving force. The deviant visual systems of bees and birds support these assumptions, as bees, but not birds, lack a photoreceptor type sensitive to red wavelengths (Altshuler 2003). There is only little lab-based experimental evidence from colour choice tests in hummingbirds and orchid bees that indeed bees preferred red colours, with an additional secondary reflection peak in the UV range of wavelengths, whereas hummingbirds did not show any preference (Lunau *et al.*, 2011). False colour photography in bee view demonstrates the striking difference of red flowers with and without additional reflection in the UV range of wavelength to bees (Verhoeven *et al.*, 2018; Fig. 1). Field tests have been done only with two

Fig. 1. Colour photo (first column A and D), UV photo (middle column B and E) and composed false-colour photo (right column C and F) in bee view of red bird-pollinated *Swainsonia formosa* (upper row A and C) and red bee-pollinated *Chorizema rhombeum* (lower row D and F). In the false-colour photo, the UV channel is shown as a blue channel, blue as green, green as red, and the red channel is discarded in order to meet bees' spectral sensitivities of their photoreceptor types. For more detailed information about the digital photo technique, see Verhoeven *et al.* (2018). Photo credit: Klaus Lunau.

colour morphs in one species, *Costus arabicus* (Bergamo *et al.*, 2016), and one plant community, rupestrian savannah (de Camargo *et al.* 2019), both in Brazil. In the framework of the bee-avoidance hypothesis and the bird-attraction hypothesis, Chen *et al.* (2020) elegantly demonstrate that the selective attractiveness to birds and sensory exclusion of bees as documented by the spectral reflectance properties of red flowers occurs in the Neotropics, Palaeotropics and Australis.

The approach of Chen *et al.* (2020) is focused on comparison between the spectral reflectance curves of 130 red flowers and calculated colour parameters to show that bee-pollinated red flowers differ from bird-pollinated red flowers in terms of conspicuousness to bees and, to a lesser degree, also to birds. They show that red flowers are more conspicuous to birds than to bees and that red bird-pollinated flowers are inconspicuous to bees due to the absence of a secondary reflection peak at shorter wavelengths.

The condensed information of the comparative study of Chen *et al.* (2020) on the meaning of red bird-pollinated flowers for the sensory exclusion of bees across continents creates new grounds for follow-up studies. Future research should focus more on the diversity of birds, bees and the flowers they visit. Some birds are territorial and thus do not need to detect flowers every few seconds, but simply to revisit flowers which they know already. Not all bees may be similarly competitive for bird-pollinated flowers as orchid bees which only occur in the Neotropics, and not all bees' visual capabilities may be well represented by the spectral sensitivity of bumble-bees. The phenomenon of sensory exclusion via colour has also been proposed for bird-pollinated white and yellow flowers and may rely on different colour parameters.

Colour vision is a complex study system, and is even more confusing due to the use of different terms in different fields of science. We are just beginning to understand colour vision in birds (Stoddard *et al.*, 2020), but the study of Chen *et al.* (2020) implies assumptions about colour preferences, and the role of colour purity and colour contrast for flower detection that need validation from behavioural tests. The Chen lab equates the conspicuousness for birds with higher chromatic contrast between a flower and its background, but ignores the diversity of natural backgrounds for flowers, i.e. sky, tree bark, green leaves or bare soil. Although the results of Chen *et al.* (2020) provide clear evidence that pollination by birds is associated with highly saturated flower colours with reflectance in the red waveband part only, this conspicuousness for birds calculated with colour vision models should not be confused with innate foraging preferences of birds for these colours *per se*. Hitherto, it is still unknown whether non-primate animals have a perceptual dimension of spectral purity and, furthermore, that this drives the evolution of flower colours, or that birds rely on one colour parameter only for flower detection. A better understanding of avian psychophysics, neural processing and foraging preferences with regard to colours is thus required before a definitive answer can be found to the question of whether the avoidance of bees is the only crucial parameter in the evolution of red colours in bird-pollinated flowers, or if both bee avoidance and the innate enhanced attraction to birds are key players.

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