

## Letter

# Is floral iridescence a biologically relevant cue in plant–pollinator signalling? A response to van der Kooi *et al.* (2014b)

A recent paper by van der Kooi *et al.* (2014a), entitled ‘Iridescent flowers? Contribution of surface structures to optical signaling’, has triggered debate about floral iridescence. Here, we summarize the primary issues, and reiterate our earlier point that more data are required before the significance and biological relevance of this phenomenon can be evaluated.

## Are any flowers iridescent?

van der Kooi *et al.* (2014a) presented optical analyses of the petals of six species of angiosperms. They investigated the flowers of 50 plant species (by scanning electron microscopy) and then selected four species with different surface structures (plus a further two in the Supporting Information) for optical characterization. Subsequently, van der Kooi *et al.* (2014b) repeated measurements of one of the species (*Hibiscus trionum*) and presented photographs of two of the species from their earlier paper (van der Kooi *et al.*, 2014a), plus a further two previously unreported species. They did not record as iridescent any of the eight flowers that they optically characterized and/or photographed.

By contrast, we presented optical characterization and photographs of *Hibiscus trionum* (taken in the laboratory, in daylight, with no flash), which we showed to be visibly and measurably iridescent, with an associated regular surface structure termed a diffraction grating in the central part of the flower (Vignolini *et al.*, 2014).

Although the distribution of floral iridescence within the 300 000 species of angiosperms remains to be explored (Vignolini *et al.*, 2014), this phenomenon is likely to be relatively uncommon, hence the apparent lack of records before Whitney *et al.*’s (2009) paper. Van der Kooi *et al.* (2014a,b) did not record floral iridescence in a sample of eight species. We are currently exploring this distribution in a phylogenetic context; so far we have identified iridescent flowers infrequently distributed across all major angiosperm groups.

In *Hibiscus trionum*, we found the same measurable iridescence effect in the three independent lines we investigated – our laboratory stock sourced from Chiltern seeds ([www.chilternseeds.co.uk](http://www.chilternseeds.co.uk)), the line held by the Cambridge University Botanic Garden (maintained as selfed seed from germplasm supplied by

Cluj-Napoca Botanic Garden in 1996), and a native New Zealand line grown from seed of Auckland Museum Herbarium voucher AK253689 (kindly supplied by Brian Murray). Our usual laboratory growth conditions are described in Vignolini *et al.* (2014), and the flower also develops well outdoors in sheltered glasshouse bays of the Cambridge University Botanic Garden (a relatively dry temperate habitat). The difference between our results and those of van der Kooi *et al.* (2014a,b) on this species could be due to one (or more) of several possible factors, but we currently lack details of their seed source or growth conditions to better resolve these discrepancies. (1) As they propose, they could be working with a distinct genetic lineage that lacks iridescence; the flower photographed in van der Kooi *et al.* (2014b) does appear morphologically distinct from our lines. (2) Van der Kooi *et al.* (2014a,b) may lack access to fully developed specimens, since the flower of *H. trionum* only opens fully in optimal growth conditions. (3) There could be a temporal effect, because the flower of *H. trionum* lasts for only a few hours on the plant, and the iridescent effect deteriorates rapidly when the flower wilts after removal.

Whatever the explanation for the lack of iridescence recorded by van der Kooi *et al.* (2014a,b), the photographs and optical measurements presented in Vignolini *et al.* (2014) demonstrate, unequivocally, that some flowers are iridescent.

## Is floral iridescence of significance in plant–pollinator signalling?

We are unable to support van der Kooi *et al.*’s (2014a,b) contention that ‘floral iridescence acting as a signalling cue to pollinators is presently untenable’. At present, we know two things about petal iridescence and pollinator behaviour. First, bumblebees can distinguish between the optical signals arising from a replica of an iridescent petal surface (obtained by casting the surface of the petal in a soft mould and reproducing the structure with optical epoxy) and those from an otherwise identical replica of a noniridescent petal surface. Second, they can be trained to use the signals arising from the iridescent surface as a cue to identify rewarding flowers (Whitney *et al.*, 2009). In assessing the potential role of animal iridescence as a signal (e.g. as part of a mate-attracting or status-determining display on a beetle or a bird), scientists usually apply two criteria – visibility to target animals, and presence on those parts of the body used in displays (and absence from other parts of the body or from nondisplaying individuals (such as juveniles or females)) (e.g. Vulinec, 1997; Loyau *et al.*, 2007; reviewed by Doucet & Meadows, 2009). Likewise, the optical signal produced by the surface structure of iridescent *Hibiscus trionum* is visible to bees, and present only on the adaxial surface of the petal. While some petals have additional roles in protecting the bud, the bud of *H. trionum* is protected by a hairy calyx while the

delicate, showy petals are ephemeral and only displayed at floral anthesis – their primary function is the attraction of pollinators.

Van der Kooi *et al.* (2014b) commented that for a floral signal to influence pollinator foraging over more than a few centimetres, it must be several millimetres in size. We note that the iridescent colour in *Hibiscus trionum* overlies the red pigmented portion of the petal. The blue structural colour and the red pigment-based colour will therefore be visible over the same distances. Many flowers produce patterns of pigmentation in similar size ranges, and many of these have been shown previously to influence pollinator foraging (Waser & Price, 1983, 1985; Johnson & Midgley, 1997; Eckhart *et al.*, 2006). Indeed, studies have also shown that pigimentary patterns on a much smaller scale, such as venation patterns, petal spots, and bulls-eye patterns of 2 mm diameter, can influence pollinator behaviour (Lunau *et al.*, 2009; Hansen *et al.*, 2012; Whitney *et al.*, 2013). There is no reason to suppose that structurally-derived colour signals will influence animal behaviour to a lesser extent than pigment-derived colour signals.

In conclusion, we reiterate that further integrated studies using a range of model and real flowers in controlled and natural environments will be important in defining with precision the role (if any) of floral iridescence in pollinator signalling. We look forward to further scientific debate on this topic after such data are published. Before such data are available, it is reasonable to hypothesize that this measurable optical signal (visible both to the human and bee eye, present at the same scale as pigment colouration, and present only on the petals, an organ whose primary function is in pollinator attraction) has a role in plant–pollinator signalling.

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