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# Comment on “Floral Iridescence, Produced by Diffractive Optics, Acts As a Cue for Animal Pollinators”

Nathan I. Morehouse\* and Ronald L. Rutowski

Whitney *et al.* (Reports, 2 January 2009, p. 130) investigated the mechanism of iridescence in hibiscus and tulip flowers and suggested that bumblebees are able to use this iridescence as a pollination cue. However, their study failed to isolate iridescence from other coincident visual cues, leaving open questions regarding the importance of iridescent stimuli in foraging-based associative learning in bumblebees.

In recent years, behavioral ecologists have sought to improve our understanding of the role that complex optical phenomena play in visual signaling (1–3). Color signals produced by structural mechanisms have been of special interest because of the unique optical properties they often exhibit, including distinctive polarization, high saturation, and iridescence (4, 5). However, when experimentally evaluating whether complex optical features of a visual signal serve as behavioral cues, researchers must disentangle the optical phenomenon of interest from other, less complex cues. Doing so convincingly can be difficult, and in our estimation this challenge has not been met in two recent, high-profile articles (1, 2). Our concern is that communicatory importance may have been attributed to complex optical phenomena that play little or no functional role in the behavioral ecology of the subject species.

In their study, Whitney *et al.* (2) first characterized an epidermal diffraction grating that contributes an iridescent color to the floral displays of several plant species. They then conducted a series of behavioral experiments with bumblebees (*Bombus terrestris*) to test the hypothesis that these animals learn to associate iridescence per se with a food reward. The distinct challenge for these behavioral experiments is to isolate iridescence from other visual features of the flowers that might be perceived by the bees. Iridescence, correctly defined by Whitney *et al.*, is an optical property characterized by a “change in hue of a surface with varying observation angles.” Foraging bumblebees should experience this phenomenon in

the form of dynamic changes in floral color as their angle of approach changes over time. However, in addition to making the flower surface iridescent, epidermal diffraction gratings will also contribute to more static properties perceptible to bumblebees, such as the average hue or polarization of petal coloration.

Although Whitney *et al.* (2) took great care in their experiments to isolate the contributions of ultraviolet signals, polarization, and underlying pigmentary coloration, they did not exclude the possibility that bumblebees were attending to static rather than dynamic color features of the experimental stimuli. As the authors point out through color vision calculations, the various colors produced by the diffraction grating should be detectable and distinguishable by the bumblebee visual system. Therefore, trained bumblebees in the study may have learned to associate food reward with a particular color or combination of colors produced by the diffraction grating, rather than the iridescence of the stimuli. If bumblebees attend primarily to specific colors produced by the surfaces, rather than their changeable appearance, we expect that the iridescent properties of the diffractive coloration would make these visual stimuli more difficult for honeybees to learn. Clear predictions arise from these possibilities if experimental protocols are designed accordingly.

We offer several suggestions that would provide more convincing evidence that, as Whitney *et al.* claim, “bumblebees...learn to disentangle flower iridescence from color.” First, we suggest noniridescent experimental stimuli that control for the chromatic contributions of the diffraction grating. This could be accomplished by incorporating the color of the diffraction grating at maximum visibility (across diffraction grating striations). Alternatively, common angles of bumblebee approach and illumination could be quantified and

used to construct an ecologically relevant geometry for measuring the chromatic appearance of the diffraction grating in nature. Adding these chromatic contributions to noniridescent stimuli would help to control for color while isolating iridescence. Whitney *et al.* (2) provide no such controls in their stimuli, leaving open the possibility that trained bumblebees learned to associate differences in static color features with reward, rather than differences in iridescence. An alternative approach would be to create experimental stimuli using fiber-optic lights whose hue could be changed dynamically to simulate iridescence.

Second, Whitney *et al.* imply that the iridescence produced by the diffraction grating increases the salience and/or memorability of floral displays. If bumblebees are indeed attending to the iridescence itself, this seems plausible. However, if bumblebees instead use a specific color produced by the diffraction grating as a cue, we might expect that learning associated with this floral feature would be hampered by the iridescence of the stimuli. At face value, the learning rate associated with the diffractive floral cue appears to be slow compared with previous work on static color stimuli (6). More direct comparison of the learning rate associated with comparably bright iridescent and noniridescent stimuli would be extremely enlightening regarding the role that iridescence per se plays in associative learning in this pollinator.

In conclusion, we strongly urge researchers to use appropriate controls when testing the function of complex optical phenomena. We are not asserting that bumblebees are unable to attend to iridescence per se, but rather that the experimental design of Whitney *et al.* (2) cannot support this claim unambiguously. We suggest instead that their conclusion might better read: “We found that bumblebees learn to associate a diffraction-grating-based color signal with a food reward, despite the variable appearance of such a cue due to iridescence.” Claims that complex optical phenomena play a role in the visual ecology of species are often widely perpetuated in both the popular press and the scientific literature, further underscoring the importance of properly designing experimental stimuli.

## References

1. A. Sweeney, C. Jiggins, S. Johnsen, *Nature* **423**, 31 (2003).
2. H. M. Whitney *et al.*, *Science* **323**, 130 (2009).
3. J. M. Douglas, T. W. Cronin, T. H. Chiou, N. J. Dominy, *J. Exp. Biol.* **210**, 788 (2007).
4. P. Vukusic, J. R. Sambles, C. R. Lawrence, R. J. Wootton, *Nature* **410**, 36 (2001).
5. P. Vukusic, J. R. Sambles, *Nature* **424**, 852 (2003).
6. N. E. Raine, L. Chittka, *Proc. R. Soc. London B Biol. Sci.* **275**, 803 (2008).

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School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA.

\*To whom correspondence should be addressed. E-mail: nmorehouse@asu.edu