Trends in Ecology & Evolution

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Spotlight

Illuminating the Evolution of Iridescence

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Iridescence, a change in hue with viewing or illumination geometry, is a common feature of colour patterns in nature, though its significance remains elusive. Recent studies of floral iridescence reveal its functional versatility in enhancing the detection and discrimination of resources by insect viewers, as well as augmenting higher-level processes of memory and perception. Coupled with a known evolutionary lability, these results suggest intriguing possibilities for how this optical curiosity may act as a key to diversification.

Nature's Brilliance

Colour in nature presents a portrait of adaptive evolution, as this conspicuous facet of variation is continuously exposed to the forces of natural and social selection. Virtually all biological colour arises via two processes: the absorption of light by pigments and the scattering of light by structures that vary periodically at the nanoscale [1]. While they often act in concert, only the latter mechanism, structural colouration, is capable of generating the extreme perceived brightness and chromaticity that characterises the most striking visual displays in the natural world (e.g., Figure 1 inset). Such structures also give rise to the curious optical effect of iridescence, wherein the apparent hue of an object shifts depending on the angle at which it is illuminated or viewed. Familiar to anyone that has watched soap bubbles or handled a compact disc, the phenomenon is widespread throughout the plant and animal kingdoms and has been variously implicated in sexual signalling, mutualism, antipredator defence, and deception [2–6]. Despite its ubiquity, an unequal focus on diffuse, pigment-dominated colouration means that our knowledge of the ecological significance of iridescence, and its evolutionary causes and consequences, remains nascent.

A View of the Ephemeral

The prevalence of colour as a channel of communication derives, in part, from its stability under the visually noisy conditions that characterise natural environments [1]. Whereas the brightness of objects will fluctuate by orders of magnitude across cloudy versus sunny conditions, the hue of an individual or resource will remain relatively constant, and so may be drawn on as a guide to (among other things) identity, category, and quality. This presents a challenge for intuiting the adaptive value of iridescence, since it subverts the inherent stability of colour-based signalling by introducing a dynamic element into an already fluid process. A central question, therefore, is how does this unique design feature enable the effective exchange of information?

Three recent papers examine this problem in the context of flower–pollinator mutualism. In the first, Whitney *et al.* [4] use behavioural assays to show that iridescence improves the speed with which trained bumblebees (*Bombus terrestris*) locate flowers, most likely by enhancing their detectability. By manipulating the magnitude of the hue-shift in artificial targets, the authors also show that the presence of less-than-perfect iridescence balances the tension between maximising visual conspicuousness and corrupting the identity of flowers as valuable resources. This thread continues through de Premorel *et al.* [7], who use artificial flowers to show that a proportionally larger area of iridescence within a colour pattern actually enhances the memorability of signals to bees. Visual modelling of the subjective appearance of flowers suggests that the broader 'perceptual footprint' generated by iridescent, as opposed to static, signals also improves the bees' ability to generalise between similarly rewarding stimuli. Finally, Moyroud *et al.* [2] take an expansive view, and present behavioural and phylogenetic evidence that optically similar 'halos', with weakly iridescent effects, have convergently evolved across angiosperm families, which enhances bees' perception of flowers as salient and attractive stimuli.

A Key Innovation?

An emerging theme from this work is the functional versatility of iridescence as a visual cue. Effective communication involves myriad processes (Figure 1), and the ultimate expression of colour patterns will be shaped by selection acting on both the design and content of signals. Even in the singular pollinator–flower context here examined, the dynamism of iridescence appears to improve the efficacy of information exchange at several stages; from the initial reception and detection of salient stimuli [2,4], through to higher-level processes of perception, memory, and generalisation [7]. These results also offer insight into contexts where the phenomenon is more common and the effects more extreme. Dramatic changes in colour are characteristic of the brilliant signals of mate identity and quality furnished by tropical butterflies and birds, yet its functional significance has proven elusive. Does the exaggerated flash of colour serve as a beacon to passing viewers to aid the detection and discrimination of conspecifics [2,4]? Or might the limited-view nature of such signals offer a degree of privacy and specificity in communication, and preferentially guide 'intended' recipients [2–4]? Moving from considerations of design to content, in contexts where the corruption of identity discussed by Whitney *et al.* [4] is

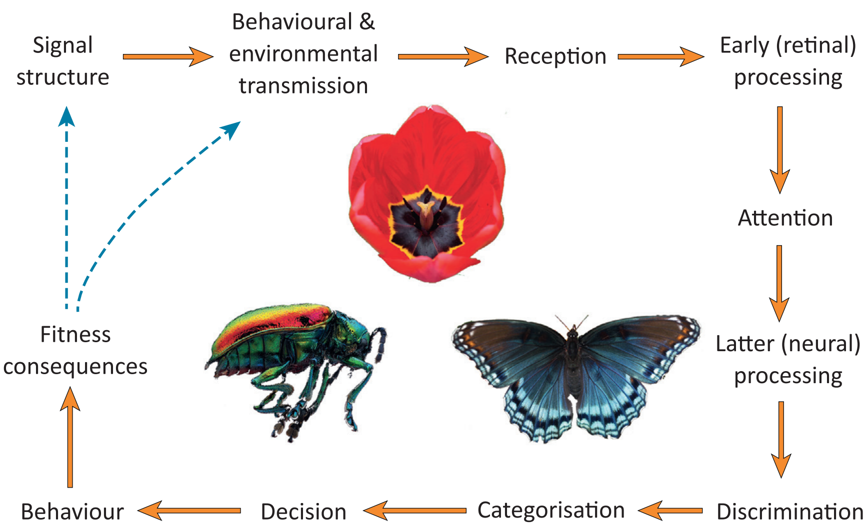

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Figure 1. The Function and Evolution of Iridescence in Visual Communication. A heuristic illustration of some the central ecological (solid arrow) and evolutionary (dashed arrow) processes involved in the exchange of visual information. Recent studies of floral iridescence [2,4,7] highlight its functional versatility in enhancing the detection and discrimination of resources by insect viewers, as well as amplifying higher-level processes of memory and perception. This versatility is equalled by an evolutionary lability, with selection able to drive dramatic changes in signal expression through only minor modifications of underlying structures and presentation behaviours.

desirable, such as camouflage, might we expect selection to favour the extremes of iridescent design to inhibit recognition by predators? The shimmering greens and golden-browns of forest-dwelling beetles offer fertile grounds for comparative tests of such possibilities, as supported by limited behavioural evidence to date [5,6].

The ecological versatility of iridescence is complemented by considerable evolutionary lability. The repeated evolution of interference colours and iridescence among angiosperms shown by Moyroud *et al.* [2] contributes to a growing body of evidence which suggests that the optical effect may have arisen early and repeatedly across taxa, including birds, butterflies, and beetles [6,8,9]. The physical basis of such colours means that, once present, subtle modifications of the underlying structures can give rise to dramatic changes in signal expression [1,9] and function (Figure 1). This modularity has been directly implicated in the diversification and adaptive radiation of starlings, for example, since selection is able to rapidly drive divergence in the iridescent, as opposed to pigment-based, ornaments used in mate signalling [8]. In a more tentative example, the simple twisting of a reflector to reduce iridescence might be exploited in service of an evolutionary transition from camouflage to aposematism or deimatism; a well-described pathway from cryptic to conspicuous defences [10], and a hypothesis for which beetles and butterflies may again be of use [6,9]. That iridescence, and structural colouration more broadly, might prove an evolutionary key to diversification seems likely in the few contexts in which the question has been asked, and may hold true more generally given the appropriate behavioural and comparative tests. While many of the above possibilities remain speculative, these compelling studies [2,4,7] suggest a pathway to understanding the function of this optical curiosity, and with it an entire dimension of biological diversity.

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