Opinion

The Paradox of Iridescent Signals

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Signals reliably convey information to a receiver. To be reliable, differences between individuals in signal properties must be consistent and easily perceived and evaluated by receivers. Iridescent objects are often striking and vivid, but their appearance can change dramatically with viewing geometry and illumination. The changeable nature of iridescent surfaces creates a paradox: how can they be reliable signals? We contend that iridescent color patches can be reliable signals only if accompanied by specific adaptations to enhance reliability, such as structures and behaviors that limit perceived hue shift or enhance and control directionality. We highlight the challenges of studying iridescence and key considerations for the evaluation of its adaptive significance.

Iridescence and the Problem of Signal Reliability

Iridescent objects are among the most vivid and visually striking in the natural world. For this reason, they are often assumed to be signals (see Glossary) that influence the behavior of receivers, whether they be predator, prey, competitor, or prospective mate. Iridescence, from the Greek word for rainbow (iridos) [1], describes a change in hue with viewing and/or illumination geometry (Figure 1). Because the appearance of iridescent objects can change dramatically in both space and time, iridescence can hamper the ability of animals to recognize objects in their environment [2–4], which is fundamental to most visual tasks, such as identifying food, enemies, or mates. The changeable nature of iridescent color patches poses a challenge for reliable signaling. How can information be reliably conveyed by signals that are inconsistent?

Advances in our ability to quantify the dynamic nature of iridescence (e.g., through advanced spectroscopy, microscopy, multispectral imaging, and high-speed video [5–9]) have highlighted the prevalence, complexity, and diversity of iridescence, but its biological function remains an enigma. Unlike diffuse or matte colors, the appearance of iridescent color patches depends on when and how they are presented relative to the viewer; for example, how the signaler moves during display and/or how the viewer visually samples the target. Most studies of iridescence measure or consider only some of these factors. There are few cases where iridescence has been shown to convey specific information independent of the constituent hues (but see [5–7]).

One problem in studies of iridescence is the pervasive inconsistency in how the term is used and how iridescence is measured. Iridescence is often confounded with structural coloration. Structural coloration arises from the interaction of light with physical structures at the microscopic scale and can produce complex, vivid colors and diverse optical effects such as white gloss, a metallic or mirror-like appearance, or polarized reflectance. Iridescence is just one of many optical effects produced by structural coloration. Sometimes, it is defined broadly to encompass angle-dependent changes in hue or intensity (luminance), because a change in intensity can cause a particular color to appear or disappear [1,10–14]. We advocate that iridescence be used exclusively to describe an angle-dependent change in hue, while specularity be used to describe the angle-dependent change in intensity. Although natural materials often show changes in both hue and intensity, the two properties are influenced by different structural...
features and are not necessarily correlated (Figures 1B and 2). For example, the plumage of the common kingfisher *Alcedo atthis* shows strong hue shift but limited intensity shift [15,16], whereas the wing spots of *Hypolimnas bolina* butterflies show dramatic intensity shift but little or no hue shift [14]. Hue (chromatic properties more generally) and intensity are processed using different physiological and neural mechanisms [17,18]. Distinguishing iridescence from specularity and other optical effects produced by structural colors is critical to evaluate how iridescence is perceived and its role in signaling.

**Diversity of Mechanism and Appearance**

Structural color is produced by the interaction of light with materials with specific arrangements and refractive indices (e.g., air vs keratin or chitin) [1,10,19–23], which causes some wavelengths to be reflected and amplified to produce vivid colors (constructive interference) while others cancel out (destructive interference). Iridescence is produced when amplified wavelengths become shorter (blue-shifted) with increasing angle of incidence (Figure 1) [21]. Depending on parameters such as the difference in refractive index [24], periodicity in different dimensions, and the layered combinations of structures [21], iridescence can be enhanced [25], reduced [21], or even inverted (redshift) [12]. In general, disorder in the structure reduces specularity [26], but specific types of irregularity, such as offsets in periodicity, can also limit iridescence [1,27]. Although the general physical principles of the production of structural color are well understood, much remains to be discovered regarding the causal relationship between structural composition and variation in iridescence or other optical effects in complex natural structures [1,10,20–23,28,29] (Figure 2).

Natural materials frequently comprise multiple components, each with different properties. For example, a layer with ordered and periodic structures can overlay a pigmented layer producing the appearance of an iridescent or colored sheen overlaying a solid color. Pigments can also act as filters that limit the wavelength range of reflectance and, thereby, the degree of iridescence [30,31]. As a consequence of the wide diversity of visual effects that can be produced by changes to one or more structural elements at different spatial scales or hierarchical levels, structural colors can play an important role in adaptive radiation [5,13,32,33]. However, the genetic, developmental basis, and evolutionary lability of structures producing iridescence remain largely unknown [34,35]. Moreover, the systematic characterization of iridescence and its structural basis in a consistent, repeatable way remains a significant challenge [26,36,37].

The appearance of iridescence depends on the angular distribution of light relative to the surface. As surfaces of natural objects are never perfectly flat or smooth, each point of a surface can have a different effective angle of incidence, even under the same illumination conditions (Figures 1E and 3). The effect on appearance depends on the spatial scale of the variation in surface geometry. Microscopic curvatures generate a mixture of reflected wavelengths, which produce the appearance of a diffuse color, whereas large-scale curvature makes iridescence more apparent to the viewer. Additionally, illumination conditions can dramatically alter the appearance of iridescent surfaces [8]. For illumination originating from a point source, such as the Sun on a clear day or a camera flash, highly specular iridescent surfaces will appear particularly brilliant, whereas under diffuse illumination such as cloudy conditions, both specularity and iridescence can be greatly diminished (Figures 1 and 3). Thus, the degree of iridescence that can be perceived must be studied in relation to specific contexts.

**How Is Iridescence Perceived?**

Iridescence has both spatial and temporal components. If we consider an animal observing an iridescent target, the wavelengths it receives will depend on its visual angle and the size and
shape of the target. If the animal’s visual system has high enough spatial resolution, it will see a complex pattern of multiple colors (spatial component). If the animal is moving, the visual angle may vary and cause the pattern of colors in the target to change shape, hue, or both (temporal component). Animals can therefore process iridescent stimuli as either a static complex collection of colors or a change in hue over time. Currently, it is unclear which mechanism(s) different animals use to process iridescent stimuli and, therefore, how they are represented in the brain.

Unlike most color patterns, the spatial variation in hue of iridescent surfaces can be continuous with few edges or boundaries. Traditional methods to analyze color pattern geometry focus on the detection of edges and boundaries characterized by distinct changes in intensity rather than hue [38]. This is because achromatic mechanisms are generally more efficient at processing spatial patterns than color mechanisms [38]. How non-human animals process continuous variation in hue independent of changes in intensity is unclear. One possibility is that local boundaries between colors appear as a function of color discrimination thresholds defined by photoreceptor sensitivities [39]. Recently, promising methods have been developed to analyze spatial variation in both the chromatic and achromatic components of visual scenes using discrimination thresholds specific to an animal’s visual system [39]. However, the spatial distribution of colors of iridescent surfaces will often vary with viewer position and illumination (Figure 1). Because of this temporal component, perception of iridescent objects cannot be understood using a single ‘snapshot’.

Due to the highly variable spatial and temporal properties of iridescent signals, their appearance will depend on how they are presented to an observer. Some signals are presented as a snapshot of edges and boundaries characterized by distinct changes in intensity rather than hue [38]. This is because achromatic mechanisms are generally more efficient at processing spatial patterns than color mechanisms [38]. How non-human animals process continuous variation in hue independent of changes in intensity is unclear. One possibility is that local boundaries between colors appear as a function of color discrimination thresholds defined by photoreceptor sensitivities [39]. Recently, promising methods have been developed to analyze spatial variation in both the chromatic and achromatic components of visual scenes using discrimination thresholds specific to an animal’s visual system [39]. However, the spatial distribution of colors of iridescent surfaces will often vary with viewer position and illumination (Figure 1). Because of this temporal component, perception of iridescent objects cannot be understood using a single ‘snapshot’.

When Might Iridescent Color Patches Be Reliable Signals?
Signals must elicit a response in the receiver, so they need to be easily detected. It is frequently suggested that iridescent signals are effective because they can enhance detectability [3,10,13], but it can be difficult to determine whether the primary signal is the vivid hue of a structural color or its iridescence. Iridescence could increase detectability because the range of hues ensures high contrast against a broad range of background colors and generates contrast between adjacent hues [9]. The detectability of iridescent objects may depend on both the hue and the specularity of the background (e.g., glossy leaves vs matte tree bark) [3], because iridescent surfaces are often highly specular. This highlights the importance of behavior, such as the choice of background and position relative to the sun, for the efficacy of iridescent signals [6,49,50].

In addition to being detectable, signals must be reliable. This is a prerequisite for honest signaling, whereby a signal reliably communicates information on individual identity or quality (e.g., condition, health, size, agility, toxicity). A recent meta-analysis indicates that structural colors, some of which
are iridescent, are associated with measures of individual quality [51]. Color is critical for object recognition [17], and mechanisms to ensure that colors appear relatively constant under a wide range of illumination conditions (color constancy) are inherent to all color vision systems (biological and artificial) [52]. Recent evidence indicates that iridescence hampers object recognition in bumblebees [2] and reduces predation on artificial beetle prey by wild bird predators, particularly on glossy backgrounds [3]. How then can iridescent signals be reliable?

Some structural colors are both highly detectable and reliable signals because the iridescence is weak or limited. The extent of hue shift can be limited by certain types of disorder in the structure (Box 1) or pigment-based filters [9]. For example, some flowers exhibit weak UV–blue iridescence produced by imperfect diffraction gratings [8,9,53]. In contrast to the strong iridescence produced by perfect diffraction gratings, this weak iridescence may enhance the visual effect of the underlying pigment-based color without compromising the signal’s identity [9]. However, it is unclear whether the iridescence itself is an important signal component for pollinators under normal viewing conditions [54]. In the context of communication, it is also important to consider whether structural features exist for signaling purposes or whether they are a secondary consequence of selection for other physical properties [55–57].

The reliability of iridescent signals can be improved through morphological adaptations to enhance directionality – producing abrupt changes in hue and often intensity over a narrow angular range. Strong directionality, even under diffuse lighting, is common in both birds and butterflies and is often achieved through the tilt of the multilayered structures in feather barbules.

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**Figure 1. Measuring Iridescence and Specularity.** Top-row panels show light interacting with a biological material to produce structural color; bottom-row panels show the spectral profile (reflectance (% ~ wavelength (nm)) measured at a fixed angle of incidence (gray unbroken line) and reflectance (black arrowheads). For any surface, incident light is reflected in multiple directions (colored halo) with a higher proportion at the specular angle (longest colored arrow). (A) A noniridescent structural color reflects light at the same wavelength. If the collector moves from position 1 to position 2, only the intensity (the area under the spectral curve) varies. (B) An iridescent structural color reflects different wavelengths of light depending on the angle. If the collector moves from position 1 to position 2, the intensity drops and the hue (the peak in the spectral profile) becomes blue shifted. (C) Iridescence can be distinguished from intensity shift by increasing the specular angle ($\beta > \alpha$) relative to the normal (broken gray line). This will capture the angle-dependent hue shift at a constant intensity. (D) Specularity (intensity shift) can be distinguished from hue shift by maintaining a constant angle between the incident light and the collector but varying the position relative to the normal (broken gray line). This will capture the angle-dependent drop in intensity at a constant hue. (E) If the iridescent structure is not flat, a single incident beam of light can generate the same effect as described in (C) because the light beam subtends a different angle at each point on the surface ($\beta > \alpha$).
Figure 2. Variation in the Degree of Iridescence.

For a Figure360 author presentation of Figure 2, see the figure legend at https://doi.org/10.1016/j.tree.2020.10.009.

(A) In insects, iridescence is enhanced by reducing the difference in index of refraction between the alternating materials in multilayers (left). Iridescence is reduced by surface irregularities (arrows) in thin films (right), while the colors of the wing interference patterns (WIPs) are due to local changes in membrane thickness (black arrowhead) [29,62].

(B) Diffraction gratings on some peacock spiders produce strong iridescence, which in other species is reduced by irregularities at three different hierarchical levels [63].

(C) Morpho butterflies produce blue with Christmas tree-like structures on their scales. These structures are perfectly aligned in species with strong iridescence, while in others, variation in the offset of the structures (blue lines) and overlapping scales [21] cancel iridescence.

(D) Structural color in birds is commonly produced by the arrangement of melanin units called melanosomes. Ordered layers create highly iridescent feathers, whereas a disordered layer covered by a sponge-like structure (a matrix of keratin and air bubbles) produces a noniridescent, diffuse structural color [64].

Original photographs by Christian Hösl (beetle), Ekaterina Shevtsova (fly), Michael Doe (spiders), Starkey and Vukusic (butterflies), Dario Sanches (hummingbird), and Alan Vernon (Mexican jay).
or wing scale ridges [15,25,58] (but see [59]). Strong directionality can produce the appearance of abrupt switches between discrete hues rather than continuous hue change and could facilitate signal processing and evaluation [6]. For example, the extreme and abrupt hue changes that characterize the dynamic “flash” displays of male Lawes’ parotia (Parotia lawesi) are likely to be more easily perceived than gradual hue shifts [58].

Directional iridescent signals can coevolve with behavior to control appearance [7,60]. For example, males of many hummingbirds present iridescent gorgets during aerial courtship displays that require exquisite precision. Male broad-tailed hummingbirds, Selasphorus platycercus, precisely coordinate their aerial dive with both song and the display of their iridescent gorget [5]. The highly directional gorget feathers change abruptly from red to dark green, appearing as a red flash [5]. By contrast, males of Costa’s hummingbird, Calypte costae, and Anna’s hummingbird, Calypte anna, maintain their gorget at a precise, constant angle relative to the female to appear a consistent hue [7]. In North American bee hummingbirds, species with flash displays have more exaggerated display behaviors and smaller iridescent plumage patches and tend to face away from the sun while displaying, whereas those presenting a constant hue during display have less exaggerated display behaviors and larger plumage patches and tend to face the sun while displaying [7]. This raises the intriguing possibility that iridescent signals in these different species are perceived differently (e.g., intensity flash vs discrete hues) and/or convey different information.

We suggest that morphological and behavioral adaptations to ensure reliability, such as limiting hue shift, enhancing directionality, and/or precise control of angular presentation relative to the illumination and the viewer, are likely to be a hallmark of iridescent signals. By contrast, iridescent
Iridescence is a term that has been used to describe a variety of visual effects, which has arguably hampered our ability to understand its adaptive significance. We have highlighted the complexities and challenges of studying iridescent signals and their function (see Outstanding Questions). Birds, butterflies, and jumping spiders may be promising groups in which to address these surfaces in animals that show dramatic hue shifts with limited ability to control their appearance to viewers are less likely to be signals. In these cases, iridescence may have evolved for other purposes, such as reducing predation risk by hampering object recognition [2,3]. Alternatively, iridescence may be a secondary consequence of selection for other properties of structural colors such as strength, flexibility, water repellence, or thermal control [61]. This is important to consider, as many structural colors show some degree of iridescence but may not be perceived or used as a signal in natural contexts [55,56].

Concluding Remarks

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questions. Additionally, we suggest the following considerations when investigating the function of iridescence.

First, it is important to distinguish iridescence from other optical effects and to systematically measure both hue shift and intensity shift. This is essential to isolate iridescence as the relevant signal, but also to understand the full diversity of visual signals and underlying mechanisms.

Second, the position and behavior of the signaler and receiver are both critical to the appearance of the signal. It is therefore essential to record and quantify the behavior of both participants to determine the type of information that is available to the receiver’s visual system.

Third, the color, spatial, and temporal perceptual ability of the species should be considered. In particular, the capacity of the visual system to process fast-changing or fast-moving iridescent signals is important if iridescence is presented as a ‘flashy’ signal.

Fourth, we suggest that iridescent signals require accompanying adaptations to enhance signal reliability while maintaining detectability. These include morphological structures and behaviors that limit perceived hue shift and/or enhance or control directionality. Traditional studies of animal color signals implicitly assume that their appearance is constant. Iridescence highlights the dynamic nature of many color signals and may reveal new realms of biological adaptation.

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