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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.

Highlights

Iridescent color patches are often considered to be signals because they tend to be eye-catching and vivid. The appearance of iridescent color patches changes with viewing geometry and illumination, but paradoxically, signals should be consistent and reliable.

To understand the evolution of iridescent signals, iridescence, or the property of angle-dependent hue shift, must be distinguished from other optical effects produced by structural coloration.

Understanding how animals present and process both the spatial and temporal components of iridescent color patches is essential to understand their reliability as signals.

To ensure reliability, iridescent signals require accompanying adaptations, such as structures or behaviors, to limit hue shift or control directionality.

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

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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 [8,13,32,33]. 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 [6]. 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

Glossary

Achromatic: relating to the total amount of light independent of color or the wavelength. Intensity and luminance are achromatic properties.

Angle of incidence: the angle between a ray of light incident on a surface and the line perpendicular to the surface.

Chromatic: relating to color or the wavelength of light independent of the total amount of light. Both hue and saturation are chromatic properties.

Color constancy: the tendency of objects to appear a similar color under different illumination conditions.

Constructive interference: when two waves are in phase, they add together so that the amplitude of the resultant wave is the sum of the two amplitudes of the original waves.

Destructive interference: when two waves are out of phase, they cancel each other out.

Diffraction grating: a periodic structure that splits light into its different wavelengths.

Diffuse: light that is scattered in many directions rather than primarily in a single direction; can refer to illumination (e.g., a cloudy day) or reflectance (e.g., a matte surface).

Directionality: the degree to which an object's appearance changes depending on the viewing angle.

Discrimination threshold: the threshold at which a receiver can distinguish two colors or intensities.

Effective angle of incidence: the precise angle of incidence at the microscopic scale. Microstructures on the surface may not be oriented at the same plane as the macroscale surface.

Gloss: an optical property of a material related to how well it reflects light in the specular (mirror-like) direction. Gloss is independent of hue and perceived as white highlights or shine on a surface.

Hue: the common use of the word 'color' (i.e., blue, green, red), associated with the dominant wavelength(s) of light.

Intensity: the absolute amount of light or rate of photons reaching the eye. It is associated with how light or dark a color appears.

Iridescence: a change in hue with viewing and/or illumination geometry.

Luminance: see 'intensity'.

Pigments: chemicals that selectively absorb certain wavelengths. Wavelengths that are not absorbed may be reflected from the surrounding material, resulting in specific colors.

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 'flash' to the receiver, as in certain hummingbirds [6,7] and butterflies [12,25] (although flash signals labeled as iridescent in some butterfly species [14,40] involve an intensity shift only and would not meet the narrower definition of iridescence advocated here). How an animal processes iridescent flashes depends on the **temporal resolution** of its color vision (e.g., [41–43]). Even if an animal's color vision has a high temporal resolution, it may use other neural mechanisms to process iridescence. For example, the processing of achromatic signals is faster than processing of chromatic signals in humans and bees [44–46]. Animals may therefore perceive flash signals only as an intensity change, despite an accompanying hue change. Finally, flashy iridescent signals that are constantly moving may be processed by motion-processing mechanisms. In human motion perception, distinct mechanisms process chromatic and achromatic information [47] and may be dependent on velocity [48], but how other animals process fast-moving colors is unclear. Therefore, understanding how animals communicate using iridescent signals requires a precise understanding of how the signaler presents the signal and how the receiver processes the information.

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 [9,10,13], 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

Polarized reflectance: reflected light waves that oscillate in the same plane.
Refractive index: a number describing how fast light travels through a given material (relative to the speed of light in a vacuum).
Signal: a feature (e.g., structure, chemical, sound) or behavior that has evolved for the purpose of influencing the behavior of a receiver.
Spectral: the distribution of light as a function of wavelength.
Specularity: proportion of incident light reflected at an equal but opposite angle to the angle of incidence (i.e., the specular angle).
Structural coloration: color that is produced by light interacting with micro- or nanometer-scale structures.
Temporal resolution: in relation to vision, refers to the speed of changes in light intensity that can be perceived. Measured as the speed at which a flickering light can no longer be distinguished from a continuous light.
Visual angle: an angular measure of the size of a visual stimulus on the eye; related to viewing distance and size of the stimulus.

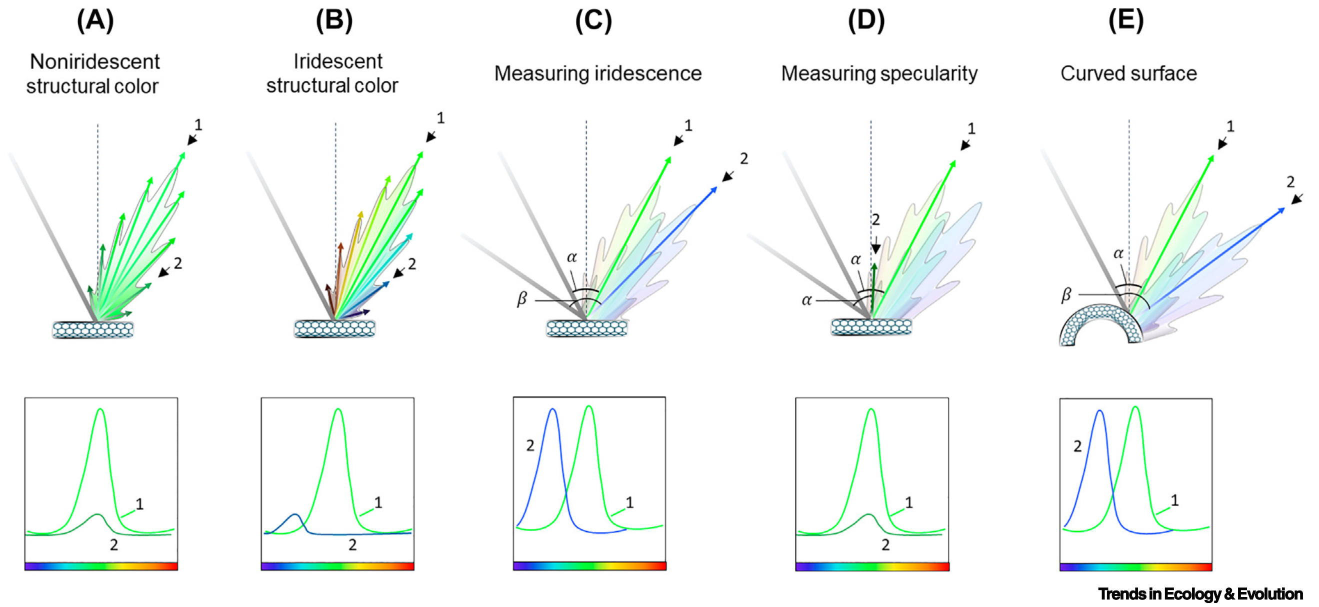

Figure 1. Measuring Iridescence and Specularity. Top-row panels show light interacting with a biological material to produce structural color; bottom-row panels show the **spectral** profile [reflectance (%) ~ wavelength (nm)] measured at a fixed angle of incidence (gray unbroken line) and reflectance (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 ($\beta > \alpha$).

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

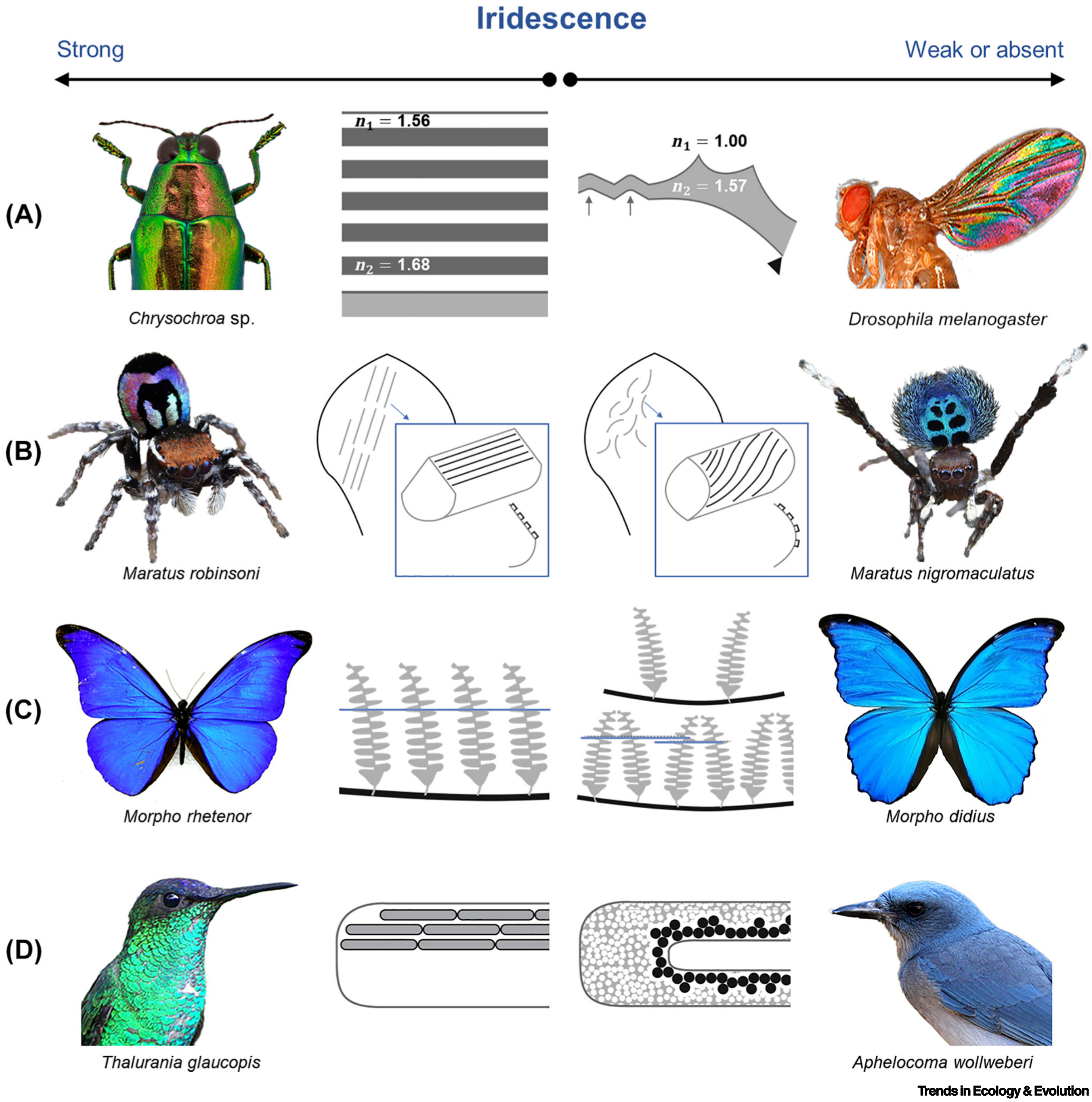

Figure 2. Variation in the Degree of Iridescence.

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).

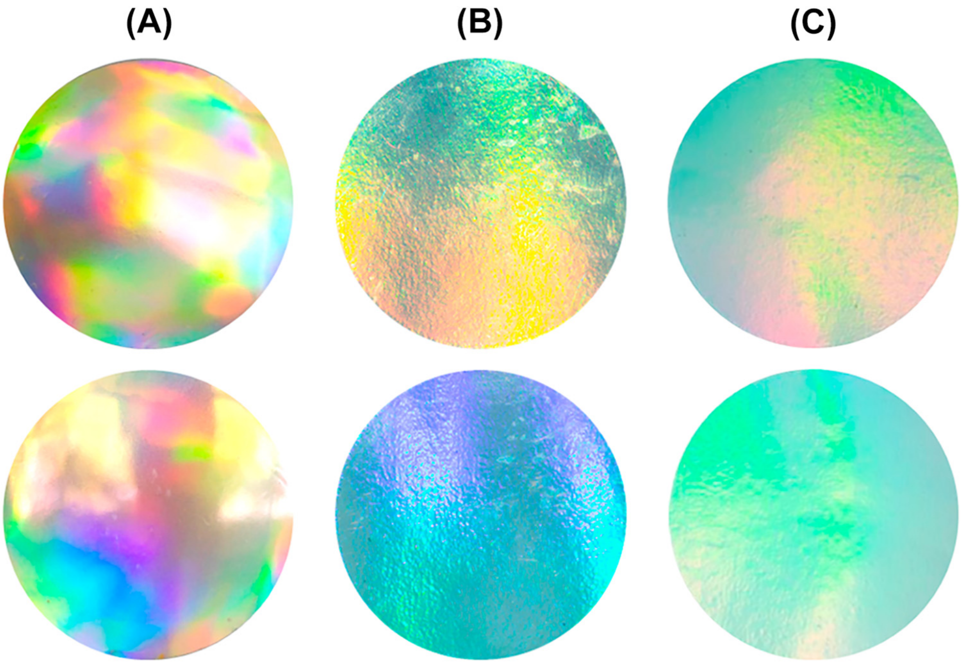

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Figure 3. The Appearance of an Iridescent Surface Can Change Dramatically Depending on Illumination. The same iridescent thin film under (A) artificial lighting (in this case multiple fluorescent lights) or (B) direct sunlight will appear strongly iridescent compared with (C) diffuse (cloudy) illumination conditions. Under all three conditions, the hue shifts to shorter wavelengths as the illumination and viewing angle change from above the sample (top row) to more oblique angles (bottom row), but the complex patterns can vary dramatically.

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 lawesii*) 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

Box 1. Wing Interference Patterns

Wing interference patterns (WIPs) are the colorful highlights that can sometimes be seen on the transparent wings of many insects (Figure I). These patterns are often compared with the rainbow highlights on soap bubbles because both visual effects are produced when specific wavelengths reflected from the upper and lower boundary of a thin, transparent film are amplified by constructive interference. A perfect thin film is iridescent; hue is angle dependent because the distance that light travels from the upper to the lower boundary increases with increasing angle (Figure 1). However, wing membranes often have surface microstructures that greatly reduce angle dependence (Figure 2A) [62]. At any given point on the wing, the hue produced through constructive interference is a function of membrane thickness but shows little or no change with angle. The patchwork of hues seen in WIPs is caused by fine-scale spatial variation in wing membrane thickness. These stable patterns can be species or sex specific [62,65,66], which has led to predictions that WIPs may be used as signals.

Although WIPs may not be iridescent, they can produce a similar perceptual effect and present challenges similar to iridescence in studies of their potential signaling role. Like iridescence, WIPs are dynamic and depend on receiver behavior because they are visible only under specific conditions. In the laboratory, studies characterize WIPs by photographing wings on a black background with a bright light and sometimes even enhance the image so the colors are clearly visible [62,66]. Under natural conditions, WIPs are subtle or absent under most circumstances, but can be visible on sunny days against dark backgrounds. For example, on a sunny day against a dark background, the twisting wing displays of dance-flies or the wing displays associated with the courtship song in *Drosophila* produce flashes of color alternating with the color of the background because of the wings' transparency. The saturation and specific hue (corresponding to membrane thickness) respond to sexual selection in laboratory experiments [66,67]. However, we do not yet know how WIPs are perceived, how they interact with behavioral or acoustic displays, or whether they convey information about individual quality. The signaling function of WIPs therefore remains contentious because there is limited evidence that WIPs affect receiver behavior.

Figure I. Wing Interference Patterns in a Platypezid Fly. The orange hue is consistent from different viewing angles. Photographs by Thomas Shahan.

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

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

Outstanding Questions

What structural mechanisms produce and limit iridescence? How does this relate to other optical effects produced by complex natural structures?

What are the developmental mechanisms underlying structures producing iridescence? How do these mechanisms enhance or constrain the evolutionary lability of iridescent signals?

How does the appearance of iridescent signals vary in relation to signaler and receiver behavior (how are the signals presented and viewed)? How do signalers control viewing geometry and conditions to ensure signal reliability?

How are iridescent signals perceived and processed by receiver visual systems? Can existing models of animal color vision be modified to model an animal's perception of iridescence?

What are the relative roles of hue shift and intensity shift in the efficacy and information content of 'flashy' iridescent signals?

How does selection for other functions (thermal, physical protection, water repellency, etc.) shape the evolution of iridescence? Is there a trade-off between these functions and iridescent signal quality?

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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