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REVIEW

Animal transparency: How should we define form and function?

James B. Barnett[1] | **Justin Yeager**[2] | **Karin Kjernsmo**[3]

[1]School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[2]Biodiversidad Medio Ambiente y Salud, Universidad de Las Américas, Quito, Ecuador

[3]School of Biological Sciences, University of Bristol, Bristol, UK

Correspondence
James B. Barnett
Email: jbarnett@tcd.ie

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Abstract

1. Animals use colour for a wide range of adaptive functions, ranging from cryptic colours that blend into their environments to bright, conspicuous signals that convey information, either to attract mates or to ward off predators and rivals. However, perhaps one of the most intriguing adaptations is how animals can make use of the absence of colour through transparency.
2. Animal transparency has long been understood as a form of camouflage, allowing predators to see straight through their prey as if it were not there. However, transparency can take many different forms, both in terms of the degree of transparency, ranging from opaque through translucent to transparent and in the extent of coverage, with different combinations of transparent and opaque regions.
3. Despite this variation, transparency has often either been regarded as a unique form of concealment or synonymised with background-matching camouflage. Yet, empirical evidence is increasingly demonstrating how different forms of transparency may facilitate different defensive and communicative strategies. Here, we contextualise the potential functions of transparency into the wider framework of visual ecology, review the evidence for different strategies and highlight areas in need of continued research.
4. We find that, despite its seemingly intuitive role in camouflage, transparency can fulfil many different functions, including facilitating several conceptually distinct forms of camouflage (e.g. background matching, disruption, masquerade and edge diffusion), mimicry (both Batesian and Müllerian) and enhancing communicative signals (such as aposematism, mate choice and territory defence). Yet, many ecological and behavioural questions remain to be addressed, and caution is needed when assessing or interpreting the function of transparency.

KEYWORDS
aposematism, camouflage, colouration, communication, mimicry, signalling, transparency, visual ecology

1 | INTRODUCTION

Transparency is often described as the 'optimal form of camouflage' and for good reason. In its most basic form being see-through appears to offer true invisibility; perfect camouflage that instantaneously matches any environment regardless of how visually complex or dynamic it may be (Bagge, 2019; Cuthill, 2019; Galloway et al., 2020; Gomez et al., 2021; Johnsen, 2001; McFall-Ngai, 1990). The reality is, of course, more complex and animal transparency is highly variable, being better described along a spectrum that ranges from opaque to transparent, and from uniform to gradated or patchy (Figure 1). Although often assumed to be rare, or largely confined to the oceans (Bagge, 2019), examples include species as diverse as almost completely transparent shrimp and jellyfish, translucent frogs and cephalopods and butterflies with wings which range from being mostly opaque to fully transparent.

Despite this variability, transparency is often erroneously discussed as though it were a single independent defensive strategy or synonymous with background-matching camouflage. However, the diversity of transparent organisms suggests that rather than being a single discrete form of defence, transparency may instead encompass a myriad of different defensive strategies (Box 1), communicative signals and non-signalling functions (Caro & Koneru, 2021; Gomez et al., 2021; Kikuchi et al., 2023). Here we discuss how to incorporate the form and function of transparency into the broader conceptual framework of animal colouration and highlight potential directions for further research.

2 | DEFINING FORM AND FUNCTION

Our understanding of colouration is defined not by an animal's appearance but instead by the effects colour has on the perceptual and cognitive processes of the observer (Cuthill, 2019; Troscianko et al., 2009). Function is therefore a context-dependent trait, where a single colour pattern may achieve multiple functions simultaneously (Kikuchi et al., 2023; Postema et al., 2022). As such, elucidating the function, or functions, of any colour pattern requires an understanding of the environmental context, the characteristics of the observer's visual system and the behavioural responses elicited under natural conditions.

For transparency, a common and intuitive assumption has been that greater transparency equates to more effective camouflage by increasing the degree to which the background is visible through the organism (Bagge, 2019; Cuthill, 2019; Galloway et al., 2020; Gomez et al., 2021; Johnsen, 2001; McFall-Ngai, 1990). In this paradigm, optimal camouflage is achieved by maximising the area of true transparency such that any inconsistency between an animal's appearance and the background (i.e. the signal-to-noise ratio) is minimised and the likelihood of detection is reduced. From the observer's perspective, the perceptual mechanisms at play here are akin to background matching (Box 1) as has frequently been studied in opaque, pigmented organisms (Merilaita et al., 2017; Merilaita & Stevens, 2011). Therefore, rather than being considered a distinct form of camouflage, we argue that transparency would be more accurately described as a mechanism by which background matching is facilitated through transparent body regions (Caro & Koneru, 2021; Cuthill, 2019; Gomez et al., 2021).

However, the assumption that the primary function of transparency is background matching, although likely valid in many circumstances, neglects the possibility that equally effective concealment may be achieved through alternative perceptual processes such as disruptive camouflage or masquerade (Box 1). These alternate forms of camouflage may evolve where complete transparency is not possible, yet it may also be the case that greater light transmission (either through increased transparency or larger patch size) does not increase the efficacy of camouflage. Indeed, it also cannot be assumed that the primary driver of transparency is always concealment and evidence is mounting to support the notion that transparency may also be an important component of certain aposematic, mimetic and other communicative signals (Box 1).

3 | IMPERFECT TRANSPARENCY

Achieving high levels of transparency requires the modification of bodily tissues to maximise light transmission by minimising the amount

FIGURE 1 Variation among transparent strategies. (a, b) The background visible through the almost completely transparent bodies of (a) a marine salp (*Salpa* sp.), (b) a shrimp (*Palaemon elegans*) and (c) a clearwing-satyr butterfly (*Dulcedo polita*). (d) Irregular transparent patches in the wings of a tussock moth (*Carriola* sp.) are reminiscent of disruptive camouflage. (e, f) The degree of translucency/semi-transparency in (e) a glass frog (*Hyalinobatrachium orientale*) and (f) the Puerto Rican semi-slug (*Gaeotis nigrolineata*) varies across the body. (g) Transparent patches may change the apparent shape of the wire coral goby (*Bryaninops yongei*) to mimic coral polyps. (h) A leaf-mimicking katydid (*Pycnopalpa bicordata*) has translucent patches which resemble holes in leaves. (i) The transparent wings of the lunar hornet moth (*Sesia bemeciformis*) appear to mimic the wings of wasps. (j) A gliding lizard (*Draco* sp.) has a translucent dewlap which, when orientated to the sun, appears to glow. (k, l) Variation in the degree of transparency and in conspicuous colouring among Ithomiini clearwing butterflies [(k) *Dircenna klugii*, (l) *Greta morgana*] may include elements of both camouflage and salient signalling. Photo credits. (a) Sarah Faulwetter (2021, CC-BY. https://www.inaturalist.org/observations/130620754), (b) Valentin Moser (2022, CC-BY. https://www.inaturalist.org/observations/105517736), (c) Abhas Misraraj (2023, CC-BY-NC. https://www.inaturalist.org/observations/153228259), (d) Lawrence Hylton (2023, CC-BY. https://www.inaturalist.org/observations/154398149), (e) Stephanie Tran (2022, CC-BY. https://www.inaturalist.org/observations/143897116), (f) Logan Crees (2020, CC-BY-NC. https://www.inaturalist.org/observations/39596409), (g) Joe Thompson (2019, CC-BY. https://www.inaturalist.org/observations/20934777), (h) Carlos Funes (2024, CC-BY. https://www.inaturalist.org/observations/197620846), (i) Christoph Moning (2023, CC-BY. https://www.inaturalist.org/observations/179513884), (j) Samuel Guiraudou (2024, CC-BY. https://www.inaturalist.org/observations/209809201), (k) Diego Huet (2018, CC-BY. https://www.inaturalist.org/observations/16470694), (l) Luis Fernando Valdez Ojeda (2021, CC-BY. https://www.inaturalist.org/observations/89388732) [images from iNaturalist under CC-BY (a, b, d, e, g–l) https://creativecommons.org/licenses/by/4.0/] and CC-BY-NC [(c, f) https://creativecommons.org/licenses/by-nc/4.0/].

of visible light absorbed, reflected, scattered or refracted as it passes through the body (Bagge, 2019; Gomez et al., 2021; Johnsen, 2001). Understanding the many different structural and developmental processes by which transparency can be achieved is currently an active area of research which continues to reveal the complexity behind the physiological changes required to attain broadband light transmission (Finet et al., 2023; Gomez et al., 2021; Pinna et al., 2021; Pomerantz et al., 2021; Taboada et al., 2022). This interplay between bodily structure and the environment results in an apparent bias favouring certain habitats and body parts which are seemingly more amenable to the evolution of transparency. For example, transparency is apparently most common in the open ocean where the refractive index of seawater is similar to that of body tissue, buoyancy reduces the need for reinforced structural body parts, harmful UV light is minimal and the background is relatively simple (Bagge, 2019; Johnsen, 2001; McFall-Ngai, 1990). Similarly, thinner and less complex body parts like

BOX 1 Glossary of key functions in defensive colouration

Background matching	Camouflage patterns which prevent detection by replicating the colours and patterns of the underlying substrate (Merilaita & Stevens, 2011)
Disruptive colouration	High contrast patterns which prevent detection and/or recognition by breaking up the organism into a series of unrecognisable features. Such patterns may intersect the edge to break up the organism's outline (edge disruption) or be concentrated in the centre to create false edges (surface disruption) (Stevens & Merilaita, 2009)
Edge diffusion	Camouflage patterns characterised by a gradient from an opaque centre to a transparent edge that minimises boundary contrast and smoothly blends an organism into the underlying substrate (Barnett et al., 2020)
Masquerade	Camouflage through the mimicry of an uninteresting/inedible object (e.g. sticks or rocks) such that even if detected the organism is not recognised (Skelhorn et al., 2009)
Aposematism	Recognisable (often conspicuous) colour patterns which signal to predators that the organism in unpalatable, defended, or otherwise unprofitable as prey (Stevens & Ruxton, 2012)
Müllerian mimicry	Convergence in the aposematic signals of multiple defended species (Müllerian co-mimics) (Sherratt, 2008)
Batesian mimicry	Deceptive signalling where an undefended species (the Batesian mimic) replicates the aposematic signal of a defended species (the model) (Jamie, 2017)

membranous insect wings may be more conducive to light transmission than thicker and more complex organs and structural tissues, such as eyes (which necessarily absorb light) or bones.

These factors do, however, also introduce a unique set of optical properties which may not be applicable to opaque organisms in the same manner. For example, deviation from true transparency due to reflection can introduce spectral highlights, gloss, polarisation and iridescence (Douglas et al., 2007; Fan et al., 2023; Shevtsova et al., 2011) (Figure 2a,b), whereas 'imperfect' transmittance can result in translucency and colour-shifted or polarised light reaching the observer (Bagge, 2019; Johnsen et al., 2011). The perception of such effects will also depend on the positioning and orientation of the transparent organism relative to the observer and the light source. These optical properties can result in increased detectability which may then impose costs that need to be mitigated (Johnsen et al., 2011). For example, we can see how such optical artefacts are under selection in species, including amphipods (Bagge et al., 2016) and butterflies (Pomerantz et al., 2021), which have developed specialised nanoscale structures to reduce surface reflection and scattering. Species, such as cleaner shrimp and glass frogs, which control or hide metabolic by-products that can reduce their transparency (Bagge et al., 2017; Taboada et al., 2022). As well as species which disguise internal structures with mirrored surfaces that channel light around opaque organs, such as the digestive systems of certain gastropods (Sakai et al., 2022) and glass frogs (Taboada et al., 2022) and the eyes of stomatopod larvae (Feller & Cronin, 2014).

Yet, despite these innovations meant to reduce detectability, transparent elements are often combined with bright, seemingly highly salient colour patches, gloss, iridescence and polarisation, which in opaque species have all been variously linked to alternative forms of camouflage as well as aposematism and mate choice (Doucet & Meadows, 2009; Franklin et al., 2022; Henríquez-Piskulich et al., 2023; Kjernsmo et al., 2020, 2022; Marshall et al., 2019; Thomas et al., 2023; Waldron et al., 2017). This raises the question of whether conspicuous colours necessarily impose costs, or whether they may instead be co-opted into alternate defensive or communicative strategies visible only to some observers, during particular behaviours or in certain microhabitats (Cuthill et al., 2017; Kikuchi et al., 2023; Postema et al., 2022).

4 | CONCEALMENT

To camouflage is to 'hide in plain sight'; a strategy which may be achieved using a diverse set of optical and perceptual mechanisms that disrupt the ability of an observer to detect and/or recognise the organism (Box 1) (Cuthill, 2019; Merilaita et al., 2017; Troscianko et al., 2018). In opaque species, pigments and structural colours may replicate the reflectance properties of the underlying substrate, i.e., background matching, or create high contrast patches which break up the organism into a series of unrecognisable features, i.e., disruptive camouflage (Merilaita & Stevens, 2011; Stevens & Merilaita, 2009). Transparency offers an alternate route where reflectance is transmitted from the substrate itself as light travels through the organism (largely) unimpeded. If transparency extends across the whole organism, then transparent camouflage would be mechanistically equivalent to background matching (Figure 1a–c) (Arias et al., 2020; Merilaita & Stevens, 2011; Michalis, 2017). However, if transparent patches are combined with high contrast opaque regions concealment may instead primarily result from disruptive camouflage (Figure 1d) (Arias, Leroy, et al., 2021; Costello et al., 2020; Stevens & Merilaita, 2009).

4.1 | Background matching

Despite the logical inference that transparency may facilitate background matching, or perhaps because of it, surprisingly few studies have empirically tested whether transparency reduces detection

FIGURE 2 The angle and intensity of light can affect our interpretation of transparency. (a–c) Ithomiini clearwing butterflies exhibiting angle-dependent iridescence [(a, b) *Greta annette*] and matching of an irradiant background against which an opaque wing would be silhouetted [(c) *Episcada salvinia*]. (d–f) The degree of transparency observed in glass frogs can vary greatly between reflected [(d) *Cochranella euknemos*; (e) *Teratohyla midas* on different backgrounds] and transmitted light [(f) unknown sp. backlit by an artificial light]. Photo credits: (a, b) Alan Rockefeller (2013, CC-BY. https://www.inaturalist.org/observations/3365480); (c) Maria Auxiliadora Mora Cross (2021, CC-BY. https://www.inaturalist.org/observations/100814585); (d) Kai Squires (2022, CC-BY. https://www.inaturalist.org/observations/105311643); (e) James B. Barnett (2014); (f) Juan Carlos Caicedo Hernández (2019, CC-BY. https://www.inaturalist.org/observations/35307788) [images (except e) from iNaturalist under a CC-BY: https://creativecommons.org/licenses/by/4.0/].

or predation rates relative to other forms of concealment. In field experiments using artificial lepidopteran-like targets being predated by wild birds, Arias et al. (2020) and Michalis (2017) both found that targets with transparent wings were attacked less frequently than opaque treatments. Moreover, there was no difference in survival between mostly transparent wings and no wings (Arias et al., 2020) or fully transparent wings (Michalis, 2017). In both cases, the benefit of transparency in mitigating predation risk is clearly demonstrated, and the most likely mechanism is through background matching. However, as the opaque targets mismatched background colour and/or luminance and lacked patterning, questions remain regarding whether concealment through transparency is fundamentally more effective than what is possible with opaque background matching.

4.2 | Disruptive camouflage

Disruptive camouflage can offer an alternative to background matching and may incorporate both transparent and opaque elements together (Figure 1d) (Arias, Leroy, et al., 2021; Stevens & Merilaita, 2009). Small areas of transparency can be distributed around obligate opaque structures, and thus disruptive patches may evolve more readily than or prior to full transparency. Here, artificial prey experiments have once again been used to measure and compare predation risk, and moth-like targets with small transparent patches within an otherwise opaque wing have a lower risk of detection than fully opaque targets. This effect has been found for both edge disruption, where transparent patches that intersect the target's outline have an advantage (Arias, Leroy, et al., 2021), and surface disruption, where transparent patches occur within the wing surface (Costello et al., 2020). Again, more work is necessary to clarify whether transparency is an alternate or a superior form of disruptive camouflage. However, Costello et al. (2020) suggest that seeing through to the true background is more effective at disrupting surface continuity than homogeneous, high-contrast, opaque markings. It remains to be seen whether background patterning is important for this effect or whether translucency (i.e. changing brightness but not displaying background pattern) may also provide disruptive camouflage in this manner.

4.3 | Translucency and edge diffusion

We also see that full transparency is not always necessary for camouflage to function. For example, when ranking the wings of clearwing butterflies (Ithomiini) by the degree of light transmission, Arias et al. (2019) found that incremental steps in transparency were mirrored by the rate at which each species was detected even when combined with conspicuous-seeming colours (Figure 1k,l). Translucency may, therefore, improve concealment even if a clear picture of the background is not visible through the animal. Consequently, transparency and pigmentation are not mutually exclusive, and translucency may offer a common route by which the colour or brightness of camouflaged patterns (both background matching and disruptive) can be tailored towards matching the immediate surroundings (Barnett et al., 2020) (Figure 1e,f).

In camouflage, it is often the organisms' edge (body outline) that is the most salient feature and one that needs to be disguised in order to reduce the risk of detection (Stevens, 2007; Stevens & Cuthill, 2006; Troscianko et al., 2009). Here, translucency may facilitate a complimentary process of edge diffusion, whereby a sharp colour boundary between a substrate and an organism can be smoothed into a less salient gradient, one that transitions from a more transparent edge to a more opaque centre (Barnett et al., 2020) (Figure 2d,e). Parallels exist to the benefits of an irregular or feathered edge which may blur the boundary of two objects together, but gradients of transparency can alter the apparent shape of an edge while allowing the true edge to remain structurally cohesive (Figure 1e,f) (Webster et al., 2015).

These two processes can be observed in glass frogs where pigments provide generalist background-matching camouflage, and a gradient of colour matching is formed when the frog is at rest by the more translucent legs surrounding the body (Barnett et al., 2020; Taboada et al., 2022). However, these processes have not been studied in detail and may be more widespread than currently recognised in translucent species like molluscs, beetles and fish (Figure 1e,f).

4.4 | When and where does transparent camouflage have an advantage?

Transparency is therefore compatible with our definitions of both background matching and disruptive camouflage (Merilaita et al., 2017; Merilaita & Stevens, 2011; Stevens & Merilaita, 2009). However, the question remains as to whether transparency may be an alternative, inferior or superior form of concealment to opaque camouflage, and under which scenarios any such differences would be most evident.

Perhaps the most intuitive advantage of transparency over opaque forms of camouflage is the ability to rapidly match multiple backgrounds. Static patterns are limited in how well they can match variable backgrounds (Hughes et al., 2019), and although we currently know of no study that has tested this assertion directly, transparency is expected to be effective over a wider range of backgrounds than any opaque pattern. Similarly, the efficacy of a static opaque pattern will be compromised by motion (Ioannou & Krause, 2009; Smart et al., 2020; Stevens & Ruxton, 2019), whereas the dynamic background matching produced by transparency may better disguise a moving organism. We may then expect transparency to be more likely to evolve in species that regularly switch between different backgrounds or are frequently in motion (Arias, Barbut, et al., 2021; Gomez et al., 2021).

Moreover, we may also expect transparency to evolve where there is no specific background against which camouflage may function (Galloway et al., 2020; Gomez et al., 2021). Where animals are not in contact with a solid substrate, such as pelagic species found suspended in the water column and flying species observed in the air, it may be nearly impossible to attain background matching using opaque colouration. Here, any opaque pattern is likely to be highly detectable as the background is both distant and orientation-dependent and camouflage may be broken by silhouetting and various depth cues.

Some support for these hypotheses may be inferred from the polymorphic shrimp, *Hippolyte obliquimanus*, where the transparent form is a more generalist forager, being more likely to move between substrates and spending more time exposed while swimming than the more sedentary opaque form (Duarte et al., 2016, 2017; Duarte & Flores, 2017). Moreover, in a predation study using artificial clearwing butterflies, Yeager et al. (2024) found some evidence to suggest that opaque but not transparent models suffered higher predation when flying than when perched. While these specific examples may be suggestive of a trend, more research is necessary to establish whether this pattern truly applies more generally across different taxa.

Alternatively, transparent camouflage may be favoured in, or restricted to, certain lighting conditions (Gomez et al., 2021; Johnsen, 2001; McFall-Ngai, 1990). High-light environments have been suggested to disadvantage transparent organisms, as they may induce specular reflectance (shine) and increase the need for UV protective pigments (Johnsen, 2001). Accordingly, in deep-sea cephalopods, which can switch from being transparent to being opaque, transparency is utilised in low light, but dark red/black pigments are revealed when the animal is illuminated (Zylinski & Johnsen, 2011). However, others have suggested the opposite for pelagic plankton and terrestrial lepidopterans. Here, although transparency may be more effective in low-light environments, selection for increased transparency may be greater in open, high-light environments where predators are better able to detect imperfections (Arias, Barbut, et al., 2021; Johnsen & Widder, 1998). Empirical studies have hitherto produced mixed results, and more work is needed to understand how lighting affects transparency more broadly.

Moreover, unlike opaque camouflage, transparency can also allow for camouflage against irradiant backgrounds where opaque bodies would cast a noticeable silhouette (Figure 2c). In the open ocean, pelagic animals may be viewed from below, silhouetted against the water column as they block downwelling light (Warrant & Locket, 2004). Silhouettes cannot easily be hidden with reflected light [but see mirroring (Cuthill, 2019; Johnsen, 2014)] and many oceanic predators have evolved specialised adaptations to search for the shadows cast by their prey (Johnsen, 2001, 2003, 2014; Warrant & Locket, 2004). Opaque species may evolve bioluminescent patches on their undersides to actively counterilluminate and disguise their silhouettes, but transparency offers a passive alternative (Johnsen, 2001, 2003, 2014). Intriguingly, such an effect may not be restricted to aquatic species, and the translucent wings of certain bats have been suggested to produce a similar background-matching effect against the night sky (Rydell et al., 2020). However, the benefits of such a strategy have thus far largely been inferred, rather than examined experimentally.

4.5 | Masquerade

An alternative to background matching or disruptive camouflage is to mimic an irrelevant inanimate object found in the environment, i.e., masquerade (Skelhorn et al., 2009). Many environmental structures mimicked by masquerading species include transparent or translucent elements, the most common of which may be damaged vegetation. Examples may include leaf-mimicking katydids (Tettigoniidae), leaf insects (Phyliidae) and mantids (Deroplatyidae) which have small translucent patches on the body or wing cases that may mimic holes in, or thinning of, the leaf membrane (Figure 1h). Including transparent elements will likely make masquerading species a closer match to their models; however, it remains to be seen whether apparent holes may also violate predator assumptions about the opacity or surface continuity of their prey (Costello et al., 2020).

Moreover, as masquerade can be size-dependent (Skelhorn et al., 2010), transparency may allow an organism to alter its apparent size and shape to mimic objects smaller than itself (Figure 1g). Empirical evidence to date is weak, but one example may be seen in the transparent shrimp, *Tozeuma carolinense*, where a thin dorsal line has been suggested to mimic a blade of seagrass (Cournoyer & Cohen, 2011). The role of transparency in masquerade strategies largely remains in a nascent state but is worthy of further examination given the findings from opaque species (Skelhorn et al., 2009).

4.6 | Concealing identity and motion

Thus far we have considered forms of concealment which are facilitated directly by transparency. Transparency may, however, be compatible with a range of other defensive strategies which deflect attacks, startle or conceal features such as identity, size, shape or motion (Kikuchi et al., 2023; Postema et al., 2022). In many cases, transparency itself may be best described as background matching, but combining multiple forms of concealment simultaneously may explain some deviation from hypothetical full transparency. These concepts have not yet been studied in transparent species, but we can identify some possible functions from studies on opaque species, which can help guide future research into transparency.

For example, iridescence can act as camouflage when the observer receives inconsistent and dynamic colour signals depending on viewing angle or lighting conditions (Kjernsmo et al., 2020; Thomas et al., 2023). The wings of certain butterflies (e.g. *Phanus vitreus* or *Greta annette*) and the bodies of certain fishes (e.g. *Kryptopterus vitreolus*) can exhibit either iridescence or transparency depending on the viewpoint (Figure 2a,b) (Fan et al., 2023; Finet et al., 2023). Iridescent transparency may provide similar benefits to those seen in opaque species by combining background matching with salient colours that distract or disrupt recognition (Kjernsmo et al., 2020; Thomas et al., 2023). Such effects may be particularly effective when in motion, as intermittent flashes of salient colouring may disrupt search image formation and motion tracking in opaque species (Loeffler-Henry et al., 2021; Murali, 2018).

5 | SIGNALLING

Transparency may intuitively be best suited for concealment, but can being transparent also help convey information? Camouflage and signalling are not mutually exclusive (Kikuchi et al., 2023; Postema et al., 2022) and transparent elements may be combined with opaque colours to alter the apparent size, shape or contrast of a signal. Alternatively, seemingly transparent surfaces may also selectively reflect and transmit particular wavelengths that are only visible under certain viewing conditions or only salient to the visual capabilities of certain observers. However, we should again distinguish between questions of whether transparency can be compatible with additional signalling elements and whether transparency itself can be utilised in communication.

5.1 | Communication

The role of transparency in social communication has not yet received much attention. However, by manipulating light transmission, novel communicative signals can be facilitated by transparency. One particularly noteworthy case is the brightly coloured, yet translucent, dewlaps of certain *Anolis* spp. and *Draco* spp. lizards (Fleishman et al., 2016; Klomp et al., 2017). By orienting themselves relative to the sun, the lizards can increase the amount of sunlight transmitted through the coloured skin to create a brighter and more salient signal than can be achieved by reflectance alone (Figure 1j) (Fleishman et al., 2016; Klomp et al., 2017). A similar effect has recently been suggested for certain *Papilio* spp. butterflies (Stavenga et al., 2023), but it is unknown how far such behaviour may extend to other species with translucent display structures, whether they be made of skin, scales, chitin or feathers.

Imperfect transparency may also permit communicative signals to evolve even if transparency itself may primarily act to promote camouflage. Iridescence, gloss and polarisation are often associated with communication in opaque species but in transparent species they have largely been assumed to be structural costs imposed on camouflage (Doucet & Meadows, 2009; Douglas et al., 2007). However, evidence from flies suggests that communication via such signals may be more widespread than currently recognised. For example, iridescent 'wing interference patterns' found on the otherwise transparent wings of male *Lispe*, *Chrysomya* and *Drosophilia* spp. are directed at females during courtship displays and specular reflectance (gloss) from the transparent wings of *Lucilia sericata* is used by males to locate females (Butterworth et al., 2021; Eichorn et al., 2017; Hawkes et al., 2019; Katayama et al., 2014; White et al., 2020; White & Latty, 2020). Similar deviations from true transparency are common and could facilitate salient intraspecific communicative signals more widely. However, many questions remain unanswered regarding how different species may perceive and respond to these colours under natural viewing and lighting conditions.

5.2 | Aposematism and mimicry

Aposematic species signal directly to predators that they are unpalatable or otherwise defended (Caro & Ruxton, 2019; Stevens & Ruxton, 2012). These signals are usually associated with conspicuous colours, but they may also be cryptic, as long as they are recognisable (Postema et al., 2022). We know of no studies directly testing whether predators can learn transparency as an aversive signal per se; however, as with communicative signals (see above) it is possible warning signals may be conveyed by apparent imperfections in transparency or emphasised when translucent species are backlit (e.g. Figure 1k).

The prevalence of transparency among both Batesian and Müllerian mimics (Box 1), however, does suggest that transparency itself can play at least some part in how predators recognise defended prey. Although aposematism is often associated with salient colouration, mimics often go beyond replicating these characteristics to also more generally approximate the features of the model's body shape and behaviour (Figure 1i). Consequently, if a model species exhibits transparent body elements, it stands to reason that transparency should also evolve in mimetic species, even if it initially had no direct role in camouflage or aversive signalling. Moreover, as defended species may incorporate camouflage into their aposematic signals, the role of transparency may counterintuitively differ between species within the same mimicry system. For example, it may arise primarily for camouflage in the model, but for aversion in the (co)mimic. Regardless of its initial evolution, however, once established mimics may be constrained to retain transparency, or risk undermining the overall efficacy of their defence.

In the Neotropics, many different unpalatable butterflies (predominantly the Ithomiini clearwings) belong to a Müllerian mimicry complex where members combine wing transparency with a bright white band (e.g. *Greta* spp., *Ithomia* spp. and *Oleria* spp.; Figure 1l) (Beccaloni, 1997; Chazot et al., 2016; McClure et al., 2019). These butterflies are less easily detected than closely related opaque and conspicuously coloured species (Arias et al., 2019; McClure et al., 2019). However, the white band has been shown to increase conspicuousness and act as an aposematic signal, increasing predation from naïve predators (Michalis, 2017) but decreasing attack rates from educated predators (Corral-Lopez et al., 2021). Although camouflage is likely playing some role, the importance and function of transparency may well differ between co-mimics, depending on whether advergence/convergence in camouflage or in aposematism was the predominant driving force behind the evolution of the phenotype.

Conversely, whereas unpalatable clearwing butterflies likely evolved transparency from an opaque ancestor for camouflage (McClure et al., 2019), we see the opposite trajectory in the mimetic damselfly, *Euthore fasciata*, which is a non-toxic Batesian mimic of clearwing butterflies (Corral-Lopez et al., 2021). Here, although the white band likely originated for mimicry, transparency was inherited from a non-mimetic ancestor and only later co-opted to further facilitate mimicry.

Intriguingly, among the putative mimics, transparency and the white wing band are both highly variable traits, with some sympatric opaque species having, and some transparent species lacking, the white band (e.g. *Pedaliodes peucestas* and *Ithomia pseudoagalla*, respectively). This raises the question of whether certain species are forgoing the aposematic or cryptic components of their defence, or whether predators now recognise both the opaque and transparent components as indicators of secondary defences. Indeed, a recent predation study, conducted in an area where Ithomiini clearwings are common, suggests that birds are broadly cautious of the clearwing phenotype, with low rates of predation being recorded for both local and novel combinations of bright colour and transparent wings (Yeager et al., 2024). Future work is needed to tease apart the role of camouflage and aposematism in mimicry complexes and test whether transparency itself can be recognised as an aversive signal (Gomez et al., 2021; Pinna et al., 2021).

6 | AVOIDING THE FUNCTION TRAP

The seemingly intuitive nature of transparency can risk leading us to make unsupported assumptions and premature conclusions about likely function. Concealment may be the most natural interpretation, but camouflage is not a single mechanism, and different perceptual processes may be disrupted depending on the size, arrangement and degree of transparency, as well as the environmental conditions under which the organism is observed. As we have discussed, transparency does not preclude additional functions, including signals related to communication, aposematism and/or mimicry, which may act independently, interactively or in the absence of camouflage.

Indeed, beyond visual ecology, transparency may also arise for thermoregulation, protection from UV irradiance, or as a non-functional by-product of other evolutionary and developmental processes (Gomez et al., 2021). For example, in the absence of pigmentation, many biological compounds may be naturally translucent such that some degree of light transmission is often the default state unless selection acts to increase opacity. This may be particularly relevant when examining small and thin organisms, as well as larvae/juveniles prior to the onset of pigment synthesis. However, care must be taken as the opposite also applies, and relaxed selection can result in the loss of unnecessary pigments (e.g. in cave dwelling fish or salamanders) which may then be erroneously interpreted as selection towards transparent camouflage.

How then can we best ensure that we correctly identify the function of transparency?

6.1 | Defining the evolutionary context and ecological significance

Transparency is often used as a catch-all descriptive term that has been applied to a wide variety of different phenotypes. To understand the function, we must therefore first define transparency and place it within its natural context. Terms such as *transparent*, *imperfect transparency*, *semi-transparent* and *translucent* have on occasion been used interchangeably to describe variation in the size of transparent patches, the amount of light transmitted through a structure and the degree to which a clear image is visible through the organism. These characteristics cannot easily be restricted to discrete categories, and as such terms are used extensively in common parlance, we refrain from defining them here. However, we encourage the use of clear descriptive terminology that defines the parameters and metrics used to assess transparency. We also emphasise the need for a whole phenotype perspective that highlights the effect transparency may have on the appearance of the organism, in the context of any opaque, semi-transparent or gradated regions, as well as the range of natural backgrounds and viewing conditions.

We should also exercise caution to avoid conflating questions regarding the evolutionary origins of transparency and the ecological role it may play today. As we have seen, in aposematic and mimetic species especially, transparency may evolve for reasons separate from the mechanisms studied in visual ecology but may later be co-opted into new functions. For example, many hoverflies (Syrphidae) and clearwing moths (Sesiidae) are Batesian mimics of aposematic wasps (Vespidae), and all three groups have transparent wings (Figure 1i). Matching the wing characteristics of their model therefore appears important for effective mimicry; however, hoverflies have inherited transparent wings from a non-mimetic ancestor, whereas clearwing moths have evolved transparency from an opaque ancestor.

Moreover, we should also be cautious in assuming a role of camouflage in transparency, despite the fact that transparency will unavoidably impart some reduction in detectability compared to many opaque alternatives. Indeed, although an apparent reduction in detectability does not necessarily mean camouflage has been an important part of the evolution of transparency, any concurrent effect of crypsis cannot be easily dismissed as irrelevant. We therefore suggest that care be taken to recognise the evolutionary context and identify the most likely alternative to transparency, as the most appropriate opaque comparison may not always be obvious. For example, should we be comparing transparency to a reduction in light transmission (e.g. darkening or increasing saturation), an increase in scattering (e.g. translucency) or a particular opaque pattern (e.g. the average colour of the background, random sample background matching or the patterning of a closely related species)?

6.2 | Understanding how transparency is perceived under natural conditions

Animal colouration (including transparency) evolves due to an interaction between the animal, its physical environment and the visual processing systems of the observer (Cuthill et al., 2017; Postema et al., 2022; Stevens, 2007; Troscianko et al., 2009). As with opaque colouration, to understand how transparency functions we first need to know how the organism appears to the observers that have driven its evolution. Depending on the focal organism, care must be taken as differences in colour perception and visual acuity mean that these species may perceive the signals in a manner quite different from that which our own vision permits (Cuthill et al., 2017). Consequently, we must identify the full range of ecologically important observers and signalling environments, so we can better assess the reflectance, absorption and crucially also transmittance of light we cannot perceive (e.g. UV and polarised light).

The perception of transparency will also depend on the physical characteristics and proximity of the background, as well as the dynamics of the lighting environment. Again, unlike opaque colouration, we need to consider the transmittance properties of the transparent organism, how this may be affected by the spectrum, intensity and angularity of natural illumination, and the importance of background luminance, colour and/or patterning. In this regard, observer orientation may be of particular consequence and will dictate whether an animal is perceived predominantly against an opaque reflective background, an irradiant background or suspended within a transparent medium (Figure 2).

Many authors have previously described in great detail how best to characterise colour, model visual perception and experimentally assess behavioural responses to visual cues, in a way that can help reveal the underlying functional mechanisms (Berg et al., 2020; Endler, 1978; Maia et al., 2019; Stevens et al., 2007; Tedore, 2024; Troscianko et al., 2017; Troscianko & Stevens, 2015; Vorobyev & Osorio, 1998). However, the context-dependent nature of transparency requires some careful methodological consideration, which will differ from those required for opaque signals. For example, artificial light (e.g. spectrophotometry lamps and camera flashes) can be extremely bright, so careful calibration is necessary to replicate the degree of light transmission occurring under natural conditions (Figure 2f). Similarly, quantifying colour will be background-dependent, requiring in situ measurements or modelling of wavelength absorption independent of background, especially when considering backlit visual scenes that can cause silhouettes.

7 | FUTURE DIRECTIONS

As we have seen, transparency appears to be associated with a wide range of different defensive and communicative functions. However, while there is some evidence to suggest a wide breadth of different applications, there is still a paucity of empirical studies into how transparency functions. As such, many potential functions that may seem likely or are predicted by theory are, in practice, strongly reliant on casual observations or inferences from experiments designed to address other questions. Yet, building off decades of work on opaque colouration offers a strong theoretical and conceptual foundation on which to build and contrast future work into transparency. Here, we highlight three particularly promising questions in need of renewed experimental attention:

1. *Where is transparency most effective, and where does it have an advantage over opaque colouration?*

Transparency and opaque colouration may fulfil the same function and be perceived by observers in a similar manner. Yet, it remains uncertain whether transparency may be a more, or indeed less, effective means of concealment or signalling. Some direct comparisons between opaque and transparent versions of the same signal (e.g. opaque versus transparent background matching or disruptive camouflage) have been conducted (Arias et al., 2020; Arias, Leroy, et al., 2021). However, it is still unknown how factors such as behaviour and background opacity, patterning, complexity, heterogeneity or lighting may affect the efficacy of both cryptic and salient functions of transparency. For example, there is no clear consensus on what lighting conditions may favour transparency, and it remains unknown whether transparency may be more effective than opaque forms of concealment where the background or lighting is heterogeneous or dynamic, or where the organism is frequently viewed against an irradiant or distant background.

2. *How do different observers perceive and understand transparent structures?*

We also lack a deeper understanding of how transparent organisms are perceived and recognised by different observers. This is true both in terms of the processing of visual information and the cognitive interpretation of transparent surfaces. For example, although cone capture models are widely used, the reflectance and transmittance properties of many seemingly transparent organisms have not yet been fully characterised across the whole range of visible light (e.g. ultraviolet or polarised light). Similarly, we also do not have a clear picture of how differences in observer colour perception, visual acuity, viewing distance, viewing angle and depth perception may affect the perception of transparent organisms. What is more, cognitive processing also deserves empirical examination. Here, innate assumptions about surface continuity, integrity or the opacity of other organisms may be violated in a manner distinct from that produced by opaque colouration. Such effects may have implications for target recognition, identification, segmentation and search image formation.

3. *How do multiple functions interact?*

The field of visual ecology is increasingly examining how multiple, often competing or seemingly contradictory, functions may be expressed and successfully function sequentially or simultaneously (Kikuchi et al., 2023; Postema et al., 2022). As we have noted, transparency is often combined with salient opaque or structural colours that have the potential to facilitate concealment, confuse observers or convey information. As with opaque colouration, the dominant strategy may differ depending on microhabitat context, observer visual perception, viewing distance and angle or through hidden signals and behavioural displays. Many questions remain regarding how transparent components may alter the apparent size or contrast of opaque signals as well as whether opaque or incidental colours necessarily impart costs or if they may instead be co-opted into other anti-predatory or signalling functions.

8 | CONCLUSION

Transparency is perhaps one of the most intriguing morphological adaptations. Far from being a simple means by which to achieve camouflage, it instead represents a multitude of different complimentary and potentially competing functions. Although transparency has currently only been studied in a small number of species, varying degrees of 'imperfect' transparency are likely much more common than currently recognised. While camouflage has clearly played a major role in the evolution of transparency, concealment can be achieved in many ways and aposematism, mimicry and communication can all function through or in conjunction with transparency. As such, rather than being a unique defensive strategy, transparency instead provides an alternate route by which other functions can be achieved. Transparency does, however, also produce a unique set of optical effects, physiological constraints and ecological opportunities that may differ greatly from species with opaque colouration. Understanding these differences opens the door to a diverse array of studies which can blend diverse disciplines including evolution, development, sensory ecology and biophysics. Yet, despite transparency being of interest to many different fields, many basic questions remain in behavioural and evolutionary ecology.

AUTHOR CONTRIBUTIONS

James B. Barnett, Justin Yeager and Karin Kjernsmo conceived of the project and contributed equally to the development of the ideas. James B. Barnett led the writing of the first draft. James B. Barnett, Justin Yeager and Karin Kjernsmo contributed to the subsequent drafts and gave final approval for publication.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

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This manuscript contains no data.

ORCID

James B. Barnett https://orcid.org/0000-0001-9789-4132
Justin Yeager https://orcid.org/0000-0001-8692-6311

Karin Kjernsmo https://orcid.org/0000-0002-8570-0406

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