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COMMENTARY

# Emerging frontiers in visual ecology

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## ABSTRACT

Visual ecology, the study of how animals acquire and respond to visual information in nature, has grown rapidly over the past few decades. Research in this field has transformed our understanding of fundamental processes, such as the neurobiological basis of behavior and the diversification of species through sensory drive. The recent growth in the field has been accompanied by leaps in our understanding of the diversity of visual systems and in the development of novel technologies and techniques (for example, those allowing us to measure scenes and signals). With such growth, however, it is more important than ever to integrate wide perspectives and expertise to move the field forward in the most productive way. To that end, in summer 2024, 30 visual ecologists from around the world – spanning all career stages – met to discuss the state of the field. From that meeting, we identified two broad emerging themes in the study of visual ecology. (1) Can we further 'step inside' the perceptual experience of a non-human animal? (2) Can foundational 'rules' of vision and visual stimuli be identified? Although large questions such as these can feel unanswerable, this is where some of the most exciting discoveries in visual ecology remain to be made. Here, we outline eight relevant areas of research and identify ways in which researchers can bring us closer to answering these complex questions.

**KEY WORDS: Animal vision, Visual physiology, Color vision, Spatial vision, Motion vision, Perceptual processing**

## Introduction

Visual ecology – the study of how animals perceive and use visual information in interactions with each other and their environments – has advanced significantly since its inception in the early 20th century. Visual ecology as a field was born out of the realization that the visual capabilities of animals are diverse and thus, must be taken into account when studying how animals appear to others, and how they respond to or perceive visual stimuli (Cronin, 1988; Cronin et al., 2014; Hughes, 1977; Land, 1997; Land and Nilsson, 2002; Loew and Lythgoe, 1978; Lythgoe, 1979; Walls, 1942; Warrant and Nilsson, 2006). The field has grown enormously as visual ecology has moved from descriptive studies to more quantitative analyses, and as researchers have developed sophisticated tools to measure numerous aspects of animal vision and visual scenes. With these recent advancements, we are now poised to answer fundamental, yet unresolved, questions. Applying integrative approaches to address these open questions may not only shape the future of visual ecology, but also increase our understanding of evolution and biological diversity, and inspire new technologies. In light of this, 30 visual ecologists from around the globe, representing a variety of career stages and sub-fields, met in 2024 to share their research, discuss the current state of the field, and identify emerging frontiers in visual ecology. From this meeting, two overarching questions emerged. Firstly, can we 'step inside' the perceptual experience of an animal? In other words, can we truly see the world from the perspective of another species, and understand how ecological and evolutionary forces shape these perceptual worlds? Despite years of research on vision and animal behavior, we still lack a deep understanding of how different species perceive their environments, and how these perceptions affect survival, communication and behavior. Secondly, can foundational 'rules' of vision and visual stimuli be identified? We are poised to ask why so many aspects of visual mechanism and visual stimuli seem consistent across species. Certain phenomena seem to have near universal significance in the visual world (e.g. red as a terrestrial warning coloration; Stevens and Ruxton, 2012), but the optical, physiological and behavioral underpinnings of that universality remain to be explored.

Such large questions can feel unanswerable, so our aim here is to identify feasible ways in which researchers can contribute. Thus, within this Commentary, we identify and discuss eight specific areas of research that fall within the two overarching questions. We hope this discussion will spark new investigations that bring us closer to answering these complex and exciting questions.

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## Glossary

**Contrast sensitivity**
The ability of a visual system to discriminate two adjacent regions of differing brightnesses. Formally defined as the inverse of the minimum percent difference in brightness that can be detected.

**Photopic vision**
Vision under bright illumination, typically daylight either on land or in shallow water, as opposed to scotopic vision, which is found at night or in the deep sea. The distinction is most often used in vertebrates, where photopic vision is typically dominated by cones and thus includes the ability to see color, and scotopic vision is typically dominated by rods and thus is monochromatic. In humans, the transition from photopic to scotopic vision occurs in late twilight.

**Pseudogenized**
A process by which a gene cannot encode its original functional products, often due to mutations or deletions in its genomic sequence.

**Sensory drive**
A hypothesis in visual ecology that states that the evolution of both visual signals and visual perception is influenced by the optical environment. For example, the eyes of deep-sea organisms are typically most sensitive to the predominant wavelengths of sunlight that transmit best through deep water.

**Spectral sensitivity**
The differential sensitivity of a visual system to different wavelengths of light. This is affected not only by the classes of expressed opsins, but also by the transmission characteristics of various components of the eye and downstream visual processing, and the abundances and classes of photoreceptor cells.

**Temporal resolution**
The ability of the visual system to accurately differentiate visual information that varies in time; often thought of as the ‘shutter speed’ of the eye. Formally defined as the maximum frequency of a square wave stimulus of light pulses that can be accurately transduced into neural signals.

**Visual acuity**
The ability of the visual system to render spatial detail. Formally defined as the number of line pairs of alternating black and white stripes that can be resolved within a degree of visual space, and thus given in units of cycles per degree.

## Can we step inside the perceptual experience of an animal?

Visual perception begins when light is transduced by the retina, after which retinal and higher-level processes filter, transform, enhance or simplify information, resulting in perception (Akre and Johnsen, 2014; Tibbetts et al., 2024; Wehner, 1987; Fig. 1). Much research has focused on characterizing animal visual systems, particularly the number, proportion and sensitivities of photoreceptor types (Cronin et al., 2014; Land and Nilsson, 2002). As yet, however, we have a limited understanding of how numerous factors, from variation in visual capability within and between individuals to environmental context, influence perceptual experiences. The four areas of research that we outline within this section should help to address these unknowns.

### How much does vision vary between and within individuals, and what are the consequences of this variation?

Within an individual, there is often considerable variation in photoreceptor types and their distribution, including spatially across the retina (Temple et al., 2010), throughout development (Shand et al., 2002), between eyes (Hart et al., 2000), between individuals (Hofer et al., 2005) and across habitats (Fuller et al., 2003). Although the mechanistic bases for much of this variability are well established (e.g. changes in opsin expression, chromophore type, intraocular filtering; reviewed in Temple, 2011), the functional consequences and ultimate causes of this variation are less well understood.

Spatial, ontogenetic and phenotypic variation in photoreceptor spectral sensitivities (see Glossary) may reflect changes in the intensity and spectrum of ambient light (Owens et al., 2012; Novales Flamarique et al., 2013). The assumption is that such changes improve absolute sensitivity, contrast detection or color discrimination in ways that facilitate prey capture, predator avoidance or other behaviors. However, although this is broadly true for some taxa (Loew and Lythgoe, 1978), the correlation between visual system variation and optical habitat can be elusive (Hofmann et al., 2010). Fine-scale intra- and inter-individual variation in spectral sensitivity have been observed in few species, and in fewer still have the functional consequences been tested empirically (Wortel et al., 1984), making it difficult to know whether such variations are adaptive, result from developmental/ontogenetic constraints or are neutral polymorphisms.

Spatial variation in the density of photoreceptive units (e.g. photoreceptors, ommatidia) affects visual acuity (see Glossary) and may be correlated with aspects of ecology, including behavior (Querubin et al., 2009), illumination (Warrant, 2004) and habitat (Hughes, 1977). However, much remains to be learned by, for example, pairing information about the spatial distribution of cell types in the retina with natural scene statistics in diverse taxa. Future studies should assess intraspecific differences, for example, those occurring between left and right eyes (Coimbra et al., 2014; Hunt et al., 2018), among age classes (Fitzgerald et al., 2001) and between sexes (Zeil, 1983).

### What is the relationship between the stimuli that strike the retina and what is perceived?

Our knowledge about how visual information is encoded in the brain across species is limited, despite recent advances in non-primates (e.g. Baden, 2021; Szatko et al., 2020; Heath et al., 2020; Matsushita et al., 2022). Comparative studies are needed to further understand processes such as opponency between photoreceptors (Fig. 1C), which underpins color vision. Examining visual system structure and circuitry may inspire novel approaches for ecologically valid explorations of animal vision. For example, color testing with spatially and temporally dynamic stimuli that leverage natural behavior has been used to dissect chromatic and achromatic pathways in *Drosophila* (Schnaitmann et al., 2018).

In most species, investigating neural circuitry is challenging because we lack genetic and molecular tools. As a result, downstream processes are typically inferred by linking sensory input measures, such as photon catch and image statistics, to behavioral output. Indeed, some aspects of retinal and early visual processing, such as contrast coding, edge enhancement and chromatic/achromatic segregation, play critical roles in shaping perception (e.g. Wertlen et al., 2008; Mitchell, et al., 2017). However, such measures may account for only a fraction of the visual and cognitive processes driving behavior (e.g. Green et al., 2022; Troscianko et al., 2017), given that downstream neural pathways accomplish filtering, color constancy, feature extraction, categorization and object recognition (e.g. Jones et al., 2001; Caves et al., 2018b; Avargues-Weber et al., 2010; Kinoshita et al., 2012; Langridge et al., 2021). Further understanding of both peripheral and central visual processing will help us to better understand how retinal input is related to perception.

Although key principles in visual coding are conserved across phyla (Sanes and Zipursky, 2010), expanding behavioral studies to a wider range of species is crucial for identifying the mechanisms and specializations of visually guided behaviors. Developing novel and ecologically relevant stimuli is vital, as in studies on the triggerfish

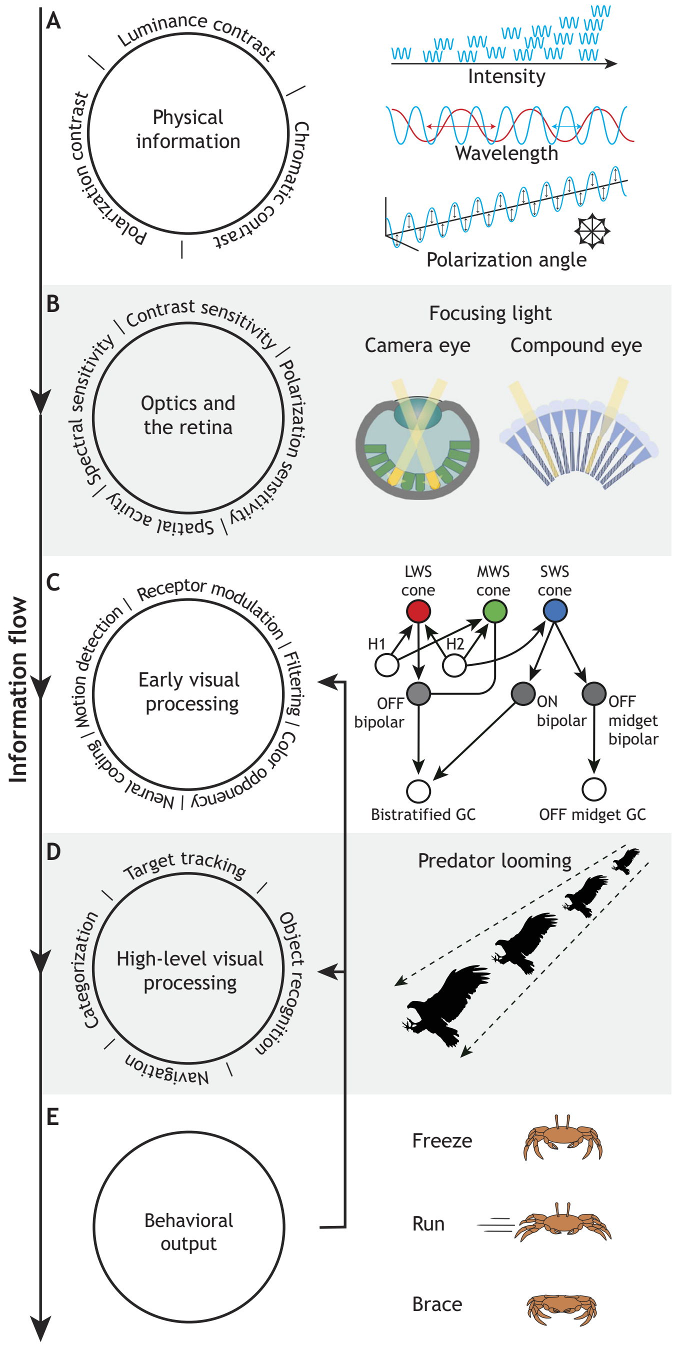

**Fig. 1. The flow of information from environmental light to behavioral output.** For each step along the pathway of information flow (left), the figure also shows relevant illustrative examples (right). (A) The properties of light used by an organism's visual system include its intensity (luminance contrast), wavelength (chromatic contrast), and degree and angle of polarization (polarization contrast). Whether an organism uses these properties depends on their ability to sense differences within each property. (B) The optics of the eye and the composition of the retina are the first limiting factors to vision. To see differences in the properties of light, light must be reasonably focused onto a retina comprising an array of photoreceptive cells (images on the right are redrawn from Nilsson, 2021 and show two different eye types with different focusing mechanisms). These factors determine visual capabilities including contrast sensitivity, spatial acuity, polarization sensitivity and spectral sensitivity. (C) Once light has entered the eye and been converted to a neural signal, early visual processing occurs within the retina and beyond. This early visual processing includes receptor modulation, for example by the horizontal cells (H1 and H2 in the schematic) in vertebrate eyes, spatial filtering, neural coding, motion detection and color-opponent processing. The schematic on the right is redrawn from Kelber, 2016, and shows an example of the mammalian color-opponent process illustrating the processing of signals from different photoreceptors in an antagonistic manner. LWS, long-wavelength sensitive; MWS, medium-wavelength sensitive; SWS, short-wavelength sensitive cones; GC, ganglion cell. (D) Stimuli and signals then undergo higher-level visual processing, such as categorization, target tracking, object recognition and navigation. For example, looming stimuli can be used to investigate predator detection and identify the visual circuits involved in the defensive responses of prey animals. (E) Higher-level visual processing of stimuli elicits reliable behavioral outputs (such as those investigated in fiddler crabs; Donohue et al., 2022) that can be used to predict the detection mechanisms involved in visual processing. These behavioral outputs are also known to influence processing in a top-down manner, whereby neurons involved in visual processing adapt their responses according to behavioral context, generating a feedback pathway (represented by the upwards arrow between 'Behavioral output' and 'Early visual processing').

*Rhinecanthus aculeatus*; these studies integrate visual stimuli with foraging tasks (Fig. 2A) (e.g. Cheney et al., 2019).

### How does context affect perception, processing and behavioural output?

Linking retinal and higher-order processes with behavioral output will be crucial to understand perception, but studies must also consider a range of contextual factors that determine how visual cues are processed, perceived and responded to (Ulanovsky, 2025). Both environmental conditions and an animal's internal state can impact the detectability of visual cues and the motivation to respond. For instance, the response of prey to visual danger can vary moment to moment as predator detectability changes with visibility or background characteristics (Fleishman, 1986; Metcalfe, 1984), or over longer time periods with changes in hunger levels (Oates et al., 2019) or seasonal changes in visual neurophysiology (Sztarker and Tomsic, 2008). These contextual influences on responses to visual stimuli have been demonstrated in many essential tasks, including mate choice, foraging and navigation.

Contextual influences are well illustrated in studies on navigation. As animals move through the world, directional cues – such as the sun, stars, geomagnetic field or wind – can fluctuate in relevance, availability and salience depending on location, weather, time of day or terrain. Navigators thus need to weigh and prioritize cues according to their current information value. Such dynamic weighting of directional cues has, for example, been identified in a day-active dung beetle (Fig. 2B): at noon, when sun compass input is unreliable, this information is temporarily de-prioritized by the beetle (Dacke et al., 2019). However, we still do not understand the fundamental principles for how weighting of varying directional inputs is controlled in biological compass systems.

Despite the importance of context, stimuli and scenes presented in visual ecology experiments are often simplified to target one aspect of vision. Although this approach can provide an understanding of mechanisms or functions, we risk overlooking the influence of contextual factors on visual behavior. Improved foundational knowledge and advances in technology – such as UV-visible virtual reality equipment (Kócsi et al., 2020) and physiological recordings from behaving animals (Ache et al., 2019) – paired with research that addresses how internal and external factors affect visual processing, perception and behavior, will help the field of visual ecology become more multidimensional and holistic.

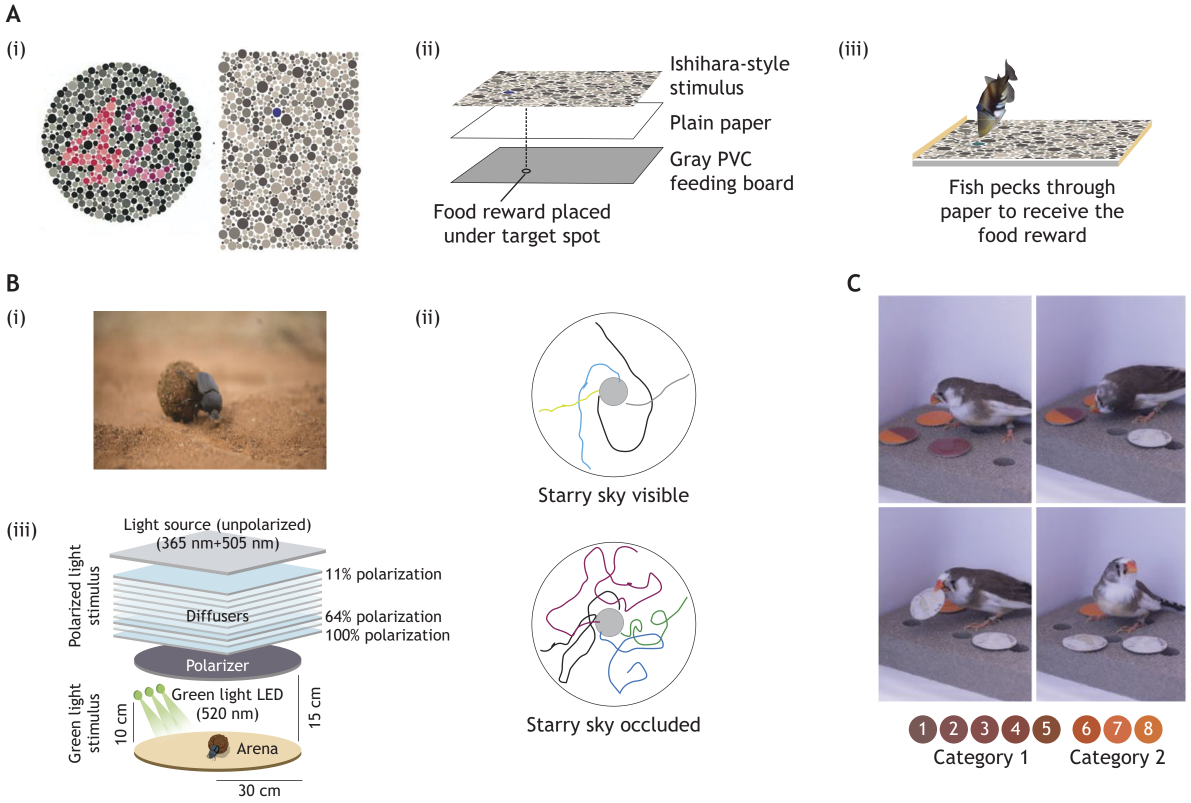

**Fig. 2. A variety of experimental techniques are moving us towards greater understanding of animal perceptual experiences.** (A) In the triggerfish *Rhinecanthus aculeatus*, Ishihara-style stimuli (i) have been developed and combined with a naturalistic foraging task (ii) to test whether triggerfish (iii) can discriminate various differences in chromaticity (saturation and hue). (B) Navigation in (i) the dung beetle *Scarabaeus satyrus* has been explored both (ii) under naturalistic circumstances in which visibility of the night sky varied (either due to weather or 'occlusion' of dung beetle vision) as well as (iii) under experimental conditions that allowed for visual factors, such as polarization of light, to be manipulated to test how those cues are weighted in navigation decisions under different circumstances. (C) Categorical color perception has been shown in zebra finches using (i) a colour-discrimination foraging task on (ii) a continuous range of colors similar to those of male beaks, a mate choice signal, which revealed that zebra finches perceive these color variants as belonging to two distinct categories. Images in A reproduced from Cheney et al., 2019; photo credit for Bi: Marie Dacke; Bii tracks redrawn from Dacke et al., 2013; Biii reproduced from Khaldy et al., 2022; photo credit for C: Ryan Huang, Terra Communications LLC.

### What are the ecological and evolutionary impacts of perception?

What an animal perceives ultimately informs its decisions. Thus, perception can influence ecology (e.g. navigation, communication and foraging) and evolution (e.g. coevolution between signalers and receivers). However, we currently have a limited understanding of the ecological and evolutionary impacts of many aspects of visual experience. Beyond color, which is relatively well studied, visual scenes comprise spatial (Caves et al., 2018a; Stoddard and Osorio, 2019), achromatic and temporal information (Rosenthal, 2007). Perception of this information depends on visual acuity, contrast sensitivity and temporal resolution (see Glossary; Bruce et al., 2014). More research into these aspects of vision would improve our understanding of evolutionary processes, including co-evolutionary dynamics, speciation and how sensory preferences evolve. Exploring perception holistically could be particularly fruitful in investigations of sensory drive (see Glossary; Endler, 1992), a foundational hypothesis positing that visual signals and receiver visual capabilities both evolve under selection to optimize signal efficacy. Although current support for sensory drive is not strong in terrestrial environments (Cummings and Endler, 2018), expanding our view of sensory drive beyond color to include other aspects of scenes (e.g. spatial information, Hulse et al., 2020), information processing (Renoult and Mendelson, 2019) or higher-order processing could reveal stronger support for this hypothesis.

As discussed above, visual experiences also involve higher-level processes and are influenced by context (e.g. Simpson et al., 2016; Sandkam et al., 2016). Such processes include generalization, categorical perception (Fig. 2C), learning and proportional processing. Although these factors are receiving increased attention (Akre and Johnsen, 2014; Caves and Kelley, 2023; Caves et al., 2018b; Dixit et al., 2021; Green et al., 2020; Hanley et al., 2021; Kelley and Kelley, 2014; Zipple et al., 2019), our understanding of perception would benefit from studying why they arise (e.g. due to selection or as byproducts of sensory physiology) and how they vary with contextual factors and across taxa (e.g. Worsley et al., 2025). Additionally, the hypothesized consequences of higher-order perceptual biases and processes – such as evolved mechanisms for generalizing similarly colored food sources or potential mates – offer promising avenues for future research (Ryan and Cummings, 2013).

### Can foundational 'rules' of vision and visual stimuli be identified?

A historical perspective in visual ecology centers on the idea that the various features of visual systems, at least at the level of the retina, have evolved as adaptations to the optical environment, assigning functional significance to each feature and a predominant role of ecology in their evolution (e.g. Walls, 1942; Lythgoe, 1979). However, research syntheses have revealed that visual system traits

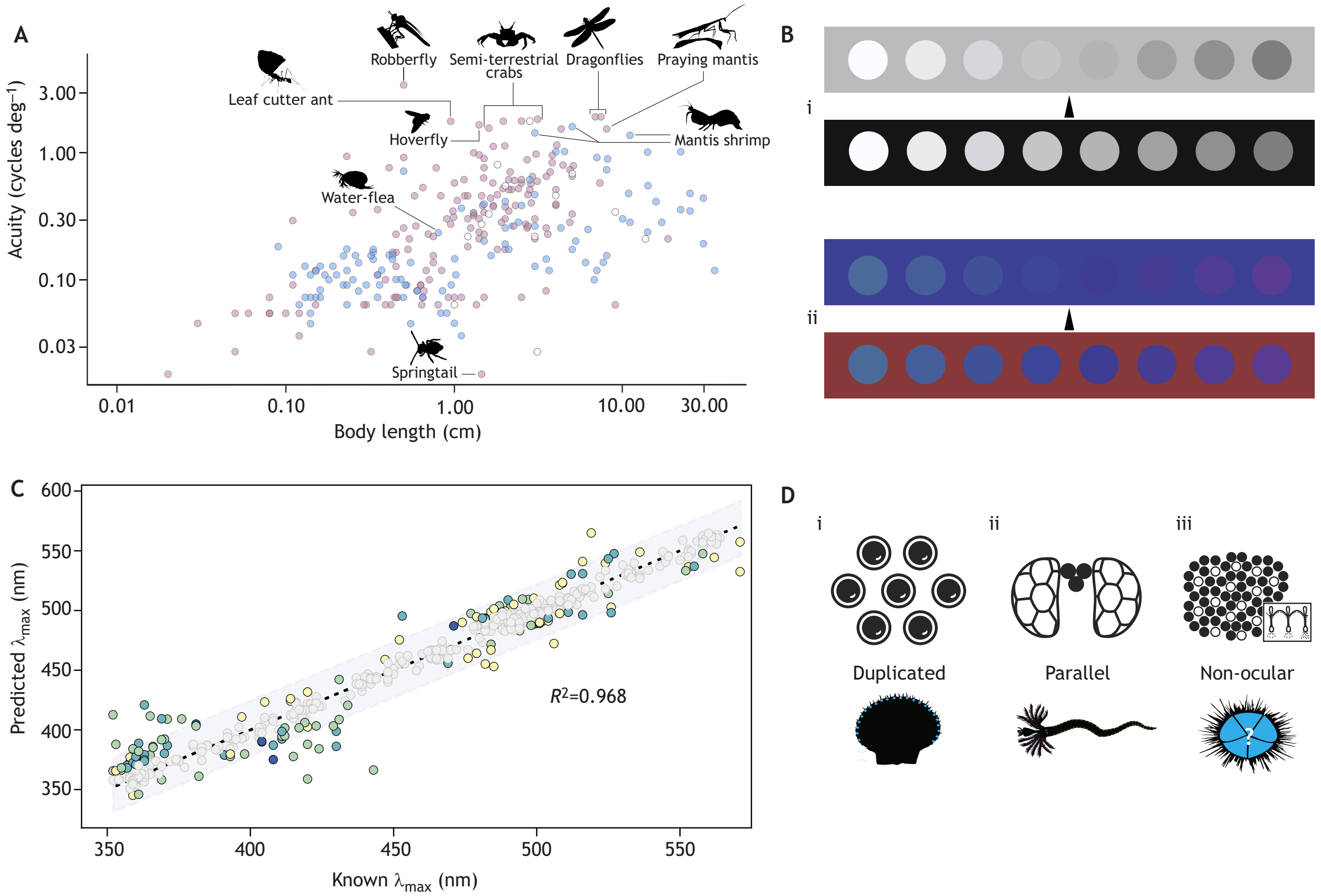

**Fig. 3. Non-classical considerations in visual ecology reveal both predictable trends and evolutionary novelty in animal vision.** (A) Visual acuity among arthropods scales with body length and is predicted by factors that include being a species that is terrestrial (pink markers), aquatic (blue markers) or both (white markers). (B) In an effect known as 'crispening,' discrimination between neighboring circles is easiest when the background (i) brightness or (ii) chromaticity is intermediate to the stimuli being compared; this location is indicated by the black arrows. Additionally, discriminating between the circles on either side of the black arrow is easier when the background is more similar in brightness or hue to the stimuli being compared (the upper bar in each case). (C) Spectral tuning by variation in opsin amino acid sequences allows machine learning to predict the wavelengths of maximum absorbance ($\lambda_{max}$) for vertebrate opsins. Predictions where the difference between the 'known' and 'predicted' $\lambda_{max}$ is less than 10 nm are shown as gray dots, whereas those greater than 10 nm are shown as colored dots. The colors indicate differences in the types of opsin variants used, and the light gray area surrounding the trend line is a 95% confidence interval. (D) Distributed visual system architectures can be (i) 'duplicated' with functionally identical eyes repeated many times, (ii) 'parallel' by using multiple types of eye or (iii) 'non-ocular' with individual photoreceptors interspersed with pigment cells over the body surface. Images in A are modified from Feller et al., 2021; B from Caves et al., 2024 (https://creativecommons.org/licenses/by-nc/4.0/); C is reproduced from Frazer et al., 2024 (https://creativecommons.org/licenses/by-nc/4.0/); and D from Sumner-Rooney, 2023.

are not always predicted by the optical environment, challenging this view of how visual systems evolve (e.g. Caves et al., 2017; Schweikert et al., 2018). One important pursuit is a more holistic understanding of the forces that shape visual systems, considering the optical environment along with other determining factors, and the real-world sensory experiences that have resulted in both predictable trends and evolutionary novelty in animal vision (Fig. 3). Four specific areas of research that would contribute to this goal are discussed in more detail below.

### To what extent can observed commonalities among signals and senses be attributed to the spectral and spatiotemporal aspects of optical habitats?

All animals exist in the context of their habitats, which shape the evolution of sensory systems and signals (Endler, 1992). For example, animals in dim light often rely on contrast instead of color (Penteriani and Delgado, 2017; Burford and Robison, 2020), and aquatic spectra are limited relative to those on land (Warrant and Johnsen, 2013), leading to tuning of both signals and vision (Cummings and Endler, 2018; Warrant and Locket, 2004). However, habitat variability and complexity can make elucidating environmental effects challenging, because species can evolve signals that achieve equal visibility in multiple ways (Kemp et al., 2023). Moreover, signal perception is shaped by habitat and by perceptual processing, which collectively determine which signal traits are salient (Fig. 3B). Thus, we must treat signals as integrated phenotypes (van den Berg et al., 2020; Caves et al., 2024) and assess how they appear across the range of signaling conditions (e.g. time of day, microhabitat). By modelling what information from a signal is available and how it shifts with changes in conditions and receivers, we can identify which aspects of habitats are predictive of signaling traits. For instance, changing illumination affects hue more than achromatic contrast. If we characterize which aspects of habitats are most important to a given signal, we can apply color or pattern spaces (Stoddard and Osorio, 2019) to compare the theoretical versus actual ranges of equally visible signals. By comparing across habitat and context, it may be possible to place habitats along a spectrum of 'restrictive' to 'permissive' and predict which environments no longer impose significant constraints on signaling.

Finally, in comparison to the spatial and chromatic aspects of vision and signals, motion remains relatively understudied (Hutton et al., 2015; Cuthill et al., 2019; Tan and Elgar, 2021). Although studies on motion in signals and habitats have been few, they underscore its importance. For example, research on *Anolis* and other lizards demonstrates effects of vegetation motion on signal detection and form (Fleishman, 1992; Ord et al., 2007; Bian et al., 2021). In shallow aquatic environments, shifting light patterns (caustics) affect prey detection (Matchette et al., 2020), camouflage strategy (Drerup et al., 2024b), habitat choice (Attwell et al., 2021) and evolution of vision (Collin et al., 2000; Venables et al., 2022). Moving forward, patterns and predictors of motion should be quantified across habitats – especially as they relate to how organisms discriminate objects from their visual background – to ask how motion in optical habitats affects signal evolution.

### What are the forces that govern the 'rules' of vision, especially as they relate to physiological and metabolic requirements along with ecological need?

Although the optical environment may shape signals, it is only one of several factors that should be considered in the evolution of visual systems. Visual systems are costly and thus are thought to operate under strong selective pressure (Niven and Laughlin, 2008), especially regarding light availability (Laughlin, 2001). This tradeoff between cost and function seems to explain many visual system characteristics, such as cellular organization of the retina (Hauzman et al., 2018), metrics of visual performance (Caves et al., 2017; Schweikert et al., 2018, 2019) and trends in relative eye size (Howland et al., 2004; Schweikert et al., 2022). Amid these characteristics, however, are conserved trends across visual systems that appear to be unexplained by the demands of the optical environment. Across animal groups, for example, eye size scales allometrically with body size and as larger eyes tend to collect more light, they often confer better sensitivity and visual acuity (Cronin et al., 2014) (Fig. 3A). As absolute eye size is guided, at least in part, by developmental program (Corral-López et al., 2017), enhanced visual capability in certain animals (and its concurrent metabolic investment; Laughlin, 2001) may not directly contribute to fitness. Thus, eye size scaling may represent one 'rule' of vision where developmental program is a greater factor in shaping visual systems than either metabolic limitations or ecological demands alone.

Similar arguments can be made for the conserved neural architectures of visual systems, such as the near ubiquity of duplex retinae (which contain both rod and cone photoreceptor cells) among mammals (Ahnelt and Kolb, 2000). Duplex retinae exist in fossorial mammals (for which photopic vision may be unimportant; Emerling and Springer, 2014) and even in those with pseudogenized (see Glossary) cone opsin genes (Schweikert et al., 2016). Studies of retinal pathology suggest that maintaining each photoreceptor type is necessary to preserve the overall structural integrity of the mammalian retina (Jones et al., 2003). Thus, the presence of cones in these animals, and by extension, any putative capacity for photopic vision (see Glossary), may only serve to protect the retina for other visual or non-visual functions (e.g. circadian photoentrainment).

Environmental factors beyond light, such as temperature (Beatty, 1984) and oxygen levels (McCormick and Levin, 2017), also shape visual systems. A retina requires substantial oxygen, so in hypoxic environments, vision will either be constrained (e.g. Robinson et al., 2013) or must overcome this limitation (e.g. Country and Jonz, 2022). In addition, higher temperatures increase spurious visual pigment activation, a problem that worsens as peak sensitivities shift towards longer wavelengths, perhaps placing a broader constraint on the spectral sensitivity of vision (Luk et al., 2016).

### What are the links between genotype and phenotype as it relates to the diversification, functional significance and ecological relevance of opsin evolution?

Although diverse factors shape animal vision, visual function is often tightly linked to the underlying structure of the visual system, providing opportunities to discover mechanistic bases for visual phenotypes. Nevertheless, connecting specific genes to organismal phenotypes remains challenging, especially because phenotypes are often complex, hierarchical and dependent on the interactions of many genes. Therefore, even the best-studied cases linking genes and phenotypes (for example, of animal visual pigments) demand caution when inferring their connection.

Visual pigments are a core building block of most animal visual systems through their role in light sensing (Porter et al., 2012). Visual pigments, composed of an opsin protein plus bound chromophore, influence sensitivity to different wavelengths of light, which is critical for environmental tuning of visual systems and for color vision (Bowmaker, 2008). Differences in spectral absorption of visual pigments often occur through amino acid differences in opsin proteins that alter chromophore binding (Yokoyama et al., 2005). Thanks to low-cost gene sequencing, opsins of many taxa are now sequenced (Ramirez et al., 2016), and new statistical techniques are helping to couple opsin sequences with functional information (e.g. visual pigment absorbance) derived from decades of research on opsin function (Frazer et al., 2024; Fig. 3C).

However, this map between opsin sequence and visual function is complicated, such that sequencing opsin genes may not necessarily allow for accurate predictions of more-complex functions, including light sensitivity, color vision or even spectral tuning. First, predicting complex visual functions depends on quantifying underlying gene expression, which remains relatively laborious and expensive. Even with knowledge of expression, we have much to learn about how expression level, co-expression and phenotypic plasticity of expression influence visual functions. Beyond expression, wavelength-specific filtering of light by lenses, screening pigments and other elements is absent from opsin-only predictions. Adding more challenges, neural processes that compare spectrally distinct photoreceptors to each other are poorly understood (van der Kooi, 2021), except for in a few model systems (Baden, 2021; Grünert and Martin, 2021; Currier et al., 2023), yet models of color vision often assume opponency. Additionally, how neural processes integrate light information with cognition and motor pathways is only beginning to be understood in some systems (Baden, 2021; Grünert and Martin, 2021; Currier et al., 2023). Each level of organization affects the interaction and evolution of organisms within their optical environments. In sum, even when the light absorption of a particular visual pigment is known, the map between genotype and organismal function remains full of critical unknowns, each requiring investigation. Therefore, although an important step forward, advances in genotype–phenotype maps highlight the significant work still needed to bridge genes and fitness.

### How do non-canonical visual systems work?

Some visual systems challenge classical views regarding the detection and processing of visual information (Fig. 3D). For example, distributed visual systems challenge expectations set by cephalic visual systems in which two primary eyes on a head are paired with visual processing centers in a brain (Buschbeck and Bok, 2023). Animals with distributed vision not only have many separate light-sensing organs, but they also tend to have relatively decentralized nervous systems that lack obvious visual processing centers. Studying distributed vision is challenging, but it also promises to expand our knowledge of how decentralized sensory networks acquire and process information, and how eyes and nervous systems co-evolve.

The first challenge in studying distributed vision is establishing mechanistic relationships between organ-level and system-level performance. Doing so will require modelling distributed visual systems as integrated multi-sensor networks (e.g. Li et al., 2023), because animals with distributed vision can demonstrate light-influenced behaviors that are not obviously predicted by the structure and function of their individual light-sensing organs. Echinoderms such as sea urchins (Kirwan et al., 2018) and brittle stars (Sumner-Rooney et al., 2019), for example, demonstrate spatial vision despite lacking eyespots or eyes. As another example, eyed chitons are sensitive to the angle of polarized light despite none of their eyes being individually polarization sensitive (Chappell and Speiser, 2023; Li et al., 2015).

A second challenge is establishing how animals with distributed vision process spatial information. Intriguingly, these animals behave as if they assemble coherent neural maps of their surroundings: box jellyfish use vision to stay close to shore while dodging underwater obstacles (Garm et al., 2007, 2011), and scallops visually track moving objects with their sensory tentacles (Chappell et al., 2021). Based on their neural architectures, animals with distributed vision must take novel approaches to visual processing, such as forming decentralized (receptive field-based) visual maps in medullary cords (Chappell and Speiser, 2023) or centralized (eye distribution-based) visual maps in non-cephalic ganglia (Spagnolia and Wilkens, 1983).

A third challenge is learning how and why distributed vision evolves so frequently. At a minimum, distributed visual systems have evolved eight times among cnidarians (Picciani et al., 2018), five times among pteriomorphian bivalves (Audino et al., 2020), four times among chitons (Varney et al., 2024) and multiple times each among fan worms (Bok et al., 2016) and echinoderms (Sumner-Rooney and Ullrich-Lüter, 2023). In many of these lineages, the origins of distributed vision do not appear to be accompanied by significant changes in neural architecture, suggesting that distributed visual systems evolve by co-opting neural circuits with ancestral roles in non-visual sensory pathways.

## Conclusions

As per Voltaire, we are better judged by our questions than our answers. From this, it follows that the field of visual ecology can be judged highly by the number and depth of the questions it now raises. From its early efforts to understand the transduction of light, basic neural processing in peripheral and central visual centers, and how these relate to visually mediated behaviors, the field has now reached the point where its questions are either very complex or so foundational as to be almost metaphysical. This Commentary has attempted to position many of these remaining questions within two major lines of inquiry: (1) can we enter the visual perception of another animal, and (2) why do the reasons for the apparent underlying order of vision and visual signals continue to elude us?

All good questions raise further good questions, but rather than ending with a well-educated shrug, we would like to state three things that we do know that will help us address these issues. (1) It is clear that simple explanations (e.g. an animal's spectral sensitivity matches the ambient illumination of the environment) do not suffice. As with everything in biology, vision and visual signals can serve multiple purposes, be constrained for non-visual reasons and be captive to their evolutionary pasts. Although the design-like qualities of the eye can invoke adaptationism, we must consider the complexity of evolutionary history, context and non-visual function to progress further. (2) After decades of study of the retina and behavior, it is now clear that assuming simple links between retinal processing and behavior does not suffice. Perhaps we can never step inside the perception of another animal, but continued exploration of the neural mechanisms that lie between light and behavior – and how they are modulated – will be fruitful. (3) As two-eyed beings with a love for color, we have marginalized perhaps the most important aspects of our field, such as distributed vision, visual acuity, temporal resolution and motion vision. Recent work (e.g. Caves et al., 2018a,b; Pallus et al., 2010; Renoult and Mendelson, 2019; Sumner-Rooney, 2023) has shown the promise of these topics, which we can only hope will continue.

In short, the field of visual ecology has reached a point where we know what we don't know, at least in part. In addition, much of what we don't know is, in principle, knowable. In all fields of science, this is perhaps the best place to be. We hope that the questions outlined in this Commentary will encourage exploration in these new areas of research and prompt the development of additional questions that have not yet been considered.

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### References

**Ache, J. M., Namiki, S., Lee, A., Branson, K. and Card, G. M.** (2019). State-dependent decoupling of sensory and motor circuits underlies behavioral flexibility in Drosophila. *Nat. Neurosci.* **22**, 1132-1139. doi:10.1038/s41593-019-0413-4

**Ahnelt, P. K. and Kolb, H.** (2000). The mammalian photoreceptor mosaic-adaptive design. *Prog. Retin. Eye Res.* **19**, 711-777. doi:10.1016/S1350-9462(00)00012-4

**Akre, K. L. and Johnsen, S.** (2014). Psychophysics and the evolution of behavior. *Trends Ecol. Evol.* **29**, 291-300. doi:10.1016/j.tree.2014.03.007

**Attwell, J. R., Ioannou, C. C., Reid, C. R. and Herbert-Read, J. E.** (2021). Fish avoid visually noisy environments where prey targeting is reduced. *Am. Nat.* **198**, 421-432. doi:10.1086/715434

**Audino, J. A., Serb, J. M. and Marian, J. E. A. R.** (2020). Hard to get, easy to lose: Evolution of mantle photoreceptor organs in bivalves (Bivalvia, Pteriomorphia). *Evolution* **74**, 2105-2120. doi:10.1111/evo.14050

**Avargues-Weber, A., De Brito Sanchez, M. G., Giurfa, M. and Dyer, A. G.** (2010). Aversive reinforcement improves visual discrimination learning in free-flying honeybees. *PLoS ONE* **5**, e13246. doi:10.1371/journal.pone.0015370

**Baden, T.** (2021). Circuit mechanisms for colour vision in zebrafish. *Curr. Biol.* **31**, R807-R820. doi:10.1016/j.cub.2021.04.053

**Beatty, D. D.** (1984). Visual pigments and the labile scotopic visual system of fish. *Vision Res.* **24**, 1563-1573. doi:10.1016/0042-6989(84)90314-6

**Bian, X., Pinilla, A., Chandler, T. and Peters, R.** (2021). Simulations with Australian dragon lizards suggest movement-based signal effectiveness is dependent on display structure and environmental conditions. *Sci. Rep.* **11**, 6383. doi:10.1038/s41598-021-85793-3

**Bok, M. J., Capa, M. and Nilsson, D.-E.** (2016). Here, there and everywhere: the radiolar eyes of fan worms (Annelida, Sabellidae). *Integr. Comp. Biol.* **56**, 784-795. doi:10.1093/icb/icw089

**Bowmaker, J. K.** (2008). Evolution of vertebrate visual pigments. *Vision Res.* **48**, 2022-2041. doi:10.1016/j.visres.2008.03.025

**Bruce, V., Georgeson, M. A. and Green, P. R.** (2014). *Visual Perception: Physiology, Psychology and Ecology*. London: Psychology Press.

**Burford, B. P. and Robison, B. H.** (2020). Bioluminescent backlighting illuminates the complex visual signals of a social squid in the deep sea. *Proc. Natl. Acad. Sci. USA* **117**, 8524-8531. doi:10.1073/pnas.1920875117

**Buschbeck, E. and Bok, M.** (ed.) (2023). *Distributed Vision*. Cham: Springer International Publishing.

**Caves, E. M., Sutton, T. T. and Johnsen, S.** (2017). Visual acuity in ray-finned fishes correlates with eye size and habitat. *J. Exp. Biol.* **220**, 1586-1596. doi:10.1242/jeb.151183

**Caves, E. M. and Kelley, L. A.** (2023). Proportional processing of a visual mate choice signal in the green swordtail, *Xiphophorus hellerii*. *Ecol. Lett.* **26**, 575-585. doi:10.1111/ele.14179

**Caves, E. M., Brandley, N. C. and Johnsen, S.** (2018a). Visual acuity and the evolution of signals. *Trends Ecol. Evol.* **33**, 358-372. doi:10.1016/j.tree.2018.03.001

**Caves, E. M., Green, P. A., Zipple, M. N., Peters, S., Johnsen, S. and Nowicki, S.** (2018b). Categorical perception of colour signals in a songbird. *Nature* **560**, 365-367. doi:10.1038/s41586-018-0377-7

**Caves, E. M., Davis, A. L., Nowicki, S. and Johnsen, S.** (2024). Backgrounds and the evolution of visual signals. *Trends Ecol. Evol.* **39**, 188-198. doi:10.1016/j.tree.2023.09.006

**Chappell, D. R. and Speiser, D. I.** (2023). Polarization sensitivity and decentralized visual processing in an animal with a distributed visual system. *J. Exp. Biol.* **226**, jeb244710. doi:10.1242/jeb.244710

**Chappell, D. R., Horan, T. M. and Speiser, D. I.** (2021). Panoramic spatial vision in the bay scallop *Argopecten irradians*. *Proc. R. Soc. B Biol. Sci.* **288**, 20211730. doi:10.1098/rspb.2021.1730

**Cheney, K. L., Green, N. F., Vibert, A. P., Vorobyev, M., Marshall, N. J., Osorio, D. C. and Endler, J. A.** (2019). An Ishihara-style test of animal colour vision. *J. Exp Biol.* **222**, jeb189787. doi:10.1242/jeb.189787

**Coimbra, J. P., Collin, S. P. and Hart, N. S.** (2014). Topographic specializations in the retinal ganglion cell layer correlate with lateralized visual behavior, ecology, and evolution in cockatoos. *J. Comp. Neurol.* **522**, 3363-3385. doi:10.1002/cne.23637

**Collin, S. P., Marshall, N. J. and Maximov, V. V.** (2000). Environmental factors which may have led to the appearance of colour vision. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **355**, 1239-1242. doi:10.1098/rstb.2000.0675

**Corral-López, A., Garate-Olaizola, M., Buechel, S. D., Kolm, N. and Kotrschal, A.** (2017). On the role of body size, brain size, and eye size in visual acuity. *Behav. Ecol. Sociobiol.* **71**, 1-10. doi:10.1007/s00265-017-2408-z

**Country, M. W. and Jonz, M. G.** (2022). Goldfish and crucian carp are natural models of anoxia tolerance in the retina. *Comp. Biochem. Phys. A Mol. Intergr. Physiol.* **270**, 111244. doi:10.1016/j.cbpa.2022.111244

**Cronin, T. W.** (1988). Vision in marine invertebrates. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R Fay, A. N. Popper and W. N. Tavolga), pp. 403-418. Springer.

**Cronin, T. W., Johnsen, S., Marshall, J. and Warrant, E. J.** (2014). *Visual Ecology*. Princeton University Press.

**Cummings, M. E. and Endler, J. A.** (2018). 25 years of sensory drive: the evidence and its watery bias. *Curr. Zool.* **64**, 471-484. doi:10.1093/cz/zoy043

**Currier, T. A., Pang, M. M. and Clandinin, T. R.** (2023). Visual processing in the fly, from photoreceptors to behavior. *Genetics* **224**, iyad064. doi:10.1093/genetics/iyad064

**Cuthill, I. C., Matchette, S. R. and Scott-Samuel, N. E.** (2019). Camouflage in a dynamic world. *Curr. Opin. Behav. Sci.* **30**, 109-115. doi:10.1016/j.cobeha.2019.07.007

**Dacke, M., Baird, E., Byrne, M., Scholtz, C. H. and Warrant, E. J.** (2013). Dung beetles use the Milky way for orientation. *Curr. Biol.* **23**, 298-300. doi:10.1016/j.cub.2012.12.034

**Dacke, M., Bell, A. T., Foster, J. J., Baird, E. J., Strube-Bloss, M. F., Byrne, M. J. and El Jundi, B.** (2019). Multimodal cue integration in the dung beetle compass. *Proc. Nat. Acad. Sci. USA* **116**, 14248-14253. doi:10.1073/pnas.1904308116

**Dixit, T., Caves, E. M., Spottiswoode, C. N. and Horrocks, N. P. C.** (2021). Why and how to apply Weber's Law to coevolution and mimicry. *Evolution* **75**, 1906-1919. doi:10.1111/evo.14290

**Donohue, C. G., Bagheri, Z. M., Partridge, J. C. and Hemmi, J. M.** (2022). Fiddler crabs are unique in timing their escape responses based on speed-dependent visual cues. *Curr. Biol.* **32**, 5159-5164. doi:10.1016/j.cub.2022.10.013

**Drerup, C., Dunkley, K., How, M. J. and Herbert-Read, J. E.** (2024b). Cuttlefish adopt disruptive camouflage under dynamic lighting. *Curr. Biol.* **34**, 3258-3264.e5. doi:10.1016/j.cub.2024.06.015

**Emerling, C. A. and Springer, M. S.** (2014). Eyes underground: regression of visual protein networks in subterranean mammals. *Mol. Phylogenet. Evol.* **78**, 260-270. doi:10.1016/j.ympev.2014.05.016

**Endler, J. A.** (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125-S153. doi:10.1086/285308

**Feller, K. D., Sharkey, C. R., McDuffee-Altekruse, A., Bracken-Grissom, H. D., Lord, N. P., Porter, M. L. and Schweikert, L. E.** (2021). Surf and turf vision: patterns and predictors of visual acuity in compound eye evolution. *Arthropod. Struct. Dev.* **60**, 101002. doi:10.1016/j.asd.2020.101002

**Fitzgerald, M. E. C., Tolley, E., Frase, S., Zagvazdin, Y., Miller, R. F., Hodos, W. and Reiner, A.** (2001). Functional and morphological assessment of age-related changes in the choroid and outer retina in pigeons. *Vis. Neurosci.* **18**, 299-317. doi:10.1017/S0952523801182143

**Fleishman, L. J.** (1986). Motion detection in the presence and absence of background motion in an Anolis lizard. *J. Comp. Physiol. A* **159**, 711-720. doi:10.1007/BF00612043

**Fleishman, L. J.** (1992). The influence of the sensory system and the environment on motion patterns in the visual displays of Anoline lizards and other vertebrates. *Am. Nat.* **139**, S36-S61. doi:10.1086/285304

**Frazer, S. A., Baghbanzadeh, M., Rahnavard, A., Crandall, K. A. and Oakley, T. H.** (2024). Discovering genotype-phenotype relationships with machine learning and the Visual Physiology Opsin Database (VPOD). *Gigascience* **13**, giae073. doi:10.1093/gigascience/giae073

**Fuller, R. C., Fleishman, L. J., Leal, M., Travis, J. and Loew, E.** (2003). Intraspecific variation in retinal cone distribution in the bluefin killifish, *Lucania goodei*. *J. Comp. Physiol. A* **189**, 609-616. doi:10.1007/s00359-003-0435-x

**Garm, A., O'Connor, M., Parkefelt, L. and Nilsson, D.-E.** (2007). Visually guided obstacle avoidance in the box jellyfish *Tripedalia cystophora* and *Chiropsella bronzie*. *J. Exp. Biol.* **210**, 3616-3623. doi:10.1242/jeb.004044

**Garm, A., Oskarsson, M. and Nilsson, D.-E.** (2011). Box jellyfish use terrestrial visual cues for navigation. *Curr. Biol.* **21**, 798-803. doi:10.1016/j.cub.2011.03.054

**Green, P. A., Brandley, N. C. and Nowicki, S.** (2020). Categorical perception in animal communication and decision-making. *Behav. Ecol.* **3**, 859-867. doi:10.1093/beheco/araa004

**Green, N. F., Guevara, E., Osorio, D. C., Endler, J. A., Marshall, N. J., Vorobyev, M. and Cheney, K. L.** (2022). Colour discrimination thresholds vary throughout colour space in a reef fish (*Rhinecanthus aculeatus*). *J. Exp. Biol.* **225**, jeb243533. doi:10.1242/jeb.243533

**Grünert, U. and Martin, P. R.** (2021). Morphology, molecular characterization, and connections of ganglion cells in primate retina. *Annu. Rev. Vis. Sci.* **7**, 73-103. doi:10.1146/annurev-vision-100419-115801

**Hanley, D., Rutledge, S. L. and Villa, J.** (2021). The perceptual and cognitive processes that govern egg rejection in hosts of avian brood parasites. *Front. Ecol. Evol.* **9**, 702934. doi:10.3389/fevo.2021.702934

**Hart, N. S., Cuthill, I. C. and Partridge, J. C.** (2000). Retinal asymmetry in birds. *Curr. Biol.* **10**, 115-117. doi:10.1016/S0960-9822(00)00297-9

**Hauzman, E., Bonci, D. M. and Ventura, D. F.** (2018). *Retinal Topographic Maps: A Glimpse into the Animals' Visual World. Sensory Nervous System*. IntechOpen.

**Heath, S. L., Christenson, M. P., Oriol, E., Saavedra-Weisenhaus, M., Kohn, J. R. and Behnia, R.** (2020). Circuit mechanisms underlying chromatic encoding in Drosophila photoreceptors. *Curr. Biol.* **30**, 264-275.e8. doi:10.1016/j.cub.2019.11.075

**Hofer, H., Carroll, J., Neitz, J., Neitz, M. and Williams, D. R.** (2005). Organization of the human trichromatic cone mosaic. *J. Neurosci.* **25**, 9669-9679. doi:10.1523/JNEUROSCI.2414-05.2005

**Hofmann, C. M., O'Quin, K. E., Smith, A. R. and Carleton, K. L.** (2010). Plasticity of opsin gene expression in cichlids from Lake Malawi. *Mol. Ecol.* **19**, 2064-2074. doi:10.1111/j.1365-294X.2010.04621.x

**Howland, H. C., Merola, S. and Basarab, J. R.** (2004). The allometry and scaling of the size of vertebrate eyes. *Vision Res.* **44**, 2043-2065. doi:10.1016/j.visres.2004.03.023

**Hughes, A**. (1977). The topography of vision in mammals of contrasting life style: comparative optics and retinal organization. In *The Visual System of Vertebrates. Handbook of Sensory Physiology* (ed. F. Crescitelli), pp. 697-756. Berlin: Springer.

**Hulse, S. V., Renoult, J. P. and Mendelson, T. C.** (2020). Sexual signaling pattern correlates with habitat pattern in visually ornamented fishes. *Nat. Commun.* **11**, 2561. doi:10.1038/s41467-020-16389-0

**Hunt, E. R., Dornan, C., Sendova-Franks, A. B. and Franks, N. R.** (ed.) (2018). Asymmetric ommatidia count and behavioural lateralization in the ant *Temnothorax albipennis*. *Sci. Rep.* **8**, 5825. doi:10.1038/s41598-018-23652-4

**Hutton, P., Seymoure, B. M., McGraw, K. J., Ligon, R. A. and Simpson, R. K.** (2015). Dynamic color communication. *Curr. Opin. Behav. Sci.* **6**, 41-49. doi:10.1016/j.cobeha.2015.08.007

**Jones, C. D., Osorio, D. and Baddeley, R. J.** (2001). Colour categorization by domestic chicks. *Proc. R. Soc. B Biol. Sci.* **268**, 2077-2084. doi:10.1098/rspb.2001.1734

**Jones, B. W., Watt, C. B., Frederick, J. M., Baehr, W., Chen, C. K., Levine, E. M., Milam, A. H. and Marc, R. E.** (2003). Retinal remodeling triggered by photoreceptor degenerations. *J. Comp. Neurol.* **464**, 1-16. doi:10.1002/cne.10703

**Kelber, A.** (2016). Colour in the eye of the beholder: receptor sensitivities and neural circuits underlying colour opponency and colour perception. *Curr Opin. Neurobiol.* **41**, 106-112. doi:10.1016/j.conb.2016.09.007

**Kelley, L. A. and Kelley, J. L.** (2014). Animal visual illusion and confusion: the importance of a perceptual perspective. *Behav. Ecol.* **25**, 450-463. doi:10.1093/beheco/art118

**Kemp, D. J., Reznick, D. N., Arendt, J., Van Den Berg, C. and Endler, J. A.** (2023). How to generate and test hypotheses about colour: insights from half a century of guppy research. *Proc. R. Soc. B Biol. Sci.* **290**, 20222492. doi:10.1098/rspb.2022.2492

**Khaldy, L., Foster, J. J., Yilmaz, A., Belušič, G., Gagnon, Y., Tocco, C., Byrne, M. J. and Dacke, M.** (2022). The interplay of directional information provided by unpolarised and polarised light in the heading direction network of the diurnal dung beetle Kheper lamarcki. *J. Exp. Biol.* **225**, jeb243734. doi:10.1242/jeb.243734

**Kinoshita, M., Takahashi, Y. and Arikawa, K.** (2012). Simultaneous brightness contrast of foraging Papilio butterflies. *Proc. R. Soc. B Biol. Sci.* **279**, 1911-1918. doi:10.1098/rspb.2011.2396

**Kirwan, J. D., Bok, M. J., Smolka, J., Foster, J. J., Hernández, J. C. and Nilsson, D.-E.** (2018). The sea urchin *Diadema africanum* uses low resolution vision to find shelter and deter enemies. *J. Exp. Biol.* **221**, jeb176271. doi:10.1242/jeb.176271

**Kócsi, Z., Murray, T., Dahmen, H., Narendra, A. and Zeil, J.** (2020). The Antarium: a reconstructed visual reality device for ant navigation research. *Front. Behav. Neurosci.* **14**, 599374. doi:10.3389/fnbeh.2020.599374

**Land, M. F.** (1997). Visual acuity in insects. *Annu. Rev. Entomol.* **42**, 147-177. doi:10.1146/annurev.ento.42.1.147

**Land, M. F. and Nilsson, D. E.** (2002). *Animal Eyes*. Oxford, UK: Oxford University Press.

**Langridge, K. V., Wilke, C., Riabinina, O., Vorobyev, M. and Hempel De Ibarra, N.** (2021). Approach direction prior to landing explains patterns of colour learning in bees. *Front. Physiol.* **12**, 697886. doi:10.3389/fphys.2021.697886

**Laughlin, S. B**. (2001). The metabolic cost of information-a fundamental factor in visual ecology. In *Ecology of Sensing* (ed. F. G. Barth and A. Schmid), pp. 169-185. Springer Berlin Heidelberg.

**Li, L., Connors, M. J., Kolle, M., England, G. T., Speiser, D. I., Xiao, X., Aizenberg, J. and Ortiz, C.** (2015). Multifunctionality of chiton biomineralized armor with an integrated visual system. *Science* **350**, 952-956. doi:10.1126/science.aad1246

**Li, T., Kirwan, J., Arnone, M. I., Nilsson, D.-E. and La Camera, G.** (2023). A model of decentralized vision in the sea urchin *Diadema africanum*. *iScience* **26**, 106295. doi:10.1016/j.isci.2023.106295

**Loew, E. R. and Lythgoe, J. N.** (1978). The ecology of cone pigments in teleost fishes. *Vision Res.* **18**, 715-722. doi:10.1016/0042-6989(78)90150-5

**Luk, H. L., Bhattacharyya, N., Montisci, F., Morrow, J. M., Melaccio, F., Wada, A., Sheves, M., Fanelli, F., Chang, B. S. and Olivucci, M.** (2016). Modulation of thermal noise and spectral sensitivity in Lake Baikal cottoid fish rhodopsins. *Sci. Rep.* **6**, 38425. doi:10.1038/srep38425

**Lythgoe, J. N.** (1979). *The Ecology of Vision*. Oxford: Oxford University Press.

**Matchette, S. R., Cuthill, I. C., Cheney, K. L., Marshall, N. J. and Scott-Samuel, N. E.** (2020). Underwater caustics disrupt prey detection by a reef fish. *Proc. R. Soc. B Biol. Sci.* **287**, 20192453. doi:10.1098/rspb.2019.2453

**Matsushita, A., Stewart, F., Ilić, M., Chen, P. J., Wakita, D., Miyazaki, N., Murata, K., Kinoshita, M., Belušič, G. and Arikawa, K.** (2022). Connectome of the lamina reveals the circuit for early color processing in the visual pathway of a butterfly. *Curr. Biol.* **32**, 2291-2299. doi:10.1016/j.cub.2022.03.066

**McCormick, L. R. and Levin, L. A.** (2017). Physiological and ecological implications of ocean deoxygenation for vision in marine organisms. *Philos. Trans. R. Soc. A* **375**, 20160322. doi:10.1098/rsta.2016.0322

**Metcalfe, N. B.** (1984). The effects of habitat on the vigilance of shorebirds: is visibility important? *Anim. Behav.* **32**, 981-985. doi:10.1016/S0003-3472(84)80210-9

**Mitchell, L., Cheney, K. L., Cortesi, F., Marshall, N. J. and Vorobyev, M.** (2017). Triggerfish uses chromaticity and lightness for object segregation. *R. Soc. Open Sci.* **4**, 171440. doi:10.1098/rsos.171440

**Nilsson, D. E.** (2021). The diversity of eyes and vision. *Ann. Rev. Vis. Sci.* **7**, 19-41. doi:10.1146/annurev-vision-121820-074736

**Niven, J. E. and Laughlin, S. B.** (2008). Energy limitation as a selective pressure on the evolution of sensory systems. *J. Exp. Biol.* **211**, 1792-1804. doi:10.1242/jeb.017574

**Novales Flamarique, I., Cheng, C. L., Bergstrom, C. and Reimchen, T. E.** (2013). Pronounced heritable variation and limited phenotypic plasticity in visual pigments and opsin expression of threespine stickleback photoreceptors. *J. Exp. Biol.* **216**, 656-667. doi:10.1242/jeb.078840

**Oates, B. A., Merkle, J. A., Kauffman, M. J., Dewey, S. R., Jimenez, M. D., Vartanian, J. M., Becker, S. A. and Goheen, J. R.** (2019). Antipredator response diminishes during periods of resource deficit for a large herbivore. *Ecology* **100**, e02618. doi:10.1002/ecy.2618

**Ord, T. J., Peters, R. A., Clucas, B. and Stamps, J. A.** (2007). Lizards speed up visual displays in noisy motion habitats. *Proc. Biol. Sci.* **274**, 1057-1062. doi:10.1098/rspb.2006.0263

**Owens, G. L., Rennison, D. J., Allison, W. T. and Taylor, J. S.** (2012). In the four-eyed fish (*Anableps anableps*), the regions of the retina exposed to aquatic and aerial light do not express the same set of opsin genes. *Biol. Lett.* **8**, 86-89. doi:10.1098/rsbl.2011.0582

**Pallus, A. C., Fleishman, L. J. and Castonguay, P. M.** (2010). Modeling and measuring the visual detection of ecologically relevant motion by an Anolis lizard. *J. Comp. Physiol.* **196**, 1-13. doi:10.1007/s00359-009-0487-7

**Penteriani, V. and Delgado, M. D. M.** (2017). Living in the dark does not mean a blind life: bird and mammal visual communication in dim light. *Philos. Trans. R. Soc. B* **372**, 20160064. doi:10.1098/rstb.2016.0064

**Picciani, N., Kerlin, J. R., Sierra, N., Swafford, A. J. M., Ramirez, M. D., Roberts, N. G., Cannon, J. T., Daly, M. and Oakley, T. H.** (2018). Prolific origination of eyes in cnidaria with co-option of non-visual opsins. *Curr. Biol.* **28**, 2413-2419.e4. doi:10.1016/j.cub.2018.05.055

**Porter, M. L., Blasic, J. R., Bok, M. J., Cameron, E. G., Pringle, T., Cronin, T. W. and Robinson, P. R.** (2012). Shedding new light on opsin evolution. *Proc. Biol. Sci.* **279**, 3-14. doi:10.1098/rspb.2011.1819

**Querubin, A., Lee, H. R., Provis, J. M. and O'Brien, K. M. B.** (2009). Photoreceptor and ganglion cell topographies correlate with information convergence and high acuity regions in the adult pigeon (*Columba livia*) retina. *J. Comp. Neurol.* **517**, 711-722. doi:10.1002/cne.22178

**Ramirez, M. D., Pairett, A. N., Pankey, M. S., Serb, J. M., Speiser, D. I., Swafford, A. J. and Oakley, T. H.** (2016). The last common ancestor of most bilaterian animals possessed at least nine opsins. *Genome Biol. Evol.* **8**, 3640-3652. doi:10.1093/gbe/evw135

**Renoult, J. P. and Mendelson, T. C.** (2019). Processing bias: extending sensory drive to include efficacy and efficiency in information processing. *Proc. R. Soc. B* **286**, 20190165. doi:10.1098/rspb.2019.0165

**Robinson, E., Jerrett, A., Black, S. and Davison, W.** (2013). Hypoxia impairs visual acuity in snapper (*Pagrus auratus*). *J. Comp. Physiol. A* **199**, 611-617. doi:10.1007/s00359-013-0809-7

**Rosenthal, G. G.** (2007). Spatiotemporal dimensions of visual signals in animal communication. *Annu. Rev. Ecol. Evol. Syst.* **38**, 155-178. doi:10.1146/annurev.ecolsys.38.091206.095745

**Ryan, M. J. and Cummings, M. E.** (2013). Perceptual biases and mate choice. *Annu. Rev. Ecol. Evol. Syst.* **44**, 437-459. doi:10.1146/annurev-ecolsys-110512-135901

**Sandkam, B. A., Deere-Machemer, K. A., Johnson, A. M., Grether, G. F., Helen Rodd, F. and Fuller, R. C.** (2016). Exploring visual plasticity: dietary carotenoids can change color vision in guppies (*Poecilia reticulata*). *J. Comp. Physiol. A* **202**, 527-534. doi:10.1007/s00359-016-1097-9

**Sanes, J. R. and Zipursky, S. L.** (2010). Design principles of insect and vertebrate visual systems. *Neuron* **66**, 15-36. doi:10.1016/j.neuron.2010.01.018

**Schnaitmann, C., Haikala, V., Abraham, E., Oberhauser, V., Thestrup, T., Griesbeck, O. and Reiff, D. F.** (2018). Color processing in the early visual system of Drosophila. *Cell* **172**, 318-330.e18. doi:10.1016/j.cell.2017.12.018

**Schweikert, L. E., Fasick, J. I. and Grace, M. S.** (2016). Evolutionary loss of cone photoreception in balaenid whales reveals circuit stability in the mammalian retina. *J. Comp. Neurol.* **524**, 2873-2885. doi:10.1002/cne.23996

**Schweikert, L. E., Fitak, R. R., Caves, E. M., Sutton, T. T. and Johnsen, S.** (2018). Spectral sensitivity in ray-finned fishes: diversity, ecology and shared descent. *J. Exp. Biol.* **221**, jeb189761. doi:10.1242/jeb.189761

**Schweikert, L. E., Caves, E. M., Solie, S. E., Sutton, T. T. and Johnsen, S.** (2019). Variation in rod spectral sensitivity of fishes is best predicted by habitat and depth. *J. Fish Biol.* **95**, 179-185. doi:10.1111/jfb.13859

**Schweikert, L. E., Thomas, K. N., Moreno, V. M., Casaubon, A., Golightly, C. and Bracken-Grissom, H. D.** (2022). Ecological predictors and functional implications of eye size in deep-sea shrimps. *Front. Ecol. Evol.* **10**, 787315. doi:10.3389/fevo.2022.787315

**Shand, J., Hart, N. S., Thomas, N. and Partridge, J. C.** (2002). Developmental changes in the cone visual pigments of black bream *Acanthopagrus butcheri*. *J. Exp. Biol.* **205**, 3661-3667. doi:10.1242/jeb.205.23.3661

**Simpson, E. E., Marshall, N. J. and Cheney, K. L.** (2016). Coral reef fish perceive lightness illusions. *Sci. Rep.* **6**, 35335. doi:10.1038/srep35335

**Spagnolia, T. and Wilkens, L. A.** (1983). Neurobiology of the scallop. II. Structure of the parietovisceral ganglion lateral lobes in relation to afferent projections from the mantle eyes. *Mar. Freshw. Behav. Physiol.* **10**, 23-55. doi:10.1080/10236248309378605

**Stevens, M. and Ruxton, G. D.** (2012). Linking the evolution and form of warning coloration in nature. *Proc. R. Soc. B Biol. Sci.* **279**, 417-426. doi:10.1098/rspb.2011.1932

**Stoddard, M. C. and Osorio, D.** (2019). Animal coloration patterns: linking spatial vision to quantitative analysis. *Am. Nat.* **193**, 164-186. doi:10.1086/701300

**Sumner-Rooney, L.** (2023). 'Distributed' vision and the architecture of animal visual systems. *J. Exp. Biol.* **226**, jeb245392. doi:10.1242/jeb.245392

**Sumner-Rooney, L. and Ullrich-Lüter, J** (2023). Extraocular vision in echinoderms. In *Distributed Vision* (ed. E. Buschbeck and M. Bok), pp. 49-85. Cham: Springer International Publishing.

**Sumner-Rooney, L., Kirwan, J. D., Lowe, E. and Ullrich-Lüter, E.** (2019). Extraocular vision in a brittle star is mediated by chromatophore movement in response to ambient light. *Curr. Biol.* **30**, R71-R73. doi:10.1016/j.cub.2019.11.042

**Szatko, K. P., Korympidou, M. M., Ran, Y., Berens, P., Dalkara, D., Schubert, T., Euler, T. and Franke, K.** (2020). Neural circuits in the mouse retina support color vision in the upper visual field. *Nat. Commun.* **11**, 3481. doi:10.1038/s41467-020-17113-8

**Sztarker, J. and Tomsic, D.** (2008). Neuronal correlates of the visually elicited escape response of the crab *Chasmagnathus* upon seasonal variations, stimuli changes and perceptual alterations. *J. Comp. Physiol. A* **194**, 587-596. doi:10.1007/s00359-008-0333-3

**Tan, E. J. and Elgar, M. A.** (2021). Motion: enhancing signals and concealing cues. *Biol. Open* **10**, bio058762. doi:10.1242/bio.058762

**Temple, S. E.** (2011). Why different regions of the retina have different spectral sensitivities: a review of mechanisms and functional significance of intraretinal variability in spectral sensitivity in vertebrates. *Visual Neurosci.* **28**, 281-293. doi:10.1017/S0952523811000113

**Temple, S., Hart, N. S., Marshall, N. J. and Collin, S. P.** (2010). A spitting image: specializations in archerfish eyes for vision at the interface between air and water. *Proc. R. Soc. B Biol. Sci.* **277**, 2607-2615. doi:10.1098/rspb.2010.0345

**Tibbetts, E. A., Harris, O. K., Morehouse, N. I. and Caves, E. M.** (2024). The evolution of simplifying heuristics in visual cognition: categorization, specialization, and visual illusions. *Annu. Rev. Vision Sci.* **10**, 123-144. doi:10.1146/annurev-vision-100923-015932

**Troscianko, J., Skelhorn, J. and Stevens, M.** (2017). Quantifying camouflage: how to predict detectability from appearance. *BMC Evol. Biol.* **17**, 7. doi:10.1186/s12862-016-0854-2

**Ulanovsky, N.** (2025). *Natural Neuroscience: Toward a Systems Neuroscience of Natural Behaviors*. Cambridge, MA: MIT Press.

**Van Den Berg, C., Troscianko, J., Endler, J. A., Marshall, N. J. and Cheney, K. L.** (2020). Quantitative Colour Pattern Analysis (QCPA): a comprehensive framework for the analysis of colour patterns in nature. *Methods Ecol. Evol.* **11**, 316-332. doi:10.1111/2041-210X.13328

**Van Der Kooi, C. J., Stavenga, D. G., Arikawa, K., Belušič, G. and Kelber, A.** (2021). Evolution of insect color vision: from spectral sensitivity to visual ecology. *Annu. Rev. Entomol.* **66**, 435-461. doi:10.1146/annurev-ento-061720-071644

**Varney, R. M., Speiser, D. I., Cannon, J. T., Aguilar, M. A., Eernisse, D. J. and Oakley, T. H.** (2024). A morphological basis for path-dependent evolution of visual systems. *Science* **383**, 983-987. doi:10.1126/science.adg2689

**Venables, S. V., Drerup, C., Powell, S. B., Marshall, N. J., Herbert-Read, J. E. and How, M. J.** (2022). Polarization vision mitigates visual noise from flickering light underwater. *Sci. Adv.* **8**, eabq2770. doi:10.1126/sciadv.abq2770

**Walls, G. L.** (1942). *The Vertebrate Eye and its Adaptive Radiation*. Bloomfield Hills, NJ: Cranbrook Press.

**Warrant, E. J.** (2004). Vision in the dimmest habitats on earth. *J. Comp. Physiol. A* **190**, 765-789. doi:10.1007/s00359-004-0546-z

**Warrant, E. J. and Johnsen, S.** (2013). Vision and the light environment. *Curr. Biol.* **23**, R990-R994. doi:10.1016/j.cub.2013.10.019

**Warrant, E. J. and Locket, N. A.** (2004). Vision in the deep sea. *Biol. Rev.* **79**, 671-712. doi:10.1017/S1464793103006420

**Warrant, E. J. and Nilsson, D. E.** (2006). *Invertebrate Vision*. Cambridge: Cambridge University Press.

**Wehner, R.** (1987). “Matched filters” - neural models of the external world. *J. Comp. Physiol. A* **161**, 511-531. doi:10.1007/BF00603659

**Wertlen, A. M., Niggebrügge, C., Vorobyev, M. and Hempel De Ibarra, N.** (2008). Detection of patches of coloured discs by bees. *J. Exp. Biol.* **211**, 2101-2104. doi:10.1242/jeb.014571

**Worsley, M. Z., Schroeder, J. and Dixit, T.** (2025). How animals discriminate between stimulus magnitudes: a meta-analysis. *Behav. Ecol.* **36**, araf025. doi:10.1093/beheco/araf025

**Wortel, J. F., Wubbels, R. J. and Nuboer, J. F. W.** (1984). Photopic spectral sensitivities of the red and the yellow field of the pigeon retina. *Vision Res.* **24**, 1107-1113. doi:10.1016/0042-6989(84)90089-0

**Yokoyama, S., Starmer, W. T., Takahashi, Y. and Tada, T.** (2005). Tertiary structure and spectral tuning of UV and violet pigments in vertebrates. *Gene* **365**, 95-103. doi:10.1016/j.gene.2005.09.028

**Zeil, J.** (1983). Sexual dimorphism in the visual system of flies: the compound eyes and neural superposition in Bibionidae (Diptera). *J. Comp. Physiol. A* **150**, 379-393. doi:10.1007/BF00605027

**Zipple, M. N., Caves, E. M., Green, P. A., Peters, S., Johnsen, S. and Nowicki, S.** (2019). Categorical colour perception occurs in both signalling and non-signalling colour ranges in a songbird. *Proc. R. Soc. B Biol. Sci.* **286**, 20190524. doi:10.1098/rspb.2019.0524