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REVIEW

Photoreception and vision in the ultraviolet

Thomas W. Cronin[1],* and Michael J. Bok[2]

ABSTRACT

Ultraviolet (UV) light occupies the spectral range of wavelengths slightly shorter than those visible to humans. Because of its shorter wavelength, it is more energetic (and potentially more photodamaging) than 'visible light', and it is scattered more efficiently in air and water. Until 1990, only a few animals were recognized as being sensitive to UV light, but we now know that a great diversity, possibly even the majority, of animal species can visually detect and respond to it. Here, we discuss the history of research on biological UV photosensitivity and review current major research trends in this field. Some animals use their UV photoreceptors to control simple, innate behaviors, but most incorporate their UV receptors into their general sense of vision. They not only detect UV light but recognize it as a separate color in light fields, on natural objects or living organisms, or in signals displayed by conspecifics. UV visual pigments are based on opsins, the same family of proteins that are used to detect light in conventional photoreceptors. Despite some interesting exceptions, most animal species have a single photoreceptor class devoted to the UV. The roles of UV in vision are manifold, from guiding navigation and orientation behavior, to detecting food and potential predators, to supporting high-level tasks such as mate assessment and intraspecific communication. Our current understanding of UV vision is restricted almost entirely to two phyla: arthropods and chordates (specifically, vertebrates), so there is much comparative work to be done.

KEY WORDS: Ultraviolet, Visual pigments, Vision, Opsin, Dorsal rim, Chromatic aberration

Introduction

In 1881, Sir John Lubbock, 1st Baron Avebury, published a fascinating paper concerning his 'Observations on Ants, Bees, and Wasps'. In it, he disputed the position of the eminent French zoologist, Paul Bert, who had claimed on the basis of limited experiments with *Daphnia* that all animals perceive the same spectral range (and thus the same colors) as humans. Sir John, a neighbor and lifelong friend of Charles Darwin and an early proponent of evolutionary theory, noted that 'Such a generalization would seem to rest on but a slight foundation', and went on to show in a series of elegant and rather charming publications that both ants and *Daphnia* are indeed capable of seeing wavelengths well below those at the violet end of the spectrum – they perceive ultraviolet (UV) light (Lubbock, 1881, 1882). To do this, Lubbock took advantage of a natural behavior of disturbed ants. He placed them and their larvae on a table top

[1]Department of Biological Sciences, University of Maryland Baltimore County, Baltimore, MD 21250, USA. [2]Lund University, Department of Biology, Sölvegatan 35, Lund 223 62, Sweden.

*Author for correspondence (cronin@umbc.edu)

T.W.C., 0000-0001-7375-9382

at a particular location in a spectrum of light thrown onto the experimental space by a glass prism. Ants will quickly scurry to move their larvae to a dark place when they are exposed like this, and Sir John found that the adult ants were particularly anxious to remove the larvae from the apparently dark region well beyond the violet end of the spread-out spectrum. They even preferred to move the larvae to the red spectral region instead of this beyond-violet location. From these results, and others on the phototaxis of *Daphnia*, he correctly concluded that these animals perceive what he called 'ultra-violet rays' of light and thus that their visual worlds differ from our own.

Lubbock's work was followed nearly a half century later by that of Alfred Kühn, who found that bees can be trained to search for sugar water in spectral lights as short as 313 nm (Kühn, 1924, 1927). At about the same time, two other Germans, Schiemenz (1924) and Wolff (1925) demonstrated that minnows learn to discriminate wavelengths down to 360 nm or so, well into the UV. None of these early vision scientists worked with terrestrial vertebrate animals, and somehow the misconception persisted until recently that UV sensitivity is rare among animals, and probably absent in terrestrial vertebrates. A number of arguments were advanced in support of this conjecture, including the traditional claim that because humans could not see UV, it probably was unimportant for most other animals. Besides this, it was noted that UV light is much more energetic than longer-wavelength radiation and known to cause cellular damage, so it was expected to be destructive to retinal tissues. Chromatic aberration (see Glossary) was another reason advanced to discount UV vision; this would cause biological optical systems to focus short-wavelength light far in front of the retinal surface. Furthermore, until quite recently it was assumed that natural waters quickly extinguish UV wavelengths, in which case aquatic animals would achieve no benefit from UV sensitivity. Finally, it was argued that the β-bands (see Glossary; sometimes called the *cis*-absorption bands or *cis*-peaks) of visual pigments are always placed at UV wavelengths anyway, so UV photosensitivity is available as a byproduct of sensitivity to visible light (see Glossary) and would in any case be corrupted by visible light, making UV photosensitivity nearly worthless.

Evolution was not aware of all these philosophical constraints. Finally, a half century after Kühn's work with bees, the first terrestrial vertebrate was demonstrated to have excellent UV vision when Goldsmith (1981) found that three different hummingbird species can discriminate UV targets from all other wavelengths. This was quickly followed by the discovery of dedicated UV photoreceptor classes in fishes (Avery et al., 1983; Hárosi and Hashimoto, 1983), birds (Chen et al., 1984), reptiles (Arnold and Neumeyer, 1987) and (after long denial) mammals (Jacobs et al., 1991). Since then, work on the dedicated UV visual receptors and visual pigments of vertebrates (and of invertebrates) has accelerated nearly exponentially. For a history of early research into UV vision in vertebrates, see Jacobs (1992). In this Review, we aim to discuss the current state of understanding of UV photoreception and vision.

Glossary

Chromatic aberration
An effect caused by the fact that the focal lengths of most lenses vary with wavelength. Thus, light of only one wavelength is focused sharply on the retina. Generally, the shorter the wavelength, the shorter the focal length of a lens.

Long-pass filter
An optical filter that transmits longer wavelengths and blocks shorter ones. When placed in front of a photoreceptor cell, it generally narrows the cell's spectral sensitivity and shifts its maximum to longer wavelengths.

Polarized light
As used here, light in which the electric vector lies within a plane. In air or water, it is usually produced by scattering of unpolarized light (with random electric vectors).

Rayleigh scattering
A scattering process caused by particles much smaller than the wavelength of light. It is most effective at short wavelengths.

Refractive index
A measure of the ability of a material to refract light. Materials with higher refractive indices refract light to greater degrees. Refractive index varies with wavelength for lenses, causing chromatic aberration.

Short-pass filter
An optical filter that transmits shorter wavelengths and blocks longer ones. When placed in front of a photoreceptor cell, it generally narrows the cell's spectral sensitivity and shifts its λ_{max} to shorter wavelengths.

Spectral tuning
Factors that affect the spectral absorbance of a visual pigment or the spectral sensitivity of a photoreceptor cell. Molecular factors of spectral tuning generally involve changes in the amino acids near the chromophore of a visual pigment. Other factors include various kinds of optical filtering, including long-pass and short-pass filtering.

Tapetum
Also called the 'tapetum lucidum', a layer behind the retina which reflects any light that has not been absorbed back through the photoreceptors, increasing sensitivity.

Ultraviolet light
Here, the region of the electromagnetic spectrum that has wavelengths between 100 and 400 nm, comprising UVA (315–400 nm), UVB (280–315 nm) and UVC (100–280 nm).

Visible light
Sometimes called 'human-visible' light. Refers to the wavelength range that is perceptible to most people, generally taken to be the range from 400 to 700 nm.

α-Band
The spectral region containing the main absorbance peak (λ_{max}) of a visual pigment, responsible for most of its overall sensitivity.

β-Band
A secondary absorbance peak placed at shorter wavelengths than the α-band that can also contribute to the spectral sensitivity of a visual pigment. The β-band lies within the UV spectral range.

UV photosensitivity and UV vision

Before going further, we need to define what part of the electromagnetic spectrum falls in the UV. The term 'ultraviolet', literally 'beyond violet', originally referred to light at wavelengths shorter than those perceptible to humans. (The human spectral range is often called 'human-visible light'; here we use the less awkward term 'visible light'.) Since the actual cutoff wavelength between violet and ultraviolet varies among individuals, for

reasons about to be discussed, the term is now defined more strictly as light between the wavelengths of 100 and 400 nm. Most of this range is not naturally present at the earth's surface, as a result of atmospheric absorption. By convention, the UV spectrum is divided into three regions: UVA extends from 315 to 400 nm, UVB between 280 and 315 nm, and UVC below 280 nm down to 100 nm. UVC is removed by the atmosphere, but a small amount of UVB and much more UVA passes through the atmosphere to the earth's surface (Fig. 1). The UVB range is significant for its biological effects resulting from its absorption by proteins and nucleic acids, but animal UV-light visual sensitivity is almost entirely restricted to the UVA. Although it is true, as noted above, that most visual pigments (including those of human retinas) have significant photosensitivity in the UV, we and many other mammals have UV-absorbing pigments in the lens that entirely block the passage of this spectral range to the retina (Douglas and Cronin, 2016). However, the density of these lens pigments varies with age, and people are actually sensitive to wavelengths extending down to at least 380 nm when young. Aphakic individuals, who have had their lenses removed, are very sensitive to UV light, nearly as far as the UVB, which compromises their color vision. This is why artificial intraocular lenses used today strongly absorb UV, much like a natural lens does.

The other distinction that will be important throughout this Review is between UV photosensitivity and UV vision. UV photosensitivity simply refers to the ability to detect UV light; as used in this paper, it means that the retina contains photoreceptor cells that absorb UV light and can transduce it to a cellular signal. UV photosensitivity is required for UV vision, but the latter term means that an animal can visualize UV patterns and recognize UV-containing images of objects, light fields and signals. The distinction is important, because many animals respond strongly to UV stimuli, but the response is stereotyped and is different from the same animal's response to longer wavelengths (most animals with such responses avoid UV or move away from a UV source, evidently interpreting such a stimulus as noxious or dangerous). Menzel discusses these responses at length, calling them 'wavelength-specific behaviors' as opposed to true color vision (Menzel, 1979). When UV is included in the color-vision system of an animal, it is discriminable from other colors and does not automatically elicit a specific response. Also, as the term implies, color vision is always associated with visual imaging and
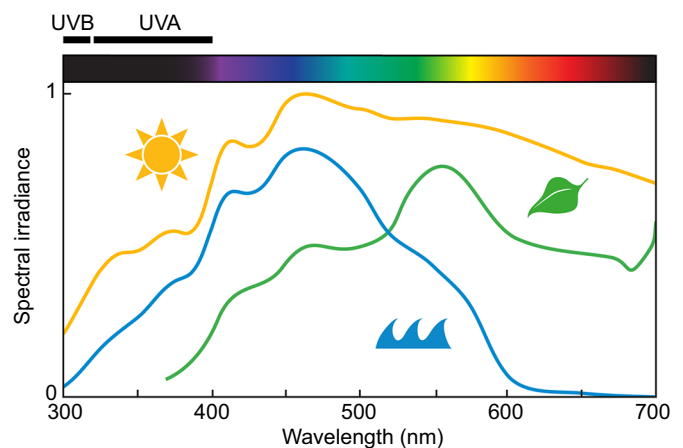

Fig. 1. Ultraviolet light in nature. Solar spectral irradiance in arbitrary units at sea level (yellow trace, indicated by a sun symbol), in clear water at 5 m depth (blue, indicated by a waves symbol) and under a forest canopy (green, indicated by a leaf symbol). UVA and UVB ranges are indicated. Adapted from ASTM G173 (A1.5) solar irradiance standard, Smith and Baker (1981) aquatic attenuation coefficients and Chiao et al., (2000).

object recognition. Many animals with UV photosensitivity, particularly invertebrates, have both wavelength-specific behaviors and color vision (Menzel, 1979; see also Kelber and Osorio, 2010).

How is UV light detected? UV visual pigments, opsins and receptors

The phototransduction cascade

Animals detect light through a phototransduction cascade mediated by visual pigments sequestered in the membranes of photoreceptor cells. Visual pigments are formed by the Schiff base covalent linkage of an opsin G-protein-coupled receptor with a vitamin A-derived chromophore. The chromophore, typically 11-*cis*-retinal in the inactive state, is nested in a binding pocket within the seven transmembrane α-helices of the opsin. Upon photon absorption, the chromophore isomerizes, causing a conformational change in the opsin protein that initiates a biochemical cascade culminating in a downstream cellular signal. On its own, the retinal chromophore maximally absorbs photons with wavelengths near 380 nm. However, by varying the amino acid residues of the opsin, especially those residues within the chromophore-binding pocket, interactions between the amino acid side chains and the chromophore can stabilize and spectrally 'tune' the wavelength of maximum absorption (λ_{max}) of the visual pigment within a range from about 330 to 570 nm. Because free retinal absorbs light at ~380 nm, the earliest opsin-based visual pigments may well have been UV sensitive.

UV visual pigments

The first visual pigment responsible for UV sensitivity was not directly characterized until nearly 50 years ago, in an owlfly (Hamdorf et al., 1971), and a *Drosophila* UV opsin was fully sequenced a few years later (Zuker et al., 1987). The first vertebrate UV visual pigment was identified in a fish, the dace (Hárosi and Hashimoto, 1983); subsequently, UV opsins were sequenced from goldfish and mice (Chiu et al., 1994; Johnson et al., 1993). UV opsin sequences are now known for many animal species, with those involved in chordate and arthropod visual systems being the best surveyed. Of the four major clades of metazoan opsins established by Porter et al. (2012), three are known to contain UV opsins: C-type, R-type and Group 4 opsins (Fig. 2A,B). Within vertebrate C-type opsins, the short-wavelength-sensitive (SWS1) clade and parapinopsins have been found to include UV-sensitive (UVS) visual pigments. The SWS1 clade contains all known vertebrate UV opsins implicated in visual tasks, whereas the parapinopsins, first identified in lamprey, exist in pineal-associated photoreceptive organs of non-mammalian vertebrates (Koyanagi et al., 2004). These organs are thought to have diverse roles, including melatonin regulation, luminance detection and even chromatic discrimination between UV and longer wavelengths (Koyanagi et al., 2015). Among invertebrates, investigations of UV opsins involved in vision have thus far been restricted to the arthropods. Their R-type opsins include a SWS opsin clade responsible for all confirmed arthropod UV visual pigments (Henze and Oakley, 2015). Sister to the arthropod SWS clade, a poorly understood 'UV7' opsin clade, homologous to *Drosophila* Rh7, contains some opsin sequences that suggest the possibility of UV tuning (see Glossary). Finally, the enigmatic neuropsins (NEUR in Fig. 2A) from the Group 4 opsin clade form UVS visual pigments and are expressed in a variety of vertebrate neuronal tissues, including retinal ganglion cells and the pineal body (Buhr et al., 2015; Yamashita et al., 2010). The function of neuropsin is poorly understood, but it appears to play a role in circadian entrainment in some cases. There may well be additional types of

UV opsins in existence, especially among non-arthropod invertebrate taxa. For instance, the giant clam *Tridacna* has UVS hyperpolarizing photoreceptors on its mantle (Wilkens, 1984; Fig. 3F). Although the actual opsin is not known in *Tridacna*, it may be homologous to scallop Go opsin (which also produces hyperpolarizing responses), placing it in the Group 4 peropsin clade (Porter et al., 2012) (PER in Fig. 2A). As noted above, functional studies of UV visual pigments are currently quite limited outside of the vertebrates and arthropods.

Spectral tuning of UV opsins

Upon examining the evolution and spectral tuning of various UV opsins, some interesting trends emerge. A unifying feature of UV opsins appears to be the conservation or coevolution of primary spectral tuning sites responsible for shifting the λ_{max} of the visual pigment between UV and violet or blue wavelengths (Yokoyama et al., 2016). Whereas longer-wavelength opsins tend to rely on smaller, additive spectral shifts from multiple tuning sites, UV/blue pigments need to alter only one or a few tuning sites to shift their λ_{max}. Amazingly, often only a single residue is involved (Shi et al., 2001; Takahashi and Ebrey, 2003; Yokoyama, 2002). Indeed, spectral shifts of over 50 nm can be achieved by the mutation of a single residue in many vertebrate SWS1 opsins (Cowing et al., 2002; Fasick et al., 2002; Wilkie et al., 2000), arthropod SWS opsins (Salcedo et al., 2003) and probably parapinopsins (Koyanagi et al., 2015). Furthermore, this dominant tuning site occurs at roughly the same location in transmembrane helix II across disparate opsin clades, at the residues homologous to position 86 or 90 in bovine rhodopsin (Fig. 2B). Positively charged residues in the binding pocket at these positions deprotonate the Schiff base (Babu et al., 2001; Dukkipati et al., 2002, 2001), returning the visual pigment λ_{max} to near that of the native chromophore and explaining the large tuning shifts inherent in UV/blue opsins. Interestingly, although most chordates primarily use SWS1 position 86 for UV tuning, birds instead use SWS1 position 90, which has independently evolved as the UV tuning site employed by arthropod SWS opsins (Hunt et al., 2004; Salcedo et al., 2003).

In both vertebrate SWS1 and arthropod SWS opsin clades, the ancestral form was probably a UV opsin (Fig. 2C) (Shi and Yokoyama, 2003; Henze and Oakley, 2015). Among vertebrates, SWS1 opsin is present in all major extant groups except elasmobranchs, including early-branching lampreys, where it forms a UV visual pigment (Collin et al., 2003, 2009). In teleosts and lungfish, SWS1 seems to form only UV visual pigments (Bailes et al., 2007; Hart et al., 2008); the single known exception is the deep-sea scabbardfish, in which the position 86 tuning site is deleted, resulting in a violet visual pigment (Tada et al., 2009) (Fig. 3E). Tetrapod SWS1 pigments, however, apparently shifted from UV into violet or blue sensitivity independently on multiple occasions in each lineage (Yokoyama et al., 2016; Hunt and Peichl, 2014). The ancestral amphibian, reptile and mammal presumably all expressed a UV SWS1, and modern reptiles have no reported violet SWS1 opsins (de Lanuza and Font, 2014). It is possible that the common reptilian ancestor of birds had a violet SWS1, but that some avian groups re-evolved UV sensitivity, often through the alternative tuning site at position 90 (Hunt et al., 2004; Ödeen and Håstad, 2013). By contrast, the recent discovery of a UVS cone type in the emu, a paleognath bird basal in avian evolution (Hart et al., 2016), is consistent with the presence of UVS visual pigments in the earliest birds and thus their ancestors. It should be noted that, with the exception of teleosts, vertebrates typically only possess one copy of SWS1, making the tuning of this opsin sequence critical in spectrally mediated visual
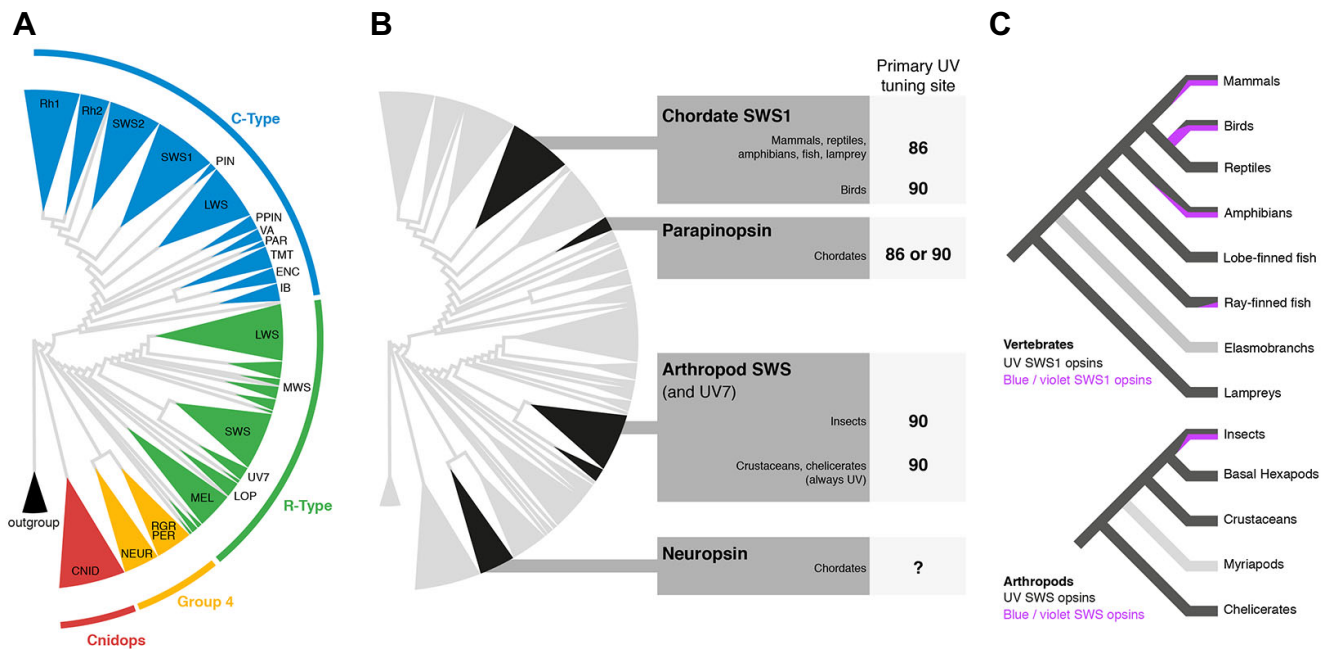
Fig. 2. Ultraviolet opsins. (A) Phylogeny of metazoan opsin sequences based on Porter et al. (2012). Abbreviations, going clockwise from top: Rh1, class 1 rhodopsin; Rh2, class 2 rhodopsin; SWS2, class 2 short-wavelength-sensitive opsin; SWS1, class 1 short-wavelength-sensitive opsin; PIN, pinopsin; LWS, long-wavelength-sensitive opsin; PPIN, parapinopsin; VA, vertebrate ancient opsin; PAR, parietopsin; TMT, teleost multiple-tissue opsin; ENC, encephalopsin; IB, invertebrate brain opsin; MWS, middle-wavelength-sensitive opsin; SWS, short-wavelength-sensitive opsin; UV7, ultraviolet-sensitive opsin 7; LOP, lophotrochozoan opsin; MEL, melanopsin; RGR, retinal G-protein coupled receptor; PER, peropsin; NEUR, neuropsin; CNID, cnidarian opsins. Clades are colored to reflect the four major groups of opsins. (B) Sub-clades containing opsins that are known to form visual pigments with λ_{max} in the UV (highlighted in black). The UV-blue/violet tuning site (amino acid residue number) is indicated for clades where representatives have been examined by sequence analysis or heterologous mutagenesis (see text). Note that phylogenetically distant opsins are all primarily tuned by the same two sites (homologous to bovine rhodopsin positions 86 and 90) located on the second transmembrane α-helix. (C) Evolutionary history of UV visual opsins in vertebrates and arthropods. Node color refers to the presence of UV (black) or blue/violet-sensitive opsins in extant lineages (purple). Branch color refers to likely ancestral states of the SWS1 and arthropod SWS opsins. Gray branches indicate groups with unknown sensitivity.

tasks. Arthropods, by contrast, often express multiple SWS opsins, and the ancestral arthropod SWS opsin also probably formed a UV visual pigment (Kashiyama et al., 2009; Koyanagi et al., 2008; Henze and Oakley, 2015). Chelicerate and crustacean SWS opsins always seem to form UV visual pigments, but in insects, one duplicated SWS clade has become blue- or violet-absorbing primarily by mutation of tuning site 90. This is perhaps in compensation for the previous loss of middle-wavelength-sensitive (MWS) opsins in insects (Henze and Oakley, 2015; M. J. Bok, The physiological, ecological, and evolutionary basis of polychromatic ultraviolet sensitivity in stomatopod crustaceans, PhD thesis, University of Maryland Baltimore County, 2013).

Although most animals with UV sensitivity possess only a single UV receptor type incorporated into a tri- or tetrachromatic color visual system, there are some notable exceptions. *Drosophila* expresses two distinct UV visual pigments with λ_{max} at 345 and 375 nm (Feiler et al., 1992). The situation in dipterans is further complicated by the frequent presence of a sensitizing pigment in the photoreceptor membranes that absorbs light strongly in the UV and transfers that energy to the visual pigment, adding a second UV sensitivity peak to longer wavelength visual pigments or augmenting the sensitivity of UV visual pigments (Hardie and Kirschfeld, 1983; Kirschfeld et al., 1977) (Fig. 3K). The significance of multiple UV receptors in flies is unknown.

Additionally, although the purpose of UV-filtering pigments in the lenses or ocular media of eyes is often to attenuate UV light falling on the retina, there are a few notable cases of spectral tuning and even the production of multiple receptor sensitivity types within the UV range

by filtering. In a rare case of short-pass optical filtering (see Glossary), at least one species of thrips (an insect) has a UV-absorbing pigment in certain facets of its compound eyes that shifts the sensitivity maximum of a probable λ_{max} 360 nm visual pigment down to below 330 nm (Mazza et al., 2010) (Fig. 3J). However, the true champions of spectral expansion and photoreceptor tuning in the UV (and throughout the entire visible spectrum) are the mantis shrimps. Many of these pugnacious crustaceans express two SWS visual pigments in their R8 photoreceptors, one with λ_{max} at 383 nm and the other at 334 nm (Bok et al., 2014; Cronin et al., 1994). This is certainly unusual, and yet they go much further: by expressing these two visual pigments in conjunction with four different short- or long-pass UV-specific filtering pigments, stomatopods expand their UV photoreceptor arsenal to at least five distinct, finely tuned photoreceptor types with λ_{max} values distributed from 310 nm to 390 nm (Bok et al., 2014, 2015; Marshall and Oberwinkler, 1999) (Fig. 3L). Furthermore, one of these photoreceptor types is also sensitive to the polarization of UV light (see Glossary; Kleinlogel and Marshall, 2009). The UV-filtering pigments are mycosporine-like amino acids, used by other animals as sunscreens or ocular filters to remove UV light, not to shape its spectrum (Bok et al., 2014).

Challenges associated with UV photosensitivity and UV vision

The problem of chromatic aberration

Chromatic aberration arises from a property that essentially all transparent materials (such as those used in biological optics) possess – their refractive index (see Glossary) decreases with
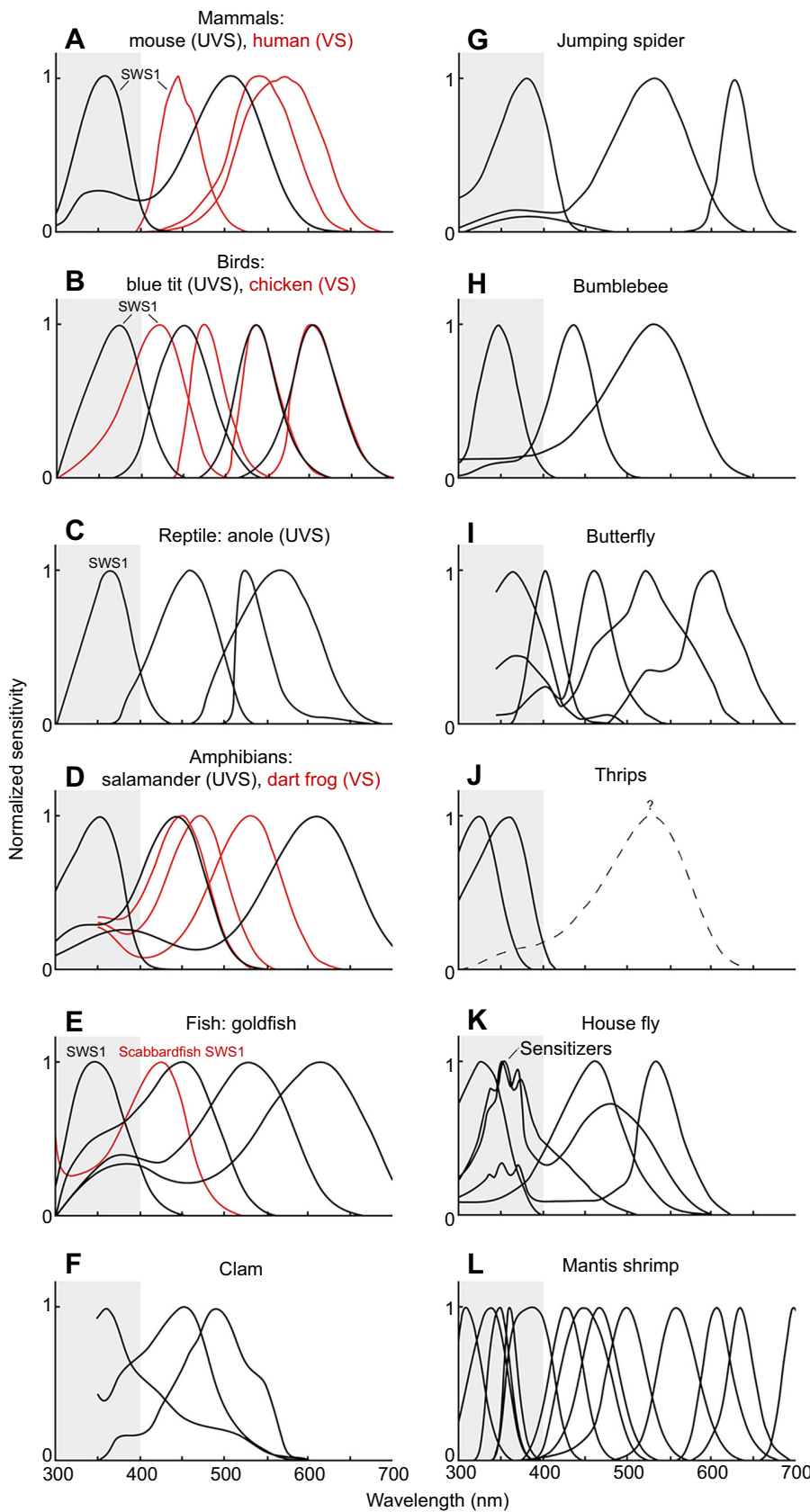
Fig. 3. Examples of photoreceptor spectral sensitivities involved in animal color vision systems. The UV range is shaded gray. Some spectra (A–E,J) are inferred based on visual pigment absorbance and lens and ocular media transmittance. The thrips spectral sensitivity (J) is inferred from behavioral response. All others are confirmed by direct electrophysiological measurements. Panels with multiple species use alternative colors, indicated on the plot. Vertebrate ultraviolet-sensitive (UVS) versus violet-sensitive (VS) SWS1 visual pigment type is indicated. See text for additional information. (A) Mammalian cones: mouse, *Mus musculus* (Sun et al., 1997; Yokoyama et al., 1998) and *Homo sapiens* (Bowmaker and Dartnall, 1980; Norren and Vos, 1974). (B) Avian cones: blue tit, *Cyanistes caeruleus* (Hart et al., 2000; Vorobyev, 2003) and chicken, *Gallus gallus* (Bowmaker et al., 1997; Olsson et al., 2015). (C) Reptilian cones: *Anolis cristatellus* (Loew et al., 2002). (D) Amphibian cones: poison dart frog, *Dendrobates pumilio* (Siddiqi et al., 2004) and tiger salamander, *Ambystoma tigrinum* (Ma et al., 2001; Perry and McNaughton, 1991). (E) Fish cones: goldfish, *Carassius auratus* (Bowmaker et al., 1991; Douglas, 1989) and scabbardfish, *Lepidopus fitchi* SWS1 (Tada et al., 2009). (F) Molluscan photoreceptors from giant clam, *Tridacna maxima* mantle eyes (Wilkens, 1984). (G) Jumping spider: *Habronattus pyrrithrix* principal eyes (Zurek et al., 2015). (H) Bumblebee: *Bombus terrestris* (Skorupski et al., 2007). (I) Butterfly: *Papilio xuthus* (Arikawa et al., 1987). (J) Thrips, *Caliothrips phaseoli* (Mazza et al., 2010). It is assumed that the thrips also has a green receptor (dashed line), but this has not been confirmed. (K) Fly: *Musca domestica* with UV-sensitizing pigment peaks indicated (Hardie, 1986). (L) Mantis shrimp: *Neogonodactylus oerstedii* (Bok et al., 2014; Marshall et al., 2007).

wavelength. Consequently, short-wavelength images are focused closer to a lens than longer-wavelength ones. Because UV has unusually short wavelengths, its focal plane lies well in front of those of visible wavelengths, thus blurring the image and decreasing

its contrast. The effect of chromatic aberration increases with eye size, so one might expect only animals with small eyes to tolerate it and thus to be UV sensitive. This is generally true, but as we show here, the exceptions are numerous.

Management of chromatic aberration in invertebrates

Given the optics of chromatic aberration, one possible way to manage it is to place UV photoreceptors closer to the lens than longer-wavelength classes. Invertebrates are generally small animals, and those that have compound eyes are essentially immune to the effects of chromatic aberration because the entire length of the photoreceptor acts as a single light guide, and resolution depends only on the separation of independent units. Nevertheless, the UV receptors are almost always found closer to the lens than other receptor types. Here, however, the reason is to boost their sensitivity, not to cope with aberrations. Because all visual pigments absorb fairly well in the UV, placing UV receptors deeper in the retina would put them at the mercy of the overlying receptors, greatly diminishing number of the UV photons that actually reach them.

Still, there are invertebrates with multiple spectral receptor types and single-lens optics. Where these species have been carefully described, they generally do manage chromatic aberration by layering UV receptor classes at the top of the retina (and also the longest-wavelength receptors in the bottom layers). Jumping spiders have large-lensed principal eyes, and their retinal tiers are nicely spaced to correct the chromatic aberration of the lens; the UV receptors are on top and the green receptors are lower – both at the correct focal plane for light to which they most strongly respond (Blest et al., 1981). As an aside, jumping spiders use focal plane changes to judge distance, but this apparently involves only green-sensitive receptors, not the UV system (Nagata et al., 2012). Of the relatively small number of other single-lensed, imaging invertebrate eyes that have been well characterized, only those of larvae of the diving beetle *Thermonectes marmoratus* definitely contain UV photoreceptors. Here, however, the UV receptors lie deeper in the retina than the middle-wavelength class, where they would be both shielded by the overlying retina and well behind the proper focal plane (Maksimovic et al., 2009). This counterintuitive arrangement has yet to be explained.

Management of chromatic aberration in vertebrates

Vertebrates have simple eyes, and nearly always large ones. Consequently, many species with UV photoreceptors potentially face chromatic aberration difficulties. In aquatic species, UV photosensitivity is mainly correlated with habitat, not with eye size. The largest fish eyes occur in high-speed predators such as tuna, swordfish or other billfishes; because these hunt away from the surface of the sea, the UV flux they experience is not strong, and they tend to be dichromats with blue and green receptor types. The lenses of most billfishes, in fact, block the entry of UV light into the eye (Fritsches et al., 2000). Amphibians tend to be small animals with rather poor spatial resolution, so they need not bother with correcting for chromatic issues.

Most terrestrial animals, however, live in a world drenched with UV photons. If they have large eyes, they must face the issues caused by chromatic defocus. Birds, as mentioned already, have two types of SWS1 cones: UVS and violet-sensitive (VS). The corresponding opsins vary at a single critical amino acid residue (Wilkie et al., 2000; Yokoyama et al., 2000; Carvalho et al., 2007). This makes it relatively easy to categorize a given species as UVS or VS using genetic approaches. It turns out that the evolution of avian UV sensitivity is complex and chaotic, and there is no clear pattern to be discerned (Ödeen et al., 2011; Ödeen and Håstad, 2013). Nevertheless, the largest birds, including cranes and ratites (ostriches and emus) are VS, consistent with their very large eyes (Wright and Bowmaker, 2001; Ödeen and Håstad, 2013; Porter

et al., 2014). A potential solution to the chromatic aberration challenge that UV sensitivity imposes is the use of multifocal lenses in many avian species (Lind et al., 2008). Such lenses have the ability to focus both short- and medium-wavelength images simultaneously. Another solution is to remove UV light by filtering it out. A comprehensive study of ocular media among birds did show decreasing UV transmittance with increasing eye size, a finding consistent with controlling chromatic aberration at very short wavelengths (Lind et al., 2014). This same study found that raptors have among the least UV-transmissive eyes of all birds, which strongly suggests that their eye designs provide very high acuity without the contamination of out-of-focus light on the retina.

Turning to terrestrial mammals, we already know from earlier sections that human lenses block UV entry very effectively. What about other species? All mammals known to have a designated UV receptor class (based, as in birds, on an SWS1 opsin) are small and/or short-lived – either rodents (mice, rats, gophers, gerbils; Jacobs et al., 1991) (Fig. 3A) or microbats (Feller et al., 2009; Müller et al., 2009). The microbat *Glossophaga soricina* is an exception that lacks a UV cone class but has UV-transmissive optics; it derives UV sensitivity from the β-band of its green-sensitive visual pigment (Winter et al., 2003). Until recently, it was assumed that larger mammals were generally similar to humans, using yellow lenses to block UV. Marine mammals lack even blue-sensitive cones (much less UV types), although this is not an adaptation for chromatic aberration (Peichl et al., 2001; Levenson and Dizon, 2003). However, in 2011, Hogg et al. published their discovery of UV sensitivity in Arctic reindeer. This came as something of a shock, because reindeer obviously have very large eyes and must view bright (and potentially photodamaging) UV-reflective snow in winter. The sensitivity is based on a standard mammalian SWS1 cone pigment absorbing maximally in the blue (Hogg et al., 2011) and being excited simply from the transparency of the optics. The finding seemed to be a strange exception until the publication of a major comparative study of mammalian ocular media (Douglas and Jeffery, 2014) revealing that the lenses of many good-sized mammals – including, surprisingly, dogs, cats and pigs – admit a sizable fraction of environmental UVA light into the eye, thus conferring UV sensitivity (albeit with the probable use in most cases of the β-bands of typical SWS or MWS cone pigments). It was subsequently found that even a deep-diving seal (*Crystophora cristata*), an animal that presumably has no UVS or blue-sensitive cones, still has the ability to detect UV light; in fact, the ability is improved by the presence of a UV-reflecting tapetum (see Glossary; Hogg et al., 2015). Clearly, the wash of largely unfocused UV images on some mammalian retinas apparently is tolerable, although it is also true that most UV-sensitive mammals have relatively poor acuity in any case; in addition, many mammals have multifocal lenses that could partially alleviate this problem (Kröger et al., 1999). Nevertheless, some mammalian groups, including primates and a few rodents, do have UV-blocking lenses. This may be related to visual acuity, or have another basis; answering this question requires yet more comparative data.

The problem of UV-associated photodamage

As noted above, it is thought that high-energy UV light is potentially damaging to retinal tissues. The energy in UV photons can break chemical bonds, potentially producing free radicals and mutating DNA, thus interfering with cellular function. At present, it is not at all obvious how large and long-living animals manage the cumulative photodamage expected from UV irradiation. Carvalho

et al. (2011) noted that – like the mammals just discussed – parrots, which are very long-lived birds (commonly attaining 50 years), also have continuous, bright UV irradiance on their corneas, lenses, ocular humors and retinas, and seem to tolerate this well. They suggest that protection from oxidative radicals produced by UV absorption may be offset by the action of carotenoid pigments in the eye. Similar mechanisms may act in mammals (Douglas and Cronin, 2016). Clearly, the costs of accepting visual damage are manageable given the widespread appearance of UV transmission in mammalian eyes.

Functions of UV vision and UV photosensitivity
Expansion of visual spectral range and color vision
It sometimes seems as if every time a new species is discovered to have UV sensitivity, some special – or secret – use is attributed to the ability. Perhaps because humans are insensitive to this part of the spectrum, we imagine that there is something unusual there. In fact, the general advantage of UV sensing is simply to extend the visual spectrum, just as adding a red cone receptor class to the retina extends the visual sense of primates to longer wavelengths compared with other mammals. It allows animals to sense stimuli that otherwise would be missed. In a later section of this Review we will explore some of the reasons why animals might wish to be aware of these stimuli. Here, we are concerned with how UV photosensitivity fits into vision itself.

Lubbock's (1881) experiments showed that ants remove larvae from patches of UV light, but because UV is photodamaging, this response simply could have been an adaptive wavelength-specific behavior. When Kühn (1924, 1927) later found that bees could be trained to forage in a UV patch, this suggested something more – that the bees recognized a color quality of UV that differed from other colors. Much later, Daumer (1956) definitively proved that bees have true color vision based on three primary colors, much like the color vision of humans, except that bee primaries turned out to be UV, blue and yellow (now known to actually be green) (Fig. 3H). Daumer also recognized that equal intensities of the primaries were equivalent to white light ('bee-white') and that mixes of UV and yellow produced a non-spectral color, which he named 'bee-purple', analogous to the human perception of non-spectral purple when blue and red light are mixed. It turns out that many insects have trichromatic color vision systems similar to those of bees (Menzel, 1979; Briscoe and Chittka, 2001; Kelber and Osorio, 2010) and, indeed, much like that of humans except for the downward shift in the spectral range.

Vertebrates have found a different solution to evolving a color vision system that includes the UV. Many years ago, Horace Barlow noted that because of the relatively broad sensitivity spectra of opsin-based visual pigments, only about three classes are needed to sample the visible spectrum fully (Barlow, 1982). If an additional class was desirable for some reason (perhaps to improve color discrimination), an extension to the visible spectrum would generally be required. Birds, reptiles and many fish have done this by adding the UV receptor, building a fourth primary and potentially achieving tetrachromatic color vision (Fig. 3B,C,E). Neumeyer (1986) showed that goldfish make UV/blue color discriminations, proving that the UV cone is involved in color vision, and later proved that these fish are true tetrachromats, requiring four primaries to match white light (Neumeyer, 1992). Subsequent research demonstrated UV color discrimination in reptiles (common slider turtle: Arnold and Neumeyer, 1987), mammals (gerbil: Jacobs and Deegan, 1994) and birds (budgerigar: Goldsmith and Butler, 2005). In the case

of birds, Goldsmith and Butler (2005) proved tetrachromacy, and it is likely that all birds with four cone classes (both UVS and VS) are true tetrachromats, as, perhaps, are many fish. Avian (and reptilian) color vision is enhanced by the presence of colored oil droplets in the inner segments of their cone photoreceptors, which sharpens the spectral sensitivity of individual cone classes and expands the range of perceptible colors, including UV colors (Vorobyev, 2003).

The overall message here is that when animals have UV photoreceptors, they generally are incorporated into the overall color vision system of the animal. Although this does not exclude color-specific responses in the UV (see Menzel, 1979), for most animals, UV is just another color dimension that affects their perception of the visual world. Mantis shrimps, with their multiple classes of UV receptors, are probably capable of color discrimination within the UV range (Bok et al., 2014) in addition to their well-documented color vision at longer wavelengths (Marshall et al., 1996). In subsequent sections, we review the utility of UV perception.

Navigation and orientation
On a clear day, UV wavelengths dominate in the atmosphere due to Rayleigh scattering (see Glossary), which has a greater effect on shorter wavelengths. It appears that insects use patches of bright UV light as a surrogate for the open sky when flying through vegetation; they certainly show strong phototaxis towards UV stimuli (Menzel, 1979). Spiders exploit this by spinning webs with silks that strongly scatter UV or by decorating the webs with ornamental patterns that reflect UV effectively. Webs from which these decorations have been removed are significantly less effective at catching insects (Craig and Bernard, 1990).

Besides its relative brightness, celestial scattered light is linearly polarized, and when the sky is clear and multiple scattering events are relatively rare, a strong and predictable polarization pattern appears in the atmosphere (Waterman, 1981; Wehner, 2001). This pattern is bilaterally symmetrical about the plane that includes the sun, the zenith and the observer, and it can be used for axial orientation. In general, UV photoreceptors are the most reliable for detecting celestial polarization (Seliger et al., 1994), so many insects (especially bees, ants and butterflies) devote a subset of their UV photoreceptors to celestial polarization analysis. The polarization analyzers are restricted to a patch of ommatidia near the dorsal margin of the eye, a region called the 'dorsal rim area'. Here, UV receptors are oriented such that each ommatidium contains a pair of polarization analyzers orthogonal to each other (Wehner and Labhart, 2006; Cronin et al., 2014). The entire array within the dorsal rims of the two eyes is organized to sample a small patch of overhead sky and to provide signals to specialized cells in the brain that respond to each of its time-varying polarization patterns (Rossel, 1989; Homberg et al., 2011). Thus, the UV array as a whole analyzes the celestial polarization at any given time, allowing the insect to orient appropriately. The system permits insects like bees and ants to make long excursions from a given location and return to it precisely. Oddly, fish are thought to have a polarization-sensitive system that also involves UVS cones in the analysis. However, the system has relatively low polarization sensitivity, and it is at present unclear whether or not it has a special function (Kamermans and Hawryshyn, 2011).

Foraging and predator/prey detection
In his very early work with bees, Kühn (1924, 1927) suggested that bees could use UV patterns to recognize flowers, and in fact, taking
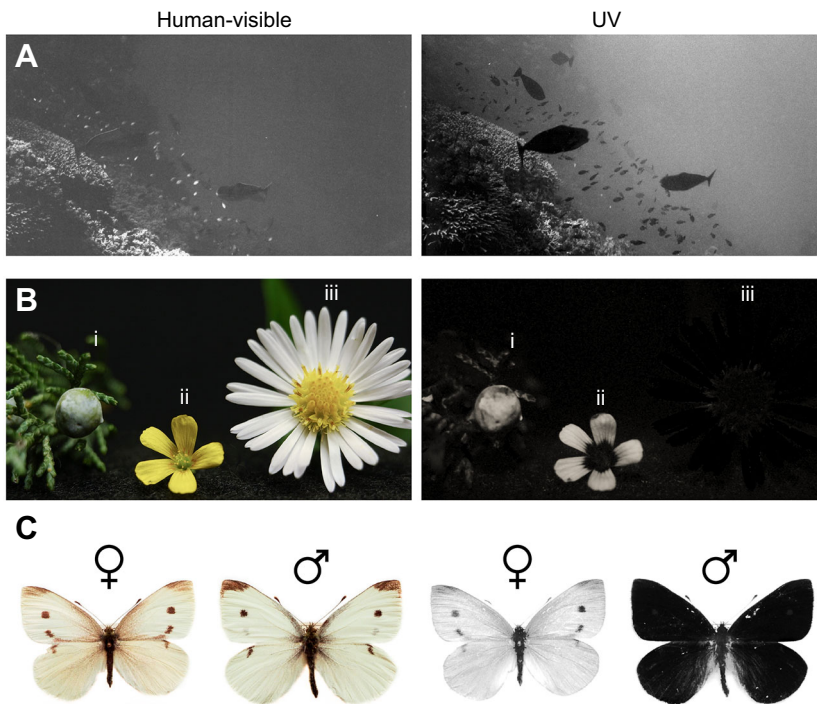
Fig. 4. Examples of uses for UV light in nature. Photographs at human-visible wavelengths (left) and in the UV (right). (A) Predator and prey detection: a coral reef scene photographed through filters for green (left) and UV (right) light. Scattered UV light in the water column silhouettes the fish. (B) Advertisements for foragers: A juniper berry (i), a buttercup (ii) and a daisy (iii). The berry and the outer ring of the buttercup reflect UV light. (C) Gender discrimination and mate choice: female and male *Pieris rapae*. Although the genders look similar in visible light, females reflect more UV light.

photographs of flowers in UV light has been possible since long before his pioneering work on UV color vision (Fig. 4B). There is nothing special about UV colors in flowers. It just happens that bees have excellent UV photoreceptors, perhaps fostered by the navigational tasks just discussed, and flower evolution has been shaped by the need to attract pollinating bees. Thus, floral UV colors and patterns are useful to plants and to bees as well (Chittka et al., 1994; Kevan et al., 2001). Similarly, many fruits and berries that are dispersed by birds (for instance those of Panamanian shrub *Psychotria emetica*) reflect UV upon ripening (Fig. 4B). Altschuler (2001) found that when their UV reflectance was blocked, they were far less likely to be taken by fruit dispersers. These dispersers are mostly UVS birds, but might include small UVS rodents as well. UV vision also may improve avian foraging success on insects, as Church et al. (1998) demonstrated with blue tits feeding on moth caterpillars. In an interesting twist, night-foraging hawkmoths (which possess UVS photoreceptors) actively avoid flowers that reflect UV, demonstrating both that UV is not itself invariably attractive and that a UV signal can be useful by its absence as well as its presence (White et al., 1994). In an analogous case from the Arctic, reindeer browse on plants including lichen and moss in dim Arctic twilight; because these plants reflect little UV light they contrast well against white snow and are easily seen by a reindeer (Tyler et al., 2014a). Thus, a major benefit of UV sensitivity in these animals could be an enhanced ability to forage effectively in snow. Reindeer have a further adaptation that is appropriate for twilight foraging in snow. Their tapetum reorganizes in the winter from a broadband, specularly reflecting structure to a form that strongly and diffusely scatters short-wavelength light (Stokkan et al., 2013). This greatly increases short-wavelength sensitivity. The change is associated with increased intraocular pressure, which apparently compresses the collagen fiber organization of the tapetum, creating a seasonally tunable reflector that produces a more UV-sensitive, albeit less acute, visual system in winter.

Because UV light is scattered effectively in marine waters, it creates a bright spacelight against which nearby objects can be seen

in silhouette (Losey et al., 1999) (Fig. 4A). Even seemingly transparent plankton may absorb in the UVA (Johnsen and Widder, 2001) and small pigmented zooplankton even more so. Consequently, planktivorous fishes should be well adapted for feeding using only UV light (Loew et al., 1993; Browman et al., 1994). Many small reef fishes have UV-transparent ocular media (Siebeck and Marshall, 2001) and there is even some evidence that zooplankton prey may adjust their vertical migration behavior when UV light is present (Leech et al., 2009). All this strongly suggests that UV vision is a critical aspect of feeding in small fishes. Recently, this was directly tested in two ways. First, Novales Flamarique (2013) used hormone treatment to encourage the early conversion of UVS cones to blue-sensitive cones in very young rainbow trout (a process that normally occurs somewhat later in these fish). The treatment made prey detection more difficult, showing that the UV system plays an important role in predation. In a later set of experiments, foraging by mutant zebrafish that have relatively few UVS cones was compared with that of wild-type fish of similar sizes. Again, diminished UV sensitivity (or resolution) decreased foraging success (Novales Flamarique, 2016). The use of UV for silhouette predation by juvenile fishes is perhaps the best-documented case of a specialized predation behavior that relies on UV sensitivity. Because the UV spacelight in clear marine water potentially permits sighting of other organisms at distances of several meters (Fig. 4A), larger predators may use this ability as well, although there is no direct evidence that they do. Similarly, small fish could detect incoming predators in the same way – unfortunately, solid evidence of this is again lacking.

There is only one published claim that credits UV vision with a role in predation by birds. Both Eurasian kestrels (Viitala et al., 1995) and rough-legged buzzards (Koivula and Viitala, 1999) are said to hunt more frequently in areas where vole trails have been marked with urine. The urine deposited by voles apparently reflects strongly in the UV, and kestrels in the laboratory spent more time inspecting vole trails that were illuminated with UV light (Viitala et al., 1995), suggesting that they use UV brightness within these

trails to look for prey. However, more recent work has questioned these conclusions. Raptors possess VS cones (with peak sensitivity near 405 nm) and have ocular media that reduce UV transmission within the eye (Lind et al., 2013). Further, Lind et al. (2013) found that, at least in Swedish bank voles, the urine is much less reflective in the UV than at visible wavelengths (and much less reflective than water alone). Together with reflectance data from urine and water on grass and sand, this research provided little evidence for UV-enhanced predation by raptors. So, the voles should be able to urinate to their hearts' content without fear of alerting nearby raptors. If anything, the shoe is on the other foot – UV sensitivity should help the voles to detect aerial predators. Mice, and likely voles as well, have regionally specialized sets of cones in the retina, and the UV cones heavily dominate in the ventral retina, which views the sky (Calderone and Jacobs, 1995). These animals should be very aware of dark objects against the bright UV sky, even at twilight (when the sky is particularly enriched at UV wavelengths) and thus able to sight hovering raptors well before they themselves are easily seen in dim twilight. Returning briefly to reindeer, their ability to sense contrast in the UV may serve them in an anti-predator role as well (Hogg et al., 2011). The white fur of wolves and polar bears weakly reflects UV light, rendering them visible to reindeer against UV-bright snow. Of course, reindeer are also more sensitive to UV light in the winter (Stokkan et al., 2013), perhaps providing improved early predator detection.

It is difficult to decide whether avoidance of power lines is predator evasion or orientation, but we will close this section with an unexpected observation related to this. Power lines emit UV discharges in the spectral range 200–400 nm as a constant 'corona' along the cable itself and as transient flashes at insulators on poles (Tyler et al., 2014b). UVS birds, and even bats, should be able to see these cables on a dark night, and potentially avoid them (Tyler et al., 2014b). Perhaps this accounts for the UV sensitivity of reindeer, as it means that Rudolph has no worries about entangling Santa's sleigh in power transmission lines!

Signaling: communicating in the UV

UV cues play major roles in animal communication, including aggression, mate choice and species recognition (Tovée, 1995). This topic easily deserves its own review, but here we will highlight a few notable cases and themes. Although much research regarding UV visual signals relies on inference based on gender- or species-specific UV reflectance differences, there is also extensive experimental evidence documenting alterations in animal interactions when UV cues are manipulated. UV-mediated intraspecific signaling was first noted in gender discrimination tasks in butterflies (Obara, 1970; Obara and Hidaka, 1968; Silberglied and Taylor, 1978). These exciting discoveries revealed how some butterflies discriminate genders using only visual cues, despite appearing nearly identical to us. Bennett et al. (1996) revealed that zebra finches evaluate UV cues when assessing mates, and a similar situation has also been identified in the blue tit, or perhaps more accurately, the 'UV tit' (Andersson et al., 1998; Hunt et al., 1998). Additionally, many animals that are dimorphic outside the UV range have nonetheless been shown to make mate choices based on UV cues (Detto and Backwell, 2009; Hausmann et al., 2003; Siitari et al., 2002; Smith et al., 2002). Furthermore, UV signals are often used in species recognition, again sometimes allowing animals to visually discriminate between otherwise identical-looking species. The most surprising example may be two species of yellow damselfish that can tell each other apart based solely on subtle differences in UV-reflective patterns on their faces

(Siebeck et al., 2010). UV cues are also involved in intraspecific aggressive displays, often male–male altercations over territory or access to females (Xu and Fincke, 2015; Stapley and Whiting, 2006; Whiting et al., 2006). It is also possible that the various UV signals discussed here can serve in covert signaling in cases where an animal's primary predators lack UV sensitivity (Cummings et al., 2003). When UV is outside the visual spectral range of potential predators, one might consider its use in signaling to be 'covert' or 'special' in some way, it is unique in this situation, but in general, the roles of UV signals are probably not different from the roles of colors and patterns in other parts of the spectrum (Hunt et al., 2001; Maddocks et al., 2001). In this sense, UV is really nothing special in signaling, only an additional way to provide species-specific signals.

Just as UV vision was long ignored because UV is not perceived by humans, most studies of UV signaling have been restricted to the UVA, where the majority of animals are maximally sensitive. However, the UVB is proving to be an important region of the spectrum for some animals. Besides the aforementioned thrips, which exhibit strong UVB attraction for an unknown purpose (Mazza et al., 2010), jumping spiders have also been found to use UVB reflectance as an important cue in mate choice (Li et al., 2008; Painting et al., 2016). Mantis shrimp may be the premiere example of UV signaling. Perhaps explaining their extreme expansion of UV photoreceptor spectral types, mantis shrimp apparently use different regions within the UV spectrum for different tasks. They can be trained to associate UV cues above 350 nm in wavelength with food rewards, and many species-specific chromatic cues reside in this area of the spectrum as well. However, untrained mantis shrimp also appear to respond antagonistically to UVB light (M. J. Bok, The physiological, ecological, and evolutionary basis of polychromatic ultraviolet sensitivity in stomatopod crustaceans, PhD thesis, University of Maryland Baltimore County, 2013). It may be no coincidence that structures presented during aggressive displays reflect light at these far-UV wavelengths, and these cues may provide covert, mantis shrimp-specific visual warnings.

Summary and outlook

Although long neglected, in part because of our own spectral deficiencies, in recent decades our understanding of UV photoreception and vision in animals has advanced tremendously. Following the original observations that animals respond to wavelengths of light beyond our perception, researchers have found UV sensitivity in an impressive diversity of animal species, mediating a variety of sophisticated behaviors. They have traced the evolution of the visual pigments responsible for UV photoreception and begun to probe the genetics and biochemical properties that confer the preferential absorption of UV photons on these molecules.

There is of course much yet to do. Firstly, because essentially all of what we know about UV photoreception and UV vision applies to only two phyla (chordates and arthropods), to gain a full understanding of the physiology and ecology of this modality it is necessary to explore UV sensitivity in a far more comparative manner. Secondly, the mechanisms used to tune visual pigments to wavelengths in the mid-UV range and below are simply not understood. The unbound chromophore, most commonly retinal1, has a λ_{max} near 385 nm, but UV visual pigments range in λ_{max} down to at least ~330 nm. Most opsins produce visual pigments with λ_{max} well above 385 nm, sometimes approaching 600 nm. The interactions between the chromophore and its surrounding amino acid residues in UV opsins that shift absorbances to wavelengths shorter than the natural absorbance of the chromophore remain a

mystery. A third potential area of research is the nature and role of UV vision in the UVB range. A few animals detect light with wavelengths as short as 300 nm. Does this extreme UV vision have special significance? If so, what? A final issue that has repeatedly arisen in our Review is the question of tolerating UV-induced photodamage. A great many animals permit UV to enter the eye and directly impact the ocular tissues, specifically the neural retina. How do the tissues of the eye protect themselves against this lifelong onslaught? Do some species tolerate the damage, evolutionarily taking their chances of making it to reproductive age? The balance between damage and repair, and the mechanisms involved, are significant research concerns that may have both basic biological and clinical implications. Research into the biology of UV photosensitivity and vision will involve approaches at every level of biological inquiry, from genetic to biochemical, cellular and neurobiological to ecological, behavioral and evolutionary aspects.

In this Review, we have attempted to provide a complete look at the rapidly expanding research on the role of UV in animal light sensitivity and vision. The ability to detect and respond to UV is largely just an extension of normal animal vision, but it is surprising that so many animals permit UV to reach the retina even when it may lower visual contrast and resolution while simultaneously damaging the tissues of the eye. An impressive range of creatures have exploited the susceptibility of UV light to scattering in air and water, using it for contrast enhancement and navigation. They use it in signals and displays, making use of mechanisms that tune their UV receptors to a surprising diversity of wavelength bands within the narrow spectral range of UV light. UV vision is a fascinating research area to vision scientists, and indeed to the public at large – perhaps in part because it seems so exotic. In the end, however, we can wonder at the UV worlds perceived by so many of our fellow creatures and hope to learn how this ability contributes to their function and survival.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Both authors contributed equally to writing and editing the manuscript.

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