

# Insights into visual pigment adaptation and diversity from model ecological and evolutionary systems

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Sensory systems provide valuable insight into the evolution of molecular mechanisms underlying organismal anatomy, physiology, and behaviour. Visual pigments, which mediate the first step in visual transduction, offer a unique window into the relationship between molecular variation and visual performance, and enhance our understanding of how ecology, life history, and physiology may shape genetic variation across a variety of organisms. Here we review recent work investigating vertebrate visual pigments from a number of perspectives. Opsin gene duplication, loss, differential expression, structural variation, and the physiological context in which they operate, have profoundly shaped the visual capabilities of vertebrates adapting to novel environments. We note the importance of conceptual frameworks in investigating visual pigment diversity in vertebrates, highlighting key examples including evolutionary transitions between different photic environments, major shifts in life history evolution and ecology, evolutionary innovations in visual system anatomy and physiology, as well as shifts in visually mediated behaviours and behavioural ecology. We emphasize the utility of studying visual pigment evolution in the context of these different perspectives, and demonstrate how the integrative approaches discussed in this review contribute to a better understanding of the underlying molecular processes mediating adaptation in sensory systems, and the contexts in which they occur.

## Addresses

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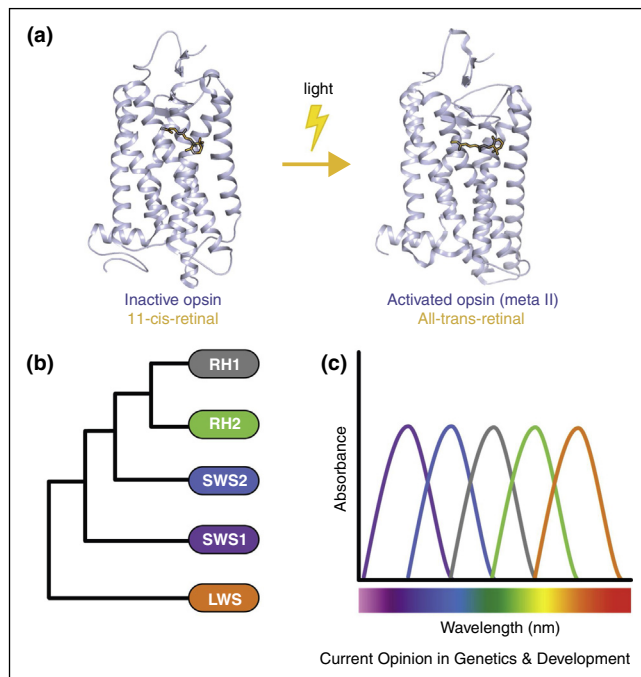
## Introduction

Sensory systems are ideal models for framing evolutionary questions about the molecular basis of organismal fitness and biology. The visual system serves as a crucial interface between many organisms and their environments, allowing for the nearly instantaneous relay of information relevant to survival [1]. Moreover, the vertebrate visual system has been extensively characterized at the molecular level due to its broad appeal across biological disciplines. For instance, numerous genes participating in vision are linked to visual impairment in humans [2], and the unprecedented rate at which visual pigments activate is considered a remarkable biochemical and evolutionary innovation [3]. Visual pigments, which mediate the first step in vision, have two components: an opsin protein, a prototypical G protein-coupled receptor (GPCR), and a covalently bound retinal chromophore (Figure 1) [4]. Upon absorption of a photon, the chromophore isomerizes from its 11-*cis* to all-*trans* form, triggering a conformational change in the opsin protein [3]. This subsequently activates the downstream visual transduction pathway within the photoreceptor and ultimately relays a signal that light has been perceived [5].

Vertebrates possess five classes of visual pigments distinguished by the wavelength of light at which they are maximally sensitive ( $\lambda_{\max}$ ) (Figure 1). Rhodopsin (RH1) is the photopigment expressed in rod photoreceptor cells that facilitates vision in dim light. With a few notable exceptions from animals living in unusual or dimly lit environments, many rhodopsins are tuned to a  $\lambda_{\max}$  of around 500 nm. On the other hand, cone photoreceptor cells, which mediate colour vision in relatively bright light, can possess multiple classes of cone opsins specialized in different regions of the visible spectrum: SWS1 (ultraviolet-sensitive or violet-sensitive); SWS2 (violet or blue-sensitive); RH2 (green-sensitive); and LWS (yellow/orange-sensitive) [6].

Adaptive changes in visual pigments can occur through several mechanisms, including variation in the size of opsin repertoire (driven by gene duplication and pseudogenization) [7,8,9\*\*], amino acid substitutions that alter spectral absorbance (i.e. spectral tuning mutations) and kinetic functions [10,11], alternative chromophore usage [12\*], and expression of different sets of opsin genes (referred to as an opsin palette) [13,14] (Figure 2). Conversely, the anatomical and physiological context (e.g. transmittance of the lens, ratios of rod and cone retinal photoreceptors, and interacting molecular partners) may

Figure 1



Overview of visual pigment structure, function, and evolution. **(a)** The opsin protein consists of seven transmembrane alpha-helices bound to a retinal chromophore derived from vitamin A [85]. Absorption of a photon triggers isomerization of 11-*cis*-retinal to all-*trans*-retinal, inducing a conformational change in rhodopsin to its active G protein-signalling form (meta II) [86]. **(b)** Five opsin classes in vertebrates evolved from an ancestrally long wavelength-sensitive opsin. **(c)** The maximum spectral absorbance of the five opsin classes defines the spectrum of light available for vision: SWS1 355–455 nm; SWS2 400–470 nm; RH1 ~500 nm; RH2 480–530 nm; LWS 500–570 nm [6].

enhance or diminish the effects of visual pigment adaptations (Figure 2). This variation in opsin gene number, sequence, and expression among vertebrates, as well as the broader anatomical context in which these proteins function, have together optimized visual system function for important fitness-related tasks. Studies examining this variation are thus able to draw on key aspects of organismal biology, anatomy and physiology, ecology, and natural history (reviewed in [15]).

Within the last decade, targeted sequencing studies, combined with increasingly available comparative genomics data, have produced excellent resources for molecular evolutionary investigations, particularly for studies of visual pigment evolution. This recent work highlights the need for appropriately framed hypotheses regarding visual pigment evolution in the context of organismal biology, and the importance of carefully selected evolutionary model systems to investigate aspects of visual function. In this review, we focus on exciting recent work showcasing the diversity of conceptual ecological and

evolutionary frameworks used to investigate visual pigment evolution. Comprehensive reviews on eye evolution [16], phototransduction [17,18], and visual pigments [15,19] spanning a broad array of organisms offer important additional context to our discussion of these studies. We devote particular attention to research that has creatively incorporated investigations of visual pigment evolution into the broader context of organismal life history, ecology, and natural history; cellular, physiological, and anatomical elements; and macroevolutionary influences on molecular variation. Importantly, the hypotheses and questions centered on visual pigments discussed in this review can extend to other sensory systems, as well as other ecologically relevant genes and gene families, ultimately contributing to a better understanding of sensory evolution, the context in which it may occur, and the underlying molecular processes mediating adaptation in sensory systems (Figure 3).

### Evolutionary transitions in photic environment

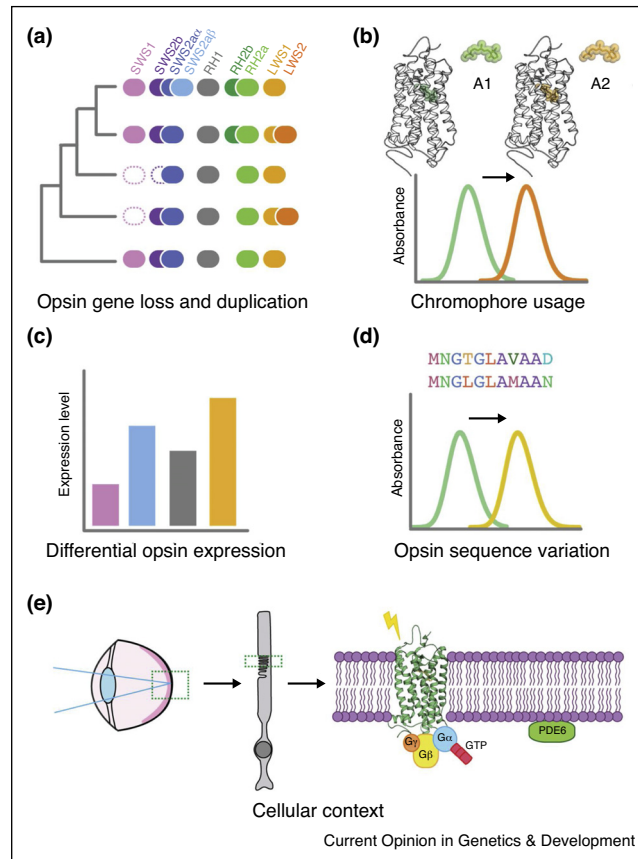
The spectral composition of ambient light exerts substantial influence on the visual system; organisms must adapt rapidly to their dominant photic regime to achieve a variety of fitness-related tasks such as foraging, inter-specific and intra-specific communication, and predator avoidance. Opsin proteins are exemplary for investigating such transitions over a range of timescales, and recent work has underscored the utility of testing hypotheses about the effect of novel light environments on opsin sequence evolution, gene expression, and other aspects of visual pigment function.

#### Transitions in aquatic habitats: marine & freshwater fishes

In aquatic environments, the spectral composition and intensity of ambient light may be influenced by the inherent properties of water (e.g. a shift to predominantly blue wavelengths with increasing depth) [20,21], as well as materials dissolved or suspended in the water (e.g. organic matter or sediments). In fishes, how transitions in photic environment have affected opsin genes has been extensively investigated for several reasons. First, many fish groups have undergone several rounds of opsin gene duplication [9<sup>••</sup>,22], and may express multiple opsins in their retinas at once, achieving trichromatic, and sometimes tetrachromatic vision [23,24]. Second, some fishes may use an alternative chromophore that dramatically red-shifts visual pigment sensitivity (A2). Third, differential opsin expression between species, through ontogeny [25], or in different regions of the retina [26,27] allows for extensive plasticity in fish visual sensitivity [28,29<sup>•</sup>] (Figure 3).

Marine habitats can be highly varied in their spectral content. Shallow habitats such as coral reefs are spectrally rich: most wavelengths of light, including rapidly attenuating UV wavelengths, may penetrate the water column.

Figure 2

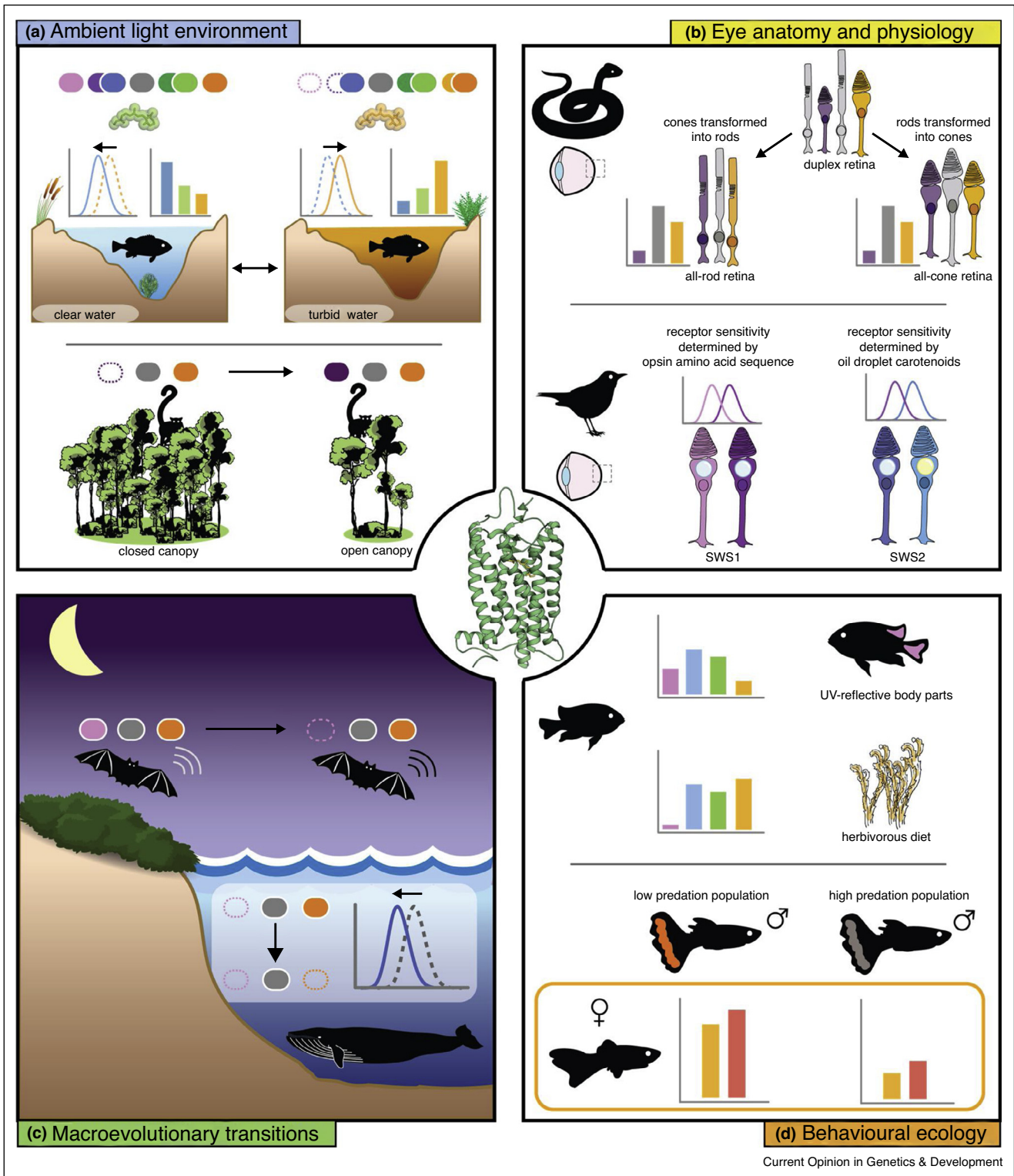


Examples of how vertebrate visual pigment variation may alter visual sensitivity. **(a)** The size of the opsin repertoire varies substantially across vertebrates, with numerous instances of both gene duplication and gene loss. In this review UV-sensitive SWS1 opsins are represented in pink. **(b)** Some vertebrates, particularly freshwater fishes, amphibians, and reptiles, may use an alternative (A2) chromophore. These A2-based pigments have a  $\lambda_{\max}$  shifted substantially into the red, and occasionally near-infrared region of the spectrum [12\*,87]. **(c)** Differential gene expression of opsin paralogs (i.e. an opsin palette) is an additional means of modulating sensitivity. **(d)** Structural differences (i.e. amino acid substitutions) in the opsin protein can dramatically shift pigment sensitivity (referred to as spectral tuning). **(e)** Anatomical, physiological, and cellular contexts will also affect how visual pigments are able to tune sensitivity, as well as the various other members of the visual transduction cascade they may interact with (e.g. G protein).

This spectral richness is reflected in the visual system diversity of reef-dwelling fishes, which may possess several differentially expressed cone opsin gene duplicates [30]. Reef fish also show considerable interspecific variation in cone opsin expression across species, and increasing depth may promote expression of a blue-shifted opsin palette [31]. In contrast to the primarily blue-dominated spectra of ocean environments, the content of ambient light in freshwater environments can vary extensively, ranging from clear to tea-stained, green-tinted, turbid or nearly opaque. For instance, dim and red-shifted freshwater habitats may have driven a reduction in the cone opsin repertoire of Amazonian cichlid fishes [32,33\*], and promoted expression of a primarily long wavelength-sensitive opsin palette (SWS2a, RH2a, and LWS) [33\*]. Differences between clear and blackwater habitats have

also mediated parallel changes in chromophore usage and opsin gene expression among closely related Midas cichlids [34\*]. With respect to sequence variation, changes in haplotype frequency at key spectral tuning sites in the stickleback blue-sensitive opsin gene (SWS2) were found after only 19 years of divergence following transplantation from a blackwater lake (red-shifted) to a clearwater pond [35\*\*]. Specifically, an SWS2 haplotype with a red-shifted SWS2 allele occurred at high frequency in blackwater stickleback populations; after 13 generations in a clearwater habitat, the frequency of blue-shifting SWS2 substitutions rose significantly [35\*\*]. Over macroevolutionary timescales, differences in freshwater aquatic habitats (e.g. between lake and riverine environments) have also driven sequence evolution in the dim-light visual pigments (RH1) of both African and

Figure 3



Ecological and evolutionary frameworks for studying visual pigment evolution. **(a)** Transitions between clear and turbid or red-shifted waters may influence all or some of the following in fishes and other vertebrates: opsin gene repertoire [33\*], expression [41\*], sequence [35\*\*], and chromophore usage [34\*]. Transitions between open versus closed canopies may also exert selection on the SWS1 opsin in primates [49]. **(b)** In snakes with 'all-cone' retinas, RH1 expression supports the hypothesis that rods transformed into cone-like photoreceptors, potentially for better visual performance under diurnal conditions [81\*\*]. Conversely, cone opsin expression in snakes with 'all-rod' retinas supports an evolutionary

Neotropical cichlids [36,37]. More recently, Central American cichlid invasion into novel spectral habitats has also been linked to functional differences among RH1 pigments [38].

Vertebrate lineages (particularly fishes) that have undergone either short-term (i.e. migratory) or long-term (macroevolutionary) transitions between marine and freshwater environments are essentially repeated evolutionary experiments in the adaptation of visual pigments to different photic environments. Fishes can have highly flexible visual systems within a single lifetime — individuals may tune visual sensitivity during migration between marine and freshwater environments via chromophore usage and differential opsin expression (e.g. salmon [39,40]). A study of heritable differences in opsin expression in marine (blue-shifted waters) versus freshwater (red-shifted waters) stickleback populations revealed lower expression of SWS1 and higher expression of RH2 in freshwater populations [41\*]. These transitions through aquatic habitats may also be reflected in opsin sequence variation. For example, a red-shifted SWS2 allele was shown to be favoured in sticklebacks that invaded blackwater lakes from marine ancestors [35\*\*]. Similarly, marine anchovy invasions into freshwater rivers likely accelerated the evolution of RH1 in several invading freshwater lineages, resulting in several amino acid substitutions that potentially red shift the pigment's sensitivity [42].

#### Nocturnal–diurnal transitions: terrestrial vertebrates

Although the visual environments of terrestrial habitats are generally not as disparate as aquatic habitats, studies of visual pigment evolution in terrestrial vertebrates have highlighted the critical role of ambient light and diel activity in shaping opsin evolution and gene expression [43]. For instance, the reduction of opsin genes in the majority of mammalian genomes to only RH1, SWS1, and LWS is likely associated with their ancestrally nocturnal lifestyle. Resurrection and functional characterization of ancestral mammalian RH1 also suggests enhanced dim light sensitivity in early mammals [44].

The mammalian (therian) ancestor likely possessed an ultraviolet-sensitive SWS1 pigment, with multiple transitions to violet sensitivity associated with shifts to diurnal

niches [45]. At the amino acid level, analyses of variation among functional SWS opsins has provided support for the loss of UV sensitivity in early nocturnal primates [46]. Nevertheless, many extant diurnal primates show extensive diversity in visual pigment genes, as well as duplication of the long-wavelength sensitive opsin (or, in New World primates, allelic variation in the LWS opsin), restoring trichromatic vision in several groups [47] (reviewed in [48]). Accordingly, there are several primate lineages in which the SWS opsin is not only intact but also highly constrained, and may mediate adaptation to open versus closed canopy environments [49] as well as foraging specializations [50] (Figure 3).

While adaptation to nocturnal or dim-light lifestyles has been most extensively investigated in mammals, reptiles also show substantial variation in activity patterns and photic niches. For instance, lizards have a relatively diverse opsin repertoire (SWS1, SWS2, RH1, RH2, and LWS), whereas snakes have a reduced set of opsins (SWS1, RH1, and LWS), a difference that may be due to an ancestrally fossorial (burrowing) lifestyle [51]. Opsin gene variation in crocodylians has also provided support for an ancestrally nocturnal lifestyle (only SWS2, LWS, and RH1 were found intact in the genome), while turtles appear to have a comparatively larger opsin repertoire (consisting of SWS1, SWS2, RH1, RH2, and LWS) [52]. Given this intriguing variation, further investigation of visual pigment evolution accompanying transitions from nocturnality to diurnality in reptiles is a promising avenue of future research.

#### Major macroevolutionary transitions in life history and ecology: bats and whales

Many mammals have visual adaptations consistent with dim-light environments and the nocturnal niche, but lineages that have undergone radical life history transitions, such as bats and whales, are particularly compelling systems to frame ecological questions about visual pigment evolution.

Bats, one of the most diverse mammalian lineages, offer an opportunity to investigate visual pigment evolution in the context of both nocturnal activity and other sensory adaptations [53,54]. For instance, the dim light visual pigment RH1 has likely undergone convergent evolution

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(Figure 3 Legend Continued) transformation of cones into rod-like structures, perhaps as an adaptation to dim light conditions [82]. In birds, SWS1 photoreceptor sensitivity is governed by point mutations in the SWS1 opsin gene, while SWS2 photoreceptor sensitivity is determined by the content of carotenoids in pigmented oil droplets, which limit the transmittance of short wavelength light [79\*]. (c) Macroevolutionary transitions in the life history of bats and whales has influenced the size of the opsin repertoire (e.g. a loss of SWS1 in bats with sophisticated echolocation [53], and all cetaceans, with further loss of LWS in some deep-diving cetaceans [59]), as well as spectral tuning (mutations in cetacean rhodopsin blue-shift  $\lambda_{max}$  to better match ambient light [60\*]). (d) In damselfish, increased expression of SWS1 and LWS has been linked to UV-reflective body parts (potentially serving as a private communication channel) and herbivorous diets, respectively [63\*]. Female guppies inhabiting regions with low predation (and therefore weaker selection acting against male guppies with conspicuous red colouration) express higher levels of two LWS paralogs [66\*].

in fruit bats with well-developed eyes [55]. Opsin variation in bats may also reflect evolutionary trade-offs in sensory capabilities. The SWS1 opsin has become pseudogenized in many microbat lineages with sophisticated (high duty cycle) echolocation, likely a consequence of relaxed constraint on the visual system due to investment in an advanced alternate sensory modality [53,56]. Conversely, SWS1 remains functional in most microbats with less sophisticated (low duty cycle) echolocation capabilities, perhaps to enhance the acoustic 'image' of their surroundings [53] (Figure 3). Differences in echolocation capabilities may also mediate differential selection on the LWS opsin [57]. Additional studies investigating opsin evolution in the context of other aspects of bat ecology, such as foraging, habitat, and lifestyle, will be an intriguing extension of bat visual system evolution research.

The cetacean transition to an aquatic lifestyle from a terrestrial ancestor presents an excellent system for examining molecular changes in ecologically relevant genes within a macroevolutionary context that also reflects enormous morphological and physiological change. This transition included major modifications to enhance dim-light aquatic vision, such as a spherical lens, a flattened cornea, and an increased rod to cone ratio in the retina [58]. Accompanying these eye adaptations were several modifications to cetacean opsins. First, the SWS1 opsin was inactivated early in cetacean evolution, and LWS was subsequently pseudogenized in several descendent lineages of both toothed and baleen whales [59]. Second, amino acid substitutions have accumulated in RH1 that have likely optimized pigment function for aquatic habitats. In RH1, functional characterization of both spectral and kinetic properties found that key amino acid substitutions along the ancestral cetacean lineage tune the pigment to blue-shifted ambient light [60], and may also mediate differences in opsin activation kinetics to optimize function in dim-light conditions [61] (Figure 3).

### Visual pigment evolution in the context of behavioural ecology

The intersection among photic environment, ecological variables such as foraging or sexual selection, and variation in opsin genes can have profound effects on vertebrate fitness and diversity. For instance, in cichlid fishes, depth-driven differences in photic environment promoted variation in LWS opsin sensitivity, which in turn likely led to differences in female preference, male nuptial colouration, and speciation (i.e. sensory drive [62]). While it is often essential to examine the effects of photic environment and, in the cichlid example, sexual selection on opsin evolution together, several recent studies have linked variation in opsin sequence and expression to a variety of behavioural ecological variables beyond photic environment.

In addition to photic environment, fishes must also tune their visual systems to optimize foraging, predator avoidance, and communication-related tasks. Recent work investigating reef fish colouration via spectral reflectance measurements, as well as diet composition, has identified associations between these traits and opsin expression. UV-reflecting body parts in damselfish may be associated with increased SWS1 opsin sequence variation and expression, potentially allowing for private communication among conspecifics and heterospecifics via UV reflectance [63]. Because many damselfish predators do not show evidence for UV sensitivity, this visual communication can occur without compromising survivorship [64]. LWS expression may also be linked to diet in damselfish, where increased expression is associated with the consumption of long wavelength light-reflecting algae [63]. Conversely, diets high in carotenoids may drive high expression of LWS opsins in guppies [65] (Figure 3).

The relationship between both natural and sexual selection, and the effect of these selection pressures on opsin evolution has been elegantly examined in guppy systems, where the bright orange colouration of males is favoured by females, but may also increase their vulnerability to predation. A recent study of high predation (favouring evolution of drab males and minimal female preference for colourful males) versus low predation (favouring colourful orange males and female preference for such males) in guppy populations found an upregulation of LWS opsin paralogs in female guppies inhabiting low predation populations [66] (Figure 3). These findings suggest that LWS opsins represent an important facet of female preference for colourful mates. Systems encompassing both sexual selection (in the form of colour preference) as well as natural selection (predation on conspicuous males) are ideal for framing questions about the adaptive relevance of opsin expression and spectral tuning.

The colourful plumage, behavioural complexity, and morphological diversity of birds has inspired numerous studies linking visual pigment evolution to these various attributes, both within and between species. For instance, evolution of SWS2 [67] and RH2 [68] has been linked to plumage evolution in warblers, and differential expression of cone opsins in this group has been associated with both sexual selection and photic environment [69]. Perhaps the best-studied aspect of bird visual pigment evolution is the transition from UV sensitivity (likely the ancestral condition in birds [70]) to violet sensitivity, which occurred numerous times throughout avian evolution [71]. Although the mechanistic basis for this switch (a single amino acid substitution) is well understood [72], the ecological factors driving transitions between UV and violet vision in birds remain elusive and warrant further study.

### Integrating visual pigment evolution with visual system anatomy and physiology

Studies of visual pigments alone lend tremendous insight into both visual tuning and molecular mechanisms of adaptation, but visual pigments participate in vision alongside other key visual protein partners, and investigations into the evolution of these proteins across vertebrates has provided additional depth of understanding into the evolution of vision [73,74]. Moreover, investigating visual pigment variation in the broader context of the photoreceptor, the retina, and/or the eye is valuable given that the physical properties of the eye interact with opsin absorption to enhance (and sometimes diminish) wavelength detection. Vertebrate eyes show remarkable diversity in overall morphology, lens shape and transmittance, photoreceptor arrangements within the retina, and photoreceptor features (e.g. wavelength-filtering oil droplets in reptiles and birds) [75–77]. These anatomical and physiological elements have substantial effects on visual performance, and may preclude any functional variation among visual pigments (e.g. if a photoreceptor oil droplet is impenetrable to UV light, UV-sensitive SWS1 opsins in the photoreceptor will not be activated) [77]. Visual opsins in these groups are ideal for testing hypotheses about the relationship between anatomical and physiological modifications and visual pigment evolution.

### Interaction between photoreceptor oil droplets and visual pigments

In addition to the aspects of behavioural ecology highlighted in the preceding section, recent studies of bird visual systems have examined underlying mechanisms of both opsin tuning (i.e. UV-sensitive versus violet-sensitive SWS1 opsin evolution) and photoreceptor-based shifts in absorption sensitivity. Oil droplet filtering, an important additional determinant of photoreceptor tuning [77], interacts with opsin evolution to modulate visual sensitivity [78]. Generally, photoreceptors housing UV-sensitive SWS1 opsins often have transparent (UV-transmitting) oil droplets, while those with violet-sensitive SWS1 pigments have droplets that do not transmit UV light. Toomey and colleagues recently demonstrated that the UV-violet transition in SWS1 sensitivity (mediated by amino acid substitutions) occurs in parallel with a shift in SWS2 cone sensitivity. Interestingly, SWS2 photoreceptor tuning is not determined by mutations in the opsin protein; rather, differences in the ratio of two apocarotenoid pigments filtering light within the photoreceptor oil droplets shift photoreceptor sensitivity [79•] (Figure 3). These modifications to the visual pigment and carotenoid molecules work in concert to enhance colour discrimination in the avian visual system. This integrative approach demonstrated important links between visual pigment evolution, photoreceptor and retinal physiology, and visual performance. Moreover, this study highlights that visual sensitivity can be modulated by a combination of changes in opsin structure as

well as variation in other molecules that participate in vision.

### Photoreceptor transmutation in reptiles

Relative to other vertebrates, reptiles and amphibians are comparatively understudied with respect to visual pigment evolution, but nevertheless show striking diversity in their visual systems. Several reptile lineages have reduced cone opsin repertoires (e.g. crocodiles and snakes), while others have retained all five members of the visual opsin family [52]. Recent investigations of morphological, physiological, and molecular variation in the reptilian visual systems have greatly enhanced our understanding of opsin evolution in response to physiological and structural remodelling of the retina through evolutionary time.

The retinas of squamates (lizards and snakes) are a compelling system to investigate visual pigment evolution in the context of evolutionary remodelling of the retina [80]. Some snakes have a duplex retina consisting of both rods and cones, while others possess an all-cone retina — perhaps a consequence of a diurnal lifestyle — and related nocturnal snakes have all-rod retinas. Recent work examining the snake visual system through a combination of opsin sequencing, opsin protein *in vitro* expression, and retinal imaging, revealed that ‘all-cone retinas’, despite an apparent absence of rods, indeed expressed rhodopsin [81••]. These findings provided support for the hypothesis that rods likely transformed into more cone-like structures during snake evolution. Conversely, all-rod retinas still expressed cone opsins, lending strong support to a theory proposing that rods and cones may swap identities through evolution while retaining the underlying genetic machinery of the original cell type (e.g. rods that have ‘transmuted’ into cones retain rhodopsin, rod transducin, etc.) [81••,82,83] (Figure 3). Based on examinations of photoreceptor absorbance, opsin expression, and opsin genetic variation across snakes, this phenomenon has likely occurred multiple times throughout snake evolution [82,84].

### Conclusions and future directions

Studies of visual pigment evolution and visual ecology illustrate the power of investigating genetic variation in the context of major macroevolutionary and ecological transitions to gain insight into the molecular underpinnings of sensory adaptation. Recent work has harnessed a number of fascinating evolutionary systems as a framework to examine how visual pigments evolve, and has benefitted enormously from a combination of experimental approaches including transcriptomics, whole genome sequencing, microspectrophotometry, *in vitro* opsin expression, and retinal imaging, as well as computational approaches such as analyses of interspecific genetic variation, population genetics, and phylogenetic comparative methods.

The effect of evolutionary shifts in photic environment on visual pigment evolution can be profound, particularly in the context of other major life history transitions. However, the underlying mechanisms by which adaptations involving visual pigments occur in response to shifts in photic niche are highly varied, ranging from opsin gene loss and gain, amino acid differences governing spectral tuning, differential opsin expression, and alternative chromophore usage. Most importantly, all these processes are also affected by the cellular and physiological context in which these proteins reside. Beyond photic environment, how the intersection between sexual and natural selection drives the evolution of visual pigments is a critical aspect of visual pigment evolutionary ecology. This relationship can be investigated over macroevolutionary timescales (e.g. by examining levels of selection and amino acid variation across pigments), as well as via more rapid adaptation at the level of differential opsin expression. Major transitions in the form of environmental adaptation (e.g. from terrestrial to aquatic cetaceans) or in eye anatomy and physiology (e.g. transmutation from a duplex to simplex retina) also present a compelling opportunity to test hypotheses about visual pigments spanning various levels of biological organization. Questions regarding how visual pigments may evolve in response to the diverse factors highlighted in this review are not exhaustive; indeed, novel integrative approaches, such as physiological or behavioural investigations, will further develop our understanding of the potential adaptive relevance of visual pigment variation, and complement the impressive work outlined here.

### Conflict of interest statement

Nothing declared.

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