

Guppy color vision: opsin diversity, retinal physiology, plasticity, and evolutionary significance

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Abstract. The guppy (*Poecilia reticulata*) represents a particularly informative model for understanding the molecular, physiological, and ecological foundations of vertebrate color vision. This mini-review synthesizes current evidence on the expanded visual opsin repertoire of guppies, retinal specialization, phototransduction, developmental and environmentally induced plasticity, and the ecological consequences of variation in visual sensitivity. Guppies possess an exceptionally diverse complement of cone opsins, including ultraviolet-, short-, middle-, and long-wavelength-sensitive classes, with pronounced molecular diversity among LWS paralogs. This diversity provides the molecular substrate for fine spectral discrimination, particularly within the red-orange region that is relevant to sexual signaling. However, the functional consequences of opsin diversity depend on their spatial expression within the retina, photoreceptor physiology, neural integration, chromophore availability, and adaptive regulation of visual sensitivity. Opsin expression changes with age, sex, illumination, and dietary carotenoid availability, demonstrating that the visual phenotype is both developmentally dynamic and environmentally responsive. The review further emphasizes that visual performance is constrained by the high metabolic demands of photoreceptors, oxidative stress, photoprotection, chromophore recycling, and retinal cellular maintenance. At the ecological level, variation in visual sensitivity is associated with mate preference, foraging behavior, predator detection, and population-level differences in sexually selected traits. Overall, guppy color vision emerges as an integrated phenotype in which molecular diversification, retinal organization, physiological homeostasis, environmental plasticity, and behavioral selection interact to shape visual information processing and fitness.

Keywords: *Poecilia reticulata*, phototransduction, spectral sensitivity, sexual selection, mate choice, visual ecology, sensory exploitation.

Introduction. The guppy (*Poecilia reticulata*) is an important research organism, but it also has numerous domesticated strains that are bred in aquaria by enthusiasts of aquatic organisms (Mag et al., 2009) (Figure 1). *P. reticulata* possesses one of the most expanded visual-opsin repertoires among teleost fish, with nine cone opsins and a rod opsin (RH1) that together enable trichromatic or tetrachromatic color vision tuned to the species' sexually selected signaling ecology (Archer & Lythgoe, 1990; Archer et al., 1987; Sandkam et al., 2016; Sakai et al., 2016; Laver & Taylor, 2011; Oroian et al., 2020; Petrescu-Mag et al., 2025).

This review synthesizes evidence from molecular, physiological, and behavioral studies to trace how opsin gene duplication, retinal specialization, and developmental

plasticity shape color vision, and how that visual capacity in turn drives mate choice, foraging, predator avoidance, and ultimately fitness in behavioral ecology and evolution.

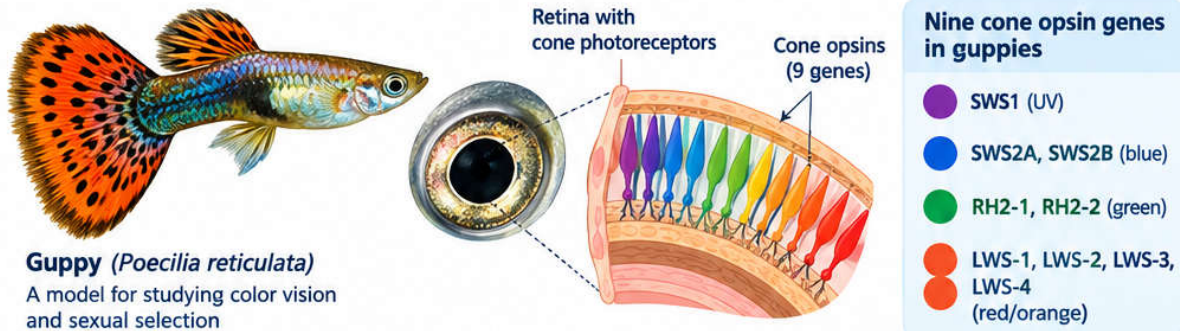
Opsin Gene Repertoire and Molecular Basis of Color Vision. Guppies express nine cone opsin genes spanning the visual spectrum: one ultraviolet-sensitive (SWS1), two blue-sensitive (SWS2A, SWS2B), two green-sensitive (RH2-1, RH2-2), and four red/orange-sensitive (LWS-1 through LWS-4, also designated A180, P180, S180, and S180r) (Sandkam et al., 2016; Sakai et al., 2016; Laver & Taylor, 2011). This LWS opsin diversity is exceptional among vertebrates, as most fish possess only one or two LWS loci (Weadick & Chang, 2007). Weadick and Chang identified six LWS opsins expressed in a single individual, arising from duplication events both pre-dating and post-dating the divergence of the guppy lineage from related killifish (Weadick & Chang, 2007). Numerous amino acid substitutions among these LWS paralogs occur at sites known to influence spectral sensitivity and G-protein activation, suggesting functionally distinct roles (Weadick & Chang, 2007).



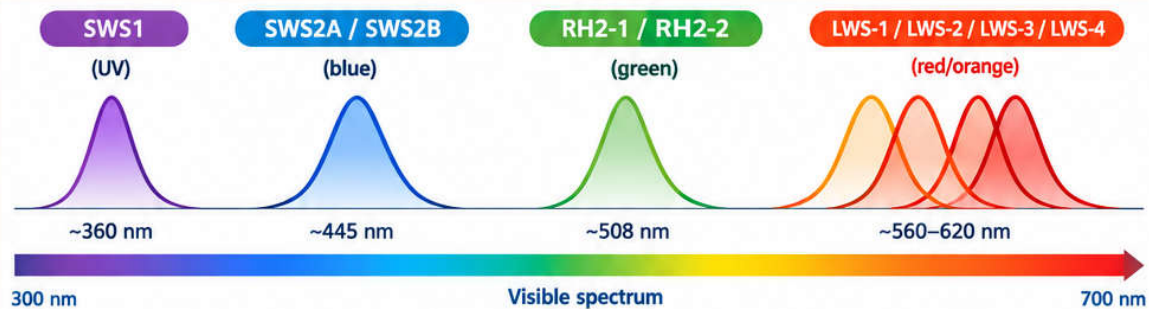
Figure 1. Rare guppy specimens from the breeding facility of the author Grzegorz Prusinowski, <https://www.facebook.com/GenetykaGupika>

Ward et al. demonstrated that three of the four LWS opsins encode proteins predicted to be maximally sensitive to different wavelengths, owing to variation at five key amino acid positions that define the "five-sites" rule for spectral tuning (Ward et al., 2008). These LWS genes were produced by a diversity of duplication events, including an intronless gene predating the divergence of Fundulidae and Poeciliidae, and an inverted tandem duplication in the common ancestor of *Poecilia* and *Xiphophorus* (Ward et al., 2008). Watson et al. confirmed that the Cumaná guppy possesses three distinct LWS cone classes by microspectrophotometry (MSP), with a novel LWS haplotype arising through gene divergence rather than duplication, potentially facilitating the strong sexual selection driven by female preference for orange coloration in the genus *Poecilia* (Watson et al., 2011; Petrescu-Mag, 2007, 2008) (Table 1; Figure 2).

Opsin Gene Repertoire and Molecular Basis of Color Vision in Guppies



Spectral sensitivity of guppy cone opsins



Guppy cone opsin gene classes, spectral sensitivities and key features

Opsin class	Gene(s)	Spectral range	Key features
SWS1	SWS1	Ultraviolet	Expressed throughout retina (Rennison et al., 2011)
SWS2	SWS2A, SWS2B	Blue/purple	Expressed throughout retina (Rennison et al., 2011)
RH2	RH2-1, RH2-2	Green	RH2-1 dorsal-enriched; RH2-2 ubiquitous (Rennison et al., 2011)
LWS	LWS-1 (A180), LWS-2 (P180), LWS-3 (S180), LWS-4 (S180r)	Red/orange	Three distinct λ_{max} values; polymorphic (Ward et al., 2008; Watson et al., 2011).

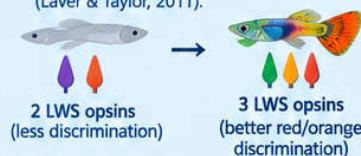
Origins and evolution of LWS opsins

- Duplication events: pre- and post-divergence of guppy lineage (Weadick & Chang, 2007).
- Three LWS opsins shaped by five key amino acid sites (Ward et al., 2008).
- Inverted tandem duplication and intronless gene events (Ward et al., 2008).



Functional significance

- Three distinct LWS cone classes (MSP) with a novel haplotype (Watson et al., 2011).
- LWS-1/LWS-3 maintained by selection to preserve red/orange discrimination (Sandkam et al., 2017).
- Enhanced color discrimination with an expanded opsin repertoire (Laver & Taylor, 2011).



The bigger picture

- ✓ A remarkable opsin repertoire (9 cone genes) allows guppies to see a wider range of colors.
- ✓ This diversity supports foraging, predator avoidance and, crucially, sexual selection for vivid coloration.
- ✓ Guppies show how gene duplication, divergence and selection can shape visual performance.

More opsins = richer color vision = stronger sexual selection

The guppy's visual system is a unique example of how evolution fine-tunes perception through an expanded set of opsin genes.

Figure 2. Opsin gene repertoire and molecular basis of color vision in guppies.

Table 1

Guppy cone opsin gene classes, their spectral sensitivities, and key functional characteristics as determined by molecular and physiological studies

<i>Opsin class</i>	<i>Gene(s)</i>	<i>Spectral range</i>	<i>Key features</i>
SWS1	SWS1	Ultraviolet	Expressed throughout retina (Rennison et al., 2011)
SWS2	SWS2A, SWS2B	Blue/purple	Expressed throughout retina (Rennison et al., 2011)
RH2	RH2-1, RH2-2	Green	RH2-1 dorsal-enriched; RH2-2 ubiquitous (Rennison et al., 2011)
LWS	LWS-1 (A180), LWS-2 (P180), LWS-3 (S180), LWS-4 (S180r)	Red/orange	Three distinct λ_{max} values; polymorphic (Ward et al., 2008; Watson et al., 2011).

Sandkam et al. (2017) examined LWS opsin evolution across 15 species in the family Poeciliidae and found low variability at amino acid tuning sites, but high rates of gene conversion between LWS-1 and LWS-3 attributable to their inverted tandem repeat arrangement (Sandkam et al., 2017). Members of the subgenus *Lebistes* (which includes guppies) appear to resist this gene conversion, suggesting that selection actively maintains LWS-1/LWS-3 differences to preserve red/orange discrimination capacity critical for sexually selected traits (Sandkam et al., 2017). Enhanced wavelength discrimination through an expanded opsin repertoire has experimental support: transgenic mice expressing three instead of two LWS opsins showed improved red-orange discrimination, and similar principles may apply to the guppy's augmented LWS repertoire (Laver & Taylor, 2011).

Retinal Anatomy and Intra-Retinal Variation. The guppy retina exhibits pronounced dorsoventral specialization in opsin expression, with LWS opsins more abundant in the dorsal retina and RH2-1 enriched ventrally, while SWS1, SWS2A, SWS2B, and RH2-2 are expressed throughout (Rennison et al., 2011). Rennison et al. (2011) used in situ hybridization to map these expression patterns and proposed that retinal regions are specialized for different visual tasks: the dorsal retina, receiving light from below, appears tuned for broad spectral sensitivity and exceptional wavelength discrimination, while the ventral retina, receiving downwelling light from above, is dominated by LWS cones suited to maximizing contrast of objects silhouetted against the surface (Rennison et al., 2011; Laver & Taylor, 2011; Endler et al., 2022).

This intra-retinal variability likely represents an adaptation to the spectral composition of light entering the eye from different directions, a pattern observed in several fish species (Rennison et al., 2011; Zhang et al., 2026; Mokhtar et al., 2024). The dorsal-central retina, containing at least three cone pigments (SWS2B, RH2-2, and A180, plus S180 in females), is well suited for color discrimination during courtship displays, which males perform in front of and slightly below females (Laver & Taylor, 2011). Conversely, the LWS-dominant ventral retina may sacrifice color discrimination for sensitivity, as a single cone class predominates in this region (Laver & Taylor, 2011). Rennison's thesis work further demonstrated that most opsin genes have distinct expression profiles and that the ventral retina appears tuned to middle-wavelength (green) light, while the dorsal retina is predicted to have exceptional discriminatory ability (Rennison, 2010).

Sibaux et al. (2019) provided behavioral evidence that this dorsoventral retinal heterogeneity has functional consequences. Testing 50 male and 50 female guppies across 4,800 trials with narrow-band wavelength stimuli presented either above or below the fish, they found that wavelength, stimulus position, and speed influenced behavior, with responses partly mediated by long-wavelength-sensitive photoreceptors (Sibaux et al., 2019). Males showed stronger behavioral responses overall, while females performed more foraging-related pecking behavior, suggesting that the spatial requirements of visual tasks and their ecological context correlate with photoreceptor arrangement in the retina (Sibaux et al., 2019).

Phototransduction and Neuroretinal Processing of Color Information. Color vision in the guppy is not determined solely by the diversity or abundance of cone opsins (Carleton et al., 2020; Hauzman et al., 2021). The physiological interpretation of spectral information begins with phototransduction within individual photoreceptors and continues through a complex network of retinal neurons that transform graded photoreceptor responses into spatially and spectrally organized neural signals (Pugh & Lamb, 2000; Kramer & Molokanova, 2001; Baden et al., 2019). From a biomedical and ophthalmological perspective, the guppy therefore provides a useful model for examining how molecular diversity at the photoreceptor level is translated into functional visual information (Kawamura et al., 2016; Rennison et al., 2011). Beyond evolutionary ecology, the fundamental phototransduction machinery of guppy photoreceptors shares deep mechanistic roots with other vertebrates, offering a clear window into how disruptions in retinal signaling can alter visual processing (Pugh & Lamb, 2000; Lamb, 2022). The presence of multiple spectrally distinct cone classes creates the potential for extensive wavelength discrimination, but the biological significance of this diversity ultimately depends on photoreceptor physiology, synaptic connectivity, adaptation mechanisms, and downstream neural processing (Carleton et al., 2020; Hauzman et al., 2021).

In cone photoreceptors, absorption of a photon by a visual pigment initiates a biochemical cascade involving activation of the opsin-associated G-protein transducin, stimulation of phosphodiesterase activity, reduction of intracellular cyclic GMP, and closure of cyclic nucleotide-gated ion channels (Pugh & Lamb, 2000; Cote, 2021; Kramer & Molokanova, 2001). This sequence produces membrane hyperpolarization and modifies neurotransmitter release at the photoreceptor synaptic terminal (Ward et al., 2008; Kramer & Molokanova, 2001; Baylor, 1987). The fundamental mechanism is conserved across vertebrates, but differences in the spectral properties, expression levels, and cellular distribution of individual visual pigments can substantially modify the probability that photons of particular wavelengths will generate a neural response (Carleton et al., 2020; Hauzman et al., 2021; Rennison et al., 2011). In guppies, the coexistence of several cone classes with overlapping spectral sensitivities consequently provides a molecular substrate for extracting wavelength information from the visual environment (Kawamura et al., 2016; Rennison et al., 2011).

Spectral coding is inherently comparative rather than dependent on the response of a single photoreceptor class (Baden, 2024ab; Rennison et al., 2011; Szatko et al., 2019). Because the absorption spectra of neighboring cone pigments overlap, a given wavelength generally produces simultaneous responses in several cone populations (Baylor, 1987; Kawamura et al., 2016). Color information can therefore be represented by relative differences in the activation of photoreceptor classes rather than by the absolute response of an individual cone (Ward et al., 2008; Szatko et al., 2019; Baden, 2024ab). The expanded LWS repertoire of the guppy may be particularly important in this context because multiple long-wavelength-sensitive pigments can generate partially distinct response profiles within the same spectral region (Ward et al., 2008; Tezuka et al., 2014; Watson et al., 2011). Such an arrangement has the potential to increase the dimensionality of chromatic information available to subsequent retinal circuits, especially when small spectral differences occur within orange and red wavelengths (Ward et al., 2008; Watson et al., 2011; Hauzman et al., 2021).

The retina subsequently converts photoreceptor signals into neural representations through horizontal, bipolar, amacrine, and ganglion cells (Günther et al., 2025; Baden et al., 2019; Ammerüller et al., 1995). Horizontal cells contribute substantially to spatial and spectral integration by pooling signals from neighboring photoreceptors and providing feedback to the photoreceptor synaptic terminals (Günther et al., 2025; Baden et al., 2019; Szatko et al., 2019). Bipolar cells transmit photoreceptor-derived information into the inner retina, where amacrine cells introduce additional temporal and spatial processing (Baden et al., 2019; Szatko et al., 2019; Ammerüller et al., 1995). Ganglion cells represent a major output stage of the retina, transforming local retinal activity into action potentials that are transmitted through the optic nerve to higher visual centers (Baden et al., 2019; Szatko et al., 2019; Ammerüller et al., 1995). Consequently, the perceptual consequences

of opsin diversity cannot be predicted from opsin expression alone because the same photoreceptor repertoire can potentially generate different visual outputs depending on retinal circuitry (Carleton et al., 2020; Baden, 2024ab; Hauzman et al., 2021).

A particularly important feature of color processing is the interaction between chromatic and achromatic information (Günther et al., 2025; Baden, 2024ab). Visual systems must distinguish spectral composition from changes in overall photon catch, particularly under conditions in which illumination intensity fluctuates (Nikolaeva et al., 2023; Kramer & Molokanova, 2001). Neural comparison of signals originating from different cone classes can provide a mechanism for separating chromatic contrast from luminance contrast (Günther et al., 2025; Szatko et al., 2019). This distinction has direct relevance to the guppy because sexual ornaments, food items, vegetation, and predators can differ simultaneously in hue, saturation, brightness, spatial configuration, and motion (Szatko et al., 2019; Rennison et al., 2011). The biological value of the guppy's visual system therefore depends not simply on its ability to detect particular wavelengths but on its capacity to integrate spectral information with spatial and temporal features (Carleton et al., 2020; Baden, 2024ab).

Retinal adaptation further modifies photoreceptor responses according to the prevailing illumination conditions (Nikolaeva et al., 2023; Kramer & Molokanova, 2001; Nikolaeva et al., 2023). Under bright illumination, cone-mediated vision predominates and photoreceptor sensitivity must be adjusted to prevent saturation while maintaining sufficient resolution for discrimination (Lamb, 2022; Fogg et al., 2026). Under dimmer conditions, changes in phototransduction gain and the relative contribution of rod pathways alter the balance between sensitivity and spectral discrimination (Lamb, 2022; Fogg et al., 2026). This dynamic regulation is particularly relevant for an aquatic species because underwater illumination changes markedly with depth, turbidity, canopy cover, water color, time of day, and weather conditions (Carleton et al., 2020; Hauzman et al., 2021). The guppy visual system must therefore operate across a broad range of photon fluxes while preserving sufficient chromatic information for biologically important visual tasks (Carleton et al., 2020; Tezuka et al., 2014).

The interaction between rods and cones is also relevant to the interpretation of color signals under changing illumination (Szatko et al., 2019; Hauzman et al., 2021). Rod photoreceptors provide high sensitivity under low-light conditions but have substantially different spectral properties from individual cone classes (Lamb, 2022; Fogg et al., 2026). As illumination decreases, the relative contribution of rod-mediated signals can increase, potentially modifying the chromatic appearance and detectability of visual objects (Fogg et al., 2026; Hauzman et al., 2021). Such changes may influence the effectiveness of visual communication because a color signal that is highly discriminable during daylight may become less informative under low-light conditions (Szatko et al., 2019). The distinction between photopic, mesopic, and scotopic visual states is therefore important when considering the ecological function of guppy coloration and the conditions under which sexual or social signals are evaluated (Lamb, 2022; Fogg et al., 2026; Watson et al., 2011; Mag-Mureşan & Pop, 2004).

The retinal response is additionally shaped by neural gain control and adaptation at multiple levels of the visual pathway (Nikolaeva et al., 2023; Kramer & Molokanova, 2001; Baden, 2024ab). These mechanisms allow the visual system to preserve information despite large changes in background illumination and stimulus contrast (Nikolaeva et al., 2023). From an ophthalmological perspective, such regulatory processes are fundamental because excessive photoreceptor stimulation, metabolic stress, or impaired adaptation can compromise retinal function (Cote, 2021). Although the guppy is primarily studied as a model of visual ecology and evolution, its retinal organization provides an opportunity to investigate general principles of photoreceptor physiology, signal amplification, sensory adaptation, and neural coding that are shared across vertebrate visual systems (Kawamura et al., 2016; Cote, 2021; Baden, 2024ab).

The relationship between photoreceptor diversity and neural processing also raises an important distinction between molecular potential and functional vision (Carleton et al., 2020). Possession of multiple opsin genes does not necessarily imply that all corresponding pigments contribute equally to perception (Carleton et al., 2020; Ward et al., 2008;

Kawamura et al., 2016). Functional expression depends on the cellular localization of each opsin, transcriptional regulation, protein production, chromophore availability, photoreceptor morphology, synaptic connectivity, and the integration of signals within retinal circuits (Carleton et al., 2020; Ward et al., 2008; Rennison et al., 2011; Hauzman et al., 2021). Thus, molecular surveys of opsin repertoires should ideally be interpreted together with physiological measurements of photoreceptor responses and behavioral measurements of visual discrimination (Carleton et al., 2020; Kawamura et al., 2016; Carleton et al., 2020).

This framework also provides a mechanistic explanation for why changes in visual ecology can influence evolutionary trajectories without requiring major alterations in the underlying neural architecture (Ward et al., 2008; Tezuka et al., 2014; Baden, 2024ab). Variation in opsin expression can modify the relative weighting of spectral channels while leaving the basic organization of the retina intact (Carleton et al., 2020; Kawamura et al., 2016; Rennison et al., 2011). Conversely, evolutionary changes in retinal circuitry could alter the functional consequences of a given opsin repertoire without requiring changes in the opsin genes themselves (Baden, 2024ab). Color vision should therefore be considered an integrated phenotype produced by interactions among photopigments, photoreceptor populations, retinal circuits, central visual pathways, and environmental illumination (Baden et al., 2019; Baden, 2024ab; Hauzman et al., 2021).

From a biomedical perspective, this integrated view is particularly valuable because retinal function is inherently vulnerable to disturbances affecting photoreceptor metabolism, oxidative balance, chromophore availability, synaptic transmission, and neural adaptation (Cote, 2021; Nikolaeva et al., 2023). The guppy consequently represents more than an ecological model of sexual signaling (Rennison et al., 2011). Its experimentally tractable visual system can also contribute to comparative understanding of vertebrate retinal physiology, particularly the relationship between photoreceptor molecular diversity and the functional organization of color vision (Kawamura et al., 2016; Baden, 2024ab; Watson et al., 2011).

Developmental Plasticity and Environmental Tuning of Opsin Expression. Opsin expression in guppies is not fixed at hatching but changes with age, sex, and environmental conditions (Popescu & Păpuc, 2025). Laver and Taylor used RT-qPCR to show that juveniles express 10 visual opsins, with SWS2B and RH2-2 accounting for over 85% of all opsin transcripts, while in adults this proportion drops to approximately 65% as LWS-A180 expression increases from roughly 3% to 20% relative abundance (Laver & Taylor, 2011). The juvenile-to-female transition also involves LWS-S180 upregulation from about 1.5% to 7% relative abundance, implicating LWS upregulation in augmenting spectral discrimination of male coloration and courtship displays in adult females (Laver & Taylor, 2011). In males, enhanced discrimination of carotenoid-rich food and rival males are strong candidate selective pressures driving LWS upregulation (Laver & Taylor, 2011). Expression within the SWS2-LWS gene cluster appears regulated in part by a common locus control region (LCR), with expression negatively correlated with distance from the candidate LCR (Laver & Taylor, 2011).

Sakai et al. (2016) demonstrated that the light environment during growth induces plastic changes in opsin expression and behavioral sensitivity. Guppies raised under orange light expressed higher levels of LWS opsins and showed greater behavioral sensitivity to 600-nm light than those raised under green light (Sakai et al., 2016). This plastically enhanced sensitivity to background light can improve detection of predators and food, thereby affecting survival, and may also alter female perception of orange male coloration, with downstream effects on mate preference (Sakai et al., 2016).

Diet represents another source of visual plasticity. Sandkam et al. (2016) showed that guppies raised on high-carotenoid diets expressed higher levels of LWS opsins than those on low-carotenoid diets, because carotenoids are precursors for vitamin A, which is essential for photopigment creation (Sandkam et al., 2016). This finding suggests that ecological differences across populations, such as variation in algal carotenoid availability, could generate mate choice differences through a previously unrecognized mechanism

involving dietary effects on opsin expression (Sandkam et al., 2016; Cole et al., 2019) (Table 2).

Table 2

Factors influencing opsin gene expression plasticity in guppies, their effects on visual tuning, and supporting evidence

<i>Factor</i>	<i>Effect on opsin expression</i>	<i>Evidence</i>
Age (juvenile → adult)	LWS-A180 increases ~3% → 20%; LWS-S180 increases ~1.5% → 7%	RT-qPCR (Laver & Taylor, 2011)
Sex	Females upregulate LWS for mate discrimination; males for food/rival detection	RT-qPCR (Laver & Taylor, 2011)
Light environment (orange vs. green)	Orange light increases LWS expression and 600-nm sensitivity	Rearing experiment (Sakai et al., 2016)
Dietary carotenoids	High-carotenoid diet increases LWS expression	Diet manipulation (Sandkam et al., 2016)
Predation pressure	LWS-R transcription changes, but overall opsin profile not strongly driven	Predation experiment (Chang, 2024).

Chang (2024) tested whether predation pressure alters cone opsin expression profiles in female guppies and detected a significant change in LWS-R transcription, but concluded that overall cone opsin expression profiles in adult females do not appear to be driven by predation pressure, leaving developmental plasticity and brain anatomy as promising avenues for further investigation (Chang, 2024).

Retinal Photoprotection, Oxidative Stress, and Visual Health. The extraordinary capacity of the guppy retina to process spectral information is accompanied by substantial metabolic and photochemical demands (Kawamura et al., 2016; Rennison et al., 2011). Photoreceptors are among the most metabolically active cells in the vertebrate body, requiring continuous energy production to maintain ion gradients, renew photoreceptor outer segments, synthesize visual pigments, and sustain synaptic transmission (Country, 2017; Wong-Riley, 2010; Neiteler et al., 2023). At the same time, exposure to light, particularly short-wavelength radiation, can promote the formation of reactive oxygen species within retinal tissues (Jarrett & Boulton, 2012; Bonilha, 2021). The combination of high oxygen consumption, abundant polyunsaturated fatty acids in photoreceptor membranes, and continuous photon exposure makes the retina intrinsically susceptible to oxidative damage (Bonilha, 2021; Benedetto & Contín, 2019; Nowak, 2013). Because photoreceptors rely on high oxygen metabolism and membranes rich in polyunsaturated fats, they are naturally prone to oxidative damage—sharing the exact same cellular vulnerabilities seen in human degenerative conditions like age-related macular degeneration (Jarrett & Boulton, 2012; Böhm et al., 2023; Sun et al., 2026). These characteristics provide a valuable biomedical perspective for understanding how visual performance is maintained despite persistent metabolic and photochemical stress (Country, 2017; Wong-Riley, 2010; Jarrett & Boulton, 2012).

Phototransduction itself requires substantial cellular energy (Wong-Riley, 2010; Muangkram et al., 2023). In darkness, photoreceptors maintain a relatively high inward current through cyclic nucleotide-gated channels, resulting in continuous ionic fluxes that must be counterbalanced by active transport mechanisms (Ingram et al., 2020; Muangkram et al., 2023; Country, 2017; Wong-Riley, 2010). Following photon absorption, the phototransduction cascade rapidly modifies this ionic balance, after which the photoreceptor must restore its dark-state biochemical and electrical condition (Yu et al., 2025; Weadick & Chang, 2007; Salesse, 2016; Wong-Riley, 2010). Continuous operation of these processes imposes a considerable energetic requirement on retinal cells (Ingram et al., 2020; Wong-Riley, 2010; Okawa et al., 2008). In guppies, extensive cone specialization may therefore represent not only an adaptation for spectral discrimination but also a physiological investment that requires efficient metabolic support (Kawamura et al., 2016; Weadick & Chang, 2007; Sakai et al., 2016).

Photoreceptor outer segments are particularly sensitive to oxidative injury because their membranes contain high concentrations of polyunsaturated fatty acids that are susceptible to lipid peroxidation (Benedetto & Contín, 2019; Nowak, 2013; Neiteler et al., 2023). Light-induced oxidative reactions can generate reactive oxygen species capable of modifying membrane lipids, proteins, nucleic acids, and cellular organelles (Jarrett & Boulton, 2012; Bonilha, 2021). Retinal tissues consequently possess multiple antioxidant and repair mechanisms that limit oxidative injury (Jarrett & Boulton, 2012; Neiteler et al., 2023; Bonilha, 2021). The balance between oxidant production and antioxidant protection is likely to influence the long-term functional stability of photoreceptors, especially under environmental conditions involving intense illumination or nutritional imbalance (Neiteler et al., 2023; Benedetto & Contín, 2019).

Visual pigments themselves require a chromophore derived from vitamin A metabolism (Yu et al., 2025; Weadick & Chang, 2007; Salesse, 2016; Saari, 2012; Rennison et al., 2011). The availability, transport, recycling, and regeneration of visual chromophore are therefore essential for sustained photoreceptor function (Yu et al., 2025; Sato & Kefalov, 2024; Choi et al., 2021; Saari, 2012). The visual cycle continuously converts chromophore molecules between different biochemical forms, allowing bleached visual pigments to be regenerated after photon absorption (Yu et al., 2025; Salesse, 2016; Choi et al., 2021; Wong-Riley, 2010). Disruption of this cycle can reduce photosensitivity and compromise visual performance (Yu et al., 2025; Choi et al., 2021; Salesse, 2016). In a species such as the guppy, in which multiple cone pigments contribute to spectral discrimination, the efficiency of chromophore metabolism may represent an important physiological constraint on the expression of the visual phenotype (Kawamura et al., 2016; Rennison et al., 2011; Sato & Kefalov, 2024).

The relationship between nutrition and visual physiology is consequently broader than the simple availability of dietary carotenoids (Sandkam et al., 2016; Von Lintig et al., 2020; Von Lintig & Bandara, 2024). Carotenoid metabolism intersects with vitamin A pathways, antioxidant defense, pigmentation, and photoreceptor function (Sandkam et al., 2016; Von Lintig et al., 2020; Liao et al., 2025; Von Lintig & Bandara, 2024). Nutritional conditions may therefore influence visual performance through several interconnected mechanisms (Sandkam et al., 2016; Von Lintig et al., 2020). Adequate nutrient availability can support chromophore regeneration and antioxidant protection, whereas nutritional imbalance may alter retinal physiology even when the underlying opsin genotype remains unchanged (Sandkam et al., 2016; Von Lintig et al., 2020; Böhm et al., 2023). This perspective is particularly relevant to guppies because environmental variation in food composition can modify both visual physiology and the expression of sexually selected traits (Sandkam et al., 2016; Zhang et al., 2019).

Photoprotection represents another important component of retinal health (Böhm et al., 2023; Chen et al., 2017). The visual system must maximize photon capture while simultaneously limiting photochemical injury (Liefbrig et al., 2023; Böhm et al., 2023). Ocular tissues can modify the quantity and spectral composition of incident radiation through absorption and filtering mechanisms before light reaches the photoreceptors (Flamarique, 2026; Von Lintig et al., 2020; Von Lintig & Bandara, 2024). Within the retina, additional protective mechanisms include antioxidant enzymes, pigment-containing structures, molecular chaperones, DNA repair pathways, and controlled turnover of damaged cellular components (Xu et al., 2023; Lunegova et al., 2024; Böhm et al., 2023; Liefbrig et al., 2023). These mechanisms create a physiological balance between sensitivity and protection (Von Lintig et al., 2020; Liefbrig et al., 2023). A highly sensitive visual system is advantageous for detecting weak signals but may also increase the potential consequences of excessive photon exposure (Liefbrig et al., 2023; Böhm et al., 2023).

The ecological environment may alter this balance substantially (Sandkam et al., 2016; Böhm et al., 2023). Water turbidity, dissolved organic matter, depth, suspended particles, vegetation, and canopy cover can modify both the intensity and spectral composition of underwater illumination (Sandkam et al., 2016). Such changes may influence the energetic requirements of photoreceptors as well as the relative contribution of different spectral channels to visual perception (Kiel et al., 2026). Consequently, environmental light should be regarded not merely as an external source of information

but also as a physiological factor capable of influencing retinal stress and visual homeostasis (Lunegova et al., 2024; Böhm et al., 2023; Chen et al., 2017).

The retina also undergoes continuous cellular renewal (Xu et al., 2024; Lieffrig et al., 2023). Photoreceptor outer segments are periodically shed and replaced, while retinal cells maintain extensive protein turnover and membrane remodeling (Kiel et al., 2026; Becerra, 2026). This regenerative capacity is essential for maintaining photoreceptor function under conditions of continuous photon exposure (Xu et al., 2024; Lieffrig et al., 2023). It also creates a strong dependence on efficient lysosomal activity, intracellular trafficking, mitochondrial function, and membrane biosynthesis (Lieffrig et al., 2023; Sun et al., 2026; Becerra, 2026). Impairment of these processes can progressively affect photoreceptor integrity and visual sensitivity (Xu et al., 2024; Lieffrig et al., 2023; Becerra, 2026).

Mitochondrial function is particularly important because photoreceptors have high energy requirements and contain specialized mitochondrial populations that support their metabolic activity (Kiel et al., 2026; Sun et al., 2026). Mitochondrial dysfunction can increase reactive oxygen species production while simultaneously reducing ATP availability, creating a potentially self-reinforcing cycle of metabolic and oxidative stress (Lunegova et al., 2024; Sun et al., 2026; Becerra, 2026). Although most studies of guppy vision have focused on ecological and evolutionary questions, consideration of mitochondrial physiology provides an additional mechanistic framework for understanding why retinal performance may respond to environmental stressors (Sandkam et al., 2016; Xu et al., 2023; Huang et al., 2020).

Environmental contaminants represent another potential interface between guppy visual ecology and biomedical retinal physiology (Gasparini et al., 2024; Zhang et al., 2019). Aquatic pollutants capable of inducing oxidative stress, disrupting endocrine signaling, altering mitochondrial function, or interfering with cellular antioxidant systems could theoretically affect photoreceptor integrity and visual processing even without directly modifying opsin genes (Gasparini et al., 2024; Zhang et al., 2022; Huang et al., 2020; Zhang et al., 2019). Because visual behavior depends on the integrity of the entire photoreceptor-retinal network, environmentally induced cellular damage could alter color discrimination, visual sensitivity, or behavioral responses before any obvious morphological abnormalities become apparent (Gasparini et al., 2024; Xu et al., 2023; Zhang et al., 2022; Zhang et al., 2019).

This possibility is especially important in the context of aquatic ecotoxicology (Huang et al., 2020; Zhang et al., 2019). The guppy is frequently exposed to environmental fluctuations and anthropogenic contaminants that can affect physiological systems at concentrations below those producing overt mortality (Gasparini et al., 2024; Huang et al., 2020; Zhang et al., 2019). Visual function may therefore represent a sensitive endpoint for detecting sublethal physiological disturbance (Gasparini et al., 2024; Zhang et al., 2019). Changes in photoreceptor activity, retinal morphology, chromophore metabolism, oxidative status, or visually guided behavior could potentially provide complementary information about environmental stress (Zhang et al., 2022; Huang et al., 2020; Gasparini et al., 2024). Such an approach would connect visual ecology with modern ecotoxicological assessment and could broaden the biomedical relevance of guppy retinal research (Gasparini et al., 2024; Huang et al., 2020).

The concept of visual health should consequently be incorporated into the interpretation of color vision (Sandkam et al., 2016). A change in color-based behavior does not necessarily indicate an adaptive modification of sensory tuning (Gasparini et al., 2024; Zhang et al., 2019). It may alternatively reflect altered photoreceptor physiology, impaired retinal adaptation, oxidative injury, nutritional limitation, or disruption of neural processing (Zhang et al., 2022; Lieffrig et al., 2023; Sun et al., 2026). Distinguishing adaptive plasticity from physiological impairment is therefore essential when interpreting variation in visual phenotypes among populations or experimental treatments (Sandkam et al., 2016).

The guppy offers a particularly useful comparative system because its visual phenotype can be examined simultaneously at molecular, cellular, physiological, and behavioral levels (Sandkam et al., 2016; Gasparini et al., 2024; Zhang et al., 2022; Huang et al., 2020). This makes it possible to conceptualize color vision as a continuum extending

from photopigment chemistry and phototransduction to retinal homeostasis, neural processing, visually guided behavior, and ecological fitness (Solano et al., 2024; Sun et al., 2026). Such integration is also relevant to ophthalmological research because many fundamental mechanisms governing photoreceptor maintenance, oxidative protection, metabolic regulation, and sensory adaptation are conserved among vertebrates (Liefbrig et al., 2023; Böhm et al., 2023; Becerra, 2026).

Taken together, the biomedical interpretation of guppy vision emphasizes that spectral discrimination is dependent on retinal health as much as on opsin diversity (Sandkam et al., 2016; Liefbrig et al., 2023; Sun et al., 2026). The evolutionary expansion of visual pigments can increase the potential information available to the visual system, but the realization of this potential requires efficient phototransduction, adequate chromophore supply, metabolic support, antioxidant protection, and continuous cellular maintenance (Solano et al., 2024; Von Lintig & Bandara, 2024; Sun et al., 2026; Xu et al., 2024). This physiological framework provides an important bridge between the molecular evolution of color vision and its ecological consequences, while also establishing the guppy as a potentially informative comparative model for investigating mechanisms of retinal resilience, environmental visual stress, and photoreceptor homeostasis (Sandkam et al., 2016; Xu et al., 2023; Zhang et al., 2022; Becerra, 2026).

Color Vision, Mate Choice, and Sexual Selection. The theory of sensory exploitation predicts that variation in visual systems drives mate preference variation through sensory bias (Sandkam et al., 2015a; Petrescu-Mag, 2025abc; Petrescu-Mag et al., 2026; Popescu et al., 2025; Bourne & Watson, 2009). Sandkam et al. (2015a) provided direct evidence that color vision co-varies with mate preference across guppy populations: in independently colonized watersheds, low-predation populations expressed higher levels of LWS-1 and LWS-3 (the most abundant LWS opsins) than high-predation populations, corresponding to differences in cone cell abundance (Sandkam et al., 2015a). Low-predation guppies, which have stronger female preferences for males with more orange/red coloration, invest more of their color vision in detecting red/orange wavelengths (Sandkam et al., 2015a). A coding polymorphism in LWS-1 also differed in frequency between high- and low-predation populations, providing candidate genes for the genetic basis of female preference variation (Sandkam et al., 2015a).

Sandkam et al. (2015b) extended this finding by comparing opsin expression across three sympatric *Poecilia* species (*P. reticulata*, *P. parae*, *P. picta*) and found that color vision was more similar within sympatric locations than across populations of the same species, demonstrating that intraspecific variation exceeds interspecific variation in visual tuning (Sandkam et al., 2015a). All three species shared the same opsin coding polymorphism that differed across populations, supporting the hypothesis that sensory system variation is involved in population divergence of mate preference (Sandkam et al., 2015a).

Endler (1991) showed that guppy color patterns represent a compromise between sexual selection and predation avoidance: color patterns are relatively more conspicuous to guppies at the times and places of courtship and relatively less conspicuous at the times and places of maximum predator risk (Endler, 1991). This differential conspicuousness arises because the guppy visual system and predator visual systems differ in spectral sensitivity, such that the "extra" chroma perceived by female guppies may not be equally conspicuous to predators (Ward et al., 2008). Yong et al. (2022), however, challenged the classic parallel-evolution narrative by using sensory-based quantification of male color patterns and finding very limited support for greater conspicuousness in low-predation populations, with only one of eight measures showing the predicted pattern (Yong et al., 2022). Fuller (2022) echoed this concern, noting that the study by Yong et al. forces a reconsideration of the validity and repeatability of this textbook example of parallel evolution (Fuller, 2022).

Male guppies also respond to color stimuli. Kline et al. found that male guppies were most attracted to orange 3D models, consistent with the prediction that longer wavelengths activate the guppy's LWS-dominated visual system (Kline et al., 2018). This male response may reflect the role of color vision in evaluating rival males or in orienting toward carotenoid-rich food items (Laver & Taylor, 2011).

Foraging, Predator Avoidance, and Ecological Fitness. Color vision in guppies extends beyond reproduction to foraging efficiency and predator avoidance, both of which directly impact fitness. Cole et al. (2019) maintained guppy populations for 6–10 generations under three light environments (green, lilac, control) and found that colour-based foraging preferences diverged, with fish from different light treatments showing different pecking behaviors toward colored stimuli when tested in a common light environment (Cole et al., 2019). Pecking behavior toward green stimuli was consistent across treatments, possibly reflecting the importance of detecting green algae as a food source in the wild (Cole et al., 2019). Blue stimuli were pecked at only by fish from control environments, and behavior toward long-wavelength stimuli varied, possibly due to the polymorphic nature of LWS opsins (Cole et al., 2019). Changes in medium-wavelength opsin expression across light environments may explain the decreased pecking toward blue and blue-green stimuli, as opsin expression has been shown to influence colour-based behaviors (Cole et al., 2019). Sakai et al. (2016) argued that plastically enhanced sensitivity to background light through changes in opsin gene expression can enhance detection and visibility of predators and food, thereby affecting survival (Sakai et al., 2016). The guppy's LWS-dominant ventral retina is tuned to the most abundant downwelling long-wavelength light, maximizing contrast of objects above the fish, including food, predators, and conspecifics (Laver & Taylor, 2011). If LWS opsin gene duplication also improves motion detection, as has been proposed, female guppies may be pre-adapted to evaluate the sigmoid courtship display, which involves rapid body oscillations (Ward et al., 2008).

Sandkam et al. (2018) reviewed the integration of molecular and physiological variation in guppy visual tuning and noted that although variation in guppy color vision was first identified over 30 years ago, the direct link between visual system variation and color preference behavior remains a "black box" (Sandkam et al., 2018). They identified multiple variables requiring further study, including ocular media transmission, ellipsosome presence, opsin allele differences, opsin expression levels, cone λ_{max} , the relationship between opsin expression and cone types, and the role of plasticity in visual tuning (Sandkam et al., 2018). Opening this black box will require studies that couple measures of color preference with measures of visual system variation from the same individual or population, varying each component of the visual pathway to determine what sets the direction and speed of mate preference evolution (Sandkam et al., 2018).

Yong et al. (2022) further noted that guppy color patterns appear more conspicuous in the chromatic channel (saturation and chromaticity) for conspecifics, whereas the pike cichlid predator is more sensitive to achromatic (luminance) elements (Yong et al., 2022), underscoring the value of adopting color measures appropriate to the visual systems of hypothesized selective agents when studying signal evolution (Yong et al., 2021). Local abiotic conditions such as substrate, water color, light transmission, and canopy cover are an explicit part of the sensory drive hypothesis and may influence in situ perception of phenotype by guppies and their predators (Yong et al., 2022).

Conclusions. The guppy provides a distinctive model for examining how molecular diversification of visual pigments is translated into physiological and behavioral variation. Its expanded complement of cone opsins, particularly the diversity of LWS paralogs, provides substantial molecular potential for fine spectral discrimination across biologically relevant wavelengths. Nevertheless, the present evidence indicates that the number of opsin genes alone cannot be considered a direct measure of functional visual capacity. Spatial patterns of opsin expression, photoreceptor physiology, retinal circuitry, phototransduction, chromophore availability, and neural processing collectively determine how spectral information is ultimately represented.

An important feature of the guppy visual system is its plasticity. Opsin expression varies with developmental stage, sex, illumination, and dietary carotenoid availability, demonstrating that visual sensitivity can be dynamically adjusted to ecological conditions. Such adjustments may modify the detection of food, predators, and conspecific signals and may consequently influence mate preferences and sexually selected traits. At the same time, the metabolic demands associated with extensive photoreceptor activity, together

with oxidative and photochemical stress, indicate that visual performance is constrained by retinal homeostasis and cellular maintenance.

Taken together, the evidence supports an integrated view of guppy color vision in which gene duplication and divergence, retinal organization, physiological regulation, environmental plasticity, and behavioral selection form interconnected components of a single sensory phenotype. The guppy therefore represents a valuable comparative system for investigating the evolution of sensory systems and the mechanisms linking visual variation to ecological performance and reproductive behavior. In short, the rich organization of the guppy visual system goes far beyond ecology, serving as a flexible comparative model to help unlock key insights into neuroprotection, photoreceptor maintenance, and adaptive mechanisms of great value to modern ophthalmology (Kawamura et al., 2016; Sandkam et al., 2018). Future research should integrate opsin genotypes and expression profiles with direct measurements of photoreceptor sensitivity, retinal physiology, neural processing, visual behavior, and environmental conditions within the same individuals or populations. Such an integrative approach would help resolve the remaining gap between molecular variation in the visual system and its ultimate consequences for perception, mate choice, and evolutionary change.

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