Poeciliid Research

Color vision, sexual dimorphism and the visual ecology of guppies

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Abstract. The Trinidadian guppy, *Poecilia reticulata* Peters, 1859, offers a compelling model for exploring the interplay between color vision, sexual dimorphism, and evolutionary adaptation. Males exhibit highly variable, conspicuous coloration, whereas females remain largely cryptic. This sexual dichotomy is underpinned by coevolution between color signals and sex-specific visual systems, particularly through diversification of opsin genes that enhance sensitivity to red-orange wavelengths. Female mating preferences align closely with these visual capabilities, shaped by both innate sensory biases and learned associations. Furthermore, environmental factors such as predation pressure and light conditions modulate both visual system development and mate choice dynamics. Together, these interactions create a complex adaptive landscape in which sexual and natural selection jointly shape guppy evolution. The integration of molecular, behavioral, and ecological evidence illustrates how visual ecology drives rapid diversification in this species.

Key Words: adaptation, color vision, guppies, mate choice, opsin genes, *Poecilia reticulata*, predation, sensory bias, sexual dimorphism, visual ecology.

Introduction. The Trinidadian guppy, *Poecilia reticulata* Peters, 1859, is a paradigmatic system for linking color vision, sexual dimorphism and mate choice with evolutionary processes of adaptation and diversification. Males bear conspicuous, polymorphic patterns of orange, black and iridescent spots, whereas females are largely cryptic. These ornaments function as visual sexual signals but simultaneously increase detectability to visually hunting predators, embedding mate choice within a trade-off between sexual and natural selection (Endler 1983; Houde & Endler 1990; Fuller 2022). Guppies inhabit light environments that vary strongly in spectral composition and predation regime, and their visual system is unusually rich in cone opsins, including multiple long-wavelength-sensitive (LWS) genes that tune sensitivity to orange-red light (Hoffmann et al 2007; Laver & Taylor 2011). This combination of variable male coloration, sex- and age-dependent visual sensitivity and heterogeneous environments has enabled detailed study of how color vision, sex, color traits and mating preferences coevolve and contribute to adaptation.

The purpose of this study is to examine how color vision, sexual dimorphism, and environmental pressures interact to shape the coevolution of visual systems and mating preferences in guppies.

Opsin diversification and sex-biased color vision. Molecular work has revealed extensive duplication and diversification of opsin genes in guppies (Oroian et al 2020). In particular, guppies possess an expanded set of LWS opsins with high sequence variability at amino acid sites affecting spectral tuning, and multiple divergent alleles can be present within single populations and even individuals (Hoffmann et al 2007). Patterns of nonsynonymous substitution indicate diversifying selection on LWS opsins, suggesting that variation in red-orange sensitivity has been favored rather than eroded by purifying selection (Hoffmann et al 2007).

Gene expression studies show that opsin expression is developmentally and sexually regulated. Juveniles express predominantly mid-wavelength opsins (SWS2B and RH2-2), whereas sexually mature adults upregulate LWS opsins, especially LWS-A180 and LWS-S180 (Laver & Taylor 2011). Females show a stronger upregulation of these LWS opsins than males, implying enhanced sensitivity or discrimination of male orange and red coloration at sexual maturity (Laver & Taylor 2011). This sex-biased tuning is consistent with the central role of female choice based on male color and supports the hypothesis that the visual system is shaped by color-mediated sexual selection.

Across wild populations experiencing different predation regimes, color vision itself varies in a way that covaries with mate preferences (Petrescu-Mag 2007a, b). In multiple independently colonized watersheds, guppies from low-predation habitats, where sexual selection is relatively stronger, express higher levels of LWS-1 and LWS-3 than fish from high-predation sites, specifically increasing investment in sensitivity to orange-red wavelengths (Sandkam et al 2015). Differences in expression coincide with variation in cone cell abundance and with allele frequency shifts at coding polymorphisms in LWS genes, indicating both regulatory and structural evolution of the visual pigments (Sandkam et al 2015). Together with broader comparative work in Poeciliidae showing selection to maintain divergence between LWS paralogs in guppies and close relatives, these findings suggest that genomic architecture of opsins both constrains and channels the evolution of color vision in lineages where visual sexual selection is intense (Sandkam et al 2017).

Female preferences, **color signals and coevolution**. Female guppies typically prefer males with greater area and intensity of orange coloration, and this preference shows striking population variation. Among Trinidadian populations, the average female preference for orange area is positively correlated with the population mean orange area in males, indicating a correlated evolution of female preferences and male color patterns (Houde & Endler 1990). Quantitative genetic analyses demonstrate substantial additive genetic variance in multiple components of male coloration, with many traits linked to the Y chromosome, and show that orange area, chroma and overall color contrast all experience positive directional sexual selection via female choice (Brooks & Endler 2001). Thus, genetic covariance between female preferences and male traits, mediated by sex-linked ornament loci, facilitates the rapid evolution and divergence of color patterns.

Color-based mate choice does not operate in isolation from other behaviors and traits. Female guppies prefer more colorful males, but they also prefer bold males that inspect predators more frequently and at closer distances; when allowed to observe male–predator interactions, females choose bolder males even when coloration is experimentally decoupled from boldness (Godin & Dugatkin 1996). Conspicuous coloration is positively associated with boldness toward predators, suggesting that color can function as an indirect indicator of male viability. In this way, sexual selection via female choice may simultaneously favor visual conspicuousness and behavioral phenotypes that enhance survival, linking color vision, color traits and risk-taking behavior within an integrated adaptive syndrome (Godin & Dugatkin 1996).

Sensory bias, **associative learning and the origin of color preferences**. The origins of female preferences for orange coloration appear to lie in nonsexual sensory biases. Both sexes exhibit strong attraction to orange objects in non-mating contexts, especially orange food-like stimuli such as fruit, and across populations the strength of attraction to orange discs in foraging assays explains 94% of interpopulation variation in female mating preference for orange spots on males (Rodd et al 2002). This supports a sensory-bias model in which a pre-existing bias for detecting carotenoid-rich resources was co-opted by sexual selection, biasing the evolution of male ornament colors and the tuning of female vision toward orange wavelengths. Opsin expression data, showing LWS upregulation coinciding with sexual maturity and stronger LWS expression in females, are consistent with this picture of a food-derived bias being refined and reinforced in a mating context (Laver & Taylor 2011).

Learning further modifies color preferences in ways that may feed back into evolution. Associative learning experiments show that females conditioned to associate food with orange or black spots subsequently shift their mating preferences toward males bearing the rewarded color, and these learned preferences translate into differential paternity success of males differing in orange:black ratios (Herdegen-Radwan 2022). Such plasticity implies that ecological experiences influencing the reward value of specific colors can be transduced into sexual preferences, potentially initiating or reinforcing divergence among populations experiencing different foraging environments.

At shorter timescales, habituation to familiar color patterns also shapes mate choice. Females repeatedly exposed to males with a given pattern show declining responsiveness to that pattern and a renewed interest in males with novel patterns, fulfilling multiple criteria for habituation including response decline, spontaneous recovery, stimulus specificity and dishabituation (Daniel et al 2019). This mechanism provides a proximate basis for the well-documented preference for rare and unfamiliar male phenotypes and the associated "rare male advantage" in guppy mating success (Hughes et al 1999; Graber et al 2014; Valvo et al 2019). Habituation-driven novelty preferences can maintain high genetic variation in male color patterns within populations by generating negative frequency-dependent sexual selection, illustrating how basic properties of the visual and cognitive systems feed directly into evolutionary dynamics.

Environmental context, **predation and visual conspicuousness**. The adaptive landscape on which color vision and color preferences evolve is structured by the light environment and predation pressure. Classic work has shown that high-predation environments favor drabber, less conspicuous males, whereas low-predation sites harbor more colorful males, consistent with the relaxation of viability selection and the relative strengthening of sexual selection (Endler 1983). Yet recent sensory-based quantification of male color patterns using models of guppy and predator vision reveals that changes in male conspicuousness across predation regimes are more complex and less parallel than previously assumed, with only weak and trait-specific effects of predation regime on overall multivariate conspicuousness (Fuller 2022; Yong et al 2022).

Despite this complexity, there is clear evidence that predation context covaries with both female preferences and visual tuning. Females from low-predation populations not only show stronger preferences for orange males but also express higher levels of LWS opsins devoted to detecting orange-red light (Sandkam et al 2015). Experimental work on opsin expression plasticity suggests that predation can induce some changes in LWS transcription, although adult female cone opsin profiles are not strongly driven by current predation pressure, pointing to a larger role for genetic differentiation and developmental history (Chang 2024). These findings imply that color vision and mating preferences have coevolved under selection mosaics shaped by spatially variable predation and light environments, with adaptation occurring in different directions in multivariate trait space rather than along a single axis of "conspicuousness" (Fuller 2022; Yong et al 2022).

Evolutionary and adaptive implications. Integrating these lines of evidence shows that the link between color vision, sex, color traits and mate choice in guppies is both tight and bidirectional. On one hand, diversification and sex-biased expression of cone opsins, particularly within the LWS family, enhance female sensitivity to the orange-red hues that characterize male ornaments, thereby sharpening the efficacy of visual mate assessment (Hoffmann et al 2007; Laver & Taylor 2011; Sandkam et al 2015). On the other hand, pre-existing sensory biases toward orange objects and learning processes such as associative conditioning and habituation generate and modulate the very preferences that drive the evolution of male color patterns (Rodd et al 2002; Daniel et al 2019; Herdegen-Radwan 2022).

Sexual selection by visually guided female choice promotes the elaboration and diversification of male coloration, while natural selection via predation constrains and redirects this elaboration depending on habitat-specific risk and visual backgrounds (Endler

1983; Fuller 2022; Yong et al 2022). Negative frequency-dependent preferences for rare and unfamiliar color patterns, underpinned by habituation, maintain high standing variation in male coloration, providing raw material for rapid adaptive responses to changing environments (Hughes et al 1999; Graber et al 2014; Daniel et al 2019; Valvo et al 2019). The coevolution of opsins and ornaments in this system illustrates how genetic architecture of sensory systems and sexually dimorphic traits can jointly shape evolutionary trajectories, making guppies a powerful model for understanding how vision, sex and color interact to drive adaptation and diversification in nature.

Conclusions. The visual ecology of guppies exemplifies a tightly integrated system in which sexual selection, sensory biology, and ecological pressures coalesce to drive evolutionary change. Female guppies' visual tuning, particularly through LWS opsin expression, is adapted to detect male coloration, a trait shaped by both natural selection from predation and sexual selection via female preference. These preferences stem from pre-existing sensory biases, further refined through learning and experience. In turn, male coloration evolves rapidly due to genetic covariance with female preferences and the selective advantage of novel traits. This dynamic, feedback-driven system highlights the guppy as a key model for understanding the genetic and ecological foundations of visual-driven sexual selection and adaptive diversification.

Conflict of interest. The authors declare that there is no conflict of interest.

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Received: 22 November 2025. Accepted: 12 December 2025. Published online: 30 December 2025.

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How to cite this article:
Petrescu-Mag I. V., Burduhos P., Iederan C., Maxim A., Bora F. D., 2025 Color vision, sexual dimorphism and the visual ecology of guppies. Poec Res 15(1):42-46.