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# Genetic and Environmental Factors Shape Rates of Plasticity: The Temporal Dynamics of Opsin Gene Expression in Aquatic Environments

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## Abstract

Phenotypic plasticity enables organisms to adjust their traits in response to environmental changes, potentially enhancing survival under fluctuating conditions. While plastic capacity—the range of phenotypic change—has been extensively studied, the rate of plastic responses remains unexplored. The rate of plasticity is crucial, as prolonged mismatches between phenotype and environment reduce fitness. Nonetheless, evolutionary models typically do not investigate rates of plasticity. Here, we measure opsin gene expression to estimate the temporal changes in predicted visual sensitivity of Nicaraguan convict cichlids (*Amatitlania siquia*) from populations exposed to changes in light conditions. We show that rates of plasticity in single cone predicted sensitivity vary significantly among populations, developmental stages, and experimental light treatments, demonstrating that rates of plastic change are shaped by both genetic and context-dependent factors. Notably, great lake cichlids—native to predominantly turbid environments—responded more rapidly to red-shifted photic conditions than crater lake fish, but more slowly when returned to clear conditions. Additionally, younger individuals exhibited faster changes in opsin gene expression than older ones, highlighting the role of developmental stage in modulating plasticity. These findings challenge the assumption of constants rates of plasticity and suggest that selection could act not only on plastic capacity but also on the rate of plastic responses. Our results demonstrate that rates of plasticity are themselves evolvable traits. Incorporating this temporal dimension into models of plasticity will improve our understanding of how organisms respond to environmental heterogeneity, with broad implications for evolutionary biology and ecology.

**Keywords:** visual ecology, plasticity evolution, cichlid fish, color vision

## Introduction

Phenotypic plasticity allows individuals to express different phenotypes throughout their lifespan in response to environmental cues (Bradshaw 1965; Stearns 1989). This ability to alter traits in a context-dependent manner should increase the match between phenotypes and environment, thereby enhancing survival in dynamic systems (Levins 1968; Padilla and Adolph 1996). Phenotypic plasticity can be understood through two key parameters: the plastic capacity and the rate of plasticity (Burton et al. 2022; Dupont et al. 2024). Plastic capacity refers to the phenotypic range within which an individual might modify its phenotype in response to environmental changes and is usually measured using reaction norms (Woltereck 1909; Schlichting and Pigliucci 1998; Einum and Burton 2022; Gomulkiewicz and Stinchcombe 2022). Conversely, the rate of plasticity describes how quickly phenotypic adjustments occur following environmental changes (Burton et al. 2022; Dupont et al. 2024). The rate at which plastic responses materialize influences how long an organism expresses a suboptimal phenotype due to environment–phenotype mismatch (Padilla and Adolph 1996; Gabriel et al. 2005; Lande 2014). Therefore, both the rate of plasticity and the plastic capacity shape how effectively organisms can respond to environmental fluctuations. However, most empirical data have focused on studying the plastic capacity of traits (Dupont et al. 2024).

The rate of plasticity, while less studied than plastic capacity, is critical for understanding the temporal dynamics of phenotypic adaptation (Levins 1968; Shapiro 1976). The rate at which organisms adjust their traits to new environments can greatly influence fitness if the rate of change in the environment outpaces the rate of the plastic response (Padilla and Adolph 1996; Gabriel 1999). For example, in rapidly changing environments, organisms with a slow rate of plasticity incur fitness costs due to prolonged mismatches between phenotype and environment (i.e. adaptive lag, Burton et al. 2022; Einum and Burton 2022; Dupont et al. 2024). Importantly, the rate of plasticity may also influence the evolution of plastic capacity itself (Lande 2014). If organisms can quickly adjust their phenotypes, they may defer the onset of trait changes until closer to when selection pressure occurs, thereby increasing environmental predictability and favoring greater plastic capacity (Lande 2014; Gomulkiewicz and Stinchcombe 2022). However, the rate of plasticity is often set to be constant in theoretical models of the evolution of phenotypic plasticity (Padilla and Adolph 1996 ; Gabriel 1999; Lande 2009, 2014). Therefore, our understanding of phenotypic plasticity remains incomplete if genetic or

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ecological influences on the rate of plasticity are left unaccounted. Despite the importance of the temporal component of phenotypic plasticity, empirical data on the factors influencing rates of plasticity in biological traits remain scarce (Einum and Burton 2022; Burton and Einum 2025).

A biological trait that exhibits reversible plasticity and may continuously modulate its phenotypic value in response to ongoing cues is the expression of cone opsin genes in teleost fish. Plasticity in opsin gene expression is common among teleost fishes and has been extensively studied in cichlids, Cichlidae (Bertinetti and Torres-Dowdall 2025). Since cone opsin genes encode the G-protein-coupled receptors that form visual pigments, opsin plasticity might enable fish to modulate spectral sensitivity in response to changing photic conditions (Fuller and Claricoates 2011; Cronin et al. 2014; Härer et al. 2017; Fogg et al. 2023). Cichlid fish inhabit heterogeneous habitats with fluctuating underwater photic conditions across time and space, e.g. stormwater runoff, algal blooms, depth or microhabitat differences, or diurnal variation (Carleton et al. 2016; Yourick et al. 2019; Carleton and Yourick 2020; Hauser et al. 2021; Torres-Dowdall et al. 2021). These rapid episodic changes in photic conditions impair visual capabilities involved in ecologically relevant tasks such as foraging, mate choice, or predator avoidance (Seehausen et al. 1997; Torres-Dowdall et al. 2014; Zanghi and Ioannou 2025). Hence, fluctuating selective pressures due to short-term photic changes favor rapid plastic adjustments. In cichlids, these responses occur on the order of a few days after a change in photic conditions (Hofmann et al. 2010; Nandamuri et al. 2017; Härer et al. 2019; Karagic et al. 2022; Schreiner et al. 2023). Although the magnitude of such changes in opsin gene expression is often known (i.e. their plastic capacity), the rate at which these plastic responses occur remains largely unexplored.

Both genetic and environmental factors influence plastic capacity in opsin gene expression among teleost fish species (Bertinetti and Torres-Dowdall 2025). For instance, closely related populations inhabiting distinct photic habitats show evolved divergence in their visual plastic capacity (Härer et al. 2017; Bertinetti et al. 2024b). Genetic differences might also affect the rate of opsin plasticity. Beyond genetic differentiation, context-dependent factors such as developmental stage or changes in the photic environment also drive differences in plastic responses (Härer et al. 2019; Carleton et al. 2020; Torres-Dowdall et al. 2024). For instance, age-dependent plasticity affects certain opsin genes (Härer et al. 2017; Nandamuri et al. 2017; Irazábal-González et al. 2024), while experimental light conditions elicit distinct expression changes (Nandamuri et al. 2017; Härer et al. 2019). Moreover, interactions among ecological factors, e.g. younger fish responding to certain photic changes, may shape both plastic capacity and its rate (Bertinetti and Torres-Dowdall 2025). Therefore, we hypothesized that both age and the nature of the photic change (e.g. from clear to turbid conditions or vice versa) influence the temporal dynamics of opsin plasticity.

In this study, we aim to evaluate the null hypothesis that the rate of plasticity is constant, independent of genetic background and ecology (e.g. Padilla and Adolph 1996; Gabriel et al. 2005; Lande 2014; Siljestam and Östman 2017). Specifically, we test if rates of plasticity in opsin gene expression are influenced by development, nature of the photic change, genetic factors, and their interactions. Therefore, we measure the effects of (i) developmental stage, (ii) experimental change in light, and (iii) genetic background on the rate and capacity of opsin plasticity. We show that rates of plasticity have diverged among populations and exhibit significant variation due to age and nature of light changes.

## Methods

### Study System and Experimental Design

One great lake and one crater lake population of Nicaraguan convict cichlids (*Amatitlania siquia*, Cichlidae) were compared in this study (Schmitter-Soto 2007). Nicaraguan convict cichlids inhabit rivers and lakes of Nicaragua, including the two largest lakes, Managua and Nicaragua, which were formed around 500,000 years ago (Kutterolf et al. 2007; Torres-Dowdall and Meyer 2021). From these lakes, convict cichlids colonized a series of smaller and younger crater lakes, including crater lake Xiloá, which formed after the last large eruption around 6,100 years ago. Hence, great lake convict cichlids represent older populations that inhabit red-shifted photic environments from which younger crater lake populations were derived (Kautt et al. 2020). Given the independent colonization of crater lakes, their differences in photic conditions, and their geographic isolation, the Nicaraguan crater lakes represent a natural setting to study phenotypic evolution (Kautt et al. 2018). Here, the visual system of Nicaraguan cichlids has been shown to evolve repeatedly in response to novel habitats, with variation in opsin gene expression being significantly predicted by photic conditions (Torres-Dowdall et al. 2017; Härer et al. 2018; Bertinetti et al. 2024a). While interpopulation differences in opsin gene expression among Nicaraguan cichlids show a strong genetic component, phenotypic plasticity also contributes to this visual diversity.

Convict cichlids possess seven cone opsin genes involved in color vision; *sws1, sws2b, sws2a, rh2b, rh2aα, rh2aβ,* and *lws*; rendering their retina sensitive to a broad spectrum, including ultraviolet (UV) light (Härer et al. 2018; Torres-Dowdall et al. 2021). Cichlid fish have two types of cone photoreceptors: single cones and double cones (Fernald 1981). The three short-wavelength-sensitive opsin genes *sws* (i.e. *sws1, sws2b,* and *sws2a*) are expressed exclusively in single cones, whereas the remaining cone opsin genes are restricted to double cones (Dalton et al. 2014 ; Torres-Dowdall et al. 2017; Härer et al. 2019). Hence, plastic changes in single cone opsin genes can serve as a proxy for visual sensitivity in the UV–blue spectral range (Sabbah et al. 2010; Torres-Dowdall et al. 2021). Although co-expression of multiple opsins within single cones has been documented, it is typically transient and reflects transitional phase during opsin switching (Cheng and Novales Flamarique 2004; Karagic et al. 2018; Härer et al. 2019). This co-expression often occurs when a cone is in the process of replacing one opsin with another, before stabilizing into a new expression state (Cheng and Novales Flamarique 2004). Short-wavelength sensitivity is particularly relevant for the foraging performance of juvenile fish that rely on zooplankton prey (Novales Flamarique 2016; Yoshimatsu et al. 2020). The ecological relevance of single cone sensitivity in early life-stages may explain the rapid reversible plasticity observed in single cone opsin expression—as opposed to double cones—which tend to show more stable expression patterns over time (Härer et al. 2019). In that study, opsin gene expression in single cones changed quickly and stabilized within days, whereas in double cones it remained relatively constant, showing limited evidence of reversible plasticity (Härer et al. 2019).

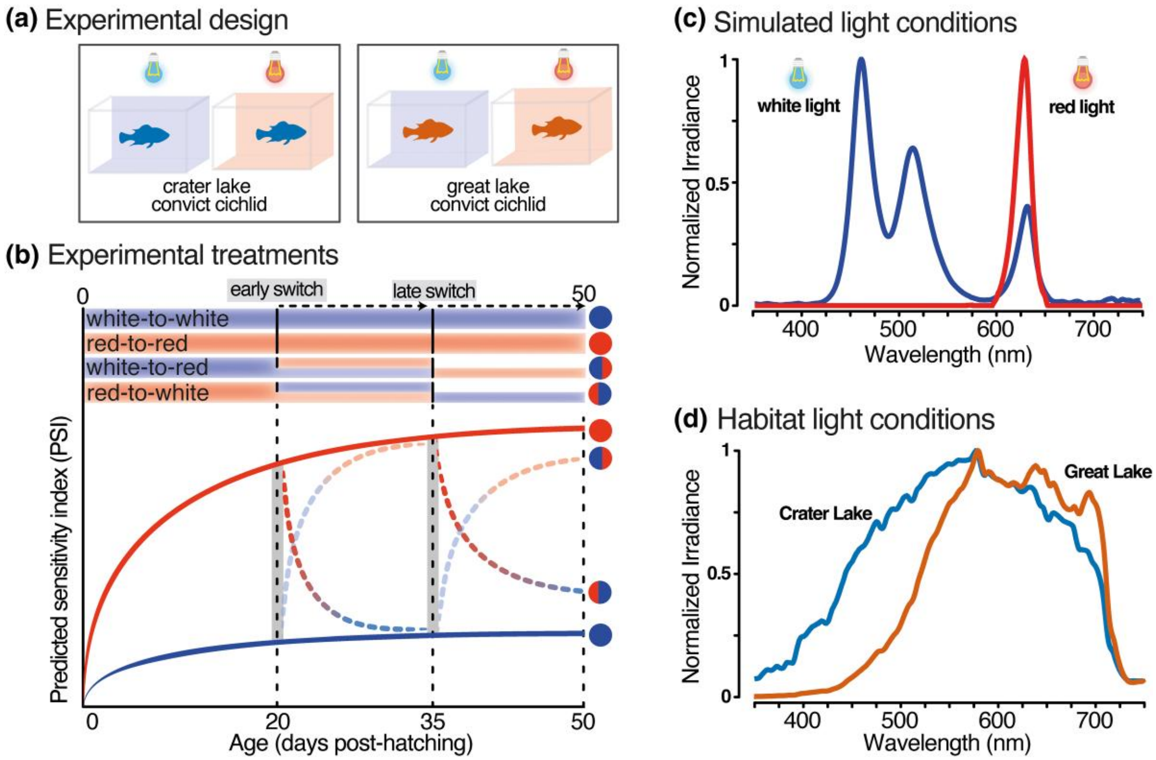


**Fig. 1.** Experimental design to test the effect of genetic background, developmental stage, and environmental change on the rate of plasticity in opsin gene expression. a) Convict cichlid populations from either a clear crater lake or a turbid great lake raised under white light and red light. b) Experimental treatments used in this study. c and d) Laboratory and native habitat normalized irradiance reference spectra.

Therefore, given the direct link between *sws* gene expression and single cone visual pigment abundance, the ecological relevance of *sws* genes for plankton feeding during juvenile stages, and their known reversible plasticity, we focused on single cone sensitivity as predicted by *sws1*, *sws2b*, and *sws2a*.

To measure the effect of genetic and context-dependent factors (e.g. age and nature of the photic change) on the rate of plasticity in opsin gene expression, we compared rates between two convict cichlid populations, two developmental stages, and two experimental light treatments. Eggs from F2 laboratory-reared descendants of wild-caught convict cichlids from Great Lake Nicaragua and Crater Lake Xiloá, referred to henceforth as great lake and crater lake convict cichlids, respectively, were used in this study. About 30 eggs per brood were placed in 2 l tanks and randomly allocated to one light treatment, either red-light or white-light, simulating the narrow and broad spectral distribution of their native environments, respectively (Fig. 1). Fish were kept at 25 °C with a 12L:12D photoperiod and fed ad libitum with live brine shrimp (*Artemia* spp.). To trigger a plastic response in opsin gene expression, half of the fry were switched from their respective light condition to the other (either red-to-white light, RW, or white-to-red light, WR), while the other half of the group were switched to a different tank but maintained under the same light conditions to control for fish handling (red-to-red, RR, and white-to-white, WW, Fig. 1b and supplementary table S1, Supplementary Material online). The light treatment switch occurred either at 20 dph (days post-hatching), referred as early treatment (E), or at 35 dph, the late treatment (L). These age stages were chosen to ensure the retina was developed (>5 dph) and that the free-swimming fry were acclimated to the first light condition prior to experiencing the novel light treatment (Karagic et al. 2018; Härer et al. 2019). Fish were sampled before the light treatment switch occurred and daily after that for 10 to 15 d. Overall, 1 to 6 fish per brood were sampled daily, in four light treatments (RR, WW, WR, and RW), two age stages (E and L), and two populations (crater and great lake), for a total of 620 fish (supplementary table S1, Supplementary Material online). All fish were collected between 1 and 3 PM to account for circadian patterns of opsin gene expression (Halstenberg et al. 2005; Johnson et al. 2013; Yourick et al. 2019). Fish were euthanized using a buffered MS-222 overdose (Syndel Laboratories, WA, USA) followed by decapitation. The eyes were dissected and stored in RNAlater (Invitrogen, CA, USA) at −20 °C. All experiments were conducted at the University of Notre Dame and approved by the Institutional Animal Care and Use Committee (Protocol 23-03-7717).

## Opsin Gene Expression and Predicted Sensitivity Index

To quantify cone opsin gene expression, RNA was extracted following a standard guanidinium thiocyanate–phenol–chloroform protocol as described in Bertinetti et al. (2024b). RNA concentration and integrity were assessed with a Qubit 4 fluorometer (Fischer Scientific, NH, USA). Following the manufacturer's protocol, 200 ng of RNA was used to synthesize cDNA using the GoScript™ Reverse Transcription System (Promega, WI, USA). The expression of single cone opsin genes: *sws1*, *sws2b*, and *sws2a* was measured for 40 cycles of 15 s, 95 °C, and 60 s, 60 °C, with an initial and final denaturation step of 2 min, 95 °C (CFX Duet, Bio-Rad Laboratories, USA). Additionally, the expression of housekeeping genes *ef1a* and *gapdh* was also measured in a subset of individuals from each treatment to validate the results. Primer sequences were as in Torres-Dowdall et al. (2021) and are reported together with amplification efficiencies in supplementary table S2, Supplementary Material online. To estimate the rate of plasticity in single cone visual sensitivity, we first computed the proportional expression of single cone opsin genes as a proxy of visual pigment ratios among single cone photoreceptors. Proportional single cone opsin gene expression was calculated as the expression of each single cone opsin ($SC_i$) relative to the total single cone opsin expression ($\sum SC$) following Fuller et al. (2004):

$$\frac{SC_i}{\sum_3^1 SC_i} = \frac{(1/((1+E_i)^{Cq_i}))}{\sum_3^1 (1/((1+E_i)^{Cq_i}))} \quad (1)$$

where $E_i$ is the primer efficiency and $Cq_i$ the quantification cycle for each gene $i$, respectively. Proportional single cone opsin gene expression was then used to compute the predicted spectral sensitivity index of single cones PSI (nm). PSI provides a theoretical estimate of single cones visual sensitivity based on proportional opsin gene expression and the absorbance peaks of each opsin protein. Hence, PSI provides a reliable single point estimate of the opsin gene expression pattern when comparing individuals that express different ratios of the same three opsin genes in one photoreceptor type. The implications for visual perception of variation in PSI are not fully resolved, but its relevance has been inferred from its correlation with ecological factors in the wild (Hofmann et al. 2009; Härer et al. 2018; Bertinetti et al. 2024a). Following Hofmann et al. (2009), we estimated PSI using visual pigment peak sensitivities from the closely related *Amphilophus citrinellus* (Torres-Dowdall et al. 2017):

$$PSI = SC_{sws1} \times 360\,nm + SC_{sws2b} \times 440\,nm + SC_{sws2a} \times 466\,nm \quad (2)$$

where SC represents the proportional expression in single cones for each short-wavelength-sensitive opsin gene $i$ (*sws1, sws2b, sws2a*).

## Statistical Analysis

To quantify the rate of plasticity in opsin gene expression, we modeled the temporal response of the predicted sensitivity index (PSI) in single cones following a change in light conditions (Fig. 1b). The response was characterized using a nonlinear least squares approach to estimate both the asymptotic expression levels and the rate of change over time using the *minpack.lm* package in R (Elzhov et al. 2023). Following Burton et al. (2022), we fitted a nonlinear exponential decay model to describe the temporal dynamics of PSI:

$$PSI(t) = PSI_f + \Delta PSI \times e^{-\lambda t} \quad (3)$$

where PSI($t$) represents the predicted sensitivity index in single cones at time $t$ (days post-switch), $PSI_f$ is the asymptotic predicted sensitivity (nm), ΔPSI the difference in predicted sensitivity between initial ($t = 0$) and final time point, i.e. the plastic capacity (nm), and λ represents the rate at which opsin gene expression approaches the asymptote, i.e. rate of plasticity (in *1/t* units).

To test the effects of genetic background, developmental stage, and light conditions; the model was extended to include fixed effects for population (great vs. crater lake), age (early vs. late switch), and experimental light treatment (RW vs. WR), as well as their interactions (supplementary table S3, Supplementary Material online). While the PSI was used as the main response variable, proportional and normalized opsin gene expression are presented in Fig. 2 and supplementary figs. S1 to S3, Supplementary Material online. Model parameters were estimated using the Levenberg–Marquardt algorithm (Elzhov et al. 2023). Nonsignificant parameters were sequentially removed to optimize model parsimony, and model selection was guided by Akaike information criterion values to determine the best-fitting model. The significance of the parameter estimates was determined using the Wald $\chi^2$ test. All statistical analyses were performed in R (R Core Team 2020).

## Results

We quantified how population, developmental stage, and change in light treatment shape the temporal dynamics of opsin gene expression. Using data from two populations of convict cichlids exposed to contrasting experimental light treatments at different developmental stages, we estimated the rate and capacity of plastic responses in single cone predicted sensitivity (Figs. 1 and 2, Table 1). Changes in predicted sensitivity occurred rapidly, with half-time change—the time for the phenotypic value to reach half of the plastic capacity —ranging from <1 d to nearly 3 d (Figs. 2 and 3). WR light changes led to a shift in the PSI toward longer wavelengths (Fig. 3a and c), whereas RW transitions led to a shift in the sensitivity index toward shorter wavelengths (Fig. 3 and d). However, crater lake fish showed a slower response than great lake fish in WR light changes (Fig. 3a and c), whereas crater lake individuals exhibited faster response than great lake fish in RW treatment (Fig. 3b and d). Broadly, younger fish showed faster responses and higher plastic capacity than older ones (Figs. 3 and 4). However, the response was context-dependent, as older great lake cichlids showed the fastest plastic response in WR light changes but a lack of response when exposed to the inverted light change RW (Fig. 3c to d). Overall, the rate of plasticity was significantly affected by experimental treatments of light condition changes ($t = -3.167$, df = 102, $P = 0.002$, Fig. 4 and Table 1) and the interaction lake × age ($t = -2.075$, df = 102, $P = 0.04$). The plastic capacity was significantly influenced by the three-way interaction of environmental light change × age × lake ($t = 3.773$, df = 102, $P < 0.001$, Fig. 4 and Table 1).

## Discussion

Phenotypic plasticity is most often understood as the phenotypic range of an organism in response to different environmental cues, i.e. plastic capacity (Dupont et al. 2024; Burton and Einum 2025). Influenced by the empirical data on reaction norms for plastic traits, models of plasticity evolution have focused predominantly on the evolution of plastic capacity (Lande 2014; Siljestam and Östman 2017). Given that rates of plasticity determine the duration of mismatches between phenotypes and the environment, selection pressures targeting the timing of plastic responses might lead to their evolution (Dupont et al. 2024; Burton and Einum 2025). Besides evolved differences in rates of plasticity, environmental conditions might also shape the rate and capacity of plasticity. Here, we exposed distinct populations of convict cichlids to light treatment changes at two different age stages to test the influence of genetic and context-dependent factors (i.e. age and type of photic change) on phenotypic plasticity. Plastic responses in

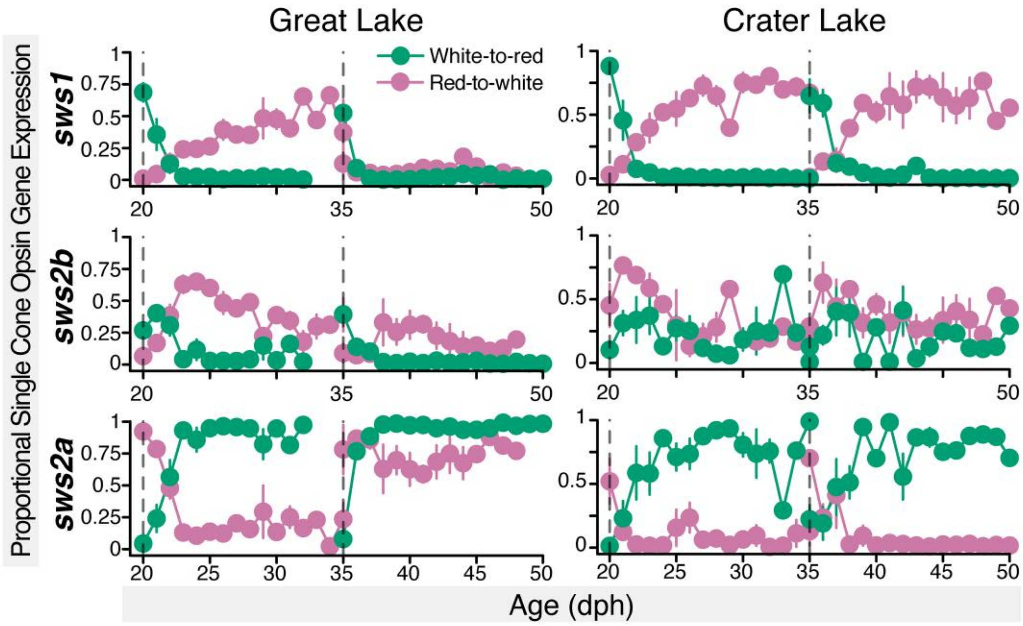


**Fig. 2.** Proportional expression of single cone opsin genes *sws1*, *sws2b*, and *sws2a* in Great Lake Nicaragua and Crater Lake Xiloá convict cichlids (*A. siquia)* experiencing different light treatments (red-to-white, RW vs. white-to-red, WR). Dashed lines represent different ages; either Early (20 dph) or Late (35 dph) treatments. Dots and error bars represent mean ± SE. Control groups and relative expression are shown in supplementary figs. S1 and S2, Supplementary Material online).

**Table 1** Summary statistics of best supported model of temporal dynamics of single cone PSI

| Parameter | Estimate | Std. error | *t* value | *P*-value |
|---|---|---|---|---|
| Plastic capacity (ΔPSI) | | | | |
| Intercept | −79.881 | 6.679 | −11.959 | **<2e−16** |
| Lake of origin | −12.899 | 9.432 | −1.368 | 0.174456 |
| Age at change | 16.098 | 9.557 | 1.684 | 0.095147 |
| Direction of light change | 143.559 | 8.829 | 16.260 | **<2e−16** |
| Lake × light change | 16.053 | 12.542 | 1.280 | 0.203469 |
| Light change × age | −82.271 | 13.102 | −6.279 | 8.41e−9 |
| Lake × age | 2.222 | 13.261 | 0.168 | 0.867258 |
| Lake × age × light change | 68.354 | 18.119 | 3.773 | **0.000271** |
| Rate of plasticity ($\lambda$) | | | | |
| Intercept | 0.711 | 0.132 | 5.385 | **4.66e−07** |
| Lake of origin | 0.079 | 0.181 | 0.435 | 0.664436 |
| Age at change | 1.071 | 0.633 | 1.692 | 0.093743 |
| Direction of light change | −0.460 | 0.145 | −3.167 | **0.002033** |
| Lake × light change | 0.004 | 0.203 | 0.019 | 0.98449 |
| Light change × age | 0.363 | 0.185 | 1.965 | 0.052093 |
| Lake × age | −1.352 | 0.651 | −2.075 | **0.040516** |
| Asymptotic PSI (i.e. plateau phase of new phenotypic value) | | | | |
| Intercept | 463.817 | 2.470 | 187.758 | **<2e−16** |
| Lake of origin | −3.393 | 3.192 | −1.063 | 0.290291 |
| Age at change | −0.084 | 3.067 | −0.027 | 0.978333 |
| Direction of light change | −62.157 | 4.841 | −12.841 | **<2e−16** |
| Lake × light change | −13.514 | 6.081 | −2.222 | **0.028483** |
| Light change × age | 52.007 | 5.495 | 9.465 | **1.24e−15** |
| Lake × Age | 1.136 | 4.352 | 0.261 | 0.79452 |
| Lake × age × light change | −47.767 | 7.374 | −6.478 | **3.33e−09** |

*Lake of origin* refers to either Crater Lake Xiloá or Great Lake Nicaragua convict cichlids (*A. siquia*). *Direction of light change* refers to experimental light change treatment, either RW or WR. *Age at change* refers to either early (20 dph) or late (35 dph) developmental states. Significant factors ($P < 0.05$) in bold and marginally significant are underlined ($P = 0.05$ to 0.1). See supplementary table 3, Supplementary Material online for details.

opsin gene expression varied in their capacity and rate across populations, light treatments, and developmental stages (Figs. 2 and 3) evidencing that opsin plasticity itself is evolvable and context-dependent.

Our study demonstrates that both the rate of plasticity and its capacity can evolve. These findings expand the current evidence about the evolution of plasticity since most examples of plasticity evolution have addressed only its capacity (Day et al. 1994; Kingsolver et al. 2007; Scoville and Pfrender 2010; Torres-Dowdall et al. 2012; Levis et al. 2017; Relyea et al. 2021). Recently, meta-analyses of thermal tolerance have shown that rates of plasticity differ among distantly related phylogenetic groups (Einum and Burton 2022; Burton and Einum 2025). In contrast, by comparing the plastic responses between two recently diverged convict cichlid populations, our study shows that rates of plasticity in opsin gene expression—not only their plastic capacity—might evolve over relatively short divergence times (<6,100 years, Kutterolf et al. 2007). Genetic divergence of plastic capacity in fish visual traits has been previously reported (Luehrmann et al. 2018; Härer et al. 2019; Bertinetti et al. 2024b). Complementarily, our study hints at the evolution of rates of plasticity in natural populations, as suggested by differences in the rate of plastic responses between crater and great lake convict cichlids (Figs. 3 and 4). The finding that both the plastic capacity and the rate of opsin plasticity might evolve adds complexity to our understanding of the evolution of plasticity. Hence, future research should aim to incorporate temporal dynamics into the classical approach of reaction norms (Burton et al. 2022; Dupont et al. 2024).

Rates of plasticity are also context-dependent. Fish differed in their rates of plasticity when exposed to identical light changes in opposite directions (WR vs. RW; Fig. 1). Generally, responses were faster in the WR than in RW change, with older great lake fish eventually being unresponsive to RW changes (Fig. 3). We hypothesize that such differences might be partially explained by selection regimes in their native habitats, where variation in the type and frequency of photic changes in crater versus great lakes could have led to divergence of plastic responses (Levis and Pfennig 2019; Dupont et al. 2024). Crater Lake Xiloá, with its high clarity and steep

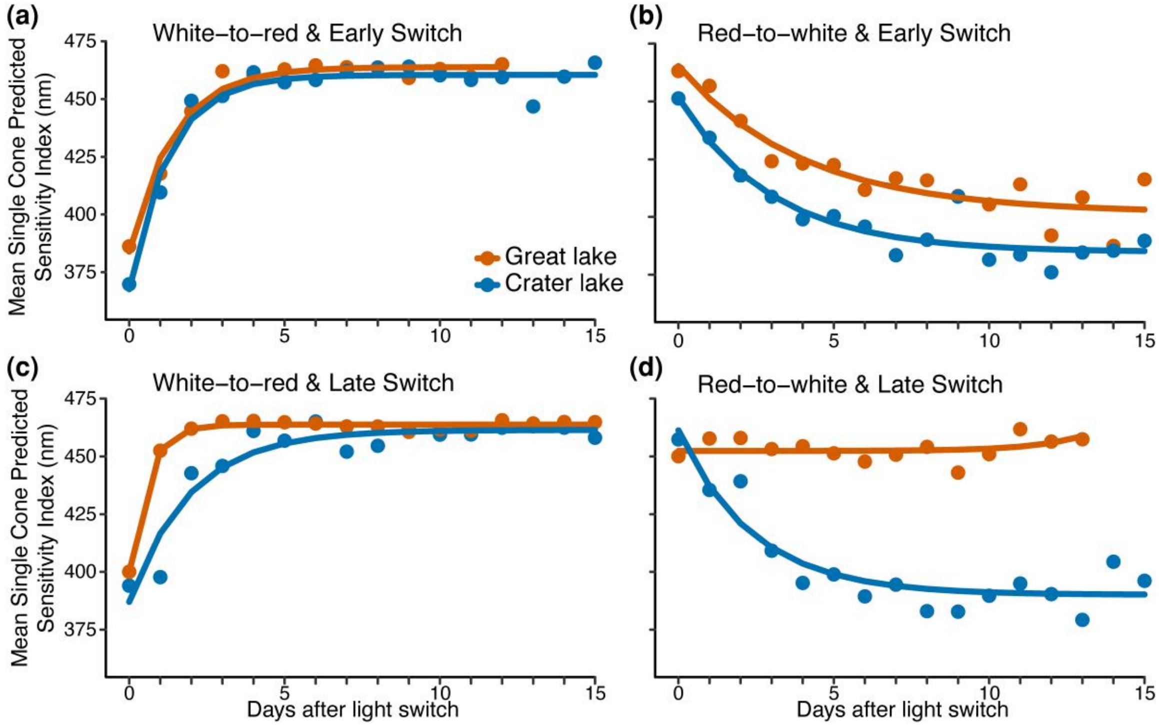


**Fig. 3.** Genetic and environmental factors influence rates of plasticity and plastic capacity in single cone predicted sensitivity PSI (nm). a) and b) depict transitions from white-light to red-light, while c) and d) show transitions from a red-light to a white-light conditions. The early (20 dph; a and b) and late (35 dph; c and d) switch conditions indicate different ages when the light shift occurred. Dots represent the mean single cone predicted sensitivity for each day after light experimental conditions changed (Fig. 1b). Solid lines show predicted values based on model outputs (Table 1). See supplementary table S1, Supplementary Material online for sample sizes.

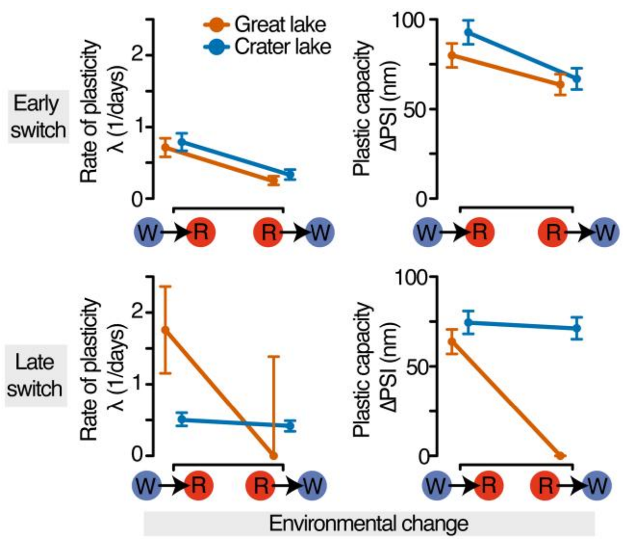


**Fig. 4.** Plastic capacity and rate of plasticity estimates of single cone predicted sensitivity differ among developmental stages, the directionality of environmental change, and populations. Plastic capacity represents the magnitude of the plastic change in single cone predicted sensitivity, an estimate of the extent to which visual sensitivity can be modulated. The rate of plasticity represents the decay constant (λ), i.e. reciprocal of time of the plastic response (see Eq. 2, supplementary table S3, Supplementary Material online). Great lake fish older than 35 dph in RW treatment lacked a plastic response resulting in inaccurate model estimates. Dots and error bars represent estimate ± SE.

rims, undergoes episodic turbidity due to precipitation runoff, resembling the WR treatment (Elmer et al. 2010; Torres-Dowdall and Meyer 2021). These shifts are temporary, as the lake eventually returns to high clarity (RW). In contrast, the turbid eutrophic Great Lake Nicaragua rarely experiences fluctuations that resemble Xiloá's clear water conditions (Torres-Dowdall et al. 2017; Härer et al. 2018; Bertinetti et al. 2024a). Great lake cichlids frequently experience increased turbidity (WR) but rarely encounter reversals to clear water (RW). Consequently, crater lake fish respond similarly fast to both experimental light treatments, whereas great lake fish show slower responses in RW than in WR (Fig. 4). These findings align with predictions that encounter frequencies of environmental fluctuations shape the evolution of plastic responses (Gomulkiewicz and Stinchcombe 2022; Dupont et al. 2024). Given the demography of the crater lake populations, which were colonized by a small number of individuals, research on additional populations and their long-term environmental data is required to understand how the frequency of photic fluctuations influences the temporal dynamics of plasticity and its genetic underpinnings.

The developmental stage when the light switch occurs also affects opsin gene expression plasticity. Fish from the same population exhibited different plasticity rates between age stages (lake × age interaction, Fig. 4). Such age-dependent effects align with the developmental trajectories of opsin gene expression in cichlids (Carleton et al. 2016; Härer et al. 2019; Lupše et al. 2022). Early larval stages are typically dominated by the expression of the UV-sensitive opsin *sws1* (Fig. 2), likely due to its relevance for foraging performance on zooplankton prey (Novales Flamarique 2016; Yoshimatsu et al. 2020). As fish grow, juveniles transition to violet and then blue-sensitive opsins, i.e. *sws2b* and *sws2a* (Härer et al. 2017; Schreiner et al. 2023). This ontogenetic shift is also influenced by photic conditions, with fish in long-wavelength-shifted environments transitioning earlier (i.e. fish reared in red-light before the experimental light change, Fig. 2). Our results suggest an interplay between developmental trajectories and reversible plasticity. Here, plastic responses aligned with the developmental trajectory (WR) occur faster than those against it (RW), suggesting that ontogeny facilitates plasticity. Alternatively, younger fish relying on UV-sensitivity for foraging may be particularly impacted by photic changes, thus generating strong selective pressures for maintaining high plasticity in WR transitions. In contrast, reversal to UV-sensitivity in RW changes might represent a smaller fitness advantage, as clear water conditions represent broad spectra and weaker selection pressures around a single optimal phenotype (Loew 1995; Bertinetti et al. 2024a). Nonetheless, our findings demonstrate that rates of plasticity are influenced by both the developmental stage and the directionality of the change in light conditions.

Our finding that both the rate and capacity of plasticity can evolve has important implications for understanding phenotypic plasticity. Evolutionary models suggest that predictable environments favor high plastic capacity (Lande 2014). These models imply that high plasticity rates lead to fast plastic responses, enabling organisms to accurately respond to environmental change; thereby, increasing predictability and selecting for high plastic capacity (Lande 2014; Siljestam and Östman 2017). This framework suggests a positive correlation between plasticity rate and capacity. Yet a recent meta-analysis of thermal plasticity reported the opposite—a negative correlation (Burton and Einum 2025). The genetic and context-dependent interactions observed in our study may help reconcile this discrepancy. We found a weak, non-significant correlation between opsin plasticity rate and capacity, $r\ (6) = 0.41$, $t = 1.1$, $P = 0.311$, driven by two outliers groups—older great lake fish that either showed no plasticity (RW) or exhibited the fastest response (WR, Fig. 4). Removing these groups revealed a strong, significant positive correlation between the rate of plasticity and plastic capacity, $r\ (4) = 0.96$, $t = 6.8$, $P = 0.002$, consistent with theoretical predictions, but opposite to the empirical results of thermal plasticity (Burton and Einum 2025). These results suggest that developmental state and environmental context may obscure rate–capacity relationships, especially in macroevolutionary analyses. This is particularly relevant for reversible traits that shift with age or occur near evolutionary tipping points of reversible versus irreversible, developmental responses (West-Eberhard 2003; Hoverman and Relyea 2007; Fischer et al. 2014; Botero et al. 2015; Fawcett and Frankenhuis 2015; Murren et al. 2015). The lack of response in older great lake fish in RW may reflect such a threshold—driven by frequency of photic fluctuations and their predictability—where the costs of phenotypic adjustment outweigh benefits (Botero et al. 2015). Clarifying how developmental trajectories interact with reversible plasticity is relevant to understanding the evolution of reaction norms and the temporal dynamics of plasticity.

Our study demonstrates that both the rate and capacity of phenotypic plasticity are evolvable traits. The Nicaraguan crater lakes provide a valuable system to understand how the frequency and magnitude of environmental fluctuations might drive the evolution of phenotypic plasticity. By examining opsin gene expression in Nicaraguan cichlids, we show that genetic background, the type of experimental light treatment, and developmental state influence plastic responses. We hypothesize that the variability and frequency of photic conditions in their native habitats might lead to population-specific plasticity rates. However, addressing whether encounter frequencies in natural populations shape rates of plasticity requires testing additional population replicates and long-term environmental data. Additionally, we show that developmental trajectories seem to facilitate plasticity when reversible changes align with ontogenetic shifts. Our findings suggest that genetic and context-dependent factors influence the positive correlation predicted between rates of plasticity and plastic capacity. Our results emphasize the need to acknowledge rates of plasticity as an evolvable trait to advance plasticity research. By integrating ecological, genetic, and developmental perspectives, this study advances our understanding of visual plasticity and provides a framework for investigating plasticity evolution in other biological systems.

## Supplementary Material

Supplementary material is available at *Molecular Biology and Evolution* online.

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## Data Availability

The data and code used for analysis are publicly available at the Zenodo Digital Repository doi.org/10.5281/zenodo.15053154 (Bertinetti 2025).

## References

Bertinetti C. 2025. Data from: Genetic and environmental factors shape rates of plasticity: the temporal dynamics of opsin gene expression in aquatic environments [Data set]. Zenodo. https://doi.org/10.5281/zenodo.15053154.

Bertinetti C, Härer A, Karagic N, Meyer A, Torres-Dowdall J. Repeated divergence in opsin gene expression mirrors photic habitat changes in rapidly evolving crater lake cichlid fishes. *Am Nat*. 2024a:203(5):604–617. https://doi.org/10.1086/729420.

Bertinetti C, Meyer A, Torres-Dowdall J. Visual pigment chromophore usage in Nicaraguan Midas cichlids: phenotypic plasticity and genetic assimilation of *cyp27c1* expression. *Hydrobiologia*. 2024b. https://doi.org/10.1007/s10750-024-05660-w.

Bertinetti C, Torres-Dowdall J. Phenotypic plasticity in visual opsin gene expression: a meta-analysis in teleost fish. *J Exp Biol*. 2025. https://doi.org/10.1242/jeb.250332.

Botero CA, Weissing FJ, Wright J, Rubenstein DR. Evolutionary tipping points in the capacity to adapt to environmental change. *Proc Natl Acad Sci U S A*. 2015:112(1):184–189. https://doi.org/10.1073/pnas.1408589111.

Bradshaw AD. Evolutionary significance of phenotypic plasticity in plants. In: Caspari EW, Thoday JM, editors. *Advances in genetics*. New York and London: Academic Press; 1965. p. 115–155.

Burton T, Einum S. High capacity for physiological plasticity occurs at a slow rate in ectotherms. *Ecol Lett*. 2025:28(1):e70046. https://doi.org/10.1111/ele.70046.

Burton T, Ratikainen II, Einum S. Environmental change and the rate of phenotypic plasticity. *Glob Chang Biol*. 2022:28(18):5337–5345. https://doi.org/10.1111/gcb.16291.

Carleton KL, Dalton BE, Escobar-Camacho D, Nandamuri SP. Proximate and ultimate causes of variable visual sensitivities: insights from cichlid fish radiations. *Genesis*. 2016:54(6):299–325. https://doi.org/10.1002/dvg.22940.

Carleton KL, Escobar-Camacho D, Stieb SM, Cortesi F, Marshall NJ. Seeing the rainbow: mechanisms underlying spectral sensitivity in teleost fishes. *J Exp Biol*. 2020:223(Pt 8):jeb193334. https://doi.org/10.1242/jeb.193334.

Carleton KL, Yourick MR. Axes of visual adaptation in the ecologically diverse family Cichlidae. *Semin Cell Dev Biol*. 2020:106:43–52. https://doi.org/10.1016/j.semcdb.2020.04.015.

Cheng CL, Novales Flamarique I. New mechanism for modulating colour vision. *Nature*. 2004:428(6980):279–279. https://doi.org/10.1038/428279a.

Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. *Visual ecology*. Princeton, NJ: Princeton University Press; 2014.

Dalton BE, Loew ER, Cronin TW, Carleton KL. Spectral tuning by opsin coexpression in retinal regions that view different parts of the visual field. *Proc R Soc Edinb Biol*. 2014:281:20141980. https://doi.org/10.1098/rspb.2014.1980.

Day T, Pritchard J, Schluter D. A comparison of two sticklebacks. *Evolution*. 1994:48(5):1723–1734. https://doi.org/10.2307/2410260.

Dupont L, Thierry M, Zinger L, Legrand D, Jacob S. Beyond reaction norms: the temporal dynamics of phenotypic plasticity. *Trends Ecol Evol*. 2024:39(1):41–51. https://doi.org/10.1016/j.tree.2023.08.014.

Einum S, Burton T. Divergence in rates of phenotypic plasticity among ectotherms. *Ecol Lett*. 2022:26(1):147–156. https://doi.org/10.1111/ele.14147.

Elmer KR, Kusche H, Lehtonen TK, Meyer A. Local variation and parallel evolution: morphological and genetic diversity across a species complex of neotropical crater lake cichlid fishes. *Philos Trans R Soc Lond B Biol Sci*. 2010:365(1547):1763–1782. https://doi.org/10.1098/rstb.2009.0271.

Elzhov TV, Mullen KM, Spiess A-N, Bolker B. 2023. minpack.lm: R interface to the Levenberg-Marquardt nonlinear least-squares algorithm found in MINPACK, plus support for bounds. https://cran.r-project.org/package=minpack.lm.

Fawcett TW, Frankenhuis WE. Adaptive explanations for sensitive windows in development. *Front Zool*. 2015:12(Suppl 1):S3. https://doi.org/10.1186/1742-9994-12-S1-S3.

Fernald RD. Chromatic organization of a cichlid fish retina. *Vision Res*. 1981:21(12):1749–1753. https://doi.org/10.1016/0042-6989(81)90207-8.

Fischer B, Van Doorn GS, Dieckmann U, Taborsky B. The evolution of age-dependent plasticity. *Am Nat*. 2014:183(1):108–125. https://doi.org/10.1086/674008.

Fogg LG, Cortesi F, Gache C, Lecchini D, Marshall NJ, de Busserolles F. Developing and adult reef fish show rapid light-induced plasticity in their visual system. *Mol Ecol*. 2023:32(1):167–181. https://doi.org/10.1111/mec.16744.

Fuller RC, Carleton KL, Fadool JM, Spady TC, Travis J. Population variation in opsin expression in the bluefin killifish, Lucania goodei: a real-time PCR study. *J Comp Physiol A*. 2004:190(2):147–154. https://doi.org/10.1007/s00359-003-0478-z.

Fuller RC, Claricoates KM. Rapid light-induced shifts in opsin expression: finding new opsins, discerning mechanisms of change, and implications for visual sensitivity. *Mol Ecol*. 2011:20(16):3321–3335. https://doi.org/10.1111/j.1365-294X.2011.05180.x.

Gabriel W. Evolution of reversible plastic responses: inducible defenses and environmental tolerance. In: Tollrian R, Harvell CD, editors. *The ecology and evolution of inducible defenses*. Princeton, NJ: Princeton University Press; 1999. p. 286–305.

Gabriel W, Luttbeg B, Sih A, Tollrian R. Environmental tolerance, heterogeneity, and the evolution of reversible plastic responses. *Am Nat*. 2005:166(3):339–353. https://doi.org/10.1086/432558.

Gomulkiewicz R, Stinchcombe JR. Phenotypic plasticity made simple, but not too simple. *Am J Bot*. 2022:109(10):1519–1524. https://doi.org/10.1002/ajb2.16068.

Halstenberg S, Lindgren KM, Samagh SPS, Nadal-Vicens M, Balt S, Fernald RD. Diurnal rhythm of cone opsin expression in the teleost fish *Haplochromis burtoni*. *Vis Neurosci*. 2005:22(2):135–141. https://doi.org/10.1017/S0952523805222022.

Härer A, Karagic N, Meyer A, Torres-Dowdall J. Reverting ontogeny: rapid phenotypic plasticity of colour vision in cichlid fish. *R Soc Open Sci*. 2019:6(7):190841. https://doi.org/10.1098/rsos.190841.

Härer A, Meyer A, Torres-Dowdall J. Convergent phenotypic evolution of the visual system via different molecular routes: how Neotropical cichlid fishes adapt to novel light environments. *Evol Lett*. 2018:2(4):341–354. https://doi.org/10.1002/evl3.71.

Härer A, Torres-Dowdall J, Meyer A. Rapid adaptation to a novel light environment: the importance of ontogeny and phenotypic plasticity in shaping the visual system of Nicaraguan Midas cichlid fish (*Amphilophus citrinellus* spp.). *Mol Ecol*. 2017:26(20):5582–5593. https://doi.org/10.1111/mec.14289.

Hauser FE, Ilves KL, Schott RK, Alvi E, López-Fernández H, Chang BSW. Evolution, inactivation and loss of short wavelength-sensitive opsin genes during the diversification of Neotropical cichlids. *Mol Ecol*. 2021:30(7):1688–1703. https://doi.org/10.1111/mec.15838.

Hofmann CM, O'Quin KE, Marshall NJ, Cronin TW, Seehausen O, Carleton KL. The eyes have it: regulatory and structural changes both underlie cichlid visual pigment diversity. *PLoS Biol*. 2009:7(12):e1000266. https://doi.org/10.1371/journal.pbio.1000266.

Hofmann CM, O'Quin KE, Smith AR, Carleton KL. Plasticity of opsin gene expression in cichlids from Lake Malawi. *Mol Ecol*. 2010:19(10):2064–2074. https://doi.org/10.1111/j.1365-294X.2010.04621.x.

Hoverman JT, Relyea RA. How flexible is phenotypic plasticity? Developmental windows for trait induction and reversal. *Ecology*. 2007:88(3):693–705. https://doi.org/10.1890/05-1697.

Irazábal-González L, Wright DS, Maan ME. Developmental and environmental plasticity in opsin gene expression in Lake Victoria cichlid fish. *Evol Dev*. 2024:26(1):e12465. https://doi.org/10.1111/ede.12465.

Johnson AM, Stanis S, Fuller RC. Diurnal lighting patterns and habitat alter opsin expression and colour preferences in a killifish. *Proc R Soc Lond B Biol Sci*. 2013:280(1763):20130796. https://doi.org/10.1098/rspb.2013.0796.

Karagic N, Härer A, Meyer A, Torres-Dowdall J. Heterochronic opsin expression due to early light deprivation results in drastically shifted visual sensitivity in a cichlid fish: possible role of thyroid hormone signaling. *J Exp Zool B Mol Dev Evol*. 2018:330(4):202–214. https://doi.org/10.1002/jez.b.22806.

Karagic N, Härer A, Meyer A, Torres-Dowdall J. Thyroid hormone tinkering elicits integrated phenotypic changes potentially explaining rapid adaptation of color vision in cichlid fish. *Evolution*. 2022:76(4):837–845. https://doi.org/10.1111/evo.14455.

Kautt AF, Kratochwil CF, Nater A, Machado-Schiaffino G, Olave M, Henning F, Torres-Dowdall J, Harer A, Hulsey CD, Franchini P, *et al*. Contrasting signatures of genomic divergence during sympatric speciation. *Nature*. 2020:588(7836):106–111. https://doi.org/10.1038/s41586-020-2845-0.

Kautt AF, Machado-Schiaffino G, Meyer A. Lessons from a natural experiment: allopatric morphological divergence and sympatric diversification in the Midas cichlid species complex are largely influenced by ecology in a deterministic way. *Evol Lett*. 2018:2(4):323–340. https://doi.org/10.1002/evl3.64.

Kingsolver JG, Massie KR, Ragland GJ, Smith MH. Rapid population divergence in thermal reaction norms for an invading species: breaking the temperature–size rule. *J Evol Biol*. 2007:20(3):892–900. https://doi.org/10.1111/j.1420-9101.2007.01318.x.

Kutterolf S, Freundt A, Pérez W, Wehrmann H, Schmincke HU. Late Pleistocene to Holocene temporal succession and magnitudes of highly-explosive volcanic eruptions in west-central Nicaragua.

*J Volcanol Geotherm Res*. 2007:163(1-4):55–82. https://doi.org/10.1016/j.jvolgeores.2007.02.006.
Lande R. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *J Evol Biol*. 2009:22(7):1435–1446. https://doi.org/10.1111/j.1420-9101.2009.01754.x.
Lande R. Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. *J Evol Biol*. 2014:27(5):866–875. https://doi.org/10.1111/jeb.12360.
Levins R. *Evolution in changing environments: some theoretical explorations*. Princeton, NJ: Princeton University Press; 1968.
Levis NA, Pfennig DW. Plasticity-led evolution: evaluating the key prediction of frequency-dependent adaptation. *Proc R Soc Lond B Biol Sci*. 2019:286(1897):20182754. https://doi.org/10.1098/rspb.2018.2754.
Levis NA, Serrato-Capuchina A, Pfennig DW. Genetic accommodation in the wild: evolution of gene expression plasticity during character displacement. *J Evol Biol*. 2017:30(9):1712–1723. https://doi.org/10.1111/jeb.13133.
Loew ER. Determinants of visual pigment spectral location and photoreceptor cell spectral sensitivity. In: Djamgoz MBA, Archer SN, Vallerga S, editors. *Neurobiology and clinical aspects of the outer retina*. Dordrecht: Springer Netherlands; 1995. p. 57–77.
Luehrmann M, Stieb SM, Carleton KL, Pietzker A, Cheney KL, Marshall NJ. Short-term colour vision plasticity on the reef: changes in opsin expression under varying light conditions differ between ecologically distinct fish species. *J Exp Biol*. 2018:221(Pt 22): jeb175281. https://doi.org/10.1242/jeb.175281.
Lupše N, Kłodawska M, Truhlářová V, Košátko P, Kašpar V, Bitja Nyom AR, Musilova Z. Developmental changes of opsin gene expression in ray-finned fishes (Actinopterygii). *Proc R Soc Lond B Biol Sci*. 2022:289:20221855. https://doi.org/10.1098/rspb.2022.1855.
Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskel MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H, *et al*. Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity (Edinb)*. 2015:115(4):293–301. https://doi.org/10.1038/hdy.2015.8.
Nandamuri SP, Yourick MR, Carleton KL. Adult plasticity in African cichlids: rapid changes in opsin expression in response to environmental light differences. *Mol Ecol*. 2017:26(21):6036–6052. https://doi.org/10.1111/mec.14357.
Novales Flamarique I. Diminished foraging performance of a mutant zebrafish with reduced population of ultraviolet cones. *Proc Biol Sci*. 2016:283(1826):20160058. https://doi.org/10.1098/rspb.2016.0058.
Padilla DK, Adolph SC. Plastic inducible morphologies are not always adaptive: the importance of time delays in a stochastic environment. *Evol Ecol*. 1996:10(1):105–117. https://doi.org/10.1007/BF01239351.
R Core Team. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing; 2020.
Relyea RA, Stephens PR, Hammond JI. Phylogenetic patterns of trait and trait plasticity evolution: insights from tadpoles. *Evolution*. 2021:75(10):2568–2588. https://doi.org/10.1111/evo.14338.
Sabbah S, Laria RL, Gray SM, Hawryshyn CW. Functional diversity in the color vision of cichlid fishes. *BMC Biol*. 2010:8(1):133. https://doi.org/10.1186/1741-7007-8-133.
Schlichting C, Pigliucci M. *Phenotypic evolution: a reaction norm perspective*. Sunderland, MA: Sinauer; 1998.
Schmitter-Soto JJ. A systematic revision of the genus Archocentrus (Perciformes: Cichlidae), with the description of two new genera and six new species. *Zootaxa*. 2007:1603(1):1-78–71-78. https://doi.org/10.11646/zootaxa.1603.1.1.
Schreiner M, Yourick M, Juntti S, Carleton K. Environmental plasticity in opsin expression due to light and thyroid hormone in adult and developing *Astatotilapia burtoni*. *Hydrobiologia*. 2023:850: 2315–2329. https://doi.org/10.1007/s10750-022-04957-y.
Scoville AG, Pfrender ME. Phenotypic plasticity facilitates recurrent rapid adaptation to introduced predators. *Proc Natl Acad Sci U S A*. 2010:107(9):4260–4263. https://doi.org/10.1073/pnas.0912748107.
Seehausen O, Alphen J, Witte F. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*. 1997:277(5333): 1808–1811. https://doi.org/10.1126/science.277.5333.1808.
Shapiro AM. Seasonal polyphenism. In: Hecht MK, Steere WC, Wallace B, editors. *Evolutionary biology*, Vol. 9. Boston, MA: Springer US; 1976. p. 259–333.
Siljestam M, Östman Ö. The combined effects of temporal autocorrelation and the costs of plasticity on the evolution of plasticity. *J Evol Biol*. 2017:30(7):1361–1371. https://doi.org/10.1111/jeb.13114.
Stearns SC. The evolutionary significance of phenotypic plasticity. *Bioscience*. 1989:39(7):436–445. https://doi.org/10.2307/1311135.
Torres-Dowdall J, Handelsman CA, Reznick DN, Ghalambor CK. Local adaptation and the evolution of phenotypic plasticity in Trinidadian guppies (*Poecilia reticulata*). *Evolution*. 2012:66(11): 3432–3443. https://doi.org/10.1111/j.1558-5646.2012.01694.x.
Torres-Dowdall J, Karagic N, Härer A, Meyer A. Diversity in visual sensitivity across neotropical cichlid fishes via differential expression and intraretinal variation of opsin genes. *Mol Ecol*. 2021:30(8): 1880–1891. https://doi.org/10.1111/mec.15855.
Torres-Dowdall J, Karagic N, Prabhukumar F, Meyer A. Differential regulation of opsin gene expression in response to internal and external stimuli. *Genome Biol Evol*. 2024:16(7):evae125. https://doi.org/10.1093/gbe/evae125.
Torres-Dowdall J, Machado-Schiaffino G, Kautt AF, Kusche H, Meyer A. Differential predation on the two colour morphs of Nicaraguan crater lake Midas cichlid fish: implications for the maintenance of its gold-dark polymorphism. *Biol J Linn Soc Lond*. 2014:112(1): 123–131. https://doi.org/10.1111/bij.12271.
Torres-Dowdall J, Meyer A. Sympatric and allopatric diversification in the adaptive radiations of Midas cichlids in Nicaraguan lakes. In: Abate ME, Noakes DLG, editors. *The behavior, ecology and evolution of cichlid fishes*. Dordrecht: Springer Netherlands; 2021. p. 175–216.
Torres-Dowdall J, Pierotti MER, Harer A, Karagic N, Woltering JM, Henning F, Elmer KR, Meyer A. Rapid and parallel adaptive evolution of the visual system of Neotropical Midas cichlid fishes. *Mol Biol Evol*. 2017:34(10):2469–2485. https://doi.org/10.1093/molbev/msx143.
West-Eberhard M. *Developmental plasticity and evolution*. Oxford: Oxford University Press; 2003.
Woltereck R. Weitere experimentelle Untersuchungen uber Artveranderung, speziell uber das Wesen quantitativer Artunterschiede bei Daphniden. *Verh Dtsch Zool Ges*. 1909:19:110–173.
Yoshimatsu T, Schröder C, Nevala NE, Berens P, Baden T. Fovea-like photoreceptor specializations underlie single UV cone driven prey-capture behavior in zebrafish. *Neuron*. 2020:107(2):320–337.e326. https://doi.org/10.1016/j.neuron.2020.04.021.
Yourick MR, Sandkam BA, Gammerdinger WJ, Escobar-Camacho D, Nandamuri SP, Clark FE, Joyce B, Conte MA, Kocher TD, Carleton KL. Diurnal variation in opsin expression and common housekeeping genes necessitates comprehensive normalization methods for quantitative real-time PCR analyses. *Mol Ecol Resour*. 2019:19(6): 1447–1460. https://doi.org/10.1111/1755-0998.13062.
Zanghi C, Ioannou CC. The impact of increasing turbidity on the predator–prey interactions of freshwater fishes. *Freshw Biol*. 2025:70(1): e14354. https://doi.org/10.1111/fwb.14354.