Behavioral Ecology, 2025, **36**(6), araf120
https://doi.org/10.1093/beheco/araf120

Original Article

Background color matching affects sexual behavior, growth, and mortality rate in an African cichlid

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Handling Editor: Dr. Pierre-Olivier Montiglio

Phenotypic plasticity allows organisms to adapt to changing environments within their lifetimes. However, environmentally induced changes in the plastic trait of interest may influence a range of fitness-related traits due to trade-offs, pleiotropy, linkage, or epistasis of genes regulating the plastic trait. These correlated responses may constrain or facilitate the evolution of plasticity, but their evolutionary implications are often poorly understood due to a lack of data on their direction and magnitude. Males in the African cichlid *Astatotilapia burtoni* are blue or yellow, and males are able to adjust their body coloration to the color of the background, presumably to increase crypsis. To test whether background color influences fitness-related traits, we raised mix-sex groups of juvenile *A. burtoni* to adulthood in yellow or blue tanks. We found that more males adopted the blue phenotype in blue tanks while more males adopted the yellow phenotype in the yellow tank, though the degree of background color matching decreased with age. Males, but not females, from blue tanks showed earlier sexual maturation than those held in yellow tanks. However, across the duration of the experiment, there was a higher occurrence of breeding in females housed in yellow tanks than those that were housed in blue tanks. In addition, fish in blue tanks exhibited reduced growth rate but higher survivorship relative to their yellow-reared counterparts. Our data suggest that background color affects important fitness-related traits in a color polymorphic cichlid, which may influence the evolution of phenotypic plasticity.

Keywords: background color adaptation; camouflage; cichlid; evolution.

Introduction

Many organisms can generate adaptive phenotypes in response to changes in environmental conditions in an individual's lifetime (Agrawal 2001; Charmantier et al. 2008). This ability, called phenotypic plasticity, requires an organism to obtain reliable information from the environment and translate this information into adaptive changes (Pigliucci et al. 2006; Murren et al. 2015; Alvarado 2020). Environmentally induced changes in the plastic trait of interest (eg body color to increase crypsis on specific backgrounds) could also influence other fitness-related traits due trade-offs, pleiotropy, linkage, or epistasis of genes regulating the plastic trait (Zhang et al. 2010; Dijkstra et al. 2017; Polo-Cavia and Gomez-Mestre 2017; Tiarks et al. 2024). Such correlated responses are usually considered a constraint to phenotypic plasticity if they are maladaptive (Snell-Rood et al. 2010). Correlated responses to specific environments may also be adaptive, in which case they could facilitate the evolution of plasticity (Montiglio et al. 2017). Identifying environment-specific effects of plasticity on fitness-related traits, such as growth and reproductive behavior, is an important first step in clarifying the selective forces that constrain or facilitate the evolution of phenotypic plasticity in heterogeneous environments (Van Kleunen and Fischer 2005; Murren et al. 2015).

One of the most dramatic examples of phenotypic plasticity is background color matching, which has been documented in a broad range of taxa, including insects (Edelaar et al. 2017), amphibians (Kindermann et al. 2014), reptiles (Corl et al. 2018), and fishes (Whiteley et al. 2009). Background color matching can occur via changes in the structure and organization of pigmentary cells in the skin to resemble the visual environment and increase crypsis (Sugimoto 2002; Umbers et al. 2014; Ligon and McCartney 2016). Cryptic color change is common in many prey species and has been studied extensively (Chiao et al. 2011; Smith et al. 2016; Liedtke et al. 2023). Color change in animals is regulated by a wide range of neuroendocrine systems that often also influence other fitness-related traits. In fish, exposure to a dark background promotes the release of α-melanocyte-stimulating hormone (α-MSH), a melanocortin hormone that increases black body coloration by inducing pigment dispersion and promoting proliferation of melanophores (van Eys and Peters 1981; Zhang et al. 2010). However, α-MSH can also activate melanocortin receptors in the brain and other tissues, thereby affecting a range of physiological and behavioral functions, including metabolism, the stress response, growth rate, and social behavior (Schiöth et al. 2005; Ducrest et al. 2008). Other candidate systems for changes in body coloration include melanopsins in pigment-containing cells in the integument

Received 6 May 2025; revised 9 September 2025; accepted 17 September 2025.

(Provencio et al. 1998). These opsins have been implicated as light-sensitive photopigments outside of the retina that can induce color changes in many fishes and frogs but can also cause behavioral effects, such as increased alertness and heightened photosensitivity (Bellingham et al. 2002; Bertolesi and McFarlane 2018). In addition to shared developmental pathways, links between pigmentation and somatic development can occur due to resource allocation trade-offs. For example, *Microhyla fissipes* tadpoles adapted to dark backgrounds exhibited increased pigmentation but also reduced growth, perhaps due to the metabolic cost of pigmentation (Chang et al. 2021). Studies aimed at establishing optimal growth conditions in fish reported that tank color affects a range of traits such as metabolism, behavior, and stress response, which is consistent with the notion that pigmentary adaptation to background color can have correlated effects on other traits [reviewed in (McLean 2021)]. However, few studies have examined the effect of background color or background color matching on fitness-related traits in the context of phenotypic plasticity (Chang et al. 2021; Liedtke et al. 2023; Radovanović et al. 2023).

In the East African cichlid fish *Astatotilapia burtoni*, adult males switch between blue and yellow coloration both in the field [Lake Tanganyika, (Fernald and Hirata 1979)] and the lab (Korzan et al. 2008; Dijkstra et al. 2017). Previous work on *A. burtoni* suggests that the reversible coloration allows males to adapt to variable visual environments to reduce the risk of predation, with blue males (who appear darker) better adapted to murky algae-rich environments and yellow males (who appear paler) better adapted to brighter coastal environments (Fernald and Hirata 1977; Fang et al. 2022). Data from the field suggests that ambient light conditions may vary seasonally in Lake Tanganyika, for example, due to upwellings and subsequent algal blooms in certain parts of the lake (Plisnier et al. 2023). Although more work is needed to demonstrate background color adaptation in *A. burtoni* in the field, such environmental heterogeneity could favor plasticity in body coloration to maximize cryptic coloration depending on the prevailing environmental conditions. Experimental work in the laboratory showed that *A. burtoni* males can reversibly change color according to the background color, with males becoming blue in a blue environment and yellow in a yellow environment (Fang et al. 2022). Although color change by exposing individuals to new spectral environments occurs in this species, the potential associated effects of background color adaptation on fitness-related traits are unknown. In the current study, we assessed how specific background colors affect fitness-related traits in *A. burtoni*. We were specifically interested in how background color influences growth, survival, and sexual behaviors during late development as fish are undergoing sexual maturation. To this end, we raised groups of juveniles into adulthood in yellow or blue tanks and quantified color adaptation, growth rate, social behavior, markers of sexual maturation (display of nuptial coloration; mouthbrooding), and survivorship. Examining environment-specific fitness effects during development is an important step in identifying the cost and benefits of background color adaptation, which is critical to clarifying the evolution of plastic phenotypes.

Materials and methods

Animals

The cichlid fish *A. burtoni* used in this study were bred from a laboratory population originally derived from Lake Tanganyika (Fernald and Hirata 1977). In the laboratory, the frequency of yellow relative to blue males fluctuates over time and ranges from 20 to 80% in this laboratory stock (Korzan et al. 2008; Dijkstra et al. 2017, 2024; Border et al. 2019). Fish were housed in aquaria at 28 °C with a 12-h light/dark cycle and 10 min dusk and dawn periods to mimic natural settings (light was full spectrum). Before the experiments, fish were reared in clear 110-liter tanks containing gravel substrate. Rearing tanks were separate from other tanks using brown paper. Continuous water flow and central mechanical and biological filtration occurred throughout the entirety of the experiment. Fish were fed fine granular pellets (Kyorin Food IND. LTD.) and cichlid flakes (Omega Sea LLC). All procedures were approved by Central Michigan University Institutional Animal Care and Use Committee (IACUC approval number 18-10 and 2021-460). A total of 360 fish were used in this study (initial length 13.18 mm ± 2.76 mm).

Experimental design and experimental housing conditions

To assess how background color influences fitness-related traits, we housed cichlid fish in yellow and blue aquaria (a visual of our experimental design is shown in Fig. 1). To this end, experimental juveniles were collected from mix-sex rearing tanks (110 liters, 76 cm L × 51 cm W × 30 cm H), each containing 40 to 60 juveniles (~ age range 2 to 3 months) from 2 to 4 broods. Juveniles from each rearing tank ($n = 7$ tanks) were randomly split into two groups and assigned to either a tank with blue or yellow background, and hence each experimental group consisted of individuals from the same rearing tank (again, each rearing tank contained juveniles from 2 to 4 broods). This resulted in a total of 7 blue tanks and 7 yellow tanks. Each experimental tank contained 20 to 28 fish.

Blue and yellow tanks were identical in dimensions and volume as rearing tanks and were created by fitting blue or yellow acrylic plates to the bottom, sides, and back of the tank (U.S. Plastic Corporation, #2050 Blue, #2037 Yellow, 3.175 mm thick). Initially, three terracotta flowerpot shards were placed in each experimental tank to provide shelter at the onset of the experiment but were removed after 14 days to reduce early territoriality and aggression in juvenile groups. Yellow or blue colored gravel (Estes' colored gravel) was placed along the bottoms of corresponding tanks to provide an enriching environment for juveniles. Fish were fed crushed cichlid flakes adjusted to the size and number of fish. Specifically, we ensured that food was eaten within five minutes, and we provided experimental groups that originated from the same rearing tank with the same amount of food. Juvenile groups were housed in these conditions for 140 days, during which we measured growth, survival, social behavior, the onset of sexual maturation, and body coloration as described below. Attempts were made to ensure that observations were made blind with respect to color treatment. However, because the color of the tank could be seen by the observer for most analyses, this was usually not possible except for the growth measurements, digital analysis of color phenotype, and melanophore quantification.

Maturation, breeding frequency, and social behavior

We conducted weekly observations to evaluate how color treatment influences color development, sexual maturation and the emergence and expression of reproductive behavior. These observations began approximately one month after the experiment was set up (and when fish were ~ 3 to 4 months of age). During these observations, we quantified the number of males exhibiting nuptial coloration as an indicator of sexual maturation in males. We assigned color phenotype for these males as either blue or yellow.

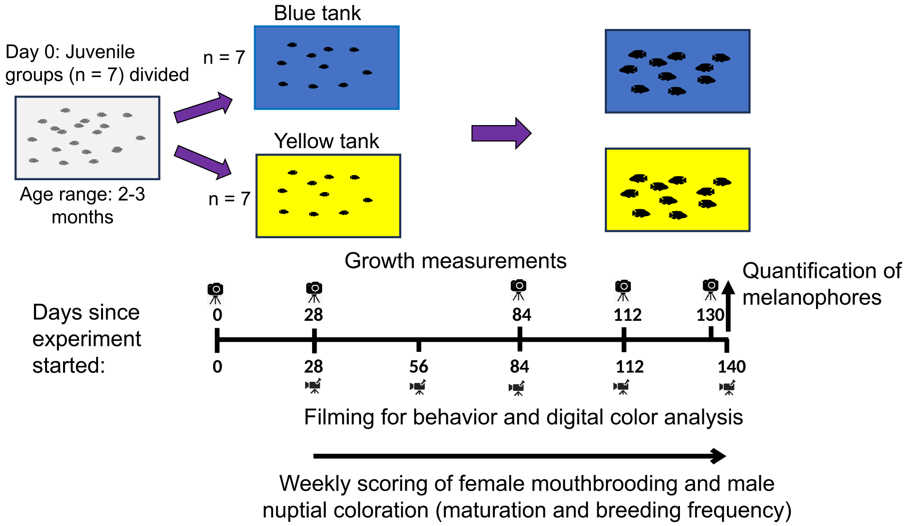

Fig. 1. General experiment design. Juvenile *A. burtoni* were raised in mixed-sex groups of 20 to 28 individuals for 140 days in yellow or blue tanks. Groups were established when juveniles were 2 to 3 months of age. In addition to photographing for growth measurements and filming for behavior and digital color analysis, we also recorded the color phenotype of mature males, the number of mouthbrooding females, and the mortality rate in each group.

We also recorded when breeding began in each group by recording the number of mouthbrooding females.

To quantify social behavior, we filmed each tank every 28 days for a total of six filming sessions with a Canon EOS 70D. For each recording, the entire tank was filmed for 5-min following a 2-min acclimation period once equipment was set up. All recordings from the group stage were uploaded to BORIS to quantify behaviors (Friard and Gamba 2016). From behavioral recordings we quantified aggressive behaviors (chases, lateral displays, and border disputes) and courtship behaviors. Aggressive and courtship behaviors were previously described (Fialkowski et al. 2021). In brief, chases consist of aggressively (rapidly) swimming after other fish, biting, and forcibly moving other fish. Lateral displays occur when an individual presents the side of his body to another fish with erect fins. Border disputes were interactions between two fish (typically males) where both fish charge head-on toward each other with extended pectoral fins and an open mouth. During border disputes, males move back and forth and do not make physical contact. We scored the total number of occurrences for each behavior in each group because it was difficult to reliably track individual fish in this group setting.

Survivorship

To estimate survivorship for each group, we recorded the number of fish in each experimental tank on a weekly basis. If a yellow-blue tank pair had a differing number of individuals, random individuals would be removed and euthanized from the tank with the higher density to match the density of the tank that experienced any mortality in that week. We performed these corrections to standardize fish density between yellow and blue tanks with fish from the same rearing tank. This standardization is important since fish density influences aggression rates and growth.

Growth

The size of all fish was measured for each group at days 0, 28, 84, 112, and 130 of the experiment. To reduce the possibility of damage or stress associated with measuring body size, we transferred each group into a small, clear plastic container to obtain photographs for digital measurements of body length. The container was placed on a Kaiser RS-1 copy stand measuring 45 cm × 50 cm with a printed grid of 1cm^2 squares within the total area. We took photographs of each group using a Pentax K-3 II SLR digital camera attached to a mounting point on the stand fixed 55 cm above the fish. Photos were then uploaded to ImageJ to measure the body length based on the dorsal view of each fish following a previously described procedure (Rizzo et al. 2017).

Color quantification

To quantify the effect of color treatment on color development, we conducted digital image analysis of 5 fish per tank for each of the six days of filming (n = 5 fish from each experimental group on each of the six filming sessions, corresponding to a total of 210 images of individual fish for each color treatment). Since stress can induce color change (Nilsson Sköld et al. 2013) we did not remove fish from the tanks but instead fish were pulled for digital image analysis from video recordings. To do so, at the end of each filming session (every 28 days), we took close-up footage of individual fish within each group for approximately 1 minute for digital color quantification. We used automatic settings with the autofocus off to prevent the camera from changing focus throughout the video. The fish were filmed at ~1.0 m away from the aquarium to obtain high-resolution pictures with a Kodak Color Separation Guide and Gray Scale (Cat 1527654) in view. In Adobe Photoshop v21.2, we standardized color based on the Kodak Color Separation Guide and Gray Scale using curves layering technique. This method standardizes collected images and eliminate differences in the lighting between collected images (Bleier et al. 2011). We attempted to randomly select fish for image analysis but typically used only fish that were closest to the front of the aquarium, where the lateral of the fish could be clearly seen. In Photoshop, images were converted to CIE $L^*a^*b^*$ after color card correction as described previously for our species (Dijkstra et al. 2017). An added advantage of CIE $L^*a^*b^*$ is that it has a single value (b^*) that constitutes the balance between blue and yellow, which is of interest to our study species (L^* indicates the level of lightness and a^* the balance between green and red). Photoshop was used to remove the image background, eyes, and fins. The removed areas were replaced with a uniform, pre-established chroma key of “true green” (CIE L^*a^*b of 88, −78, 80). The resulting edited images were then placed through a JavaScript program that collects the L, a, and b values per individual pixel.

To confirm that background color treatment influences body coloration by altering melanophore density, we took pictures of three to four randomly selected males and females from each group using a stereomicroscope (Leica DM2000LED) at the end of the 140-day experiment. Pictures were taken of the caudal fin and the head region. Pictures were analyzed in ImageJ (Schneider et al. 2012) to quantify the melanophore density in the caudal fin, forehead, and mouth regions (upper and lower lips) as described elsewhere (Border et al. 2018).

Data analysis

All analyses were conducted in R v 4.5.1 (RCore 2025) using the R packages lme4, lmerTest, MASS (Bates et al. 2015), and glmmTMB (Brooks et al. 2017). We ran linear mixed models (LMMs) or generalized linear mixed models for count data (GLMMs) with color treatment (blue or yellow tanks) and time (days since the experiment started) as fixed or continuous variables and “tank of origin identity” (ie tank in which fish were reared before the experiment started) and “tank identity” (ie experimental tank) as random variables.

To analyze digital color values, we used LMMs to compare $L^*a^*b^*$ values of images of fish from yellow and blue tanks for each observation. For analyzing the presence or absence of brooding females in experimental groups, we fitted a zero-inflation model (GLMM hurdle models) with color treatment and time as fixed effects to examine whether brooding females appeared sooner in yellow or blue tanks (a similar model was not fitted for testing the presence or absence of sexually mature males since they were already there when observations began). In addition, we analyzed whether the number of brooding females differed between yellow and blue tanks over time using a GLMM with a negative binomial distribution. We compared the number of sexually mature males between yellow and blue tanks over time using a GLMM with a Poisson distribution.

Group-level body size was compared between treatments with LMMs. In these models, we used body size measurements of individual fish and included “tank identity” as a random effect (we did not track the individual identity of each fish during the experiment). Specific growth rate was analyzed based on group-level body size differences between each growth interval. We analyzed survival using a GLMM with a negative binomial distribution and an offset argument to account for the number of fish in each group at each time point. We used color treatment and time as fixed effects to examine whether the risk of mortality varied between blue and yellow environments. In addition, we calculated the percentage of fish that survived from the beginning to the end of the experiment for each tank based on total mortality relative to the number of fish at the beginning of the experiment. We then used a Wilcoxon signed-rank (WSR) test to compare survival between yellow and blue tanks (paired based on rearing group). Social behavior was compared between yellow and blue tanks using GLMMs with a negative binomial distribution for chases, aggressive displays, and courtship displays in separate models. A significance level (α) of 0.05 was used for all tests. We report mean ± SE for our model estimates.

Results

Effect of tank color on body coloration

As expected, fish reared in yellow tanks were paler and more yellow than those reared in blue tanks throughout the experiment (males and females combined) (Fig. 2a). Specifically, lightness (L^*) was significantly higher in yellow-reared fish than in blue-reared fish (LMM, color treatment: -22.10 ± 6.16, $t_{14} = 3.589$, $P = 0.003$). Fish in yellow tanks had lower red-green a^* values (LMM: -9.00 ± 2.75, $t_{14} = -3.267$, $P = 0.00561$) but higher blue-yellow b^* values (LMM: 30.44 ± 7.30, $t_{14} = 4.173$, $P = 0.00094$) than fish reared in blue tanks. At the end of the experiment, we found that fish in blue tanks had a significantly higher melanophore density compared to those held in yellow tanks (Fig. 2b, LMM, color treatment, males: -1.001 ± 0.179, $t_{69} = -5.639$, $P < 0.001$; females: -1.057 ± 0.176, $t_{64} = -5.992$, $P < 0.001$). The results of melanophore density across body regions are shown in the supplementary materials.

We started assigning blue or yellow phenotype to males in each tank one month after the experiment was set up (only sexually mature males express blue or yellow coloration). The color phenotype of males, in general, matched the background of their tank (Fig. 2c): The proportion of yellow males was significantly higher in groups held in yellow tanks than those held in blue tanks (GLMM, color treatment: 3.50 ± 0.27, $z = 12.90$, $P < 0.001$). However, in a separate model we fitted the interaction between color treatment and time, and this effect was also significant (GLMM: -0.012 ± 0.005, $z = -2.23$, $P = 0.026$), suggesting that the degree of background color matching weakened with more mismatches (eg blue males in yellow tanks) occurring later in the experiment.

Sexual maturation and behavior

During the first observation (approximately one month after setting up the experiment when fish were ~ 3 to 4 months of age), three out of seven blue groups and one out of seven yellow groups had one sexually mature male, as indicated by the expression of nuptial coloration, presence of egg spots on the anal fin, and increased aggressive behavior. By the end of the experiment, each group had 2 to 4 males expressing nuptial coloration. We found that the first sexually mature male(s) emerged approximately 2 weeks earlier in groups reared in blue tanks compared to those reared in yellow tanks (Fig. 3a, LMM, 15.14 ± 5.10, $t_7 = 2.969$, $P = 0.021$). Across the entire experiment, the number of sexually mature males did not differ between yellow and blue tanks after correcting for a significant positive effect of day (Fig. 3b, GLMM, effect of color treatment: -0.104 ± 0.123, $z = -0.844$, $P = 0.4$, effect of day: 0.015 ± 0.002, $z = 9.648$, $P < 0.001$).

Mouthbrooding occurred in all groups and started on average 102 days after setting up the experiment (~5 to 6 months of age). The onset of mouthbrooding did not vary significantly between yellow and blue-reared groups (Fig. 3c, LMM, effect of color treatment: -4.08 ± 12.59 $t_7 = -0.324$, $P = 0.76$). However, across the entire experiment, there was a nonsignificant tendency for a higher rate of brooding in females in groups held in yellow tanks compared to those in blue tanks after controlling for the overall increase in breeding over time (Fig. 3d, GLMM, effect of color treatment: 0.737 ± 0.403, $z = 1.830$, $P = 0.067$, effect of day: 0.022 ± 0.007, $z = 3.399$, $P = 0.0007$). To test if the likelihood of groups containing one or more brooding females was different between color treatments, we fitted a zero-inflation model with a negative binomial distribution. Using this model, we found that the probability of brooding occurring was significantly higher in groups reared in yellow tanks than those reared in blue tanks (GLMM zero inflation model, color treatment: -0.84 ± 0.43, $z = -1.97$, $P = 0.049$).

Tank color did not significantly influence the frequency of chase behaviors (GLMM, color treatment: 0.22 ± 0.36, $z = 0.62$, $P = 0.54$), aggressive display behaviors (GLMM: -0.532 ± 0.826, $z = -0.643$,

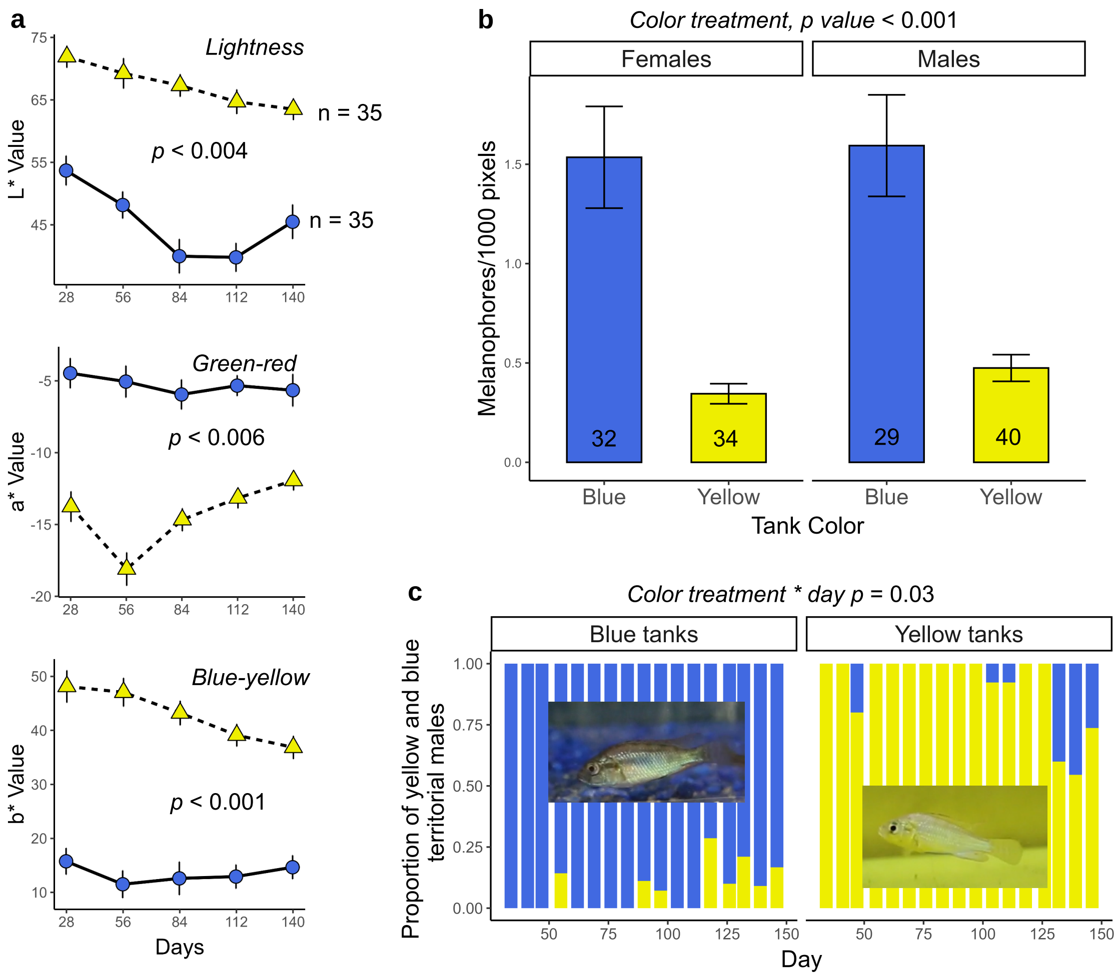

Fig. 2. Background color matching. a) Digital color quantification of fish (males and females combined) reared in blue (circles) and yellow (triangles) tanks. Digital color quantification was performed by capturing images from videos of fish (n = 35 per color treatment and day of observation) in their tanks and extracting $L^*a^*b^*$ color values. Shown are mean ± se. b) Melanophore density in males and females held in blue or yellow tanks measured at the end of the experiment. Samples sizes are also shown. Shown are mean ± se. c) The proportion of males with yellow and blue nuptial coloration during the experiment. The data is based on color phenotype scoring of a minimum of 24 males in blue tanks and 19 males in yellow tanks (7 tanks in each color treatment). Also shown are representative pictures of males housed in blue and yellow tanks.

$P = 0.52$), or courtship behaviors (GLMM: 0.255 ± 0.449, $z = 0.568$, $P = 0.57$) (Fig. 4) after controlling for the effect of time (P values < 0.05). The changes in behavior over time were not influenced by color treatment (color treatment * time, P values > 0.1, see supplementary materials for details).

Growth and survivorship

We found that fish reared in yellow tanks were approximately 4% larger than fish in blue tanks on the final day when growth was measured (Fig. 5a, day 130, LMM: 1.20 ± 0.37, $t_{297} = 3.265$, $P = 0.00123$). There was no significant size difference between color treatments at the beginning of the experiment (day 0, LMM: −0.36 ± 0.27, $t_{352} = -1.372$, $P = 0.171$). When examining specific growth rate in four consecutive intervals during the five-month experiment (calculated based on group averages, Fig. 5b), we detected significantly higher specific growth rates of yellow-reared fish compared to blue-reared fish during the second interval (days 28 through 84 of the experiment, LMM: 0.078 ± 0.023, $t_7 = 3.424$, $P = 0.011$). Specific growth rates did not vary by treatment in the other time intervals (P values > 0.3, see supplementary materials for details).

Survival probability was not significantly influenced by tank color treatment (GLMM: 0.064 ± 0.425, $z = 0.150$, $P = 0.88$) after controlling for a small but significant decline in survival probability over time (GLMM: −0.014 ± 0.005, $z = -2.809$, $P = 0.005$). However, when considering the cumulative mortality across the experiment, there was significantly more mortality or less survivorship (percentage of fish that died relative to the number of fish at the beginning of the experiment) in the yellow tank setting than the blue tank setting (WSR test, $V = 27$, $P = 0.03$) (Fig. 5c). Groups housed in blue tanks had a mean survivorship of 93.97 ± 1.87% whereas groups in yellow tanks showed a mean survivorship of 84.47 ± 3.17%. Since mortality has been linked to aggression levels in cichlid fish, we also tested whether the overall rate of aggression was linked to the mortality rate. Consistent with this idea, there was a significant positive effect of the rate of chases on cumulative mortality after correcting for the effect of color treatment (data not shown: LMM, effect of chases/attacks: 0.015 ± 0.006, $t_9 = 2.492$, $P = 0.034$).

Discussion

The occurrence of background color adaptation has been widely documented, but studies on the effect of specific background

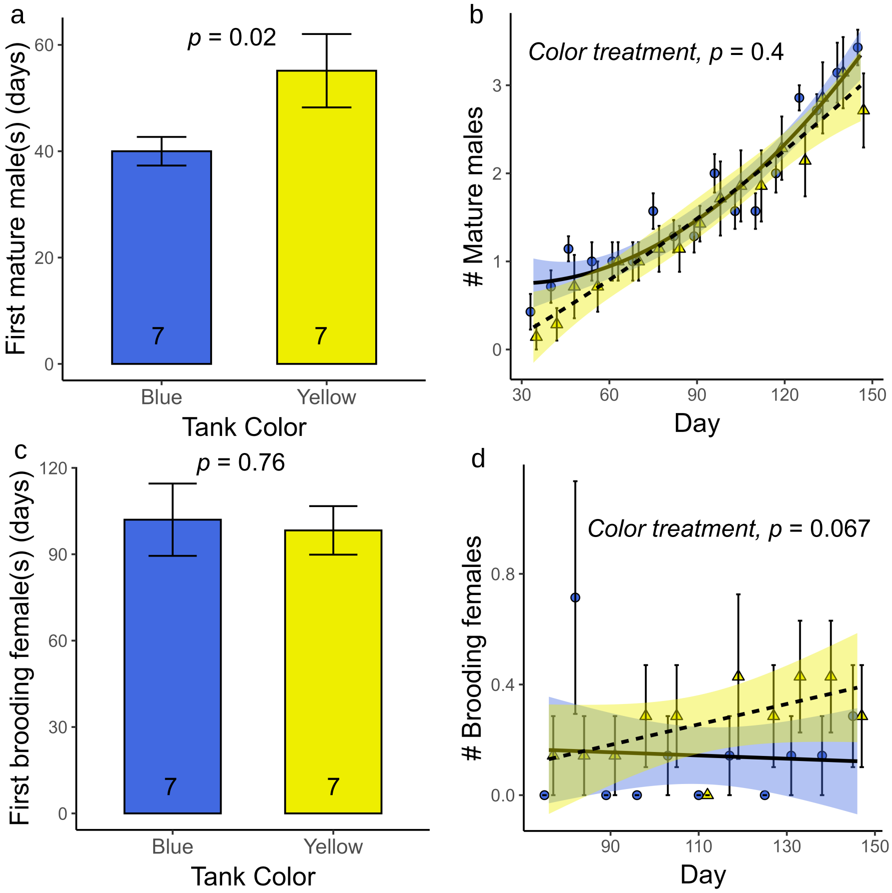

Fig. 3. a) Sexual maturation as indicated by the onset of males expressing nuptial coloration since the time the experiment was started in blue and yellow tanks (shown are the sample sizes of experimental tanks). b) Number of males with nuptial coloration per group for each color treatment per observation (numbers range from 3 to 24 and 1 to 22 mature males total per observation for blue and yellow tanks, respectively). c) The onset of mouthbrooding in blue (circles) and yellow (triangles) tanks. d) Number of brooding females in blue (circles) and yellow (triangles) tanks per observation (numbers range from 0 to 5 and 0 to 3 brooding females total per observation for blue and yellow tanks, respectively). Shown are mean ± se.

colors on fitness-related traits are relatively scarce. In this study, we investigated whether background color during (late) development influences fitness-related traits in the color polymorphic cichlid *A. burtoni* where males are either yellow or blue. As expected, we found that the background color of the tank had a robust influence on body coloration with fish held in blue tanks becoming more blue and fish held in yellow tanks becoming more yellow. Fish held in blue tanks exhibited earlier sexual maturation than fish in yellow tanks relative to the emergence of males displaying nuptial (breeding) coloration. Females reared in yellow tanks were breeding more than their counterparts in blue tanks. Finally, we found reduced growth but a tendency for increased survival in groups housed in blue tanks compared to those housed in yellow tanks.

Throughout the experiment, which started when fish were still not mature, we found that background color affected coloration with fish becoming darker and bluer in blue tanks and fish becoming paler and more yellowish in yellow tanks. It is interesting to note that these color effects in the digital image analysis and melanophore density at the end of the experiment were found in females, too, even though only male express conspicuous yellow or blue nuptial coloration. The “bluer” color scores in the digital image analysis (reflected by the “b” axis in the L^*a^*b color values) likely indicate darker coloration of fish housed in blue tanks. In sexually mature males we found similar results with most males matching their body coloration to the visual environment: more males adopted the yellow color phenotype in yellow tanks, and more males adopted the blue phenotype in blue tanks. Our results support previous studies showing that male *A. burtoni* adapt their coloration to match their environment (Fang et al. 2022). More generally, our findings are consistent with the notion that cichlids, as many other fish species, adjust body pigmentation to the background color, presumably to increase crypsis across heterogeneous environments (Sowersby et al. 2015; Takahashi 2019). However, our study shows that the degree of color matching was not perfect in *A. burtoni* males (eg, blue males did develop in yellow tanks) and the degree of background color matching declined significantly over time. The more reliable background color matching during the first part of the experiment is consistent with the degree of phenotypic plasticity being higher in early life in many animal species either due to developmental constraints or selection favoring increased environmental sensitivity during the early stage of life (Fischer et al. 2014). Examining age-dependent color plasticity in our study species requires more detailed studies, including altering color treatment at different stages of life (Wright et al. 2018).

We observed that sexually mature males emerged sooner in groups housed in blue tanks than those housed in yellow tanks. These males are characterized by yellow or blue nuptial coloration and often engage in active territorial defense. The

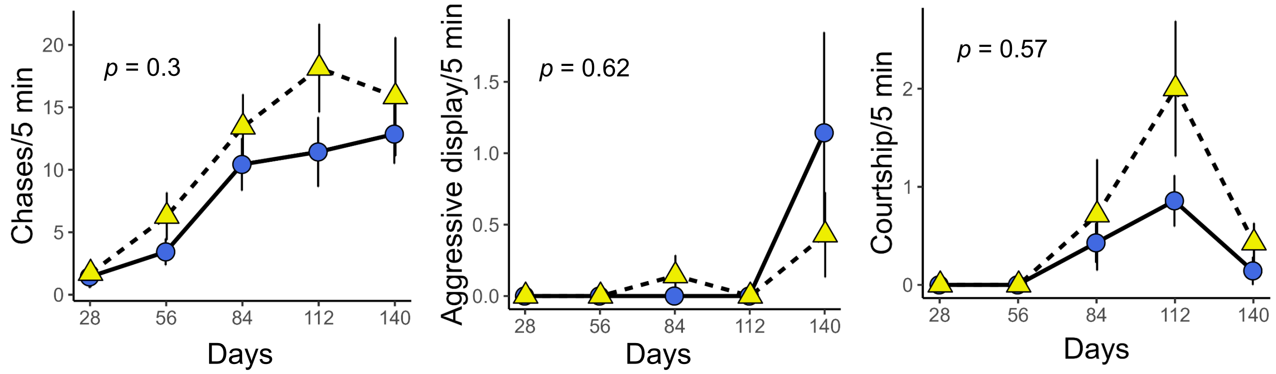

Fig. 4. Frequencies of chases (top), aggressive display (middle), and courtship (bottom) behaviors over time for groups housed in blue (circles) and yellow (triangles) tanks ($n = 7$ each). Shown are mean ± se.

expression of nuptial coloration is linked with upregulation of the hypothalamic-pituitary-gonadal axis in haplochromine cichlids (Fraley and Fernald 1982; Dijkstra et al. 2007), suggesting that blue tank color induced more rapid sexual maturation in males compared to those that were housed in yellow tanks. We also note that blue tanks induced increased pigmentation compared to yellow tanks, which is relevant to the expression of nuptial coloration given that it requires hyperpigmentation in several body regions (Dijkstra et al. 2007; Border et al. 2018). Our findings are consistent with other studies suggesting that tank colors can influence sexual maturation of fishes (Volpato et al. 2004; Amiya et al. 2008). The onset of mouthbrooding, which is an indicator of sexual maturation in females, did not vary by tank color treatment. However, we found evidence for a higher level of brooding activity in groups housed in yellow tanks than those housed in blue tanks, as indicated by a marginally nonsignificant higher number of breeding females in yellow tanks and a significantly higher probability of breeding occurring in yellow tanks throughout the entire duration of the experiment. Since egg development is metabolically costly (Sawecki et al. 2019), we hypothesize that the higher growth rate in yellow tanks drives or permits faster egg maturation, allowing females in yellow environments to reproduce more relative to those reared in blue tanks.

Fish in yellow tanks grew faster than fish in blue tanks during all examined intervals, although it was only significant during days 28 through 84 of the experiment. These growth rate differences may have important evolutionary consequences since larger body size confers an advantage in agonistic interactions (Dijkstra et al. 2005; Alward et al. 2021; Solomon-Lane et al. 2022) and mate choice (Thünken et al. 2012). The reduced growth rate in blue tanks is consistent with previous work showing that tank color impacts growth (Imanpoor and Abdollahi 2011; Montajami et al. 2012). Given that we observed fainter body coloration in juveniles and young adults housed in yellow tanks, one possibility is that these fish were able to allocate more resources toward growth because they invested less energy toward expressing pigmentation, which is a metabolically expensive process (Polo-Cavia and Gomez-Mestre 2017; Alfakih et al. 2022). However, we found that the cumulative mortality across the duration of the experiment was significantly higher in fish housed in yellow tanks compared to those housed in blue tanks. The reduced survival rate in yellow tanks is inconsistent with the potential metabolic benefits of lower pigmentation in yellow tanks. One possibility is that aggression in yellow tanks led to a higher mortality rate, as has been suggested in other cichlid species (Mohadzir et al. 2022). However, there was no significantly higher level of aggression in groups housed in yellow tanks. In addition, although average aggression rates across the entire duration of the experiment were positively correlated with the observed cumulative mortality rates, this effect was observed in both blue and yellow tanks. The visual environment can influence the level of chronic stress in different fish species (Kim et al. 2016; Costa et al. 2017), and it is possible that blue and yellow background color result in differences in activation of the hypothalamic-pituitary adrenal axis or the sympathetic nervous system, which could impact growth and survival. For example, ambient light conditions affected survival and perhaps also growth in the cichlid fish *Pundamilia pundamilia* and *P. nyererei* (Maan et al. 2017). Future studies should examine physiological markers of stress, such as cortisol levels in *A. burtoni* reared in yellow tanks compared to those reared in blue tanks.

The proximate mechanisms underlying the observed correlated responses to specific backgrounds in our study are unknown. The melanocortin system is responsive to environmental light or background color (van der Salm et al. 2005) and melanocortin hormones are known to influence color phenotype and behavior in *A. burtoni* (Dijkstra et al. 2017). Other signaling pathways that regulate background color adaptation and other traits include endothelin signaling (Fang et al. 2022) and melanocyte concentrating hormones (Zhang et al. 2010). It will be interesting to examine how these different neuroendocrine systems regulate background color adaptation and other life history traits at the cellular and molecular levels. For example, increased modularity in developmental pathways can limit pleiotropic constraint and favor adaptive plasticity (Snell-Rood et al. 2010). Hence, details about specific signaling pathways [relative to, for example, widespread changes in hormones levels versus tissue-specific expression of receptor subtypes, eg (Ducrest et al. 2008)] can provide important information about the degree of modularity, which in turn influences the conditions under which plasticity is favored or hindered.

If the background color-specific effects on fitness reported in this study are relevant to specific visual environments in nature, they could reflect a potential constraint to the evolution of color plasticity. However, if these correlated fitness effects are properly matched to their respective environments (ie advantageous), it could facilitate the evolution of color plasticity in heterogeneous environments. For example, life history theory predicts that earlier sexual maturation is typically favored when resources are unpredictable (Stearns 1992). In Lake Tanganyika, murkier (and

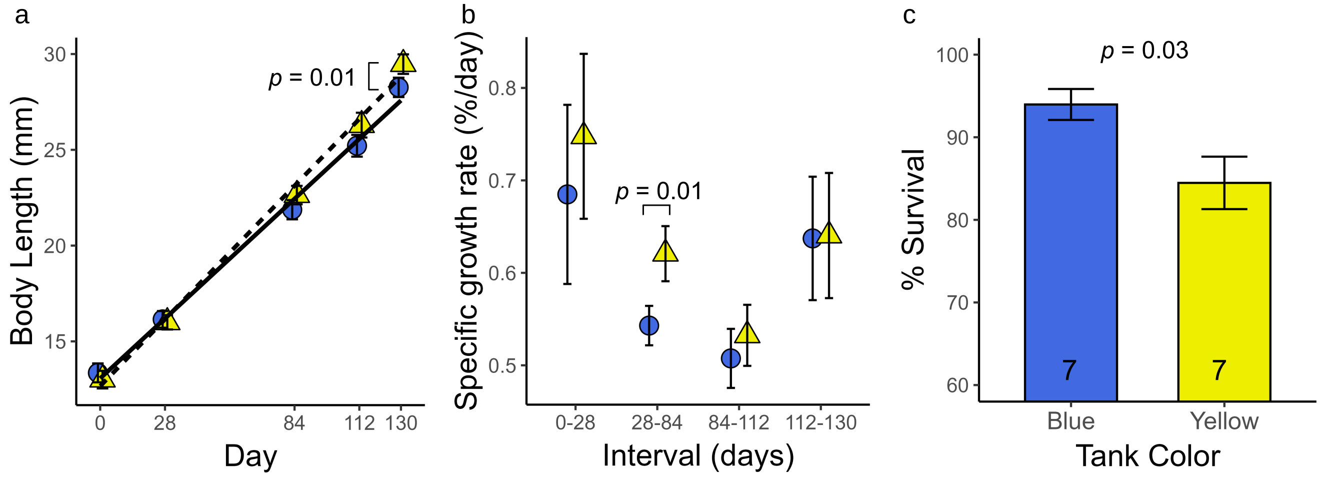

Fig. 5. Body size a) and growth rate b) in fish reared in blue (circles) and yellow (triangles) tanks (initial sample sizes, $n = 180$ in blue tanks and $n = 179$ in yellow tanks). c) Percent survival for fish reared in blue and yellow tanks (sample sizes are shown in the plot). Overall percent survival was quantified as the number of surviving fish at the end of the experiment (at day 140) in each tank divided by the total number of fish in each tank at the start of the experiment. Shown are mean ± se.

perhaps bluer) visual environments occur when lake productivity and the risk of harmful algal blooms creating anoxic conditions are high (Plisnier et al. 2023). It is possible that under these circumstances (high food availability but also high unpredictability relative to mortality risk), it may be advantageous to undergo faster sexual maturation. Testing whether correlated responses to background color adaptation are advantageous or not is not an easy task, but could be a goal for future studies.

Cichlid fish rely heavily on visual signals in both mate choice (McElroy and Kornfield 1990; Seehausen and Van Alphen 1998) and male-male competition (Dijkstra et al. 2005; Pauers et al. 2008; John et al. 2021). Variation in the visual environment has been suggested to drive variation in body coloration and even speciation (Seehausen et al. 2008; Wright et al. 2020), as has been suggested for speciation through sensory drive (Boughman 2002). In *A. burtoni*, blue males are sexually more attractive, while yellow males are superior fighters when competing for mating territories (Korzan et al. 2008; Dijkstra et al. 2024). Crucially, male-male competition influences color phenotype expression, with more males expressing yellow coloration rather than the blue color phenotype in groups with unstable dominance hierarchies (Dijkstra et al. 2024). In a more controlled setting, individually housed *A. burtoni* males with visual access to a bigger territorial neighbor were more likely to express blue coloration but only when the neighbor was in close proximity (Dijkstra et al. 2025). It will be interesting to see how background color adaptation and sexual selection interact and influence color expression and plasticity in this species. For example, a trade-off may exist where phenotypic plasticity to improve camouflage conflicts with the optimal body coloration required for mate choice or male-male competition [(Kelley et al. 2016), see also (Smith et al. 2016)]. Integrating these fitness effects may contribute to a clearer understanding of how the physical environment, in concert with sexual selection, drives the evolution of phenotypic plasticity in body coloration.

A limitation of the current study is that we did not transfer groups to a different background color during development, preventing us from assessing how subsequent background color adaptation influences fitness-related traits. Such an approach would specifically test the cost associated with color change (Radovanović et al. 2023), and this will be a focus in future studies. Additionally, early life experiences can influence behavior later in life (Solomon-Lane and Hofmann 2019), and future studies should examine how the visual environment influences male behavior and phenotype in adult life. Finally, we did not track individual fish in this study and therefore, we were not able to distinguish between the effects of color phenotype or background color on treatment-specific responses in fitness-related traits.

In summary, background color affected a variety of fitness-related traits in *A. burtoni*, including sexual maturation, breeding frequency, growth, and survivorship. Our results suggest that distinct visual environments may differentially impact important fitness-related traits, which could play a role in the evolution of color plasticity. In general, the adaptive significance of plasticity in body coloration according to background color depends on the relative cost and benefits of plastic adjustments to specific backgrounds, as well as the spatial and temporal heterogeneity of the visual environment (Wente and Phillips 2003; Corl et al. 2018; Fang et al. 2022). Given the importance of body coloration in social communication, future studies should assess how background color adaptation and social selection interact to influence the evolution of phenotypic plasticity in body coloration. Finally, phenotypic plasticity is thought to play an important role in evolutionary diversification [eg, plasticity may precede or facilitate adaptive evolution (Levis and Pfennig 2016)], and it will be interesting to see how plasticity in body coloration contributes to adaptive diversification in nuptial coloration and other traits in the East African cichlid radiations (Albertson et al. 2014; Malinsky et al. 2015; Kratochwil et al. 2018; Wright et al. 2020; Dijkstra and Seehausen 2025).

Acknowledgments

We thank members of the Dijkstra lab, the editor, and an anonymous reviewer for providing helpful comments on earlier drafts of the manuscript.

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Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

Funding

Research reported in this publication was supported by grants from Central Michigan University (Undergraduate Summer Scholars Awards to WGB and WB; a Graduate Student Award to TIM; a Faculty Research and Creative Endeavors Award to PDD); a grant from the Grants for Laboratory Animal Science (GLAS) program of the American Association for Laboratory Animal Science (AALAS) to PDD; a grant from the National Institute of General Medical Sciences (NIGMS, grant number 1R15GM150286 to PDD), and grants from the National Science Foundation (grant number 2444902 to PDD, 1921773 to SGA, and 2341006 to TKSL).

Conflicts of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data and code provided by Dijkstra (2025).

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