## ADVANCES IN CICHLID RESEARCH IV

# Courting danger: socially dominant fish adjust their escape behavior and compensate for increased conspicuousness to avian predators

Keith W. Whitaker · Marcos Alvarez · Thomas Preuss · Molly E. Cummings · Hans A. Hofmann

**Abstract** Males of many species display conspicuous colors to attract mates and deter rivals, although this benefit can incur an increased predation risk. In the African cichlid fish, *Astatotilapia burtoni,* males can change both their social status (dominant, DOM, or subordinate, SUB) and primary body color (yellow or blue). We hypothesized that these phenotypes vary in conspicuousness to predators and conspecifics, thus establishing a trade-off between intraspecific signaling and predation. We quantified the spectral reflectance of yellow and blue DOM and SUB males. We then constructed avian and conspecific visual receiver models to determine the relative conspicuousness of each phenotype. We show that there are significant differences in conspicuousness to predators and conspecifics, with the flanks of the yellow DOM males exhibiting more spectral contrast to both avian predators and conspecifics than the flanks of blue DOM males. Our measurements of escape behavior revealed that each morph exhibits distinct anti-predatory responses, with SUB males shoaling for protection, and the more conspicuous yellow DOM males executing more escape responses, potentially compensating for their increased conspicuousness. Our results suggest a novel mechanism for the maintenance of alternative male phenotypes in this species,

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where dynamically enhanced conspicuousness is off-set by plastic changes in behavior.

**Keywords** Dominant · Subordinate · Plasticity · Cichlid · Coloration · Kingfisher

## Introduction

An essential challenge in animal communication systems is standing out from the background (Endler, 1978, 1992). Being conspicuous is generally beneficial for obtaining mates and other resources, yet it can increase the risk of detection by predators as well (Stuart-Fox et al., 2003). Therefore, each signaling system represents a trade-off between the actions of sexual selection and natural selection within the signaling environment (Endler, 1992; Ryan & Cummings, 2013). For males that are socially dominant or territorial, being conspicuous may be important to advertise to both mates and rivals, which may make them vulnerable to predators. The overall territorial phenotype, therefore, is likely to represent some physiological trade-off between attention-seeking and attention-avoiding components. Experimentation on species with variable territorial phenotypes allows us to evaluate the relationship between conspicuousness and predator avoidance strategies.

Many polychromatic species are comprised of fixed phenotypes (e.g., Sinervo & Lively, 1996). In many of these species color is determined, at least in part, by genetic factors. Because color may also be linked in some way to immune function, relatedness, and/or fitness, it is essential to understand how these polymorphisms evolve. For example, when Gouldian finches, *Chloebia gouldiae* Gould, 1844, are presented with simultaneous stressors, such as competition and a large clutch, then head color predicts which stressor will be addressed by the male; red males increase territorial defense to confront the competition, while black males increase paternal care to cope with the large clutch (Pryke & Griffith, 2009). Similar correlations between color and behavioral adaption to stress have been shown in the guppy *Poecilia reticulata* Peters, 1859 (Endler, 1991) and *Pundamilia pundamilia* Seehausen & Bouton, 1998 and *Pundamilia nyererei* Witte-Maas & Witte, 1985, two closely related Lake Victoria cichlids that vary in coloration

as well as numerous other traits (Dijkstra et al., 2007). In other polychromatic species, individuals can dynamically alter their color phenotypes in real time. In instances where body coloration is not genetically determined, spectacular examples of camouflage (Chiao et al., 2011) and female mate choice (Dijkstra et al., 2009) have evolved even though coloration increases predation risk (Maan et al., 2008).

Males of the cichlid *Astatotilapia burtoni*, Günther, 1894 alter their phenotype with social status (Hofmann, 2003) in a dynamic fashion. When males are socially dominant (DOM), they display bright nuptial coloration (either blue or yellow, between which they occasionally alternate, Korzan et al., 2008), several horizontal black stripes across the forehead, a black lachrymal stripe ("eye-bar") across the face, and a red humeral patch. Most of these mutable markings serve as social signals (Heiligenberg et al., 1972; Leong, 1969; Muske & Fernald, 1987). Recent evidence suggests that yellow males might have a competitive advantage over blue males, which may increase their attractiveness to females (Korzan et al., 2008), yet it is unclear whether yellow or blue body coloration directly conveys information about social dominance (Fernald & Liebman, 1980). When males cannot obtain or maintain a territory, usually due to small relative body size, they adopt a socially subordinate (SUB) phenotype that is characterized by dull body coloration (faintly blue or yellow) with few markings. However, because SUBs grow faster than DOM males, they often challenge and defeat DOMs such that the dominance hierarchy is gradually overturned (Hofmann et al., 1999). Importantly, predation also causes instability in the social hierarchy of a lek by permanently removing individuals (Fernald & Hirata, 1977). When a territory is vacated, overt aggression often ensues as neighboring territory holders attempt to exert control over the area, while ascending non-territorial males compete to establish their own territory.

Body color has been associated with behavioral and physiological differences. Yellow DOMs are more aggressive (Korzan & Fernald, 2007; Dijkstra et al., 2017) and have higher circulating androgen levels (Huffman et al., 2012; O'Connell & Hofmann, 2012) and increased stress reactivity (Dijkstra et al., 2017) compared with blue DOMs. This difference, which appears to be regulated (in part) by the melanocortin system (Dijkstra et al., 2017; Border et al., 2019),

could be indicative of alternative reproductive tactics related to male–male competition and mate attraction (Korzan & Fernald, 2007; Dijkstra et al., 2009) or aggressive defense of limited resources (Barlow et al., 1986). We have previously shown that DOM males are more responsive to an abrupt auditory stimulus, approximating a bird breaking the water surface, compared to SUB males (Neumeister et al., 2010). Specifically, DOMs exhibit increased startle-escape responsiveness and a matched larger sound-evoked synaptic response in the escape command neuron (known as the Mauthner-cell) compared to SUBs, suggesting a social status-dependent plasticity. This could be explained as the result of a trade-off between the benefits of increased conspicuousness when inter-acting with conspecifics and the costs associated with higher predation risk (Godin & Clark, 1997; Neumeis-ter et al., 2010).

Evidence suggests that both behavioral differences and color differences between *A. burtoni* males may impact their predation rates. Field observations of *A. burtoni* males in their native Lake Tanganyika suggest that avian predators, including various species of kingfishers, are more likely to catch DOM males, though their body color was not recorded (Fernald & Hirata, 1977). Additionally, there is some evidence that birds could cue into the blue and yellow body color differences in other cichlid species. For example, highly conspicuous orange-blotched individuals of the Lake Victoria cichlid *Neochromis omnicaeruleus*, Seehausen & Bouton, 1998 are more frequently preyed upon by kingfishers compared to blue- and white-blotched fish (Maan et al., 2008). In the Midas cichlid, *Amphilophus citrinellus* Günther, 1864, field experiments have shown that dark colored young males are preferentially preyed upon by birds com-pared to other males (Torres-Dowdall et al., 2017).

In the present study, we examined the relationship between conspicuousness and startle-escape respon-siveness of *A. burtoni* color morphs. Visual conspic-uousness depends on the available spectrum of light, the reflective characteristics of the signal itself, the background reflectance and the receiver's sensory system (Endler, 1992; Cummings, 2007). Hence, to evaluate each morph's conspicuousness, we measured spectral reflectance of different body regions com-bined with avian predator and conspecific visual receiver models using irradiance measurements from aquatic habitats similar in depth and optical variability

to their native nearshore pools in Lake Tanganyika. We hypothesized that yellow DOMs, which are more aggressive, are more conspicuous than blue DOM phenotypes to both conspecific and avian viewers, and that DOMs in general are more conspicuous than SUBs or females. We further hypothesized that yellow males compensate for their enhanced conspicuousness by displaying increased escape behavior in response to a startle stimulus, compared to blue males.

## Materials and methods

### Animals

Adult *A. burtoni* from a lab-reared stock were housed in acrylic tanks (30 × 30 × 60 cm) in communities of 8–12 males and 8–12 females under conditions mimicking the natural environment in their native Lake Tanganyika (pH 8.5 ± 0.2; 27°C ± 0.2; 12 h:12 h light:dark cycle). Gravel substrate and terracotta pots were provided to allow multiple males to establish territories within each community. For the individuals used in this study, we assessed dominance status twice weekly over a period of at least 3 weeks to identify stable DOMs and SUBs using established methods (Fernald, 1977; Renn et al., 2008). Individ-uals were tracked over time by plastic beads attached to the body of the fish. All protocols were approved by the Institutional Care and Use Committee of The University of Texas at Austin.

The behavioral testing paradigm has been described elsewhere (Whitaker et al., 2011). Briefly, individual fish was transferred from the home tank to an isolated experimental tank (30 × 30 × 60 cm). A mesh net confined a circular area (20 cm diameter) in the center of the tank where the fish swam freely for a 60 min acclimation period. The experimental tank was fitted with two underwater speakers (UW-30; Electro Voice, Burnsville, MN, USA) on opposite ends and a black curtain around the tank eliminated visual cues. Startle-escape responses i.e., C-starts were evoked by high intensity sound pips (200 HZ) created by a waveform generator (Wavetek, CA, USA) and an amplifier (AudioSource, CA, USA). To avoid habituation, speaker selection, sound intensities, and time between trials (2–10 min) was randomized (Neumeister et al., 2010). In each experiment fish were presented with 16 stimuli, divided into four blocks of four different

auditory pulses at pre-set intensities (145, 155, 165, and 175 dB re. 1 µPa in water, respectively). The chosen intensities represent the linear range of a stimulus/response curve previously established for *A. burtoni* males (Neumeister et al., 2010). Fish were allowed to swim freely within the mesh net with volume adjusted based on their distance from the speaker. To identify unambiguously M-cell-related startle responses with latencies of less than 18 ms (Zottoli et al., 1999; Casagrand et al., 1999), we used a high-speed camera (Kodak Extrapro 1000 HRC; Eastman Kodak; San Diego, CA) at 1000 Hz. Startle responsiveness, or escape probability, was calculated as the response/no response ratio in a given experiment.

Of the 14 males tested in both DOM and SUB status, 7 were blue and 7 were yellow throughout the experiment. In the repeated measures design, two blue males were tested as DOM first, while the other five were first tested as SUB. Half of the yellow males were tested as DOM first. Since transitions are relatively rare in stable laboratory communities (Hofmann et al., 1999), very few males transitioned spontaneously. Instead, the fish were moved to socially engineered communities to encourage a change in the social status in the desired direction. Ascending males were left in their home tank, while the DOMs and aggressive SUBs were removed. Novel, smaller males were added to the tank to maintain the community size and density. Descending males were removed from their home tank and put into an established community of larger males. Once a new status had been established for 3 weeks, animals were re-tested for startle responsiveness. Five of the blue males experienced a second social transition and were tested a third time (data not shown).

Reflectance spectrophotometry and visual receiver modeling

Spectral reflectance measurements were collected from 10 blue DOM male, 10 yellow DOM male, 10 SUB blue male, 10 SUB yellows male and 10 female (average body width ± SD: 3.15 ± 0.14 cm) *A. burtoni* described above. Reflectance spectrometry was carried out as described in detail in Supplementary Methods.

Visual receiver modeling

Whether *A. burtoni* males vary in conspicuousness depending on body coloration depends on several factors including the spectral sensitivity of a specific viewer and the optical environment in which it is being viewed. Visual models approximate an animal's perception of visual information, have predicted behavioral sensitivities in a variety of taxa (Vorobyev & Osorio, 1998; Vorobyev et al., 2001; Goldsmith & Butler, 2003; Cummings et al., 2008), including cichlid fishes (Escobar-Camacho et al., 2017, 2019), and can provide reliable estimates of predation risk (Stuart-Fox et al., 2003; Husak et al., 2006; Stobbe & Schaefer, 2008; Maan & Cummings, 2012; Crothers & Cummings, 2013).

*Astatotilapia burtoni* occupy an unusual optical habitat in Lake Tanganyika. While most of the lake is deep and clear, *A. burtoni* occupy very shallow (< 1 m) nearshore pools and lagoons which experience a great range in water clarity (Cummings & Partridge, 2001; Cummings, 2004). Given the lack of calibrated irradiance measurements from these unique Lake Tanganyika habitats, we used proxy spectral measurements from the same depth range in a comparably variable optical environment. Specifically, we used paired downwelling and sidewelling irradiance spectra collected at high solar elevations (10 am–2 pm) at 0.1–1.5 m depths in California nearshore marine environments from clear ($n = 26$ paired measurements with horizontal visibility > 7 m) and murky ($n = 16$ paired measurements with horizontal visibility < 3 m) conditions (irradiance data from (Ödeen & Håstad, 2003; Dalton et al., 2010). We opted to use these proxy spectral irradiance from a geographically different location, because it provided variation in spectral irradiance within a very restricted depth range (< 1.5 m) not yet measured in African rift lakes.

We then constructed two viewer-specific visual models to evaluate the conspicuousness of the different phenotypes in both murky and clear optical conditions (details can be found in Supplementary Methods). Briefly, we modeled two different observers: a tetrachromatic bird [a UVS sensitive bird model, using the European starling, *Sturnus vulgaris* Linnaeus, 1758, photoreceptor absorptance and oil droplet spectra, described in (Goldsmith & Butler, 2003)] and trichromatic model for cichlid vision that assumes Weber noise and opponency processing based on trichromatic signal-to-noise estimates

(modified from (Cummings et al., 2008). Avian visual systems are generally characterized into two broad categories (Ödeen & Håstad, 2003)—species with violet-sensitive opsins (VS system) and species with sensitivity that extends further into the ultraviolet (UVS system). While both visual systems are represented in avian species that prey on fish (e.g., VS in kingfishers; UVS in gulls: Ödeen & Håstad, 2003), we selected to model bird predator using a representative UVS system in case the variation in ultraviolet reflectance we measured in flank and dorsal regions of *A. burtoni* (see Fig. 1) influenced conspicuousness to a potential bird viewer.

For the cichlid viewer model, we employed *A. burtoni* photoreceptor $\lambda_{max}$ values and chromophore type from Fernald and Liebman (1980) with SWS $\lambda_{max}$ = 455 nm, MWS $\lambda_{max}$ = 523 nm, and LWS $\lambda_{max}$ = 565 nm with the MWS and LWS photoreceptors found in twin or double cones. We conducted statistical analyses on the spectral ($\Delta S$) and luminance ($\Delta L$) contrast estimate output from our receptor-noise-limited model adapted from (Cummings et al., 2008) employing weber fractions previously recorded from goldfish (*Carassius auratus* Linnaeus, 1758) from Hawryshyn (1991) (SWS cone $v = 0.045$; MWS cone $v = 0.032$; LWS cone $v = 0.056$; see supplementary methods). Because recent behavioral research (Escobar-Camacho et al., 2017) suggests larger weber fractions might be involved in color discrimination with the rock-dwelling cichlid (*Metriaclima benetos* Stauffer et al., 1997), we additionally ran our models with recommended higher weber fractions (e.g., LWS $v = 0.16$) to determine whether our contrast measures remain above color detection thresholds ($\Delta S > 1$) with these assumptions.

Statistics

All results are stated as mean ± standard error unless otherwise noted. Significance for the differences between morphs in spectral and luminance contrasts were determined in SPSS using an ANOVA with a Tukey post hoc comparison. Where applicable, the reported post hoc *P*-values are Bonferroni-corrected due to multiple comparisons, unless otherwise noted. To analyze startle response behavior, we binned the data according to the four blocks in which the different stimuli intensities were presented (see above and Whitaker et al., 2011). To examine the role of color

and social status in escape performance, we first used a paired *t* test to compare blue and yellow males' startle responsiveness when they were SUBs to that displayed when they were DOMs. Finally, we developed a general linear model to test for main effects of social status and body coloration in startle responsiveness as well as a possible interaction effect between these two factors, while accounting for repeated measures (i.e., testing of individual fish before and after a social transition), with fish ID as a random factor. Since the data are binned by stimulus block within each test session (see above), a normal probability distribution was used with an identity link function and the Satterthwaite approximation for degrees of freedom due to the limited sample size.

Results

We first report the results that allowed us to test the hypothesis that DOMs are more conspicuous than SUBs or females as well as the more specific hypothesis that yellow DOMs are more conspicuous than blue DOMs. We then show how startle-escape responsiveness varied across these morphs to test whether yellow males display increased escape behavior in response to a startle stimulus. Representative examples of the four *A. burtoni* male phenotypes (yellow SUBs and DOMs and blue DOMs and SUBs) and of a female are shown in Fig. 1a.

Spectral reflectance measures

Mean spectral reflectance measures for each social and color phenotype in several locations across the body, specifically the dorsum, ventrum, humeral patch, and flank (where blue and yellow males qualitatively differ the most, Fig. 1b) are shown in Fig. 1c–f, respectively. Dorsal reflectances (Fig. 1d) were the darkest and most uniform across all 5 phenotypes, whereas ventral (Fig. 1c) and flank (Fig. 1f) reflectances exhibited significant variation across phenotypes (Supplementary Table 1). The reflectance spectra of the humeral patch differed greatly between females (which never show this patch) and males, with blue SUBs more similar to females and yellow SUBs more similar to DOMs (Fig. 1e). The presence and size of the expressed humeral patch has important signaling function in male–male contests (15), although we did
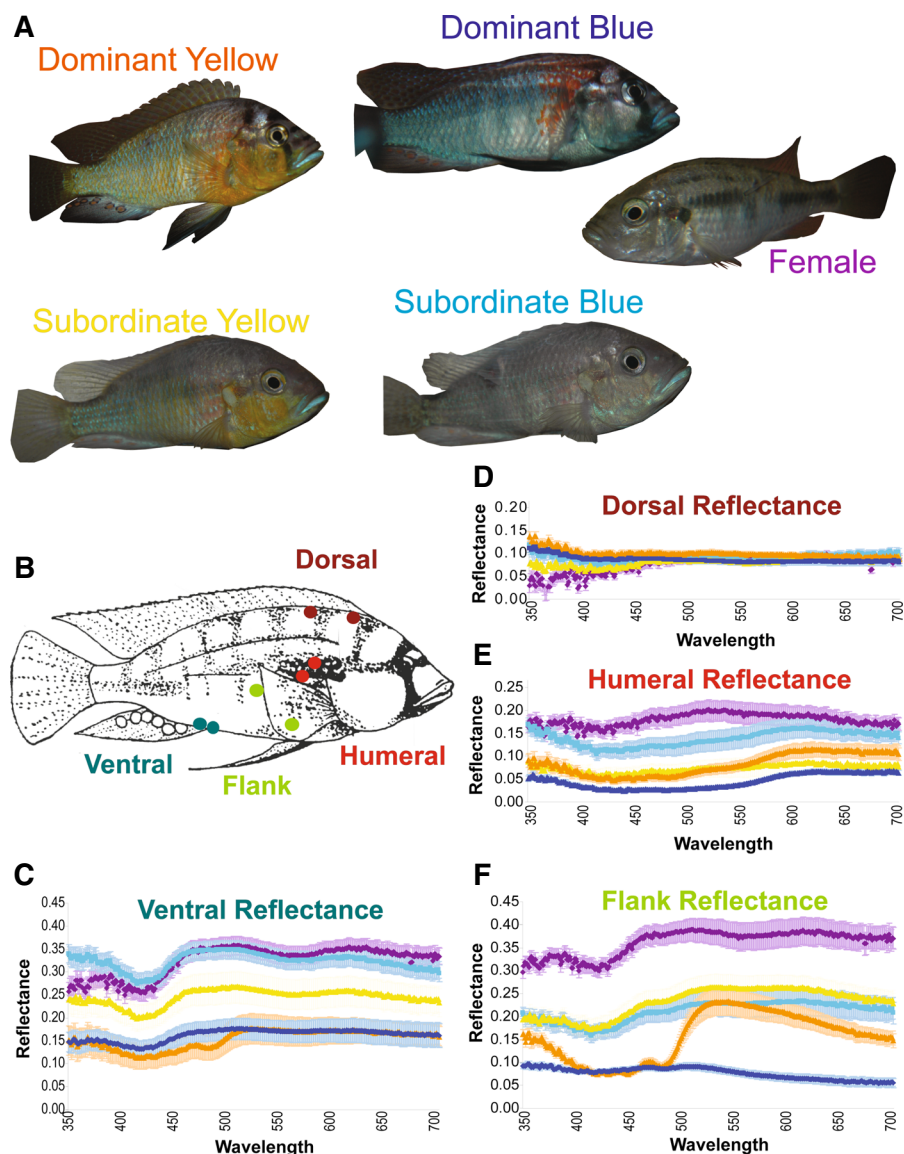
**Fig. 1** Five phenotypes of *Astatotilapia burtoni*. **A** Representative images of the four different male phenotypes are represented along with a female. Males can transition between social and color phenotypes, while females maintain the same phenotype throughout their lives. **B** Multiple points within each body area of each fish ($n = 10$ per phenotype) were measured in duplicate or triplicate to attain technical and biological replication. The mean reflectance spectra of different body regions **C** Ventral; **D** Dorsal; **E** Humeral; **F** Flank) are shown for each phenotype. Note the difference in reflectance in the UV spectrum of the flank between the two DOM phenotypes, which may indicate some social signaling in these wavelengths (<400 nm)

not quantify patch size in the present study. Comparison of the total reflectance flux, $\log \sum_{\lambda=350}^{700} (R_\lambda)$, between phenotypes showed no difference in dorsal total flux (ANOVA: $F_{4,45}=1.707$; $P = 0.165$); however, significant differences in total reflectance in other body regions were evident. Specifically, DOM males (yellow and blue) were overall darker (lower reflectance) than SUB males and females in flank ($F_{4,45} = 20.297$, $P < 0.001$) and ventral body regions ($F_{4,45} = 8.364$, $P < 0.001$). Flank regions of blue DOMs were significantly darker than all other phenotypes (Tukey

post hoc test: $P < 0.001$). The flank region of females was significantly lighter than that of DOMs of either color ($P < 0.001$), but not compared to either blue ($P = 0.101$) or yellow SUBs ($P = 0.396$). Blue SUBs are also lighter than yellow DOMs on the ventral surface ($P = 0.001$). The total reflectance flux of the humeral surface also varies significantly ($F_{4,45} = 12.135$, $P < 0.001$). Again, females are lighter in this region than DOMS of either color ($P < 0.015$). Blue SUBs are lighter than blue DOMs ($P < 0.002$). For detailed statistical results, see Supplementary Table 1.

## Visual conspicuousness to cichlid and avian viewers

To determine whether these differences in spectral reflectance measures are likely to result in differences in visual conspicuousness to conspecifics or avian predators, we evaluated these spectra in terms of color and brightness contrast ($\Delta S$, spectral contrast; and $\Delta L$, luminance contrast, respectively) against background light of shallow, aquatic environments under clear and murky conditions. Our results, expressed as signal-to-noise contrast estimates, show differences in the conspicuousness to an avian viewer and a cichlid viewer between different body parts in terms of chromatic ($\sim$ color) contrast and luminance ($\sim$ brightness) contrast in clear (Supplementary Table 2) and murky (Supplementary Table 3) conditions.

## Avian viewer

Mean dorsal reflectance for all phenotypes exhibited the lowest degree of conspicuousness to an avian viewer in clear conditions, evaluated as either spectral or luminance contrast (Supplementary Table 2; Fig. 2a). While there were no significant differences in terms of brightness contrast across all the phenotypes (for details, see Supplementary Table 4), there were significant differences in spectral contrast of the dorsal (ANOVA: $F_{4,45} = 10.362$, $P < 0.001$), flank ($F_{4,45} = 22.784$, $P < 0.001$), and ventral surfaces ($F = 5.622$, $P = 0.001$) when viewed by an avian observer under clear water conditions (respectively, Fig. 2A1-3). Tukey post hoc tests show that the spectral contrast of the dorsal surface was significantly lower for DOM males than for SUBs or females (Fig. 2A1; $P < 0.001$); however, blue and yellow DOMs did not differ from each other ($P = 1$). The flank surface contrast is

significantly lower for blue DOMs compared to yellow DOMs (Fig. 2A2, $P \leq 0.001$) and significantly higher for yellow DOMs ($P \leq 0.001$), while SUB males and females did not differ significantly from each other. Ventral surface reflectance was significantly higher in yellow DOMs compared to the other male morphs (Fig. 2A3, $P \leq 0.012$), but not when compared to females ($P = 0.116$). The SUBs and females were not significantly different from each other or from blue DOM males.

The luminance ($\sim$ brightness) contrast to an avian viewer of the dorsal surface of each morph in clear water conditions did not vary significantly across morphs (ANOVA: $F_{4,45} = 0.282$, $P = 0.888$), but the flank ($F_{4,45} = 16.372$, $P < 0.001$) and ventral surfaces ($F_{4,45} = 8.874$, $P < 0.001$) showed significant variation. Specifically, the flank surface of blue DOMs exhibited the lowest luminance compared to all other morphs (Tukey post hoc test: $P \leq 0.001$), whereas flank luminance was greatest in yellow DOMs, although this was significant only in comparison to blue DOMs and females ($P = 0.017$). Females and SUBs did not differ in this regard. Finally, for the ventral surface, luminance contrast of both blue and yellow DOM males is significantly lower than in females ($P < 0.01$) and blue SUB males ($P < 0.01$). For detailed statistical results see Supplementary Table 4.

## Cichlid viewer

To a cichlid viewer under clear water conditions (Fig. 2B), the spectral contrast of the dorsal (ANOVA: $F_{4,45} = 17.128$, $P < 0.001$), flank ($F_{4,45} = 39.457$, $P < 0.001$), ventral ($F_{4,45} = 16.644$, $P < 0.001$), and humeral surfaces ($F_{4,45} = 11.956$, $P < 0.001$) of the five morphs varied significantly (for details, see Supplementary Table 4). After correcting for multiple comparisons, we found that the spectral contrast of the dorsal and flank surfaces were significantly different between each color DOM male and all other morphs (Tukey post hoc tests: $P < 0.003$), but the SUBs and females were not significantly different from each other (see Supplementary Table 4). Flank regions showed the greatest range of spectral contrast (Supplementary Table 2), and here we found yellow DOMs to be significantly more conspicuous than all other morphs ($P < 0.001$ in all comparisons). For the ventral surface, the yellow DOM males were
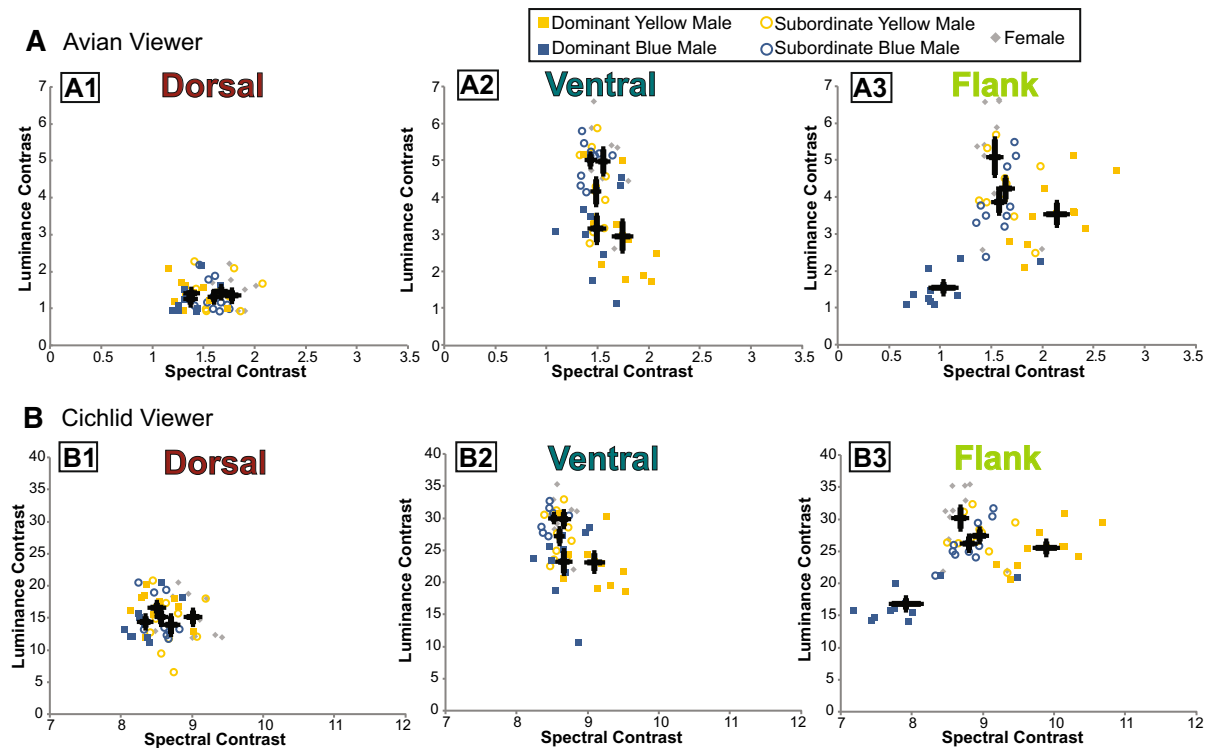
**A** Avian Viewer



**B** Cichlid Viewer



**Fig. 2** Luminance and spectral contrasts of dorsal, ventral, and flank measurements from the five *A. burtoni* phenotypes as viewed by **A** avian and **B** cichlid observer in clear water. Median model estimates for the spectral contrast ($\Delta S$, $x$ axis) and luminance contrast ($\Delta L$, $y$ axis) against background light across the 26 paired irradiance spectra representing high visibility conditions (clear, shallow nearshore waters). Individual fish ($n = 10$ per phenotype) that were expressing each phenotype are shown for the dorsal (A1, B1), ventral (A2, B2), and flank (A3, B3) body areas. Crosses represent the phenotypic mean. Refer to Supplementary Table 2 and Supplementary Table 4 for corresponding means and statistical significance, respectively. Note: incorporating larger weber fractions into the cichlid viewer receptor noise model (LWS v = 0.16) as suggested by behavioral measures of color discrimination in the rock-dwelling cichlid (*Metriaclima benetos*) in (Escobar-Camacho et al., 2019) also resulted in the majority of $\Delta S$ values (94.8%) above the assumed JND threshold ($\Delta S > 1$)

significantly different from all other morphs ($P < 0.001$), but no other comparisons yielded significance.

To a cichlid viewer, the luminance contrast of the dorsal surface did not vary significantly across the morphs (ANOVA: $F_{4,45} = 0.915$, $P = 0.464$), similar to the findings for the avian viewer. However, luminance contrasts varied significantly for the flank ($F_{4,45} = 20.108$, $P < 0.001$), ventral ($F_{4,45} = 7.699$, $P < 0.01$), and humeral surfaces ($F_{4,45} = 11.956$, $P < 0.001$).The luminance contrast for the flank surface of blue DOMs is also significantly lower than all other morphs (Tukey post hoc tests: $P < 0.001$ in all comparisons), which were not different from each other. Comparisons of the ventral surface luminance contrast are more complex as yellow SUBs are not significantly different from any other morph ($P > 0.2$ in all comparisons). DOMs have a lower spectral contrast

than blue SUBs ($P < 0.005$) and Females ($P < 0.005$) on the ventral surface, to a cichlid viewer. For detailed statistical results see Supplementary Table 4.

Alternative lighting conditions

*Astatotilapia burtoni* are found in a wide range of water quality and clarity. In murky conditions incidental and reflected spectra are shifted, which might affect conspicuousness of an animal. When we modeled the impact of murky water on conspicuousness (Fig. 3; Supplementary Table 3), we found that to an avian viewer, the five morphs varied significantly in spectral contrast at all body surfaces measured: dorsal (ANOVA: $F_{4,45} = 4.566$, $P = 0.004$), flank ($F_{4,45} = 13.733$, $P < 0.001$), ventral ($F_{4,45} = 4.306$, $P = 0.005$), and humeral ($F_{4,45} = 20.759$, $P < 0.001$) (for details,
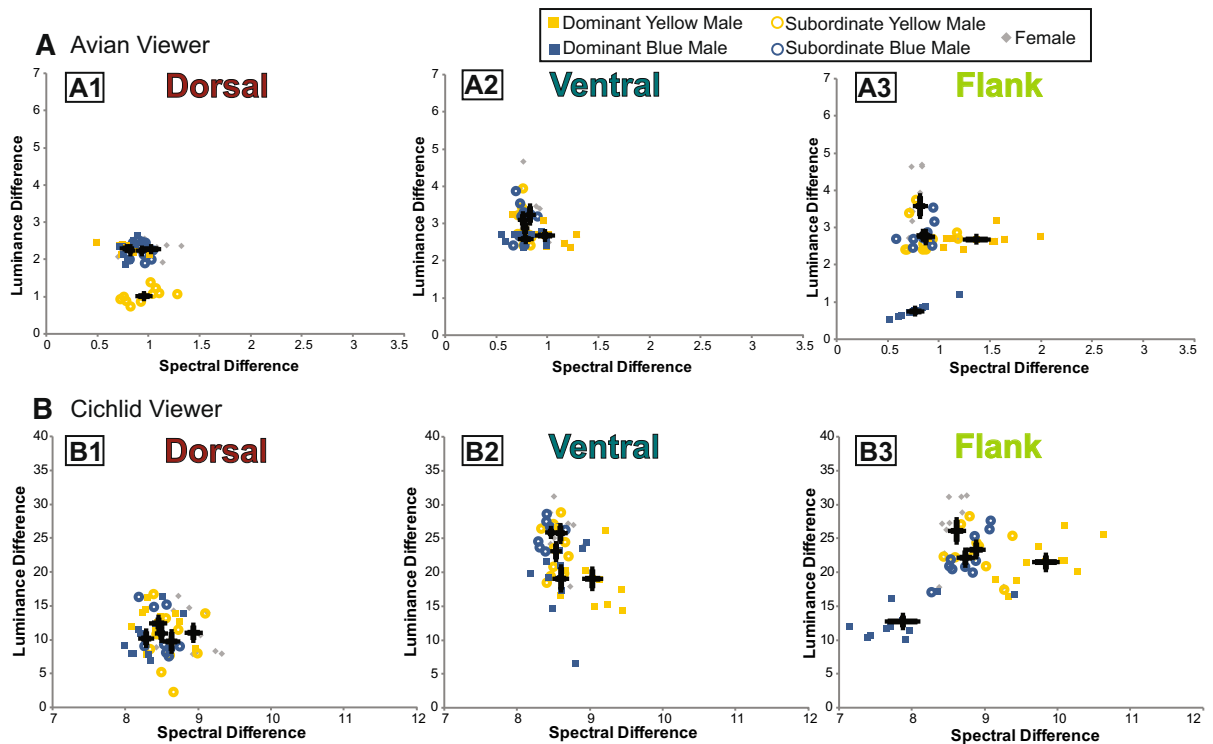
**Fig. 3** Luminance and spectral contrasts of the five *A. burtoni* phenotypes as viewed by **A** avian and **B** cichlid observer in murky water. Median model estimates for the spectral contrast ($\Delta S$, *x* axis) and luminance contrast ($\Delta L$, *y* axis) against background light across the 13 paired irradiance spectra representing low visibility conditions (murky, shallow nearshore waters).The spectral and luminance contrast values for individual fish for each phenotype are shown for the dorsal (**A**1, **B**1), ventral (**A**2, **B**2), and flank (**A**3, **B**3) body areas. The murky water conditions generally diminish the differences in conspicuousness between the different morphs when viewed by an avian observer (**A**), but have little impact on the relative conspicuousness to a cichlid observer (**B**).

To an avian observer viewing the flank (**A**2), the conspicuousness of each morph in murky conditions is reduced to the level of the Blue DOMs, though the females still stand out in terms of luminance and Yellow DOMs still stand out in spectral character. Refer to Supplementary Table 3 and Supplementary Table 5 for corresponding means and significance, respectively. Note: incorporating larger weber fractions into the cichlid viewer receptor noise model (LWS v = 0.16) as suggested by behavioral measures of color discrimination in the rock-dwelling cichlid (*Metriaclima benetos*) in (Escobar-Camacho et al., 2019) also resulted in the majority of $\Delta S$ values (90.6%) above the assumed JND threshold ($\Delta S > 1$)

see Supplementary Table 5). Interestingly, the dorsal surface of females has greater spectral contrast than that of DOM males of either color morph (Tukey post hoc tests: $P < 0.05$ for all comparisons). The five morphs also varied significantly in spectral contrast to a cichlid viewer, at all body surfaces measured: dorsal (ANOVA: $F_{4,45} = 8.349$, $P < 0.001$), flank ($F_{4,45} = 39.112$, $P < 0.001$), ventral ($F_{4,45} = 14.559$, $P < 0.001$), and humeral ($F_{4,45} = 10.094$, $P < 0.001$) (for details, see Supplementary Table 5). To a cichlid viewer, the murky conditions occlude any difference in contrast of the dorsal surface between male morphs (Tukey post hoc tests: $P > 0.3$ for all comparisons), though females still show greater spectral contrast than most morphs ($P < 0.001$ for all comparisons,

except for Blue DOMs, where $P = 0.062$). Comparing the flank and ventral surfaces, yellow DOMs stand out based on spectral contrast to both avian ($P < 0.001$ for all comparisons) and cichlid observers ($P < 0.001$ for all comparisons, except for females: $P = 0.151$). The humeral surface of either DOM color type provides strong spectral contrast to both avian ($P < 0.015$ for all comparisons) and cichlid viewers ($P < 0.035$ for all comparisons) compared to SUBs and females, though the DOM types do not differ ($P = 1.000$). See Supplementary Table 5 for detailed statistical results.

With regards to luminance contrast in murky conditions, there were no phenotype-based differences for the dorsal surface for either an avian ($F_{4,45} = 1.501$, $P = 0.218$) or cichlid viewer ($F_{4,45} = 0.930$, $P = 0.455$)

(for details, see Supplementary Table 5). Comparing the flank surfaces of morphs, which vary significantly in luminance contrast for both avian ($F_{4,45} = 10.224$, $P < 0.001$) and cichlid viewers ($F_{4,45} = 19.645$, $P < 0.001$), blue DOMs show less luminance contrast to cichlid viewers of the flank compared to all other morphs (Tukey post hoc tests: $P < 0.000$ for all comparisons), while females are more conspicuously luminous than other morphs to an avian observer ($P < 0.005$ for all comparisons). Luminance contrast of the ventral surface in murky conditions varies significantly across morphs for both avian ($F_{4,45} = 3.750$, $P = 0.010$) and cichlid viewers ($F_{4,45} = 7.653$, $P < 0.001$), with blue DOMs and females showing significantly higher (Tukey post hoc tests: $P < 0.001$ for all comparisons) and lower ($P < 0.01$ for all comparisons) contrast to an avian observer, respectively. To a cichlid observer, there is greater luminance contrast for the ventral surface of blue SUB males and females, but not against all morphs (see Supplementary Table 5). Finally, there is no significant difference in luminance contrast of the humeral surface to an avian viewer ($F_{4,45} = 0.742$, $P = 0.588$), but there is significant yet complex variation from the viewpoint of a cichlid viewer ($F_{4,45} = 12.319$, $P < 0.001$). See Supplementary Table 5 for detailed statistical results.

## Variation of startle responsiveness in relation to color and social phenotype

Given the considerable variation in conspicuousness between yellow and blue DOMs as well as the other phenotypes, we hypothesized that there could be compensatory variation in startle-escape responsiveness. We have previously shown that DOM males display increased escape probability compared to SUB males (Neumeister et al., 2010; Whitaker et al., 2011), although by chance most of the males used in those studies were yellow (Neumeister et al., 2010). In the present study, each individual fish was first tested as either SUB or DOM and then re-tested after an experimentally induced status change. As is shown in Fig. 4, yellow males indeed displayed a difference in startle responsiveness after a social transition, as expected, such that they showed a significantly increased response probability as DOMs (DOM mean ± standard deviation: 0.41 ± 0.14, SUB: 0.25 ± 0.13; paired $t$ test: $t_6 = 2.521$, $P = 0.045$). To our surprise, however, blue males failed to differ in startle
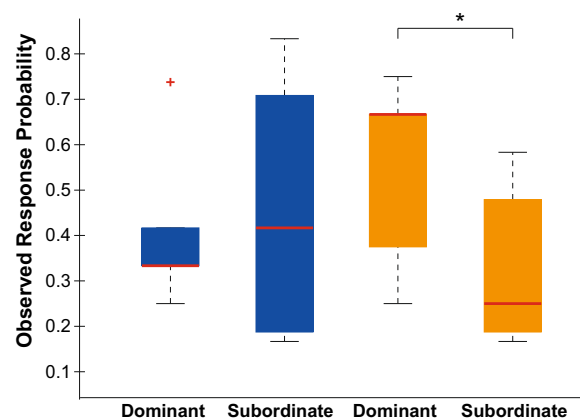


**Fig. 4** Startle-Escape Response Plasticity. Box and whisker plots show the responsiveness to twelve auditory stimuli for seven blue and seven yellow males that were tested before and after a change in social status. In blue males, responsiveness was independent of social status, whereas yellow males were more responsive as DOMs than as SUBs. Median value is marked by a bold line. Dashed lines show quartiles and outliers are marked by a cross. Asterisk indicates a significant difference at $P < 0.005$

responsiveness depending on social status (DOM: 0.30 ± 0.12, SUB: 0.34 ± 0.20; $t_6 = 0.573$, $P = 0.587$). A univariate general linear model that accounts for the retesting of individual fish after a social transition, with status and color as fixed effects, reveals no significant main effects for either color ($F_{12} = 0.017$; $P = 0.899$) or status ($F_{12} = 1.967$; $P = 0.186$). However, we found a significant interaction effect between color and status ($F_{12} = 4.865$; $P = 0.048$), such that yellow males showed an increased escape response probability only when DOM, while the response probability of blue males was independent of their social status (Fig. 4).

## Discussion

*Astatotilapia burtoni* males vary in social status and in the principal color (yellow vs. blue) reflected off their flank. Here, we showed that these male phenotypes differ in visual conspicuousness to both teleost and avian viewers under conditions similar to those observed in their native Lake Tanganyika. The more conspicuous yellow DOM males increase the probability of executing a startle-escape behavior compared to their less conspicuous blue DOM counterparts. The blue males do not change their startle-escape

probability when changing social status. The difference in startle behavior of DOM or SUB males we reported previously (Neumeister et al., 2010; Whitaker et al., 2011) is thus likely explained by the relative conspicuousness of an individual at any given point in time. Like shoaling behavior (Handegard et al., 2012), this finding may indicate a behavioral compensatory mechanism as the risk of predation increases with conspicuousness (Stuart-Fox et al., 2003).

With regard to conspicuousness of the dorsum in relation to social phenotype the situation is quite simple in *A. burtoni*. All phenotypes have converged on a dorsal coloration with low visual contrast which is predicted as a means to avoid detection from aerial predators (counter-illumination (Claes and Mallefet 2010)). However, examining other body regions (e.g., flank) that are more visible during lateral displays in both aggressive and sexual contexts, we find greater divergence across phenotypes. We predicted that DOM males (both blue and yellow) would be more conspicuous than the non-territorial phenotypes in this species (females, blue or yellow SUB males). Our visual modeling results, however, suggest that only yellow DOM males have evolved a flank coloration pattern that gives them greater color contrast ($\Delta S$) than all other phenotypes in both clear and murky waters (Fig. 2, 3; Supplementary Tables 1, 2). This finding is consistent with sexual dimorphic cichlids found in Lake Malawi, where males generally exhibit greater color contrast than females (Dalton et al., 2010).

When a diving predator hits the water during a strike, the resulting sudden and loud sound can trigger a startle-escape response (so-called 'C-start') in nearby fish (Faber & Korn, 1978). Previously, we have shown that DOM males are more likely to respond to such a stimulus than males that are SUB (Neumeister et al., 2010; Whitaker et al., 2011). This result is consistent with observations in the field that DOM *A. burtoni* males are more likely to be caught by kingfisher birds than SUBs (Fernald & Hirata, 1977). This behavioral plasticity is governed by changes in the excitability of a pair of reticulo-spinal neurons, known as Mauthner cells, in the medulla of the hindbrain (Neumeister et al., 2010), which initiate and control the likelihood, direction, and timing of the C-start behavior (Preuss & Faber, 2003; Korn & Faber, 2005; Preuss et al., 2006, Weiss et al., 2006). We have previously shown that serotonergic modulation of

inhibitory interneurons that synapse on the Mauthner neurons plays an important role in this behavioral variation (Whitaker et al., 2011). Serotonin is associated with aggressiveness and social dominance in many vertebrates (Miczek et al., 2007; Veenema, 2009) including *A. burtoni* (Winberg et al., 1997; Loveland et al., 2014) and other cichlids (Munro, 1986; Adams et al., 1996). Also, yellow DOMs are more aggressive than blue DOMs and appear to have a competitive advantage (Korzan & Fernald, 2007; Korzan et al., 2008; Dijkstra et al., 2017). Future studies will examine experiments whether and how serotonergic tone might integrate body coloration, aggression, and startle responsiveness.

We previously demonstrated that DOMs are more responsive to a startle stimulus than SUBs, although without consideration of body color, and hypothesized that this was related to differences in conspicuousness to avian predators (Neumeister et al., 2010; Whitaker et al., 2011). In the present study, we found that body coloration is an important phenotypic characteristic to consider for both behavior and conspicuousness. Specifically, we tested the same individuals before and after they changed social status to determine the extent to which the responsiveness to a startling stimulus is plastic in blue and yellow males. Remarkably, blue males responded about half of the time, regardless of status, but yellow males responded significantly more as DOM than SUB. These results suggest that yellow DOM males might increase startle-escape responsiveness when they increase in conspicuousness and social status, likely to offset their heightened risk of predation by aquatic and avian predators. The latter notion is supported by field studies that show that the highly conspicuous orange-blotched phenotype of another haplochromine cichlid, *Neochromis omnicaeruleus* from Lake Victoria, are preyed upon significantly more frequently by the Pied Kingfisher, *Ceryle rudis* Linnaeus, 1758, compared to the blue and white-blotched morphs (Maan et al., 2008). Blue DOMs, on the other hand, may offset the risk of predation by being less conspicuous and their responsiveness remains the same as the SUB males, who offset the predation risk by shoaling.

Executing a startle response could be considered disruptive and energetically costly and should, therefore, be inhibited when risk is low. Previously, we suggested that when males are SUB (regardless of color), they are less likely to be targeted by birds

because they are protected by the shoal they are part of (Jeschke & Tollrian, 2007) and their dull coloration (Stuart-Fox et al., 2003; Jeschke & Tollrian, 2007). Now we extend this reasoning to blue DOM males, arguing that they are similarly protected from avian viewers as SUBs.

The *A. burtoni* behavioral displays that reveal the flank to the surface are most commonly observed during courtship and territory defense, which are much more frequent in DOM males in the early morning (unpublished observations). The shoaling phenotypes (i.e., females and SUB males) are all visually conspicuous in terms of luminance, but protected by the shoal. Of the non-shoaling, territorial phenotypes, yellow DOM males are much more conspicuous in the flank region than blue DOM males to other *A. burtoni* (Supplementary Table 2), which may provide a mating advantage to the yellow morphs, although this hypothesis has not yet been tested rigorously (Korzan et al., 2008). Interestingly, the same appears to apply to avian observers: blue DOMs are the least conspicuous morph (lowest average chromatic contrast and luminance contrast values, see Figs. 2, 3). Yellow body coloration also provides an advantage in male–male competition (Korzan & Fernald, 2007; Dijkstra et al., 2017), thus yellow DOMs appear to be trading off the benefits of being conspicuous to conspecifics with the risk of predation.

Although there are many predators of cichlid fish in Lake Tanganyika (including water snakes, piscivorous fish, and wading birds) (Coulter, 1992), various species of kingfisher birds have been frequently recognized by field observers as a common daily threat to cichlids (Fernald & Hirata, 1977; Reyer et al., 1988; Wanink & Goudswaard, 1994). These birds nest near the lake shore, and foraging activity is highest close to the shore (Wanink & Goudswaard, 1994) and in waters less than 30 cm deep (Whitfield & Blaber, 1978). They locate prey by hovering above the water surface or by perching on suitable substrates along the shore (Reyer, 1980; Reyer et al., 1988; Maan et al., 2008). *A. burtoni* communities are naturally found in such near shore habitats such as estuaries, lagoons, and pools (mostly at a depth of less than 20 cm; Fernald & Hirata, 1977), suggesting that they are highly vulnerable to predation by kingfishers. In fact, a study on the Pied Kingfisher, *C. rudis*, in Lake Victoria estimated that during the breeding season an average kingfisher consumed approximately six haplochromine fish per day (Wanink & Goudswaard, 1994). Overall, these considerations reinforce the need for quantitative field observations as well as experiments with live predators, both of which are lacking at this point.

Polychromatism is widespread taxonomically and has been observed in lizards (Sinervo & Lively, 1996), birds (Pryke & Griffith, 2006), and insects (e.g., damselflies: Sanchez-Guillen et al., 2005; and cichlids: Border et al., 2019). The different morphs are predicted to exhibit behaviors that will optimize their fitness given their phenotype (Sinervo & Lively, 1996; Shuster & Wade, 2003). Here, we find two alternative territorial male morphs with distinct strategies to advertise to conspecifics while avoiding predation. Yellow DOM males couple high advertisement (conspicuousness) with high avoidance (startle response), while Blue DOM males minimize advertisement and conserve (presumably physiologically costly) avoidance responses. As *A. burtoni* males change social status, morphological and phenotypic changes occur to optimize either reproduction or growth (Hofmann et al., 1999; Huffman et al., 2012). In principle, any individual *A. burtoni* male can alternate between the four phenotypes throughout life and, thus, dynamically change the probability of its startle-escape response consistent with changes in conspicuousness to predators. Our results provide a foundation for future integrative studies that dissect these complex biological mechanisms across multiple levels of biological organization. The results of this study, therefore, provide a possible explanation for the maintenance of alternative male phenotypes in this species and can inform future studies in other polychromatic species.

# References

Adams, C. F., N. R. Liley & B. B. Gorzalka, 1996. PCPA increases aggression in male firemouth cichlids. Pharmacology 53: 328–330.

Barlow, G. W., W. Rogers & N. Fraley, 1986. Do Midas cichlids win through prowess or daring? It depends. Behavioral Ecology and Sociobiology 19: 1–8.

Border, S. E., T. J. Piefke, R. J. Fialkowski, M. R. Tryc, T. R. Funnell, G. M. DeOliveira & P. D. Dijkstra, 2019. Color change and pigmentation in a color polymorphic cichlid fish. Hydrobiologia 832: 175–191.

Casagrand, J. L., A. L. Guzik & R. C. Eaton, 1999. Mauthner and reticulospinal responses to the onset of acoustic pressure and acceleration stimuli. Journal of Neurophysiology 82: 1422–1437.

Chiao, C. C., J. K. Wickiser, J. J. Allen, B. Genter & R. T. Hanlon, 2011. Hyperspectral imaging of cuttlefish camouflage indicates good color match in the eyes of fish predators. Proceedings of the National Academy of Sciences USA 108: 9148–9153.

Claes, J. M. & J. Mallefet, 2010. The lantern shark's light switch: turning shallow water crypsis into midwater camouflage. Biology Letters 6: 685–687.

Coulter, G. W., 1992. Lake Tanganyika and its life. Oxford University Press, Oxford.

Crothers, L. R. & M. E. Cummings, 2013. Warning signal brightness variation: sexual selection may work under the radar of natural selection in populations of a polytypic poison frog. American Naturalist 181: E116–E124.

Cummings, M. E., 2004. Modelling divergence in luminance and chromatic detection performance across measured divergence in surfperch (Embiotocidae) habitats. Vision Research 44: 1127–1145.

Cummings, M. E., 2007. Sensory trade-offs predict signal divergence in surfperch. Evolution. 61: 530–545.

Cummings, M. E. & J. C. Partridge, 2001. Visual pigments and optical habitats of surfperch (Embiotocidae) in the California kelp forest. Journal of Comparative Physiology A 187: 875–889.

Cummings, M. E., X. E. Bernal, R. Reynaga, A. S. Rand & M. J. Ryan, 2008. Visual sensitivity to a conspicuous male cue varies by reproductive state in *Physalaemus pustulosus* females. Journal of Experimental Biology 211: 1203–1210.

Dalton, B. E., T. W. Cronin, N. J. Marshall & K. L. Carleton, 2010. The fish eye view: are cichlids conspicuous? Journal of Experimental Biology 213: 2243–2255.

Dijkstra, P. D., R. Hekman, R. Schulz & T. G. Groothuis, 2007. Social stimulation, nuptial colouration, androgens and immunocompetence in a sexual dimorphic cichlid fish. Behavioral Ecology & Sociobiology 61: 599–609.

Dijkstra, P. D., C. Hemelrijk, O. Seehausen & T. G. G. Groothuis, 2009. Color polymorphism and intrasexual competition in assemblages of cichlid fish. Behavioral Ecology 20: 138–144.

Dijkstra, P. D., S. M. Maguire, R. M. Harris, A. A. Rodriguez, R. S. DeAngelis, S. A. Flores & H. A. Hofmann, 2017. The melanocortin system regulates body pigmentation and social behaviour in the cichlid fish *Astatotilapia burtoni*. Proceedigs of the Royal Society B 284: 20162838.

Endler, J., 1978. A predator's view of animal color patterns. Evolutionary Biology 11: 319–364.

Endler, J., 1991. Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. Vision Research 31: 587–608.

Endler, J., 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139(Supplement): S125–S153.

Escobar-Camacho, D., J. Marshall & K. L. Carleton, 2017. Behavioral color vision in a cichlid fish: *Metriaclima benetos*. Journal of Experimental Biology 220: 2887–2899.

Escobar-Camacho, D., M. A. Taylor, K. L. Cheney, N. F. Green, N. J. Marshall & K. L. Carleton, 2019. Color discrimination thresholds in a cichlid fish *Metriaclima benetos*. Journal of Experimental Biology 222: jeb201160.

Faber, D. S. & H. Korn, 1978. Neurobiology of the Mauthner Cell. Raven Press, New York.

Fernald, R. D., 1977. Quantitative behavioural observations of *Haplochromis burtoni* under semi-natural conditions. Animal Behaviour 25: 643–653.

Fernald, R. D. & N. R. Hirata, 1977. Field study of *Haplochromis burtoni*: quantitative behavioural observations. Animal Behaviour 25: 964–975.

Fernald, R. D. & P. A. Liebman, 1980. Visual receptor pigments in the African cichlid fish, *Haplochromis burtoni*. Vision Research 20: 857–864.

Godin, J.-G. J. & K. A. V. Clark, 1997. Risk-taking in stickleback fishes faced with different predatory threats. Ecoscience 4: 246–251.

Goldsmith, T. H. & B. K. Butler, 2003. The roles of receptor noise and cone oil droplets in the photopic spectral sensitivity of the budgerigar, *Melopsittacus undulatus*. Journal of Comparative Physiology A 189: 135–142.

Handegard, N. O., K. M. Boswell, C. C. Ioannou, S. P. Leblanc, D. B. Tjøstheim & I. D. Couzin, 2012. The dynamics of coordinated group hunting and collective information transfer among schooling prey. Current Biology 22: 1213–1217.

Hawryshyn, C. W., 1991. Light-adaptation properties of the ultraviolet-sensitive cone mechanism in comparison to the other receptor mechanisms of goldfish. Visual Neuroscience 6: 293–301.

Heiligenberg, W., U. Kramer & V. Schulz, 1972. The angular orientation of the black eye-bar in *Haplochromis burtoni* (Cichlidae, Pisces) and its relevance to aggressivity. Zeitschrift für Vergleichende Physiology 76: 168–176.

Hofmann, H. A., 2003. Functional genomics of neural and behavioral plasticity. Journal of Neurobiology 54: 272–282.

Hofmann, H. A., M. E. Benson & R. E. Fernald, 1999. Social status regulates growth rate: consequences for life-history strategies. Proceedings of the National Academy of Sciences USA 96: 14171–14176.

Huffman, L. S., M. M. Mitchell, L. A. O'Connell & H. A. Hofmann, 2012. Rising StARs: behavioral, hormonal, and molecular responses to social challenge and opportunity. Hormones and Behavior 61: 631–641.

Husak, J. F., J. M. Macedonia, S. F. Fox & R. C. Sauceda, 2006. Predation cost of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. Ethology 112: 572–580.

Jeschke, J. M. & R. Tollrian, 2007. Prey swarming: which predators become confused and why? Animal Behavior 74: 387–393.

Korn, H. & D. S. Faber, 2005. The Mauthner cell half a century later: a neurobiological model for decision-making? Neuron 47: 13–28.

Korzan, W. J. & R. D. Fernald, 2007. Territorial male color predicts agonistic behavior of conspecifics in a color polymorphic species. Behavioral Ecology 18: 318–323.

Korzan, W. J., R. R. Robison, S. Zhao & R. D. Fernald, 2008. Color change as a potential behavioral strategy. Hormones & Behavior 54: 463–470.

Leong, C.-Y., 1969. The quantitative effect of releasers on the attack readiness of the fish *Haplochromis burtoni* (Cichlidae, Pisces). Zeitschrift für Vergleichende Physiologie 65: 29–50.

Loveland, J. L., N. Uy, K. P. Maruska, R. E. Carpenter & R. D. Fernald, 2014. Social status differences regulate the serotonergic system of a cichlid fish, *Astatotilapia burtoni*. Journal of Experimental Biology 217: 2680–2690.

Maan, M. E. & M. E. Cummings, 2012. Poison frog colors are honest signals of toxicity, particularly for bird predators. American Naturalist 179: E1–E14.

Maan, M. E., B. Eshuis, M. P. Haesler, M. V. Schneider, J. J. M. van Alphen & O. Seehausen, 2008. Color polymorphism and Predation in a Lake Victoria Cichlid fish. Copeia 2008: 621–629.

Miczek, K. A., R. M. de Almeida, E. A. Kravitz, E. F. Rissman, S. F. de Boer & A. Raine, 2007. Neurobiology of escalated aggression and violence. Journal of Neuroscience 27: 11803–11806.

Munro, A. D., 1986. Effects of melatonin, serotonin, and naloxone on aggression in isolated cichlid fish (*Aequidens pulcher*). Journal of Pineal Research 3: 257–262.

Muske, L. E. & R. D. Fernald, 1987. Control of a teleost social signal. I. Neural basis for differential expression of a color pattern. Journal of Comparative Physiology A 160: 99–107.

Neumeister, H., K. W. Whitaker, H. A. Hofmann & T. Preuss, 2010. Social and ecological regulation of a decision-making circuit. Journal of Neurophysiology 104: 3180–3188.

O'Connell, L. A. & H. A. Hofmann, 2012. Social status predicts how sex steroid receptors regulate complex behavior across levels of biological organization. Endocrinology 153: 1341–1351.

Ödeen, A. & O. Håstad, 2003. Complex distribution of avian colour vision systems revealed by sequencing the SWS1 opsin from total DNA. Molecular Biology & Evolution 20: 855–861.

Preuss, T. & D. S. Faber, 2003. Central cellular mechanisms underlying temperature-dependent changes in the goldfish startle-escape behavior. Journal of Neuroscience 23: 5617–5626.

Preuss, T., P. E. Osei-Bonsu, S. A. Weiss, C. Wang & D. S. Faber, 2006. Neural representation of object approach in a decision-making motor circuit. Journal of Neuroscience 26: 3454–3464.

Pryke, S. R. & S. C. Griffith, 2006. Red dominates black: agonistic signalling among head morphs in the colour polymorphic Gouldian finch. Proceedings of the Royal Society B 273: 949–957.

Pryke, S. R. & S. C. Griffith, 2009. Socially mediated trade-offs between aggression and parental effort in competing color morphs. American Naturalist 174: 455–464.

Renn, S. C. P., N. Aubin-Horth & H. A. Hofmann, 2008. Fish & chips: functional genomics of social plasticity in an African cichlid fish. Journal of Experimental Biology 211: 3041–3056.

Reyer, H.-U., 1980. Flexible helper structure as an ecological adaptation in the pied kingfisher. Behavioral Ecology & Sociobiology 6: 219–227.

Reyer, H.-U., W. Migongo-Bake & L. Schmidt, 1988. Field studies and experiments on distribution and foraging of pied and malachite kingfishers at Lake Nakuru (Kenya). Journal of Animal Ecology 57: 595–610.

Ryan, M. J. & M. E. Cummings, 2013. Perceptual biases and mate choice. Annual Reviews in Ecology Evolution & Systematics 44: 437–459.

Sanchez-Guillen, R. A., H. Van Gossum & A. Cordero Rivera, 2005. Hybridization and the inheritance of female colour polymorphism in two ischnurid damselflies (Odonata: Coenagrionidae). Biological Journal of the Linnean Society 85: 471–481.

Shuster, S. M. & M. J. Wade, 2003. Mating systems and strategies. In Krebs, J. R. & T. H. Clutton-Brock (eds), Monographs in Behavior and Ecology. Princeton University Press, Princeton.

Sinervo, B. & C. M. Lively, 1996. The rock-paper-scissors game and the evolution of alternative male strategies. Nature 380: 240–243.

Stobbe, N. & H. M. Schaefer, 2008. Enhancement of chromatic contrast increases predation risk for striped butterflies. Proceedings of the Royal Society B 275: 1535–1541.

Stuart-Fox, D. M., A. Moussalli, N. J. Marshall & I. P. F. Owens, 2003. Conspicuous males suffer higher predation risk: visual modelling and experimental evidence from lizards. Animal Behaviour 66: 541–550.

Torres-Dowdall, J., J. Golcher-Benavides, G. Machado-Schiaffino & A. Meyer, 2017. The role of rare morph advantage and conspicuousness in the stable gold-dark colour polymorphism of a crater lake Midas cichlid fish. Journal of Animal Ecology 86: 1044–1053.

Veenema, A. H., 2009. Early life stress, the development of aggression and neuroendocrine and neurobiological correlates: what can we learn from animal models? Frontiers in Neuroendocrinology 30: 497–518.

Vorobyev, M. & D. Osorio, 1998. Receptor noise as a determinant of colour thresholds. Proceedings of the Royal Society B 265: 351–358.

Vorobyev, M., R. Brandt, D. Peitsch, S. B. Laughlin & R. Menzel, 2001. Colour thresholds and receptor noise: behaviour and physiology compared. Vision Research 41: 639–653.

Wanink, J. H. & K. Goudswaard, 1994. Effects of Nile perch (*Lates niloticus*) introduction into Lake Victoria, East Africa, on the diet of pied kingfishers (*Ceryle rudis*). Hydrobiologia 279: 367–376.

Weiss, S. A., S. J. Zottoli, S. C. Do, D. S. Faber & T. Preuss, 2006. Correlation of C-start behaviors with neural activity recorded from the hindbrain in free-swimming goldfish (*Carassius auratus*). Journal of Experimental Biology 209: 4788–4801.

Whitaker, K. W., H. Neumeister, L. S. Huffman, C. E. Kidd, T. Preuss & H. A. Hofmann, 2011. Serotonergic modulation of startle-escape plasticity in an African cichlid fish: a single-cell molecular and physiological analysis of a vital neural circuit. Journal of Neurophysiology 106: 127–137.

Whitfield, A. K. & S. J. M. Blaber, 1978. Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. Journal of Fish Biology 13: 675–691.

Winberg, S., Y. Winberg & R. D. Fernald, 1997. Effect of social rank on brain monoaminergic activity in a cichlid fish. Brain Behavior & Evolution 49: 230–236.

Zottoli, S. J., B. C. Newman, H. I. Rieff & D. C. Winters, 1999. Decrease in occurrence of fast startle responses after selective Mauthner cell ablation in goldfish (*Carassius auratus*). Journal of Comparative Physiology A 184: 207–218.