



The role of ultraviolet coloration in intrasexual interactions in a colonial fish



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Ultraviolet (UV) coloration varies drastically across species and likely plays fundamentally different roles in facilitating social communication depending on the ecological or social context. While it is well known that UV coloration serves important social functions in species that school and flock, far less is known about the role of UV coloration in group-territorial and colonial species, where individuals have long-lasting and potentially cooperative relationships with many neighbours. We measured spectral reflectance in *Neolamprologus pulcher*, a group-living, colonial Tanganyikan cichlid fish, and found prominent UV coloration on both sexes. We manipulated the visibility of this UV coloration using a clear UV-blocking filter or a UV-transparent filter during behavioural contests across a barrier. We found that trials between similarly sized same-sex opponents involved significantly lower frequencies of aggression when opponents' UV coloration was obscured compared to when opponents' UV coloration was visible. As aggression is typically high between similarly sized same-sex individuals in *N. pulcher*, this reduction in aggression suggests that UV coloration aids in motivating individuals to engage in conspecific intrasexual interactions. We found no difference in aggression in trials between familiar and unfamiliar opponents in female–female and male–female trials, regardless of the presence of UV coloration. In male–male trials, we found significantly higher frequencies of aggression in contests between familiar male opponents than in contests between unfamiliar male opponents, but only when UV coloration was visible. Collectively, these results suggest that UV coloration is important for intrasexual interactions and prompts further investigation as to the benefits of having visual signals of communication extend into the ultraviolet spectrum.

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Although humans are unable to see in the ultraviolet (UV) range of the light spectrum, many species of birds, fish, reptiles and mammals both see UV light and have UV coloration on their bodies (Siebeck, 2014). Similar to coloration in the human visual spectrum, UV coloration serves a variety of signalling functions based on the ecological context or social structure of the focal species, including interspecific and individual recognition (Siebeck, Parker, Sprenger, Mäthger, & Wallis, 2010), sex recognition (Guillermo-Ferreira, Therézio, Gehlen, Bispo, & Marletta, 2013) and signals of individual quality (Korsten, Thomas, & Komdeur, 2007; Siebeck, 2014).

This variation in signalling function due to social or ecological context is often expressed through variation in the size, location, intensity or dimorphism of such coloration. For example, many fishes have intricate facial UV patterns that vary between species or between individuals and aid in identifying species or familiar conspecifics (Siebeck, 2014; Siebeck et al., 2010). In contrast, many birds and some fishes have general UV-reflective regions that vary in intensity (Korsten et al., 2007; Rick, Modarressie, & Bakker, 2004). These regions may be sexually monomorphic, playing a role in social functions such as shoaling decisions (Modarressie, Rick, & Bakker, 2006) and parent–nestling communication (Tanner & Richner, 2008). Conversely, UV coloration may be sexually dimorphic, used in sex recognition (Guillermo-Ferreira et al., 2013), individual quality assessments (Griggio, Zanollo, & Hoi, 2010; Pérez i de Lanuza, Carazo, & Font, 2014; Roberts, Ras, & Peters, 2009), mate choice decisions (Andersson, Ornborg, &

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Andersson, 1998; Bennett, Cuthill, Partridge, & Maier, 1996; Palmer & Hankison, 2015), intrasexual competition (Alonso-Alvarez, Doutrelant, & Sorci, 2004; Martin et al., 2016; Rick & Bakker, 2008; Siebeck, 2004) and territorial defence (Martin, Meylan, Perret, & Le Galliard, 2015; Siebeck, 2014). The variation in UV coloration present across different species underlies the idea that this coloration plays fundamentally different roles in social signalling across species (Cummings, Rosenthal, & Ryan, 2003).

These different functions across species are likely linked to differences in both the social and ecological environment of different species. For example, schooling or flocking species tend to form short-term aggregations that are not location specific, as the animals coordinate their movements to travel in a group (Soria, Freon, & Chabanet, 2007). Instantaneous visual identification of conspecifics is likely key in these species (Siebeck, 2014), as schooling animals need to recognize and coordinate with nearby conspecifics quickly to avoid predators (Barber & Ruxton, 2000) and may not have spatial recognition cues to associate with particular individuals. Furthermore, markings that signal individual identity may be critically important in these species because conspecific coordination among familiar individuals is beneficial due to reduced competition costs within the school, increased homogeneity in group behaviour and better coordinated group responses (Barber & Ruxton, 2000). However, less is known about the role of UV coloration in territorial species where conspecifics develop long-term and potentially cooperative relationships with their group members and neighbours (Drewe, Madden, & Pearce, 2009; Jungwirth, Josi, Walker, Taborsky, & Reznick, 2015; Jungwirth, Walker, & Taborsky, 2015). In these systems, individuals often need to make rapid assessments with respect to identifying and responding to possible territorial threats, cooperative partners, potential group joiners, extrapair mates and reproductive competitors (Jansen & van Baalen, 2006; Jordan, Wong, & Balshine, 2010; Ligocki et al., 2015; Temeles, 1994). Such assessments may require individually identifiable signals of sex, familiarity or quality that allow individuals to respond appropriately to a wide variety of potential social partners.

Investigating the role of UV coloration in a variety of social systems will better elucidate contexts in which UV coloration is an important mediator of social interactions. In particular, exploring the function of UV coloration across different social contexts may help us understand how and why animals might utilize UV signals. For example, signals in the UV spectrum may be concealed from other species lacking UV visual sensitivity (e.g. Cummings et al., 2003), but these signals may also be subject to fluctuations in UV light (e.g. with depth underwater) that alter their reliability across ecological contexts. Consequently, we sought to understand whether and how UV coloration facilitates social interactions in the highly social and cooperatively breeding cichlid fish, *Neolamprologus pulcher*. *Neolamprologus pulcher* lives in territorial groups composed of a dominant breeding pair with 0–20 subordinates (Wong & Balshine, 2011). *Neolamprologus pulcher* groups are located within permanent colonies of 2–200 groups, with densities reaching 60 groups within a 3 m radius at some sites (Hellmann et al., 2015; Wong & Balshine, 2011). This social structure requires *N. pulcher* to use close-range interactions to mediate mating, dominance and territorial behaviours with many individuals, including social competitors in nearby groups, current group members and potential mates (Wong & Balshine, 2011). *Neolamprologus pulcher* express the short-wavelength (SWS) visual palette typical of some African cichlids, meaning that they have UV-sensitive photoreceptors (Schulte, O'Brien, Conte, O'Quin, & Carleton, 2014). Although body coloration of *N. pulcher* is largely monomorphic to the human eye (Taborsky & Limberger, 1981), *N. pulcher* can distinguish familiarity, identity and sex using visual

cues from video playback experiments that do not capture the UV spectrum (Balshine-Earn & Lotem, 1998; Kohda et al., 2015) as well as from live experiments that do capture the full light spectrum (Frostman & Sherman, 2004; Hellmann & Hamilton, 2014). Consequently, although we know that non-UV visual cues alone are sufficient to permit recognition of conspecifics, we do not yet know whether UV coloration facilitates behavioural interactions in this highly social fish by providing additional cues regarding conspecific quality or identity.

We measured spectral reflectance in *N. pulcher*, and found prominent UV facial and body coloration on males and females. To investigate the influence of UV coloration on sex recognition and familiarity, we compared social interactions between fish when they could see their opponent's UV coloration and when that coloration was obscured or reduced. If UV coloration aids in facilitating interactions between familiar and unfamiliar individuals, we predicted that contests between familiar conspecifics would contain less aggression in UV trials (Kohda et al., 2015), but contests between familiar and unfamiliar individuals would involve similar levels of aggression when UV coloration was obscured. If UV coloration mediates intrasexual competition, then we expected to see more aggression between same-sex competitors in UV trials (Desjardins, Stiver, Fitzpatrick, & Balshine, 2008), but similar levels of aggression between same-sex and opposite-sex opponents when UV coloration was obscured.

METHODS

Experimental Design

All experimental fish were wild caught or F1 offspring of wild-caught fish from the Kambwimba region of Lake Tanganyika (8°32'S, 31°9'E). Twenty male–female pairs ($N = 40$ fish total) were housed together 30 days prior to the experiment (mean standard length (SL) \pm SE: males: 59.7 \pm 1.54 mm; females: 52.5 \pm 0.95 mm). Each pair was housed in 113.6-litre aquarium (30.5 \times 61 cm and 61 cm high) with sand substrate and two inverted terracotta flowerpot halves that served as shelter and potential breeding substrate. To mirror natural conditions, a 12:12 h light: dark cycle was maintained for the duration of the experiment and water temperatures were kept constant at 27 \pm 1 °C. Fish were fed daily and ad libitum with either TetraMin flakes (5 days per week) or frozen *Daphnia* or *Artemia* (twice per week).

We conducted 160 dyadic trials: 40 male–male trials, 40 female–female trials and 80 male–female trials. More opposite-sex trials were conducted to standardize the number of trials per individual. In a randomized order, each experimental fish faced an unfamiliar same-sex opponent, a familiar same-sex opponent, an unfamiliar opposite-sex opponent and a familiar opposite-sex opponent under UV and non-UV conditions ($N = 8$ trials per fish). To establish familiarity, fish were allowed to see and interact with pairs in neighbouring tanks for 10 days prior to the start of the experiment.

For trials, opponents were placed on opposite, randomized sides of an opaque barrier in a test tank (76 \times 32 cm and 32 cm high). After a 10 min habituation period, the opaque barrier was removed, leaving only a clear barrier (UV trials: Plexiglas, non-UV trials: Plexiglas with a clear UV-blocking film). After an additional 1 min habituation period, the observer (A.C.S.) conducted a 5 min behavioural observation and scored all aggressive behaviours between opponents on JWatcher (a behaviour recording program: Blumstein & Daniel, 2007) using a species-specific ethogram (Reddon et al., 2015). Behaviours were categorized as (1) restrained aggressive displays (fin raise, fast approach, operculum spread, head jerk, head-down display), which are often used to prevent

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