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The correlation between subordinate fish eye colour and received attacks: a negative social feedback mechanism for the reduction of aggression during the formation of dominance hierarchies

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ABSTRACT

Eye darkening has been linked to social status in fish. The subordinate's eyes darken, while the eyes of the dominant fish become pale. Although this phenomenon has been described in salmonid fishes and in the African cichlid Nile tilapia *Oreochromis niloticus*, it is unclear whether eye darkening correlates with a reduction in aggressive behaviour. Thus, we evaluated the link between social status and eye darkening. We evaluated whether the eye colours of subordinate fish correlate with the frequency of received attacks in a neotropical fish, the pearl cichlid *Geophagus brasiliensis*. We paired pearl cichlids and quantified both the aggressive behaviour and the eye darkening of each fish. As has been described for Nile tilapia and Atlantic salmon, a clear-cut hierarchical relationship formed, where dominance and subordination were associated with pale and dark eye colours, respectively. Initially, eye colour darkening was positively correlated with the frequency of received attacks; however, a negative association occurred following eye darkening, in which the intensity of aggressive interactions decreased. Thus, fish that initially received a high number of attacks signalled subordination more rapidly and intensely (rapid and dramatic eye darkening), thereby inducing a negative social feedback mechanism that led to reduced aggression.

1. Introduction

In nature, the most common type of resource competition is an aggressive dispute (Ridley, 1995; Wootton, 1998). Although it is not always the case that the most aggressive animals become dominant and/or secure access to the contested resource (Francis, 1988; Francis et al., 1992; Mazur and Booth, 1998; Staffan et al., 2002), the most aggressive ones are often more successful in exploiting a shared resource (Metcalfe, 1986; Alanärä et al., 2001; Delicio et al., 2006; Ang and Manica, 2010; Magellan and Kaiser, 2010). Moreover, the presence of a contested resource may increase aggressive activities in fish (Barreto et al., 2011). The fitness of the individual fish may be enhanced due to increased access to these resources. Thus, it is expected that aggressive individuals would be favoured by natural selection. Nevertheless, aggressive interactions may have an energetic cost for the individuals (Glass and Huntingford, 1988; Alvarenga and Volpato, 1995; Kelly and Godin, 2001; Briffa and Elwood, 2004). Therefore, it is likely that natural selection also favours mechanisms that decrease the occurrence of serious fighting. For example, ritualised displays may facilitate opponent assessment and the establishment of social hierarchies and/or territories without the need for costly physical combat (Maynard-Smith and Price, 1973; Maynard-Smith and Parker, 1976; Parker and Rubenstein, 1981; Enquist and Leimar, 1983, 1990; Enquist et al., 1990; Grosenick et al., 2007; review by Arnott and Elwood, 2009).

In the case of social hierarchies, the signalling of social status is necessary for the maintenance of stable social structures (Giaquinto and Volpato, 1997; Volpato et al., 2003); otherwise, a high rate of aggressive encounters could persist (Oliveira and Almada, 1996; Goncalves-de-Freitas et al., 2008).

Changes in body colour have been recognised as a reliable signal of social status in certain fish species. In the case of some cichlids, a subordinate status is usually associated with a darker appearance (appearance of dark stripes), while dominant fish are typically paler (Falter, 1987; Beeching, 1995). It is assumed that this link between social status and body colour is an intraspecific signal that may function to decrease aggression and to aid in the establishment of a hierarchy (O'Connor et al., 1999). Body colour is the characteristic that has been most extensively studied in this context (Abbott et al., 1985; Hulscher-Emeis, 1992; Beeching, 1995; O'Connor et al., 1999, 2000; Hoglund et al., 2000); however, some investigations have concentrated on eye colour, in species such as

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Atlantic salmon, *Salmo salar* (Suter and Huntingford, 2002), and the Nile tilapia, *Oreochromis niloticus* (Volpato et al., 2003).

Eye colour is easy to identify, but its adequacy as an indicator of social status in other fish species has yet to be thoroughly investigated. It is not clear whether variation in eye colour always corresponds to shifts in body colour. A highly significant association was reported between the body colour and the sclera colour of juvenile Atlantic salmon (O'Connor et al., 1999), and this relationship has been verified by ad hoc observations for this salmon species (Suter and Huntingford, 2002). However, for pairs of Nile tilapia (Volpato et al., 2003), it is known that eye colour is independent of body stripes because darkened stripes (vertical, horizontal, or both) can appear without alteration of eye colour. The pairs of Nile tilapia in the study by Volpato et al. (2003) varied in the number of aggressive actions they perpetrated, but there were no differences between the eye darkening levels of the two contesters in pairs with high numbers of aggressive encounters. The opposite occurred in pairs with low levels of confrontation, in which subordinate fish presented a darker eye colour than dominant fish. In these pairs of Nile tilapia, the social hierarchy was stable and, therefore, eye colour was clearly associated with social rank. These results suggest that the association between eye colour and social rank may function to reduce aggression. Although it is known that eye colour is a clear indicator of social status in cichlid fish (Volpato et al., 2003), the relationship between eye colour and a reduction in aggressive behaviour has not yet been tested.

In the present study, we examined the correlation between eye colour, social rank, and aggressive behaviour of the pearl cichlid *Geophagus brasiliensis*. This species was chosen because it is an aggressive fish species that changes eye colour during intraspecific confrontations (Kadry and Barreto, 2010). The Cichlidae are a group composed of several species with evident aggressive behaviour that have variously been used as models for studying aggression in vertebrates (Oliveira et al., 2001, 2005; Cruz and Brown, 2007; Korzan et al., 2008).

2. Methods

2.1. Fish and holding conditions

Specimens of the pearl cichlid *G. brasiliensis* (Quoy and Gaimard 1824) were collected from a lagoon system (in a rural area of São Paulo city, Jardim Britânia – 23°25′46.34″S, 46°47′19.47″W). The fish were of both sexes and were sexually immature (8.91 ± 4.7 g, 6.51 ± 0.45 cm). Fish were held in two indoor tanks with a holding density of one fish per 1.5 l of water. This stock population was held for at least one month before the test. During this time, the water was kept at a mean temperature of 25 ± 1 °C, with biological, chemical and mechanical filtering and constant aeration with an air pump (air stone connected via plastic tubing). Approximately 20% of the tank water was slowly changed at least three times a week (de-chlorinated water). Ammonia and nitrite levels were <0.5 ppm and <0.05 ppm, respectively. The photoperiod (~13 h light and 11 h dark) and illumination were natural. Fish were fed daily with a commercial fish chow containing 32% protein (Presence; Evialis do Brasil Nutrição Animal, Paulínia, SP, Brasil).

2.2. Experimental protocol and procedures

Pearl cichlid juveniles were paired, and the sclera (eye) colour and aggressive interactions were quantified in the context of an intruder–resident paradigm (Beaugrand and Zayan, 1985; Turner and Huntingford, 1986; Turner, 1994; Barreto and Volpato, 2006; Arnott and Elwood, 2008; Kadry and Barreto, 2010; Jordan et al., 2010). Thirty-six pearl cichlids of similar sizes from the stock population were completely isolated (one fish/tank) in glass tanks (40 cm × 20 cm × 25 cm; 20 l of water) for 7 consecutive days for acclimation. On day 8, the eye-darkening levels of the isolated fish were measured five consecutive times during a 10-min period, at 2-min intervals. The mean value of the five measurements for each fish was set as the baseline eye colour.

Following the baseline measurements, size-matched pairs were formed by introducing an intruder animal into the resident fish tank. The pairs were formed from fish that came from separate stock tanks. The mean weight and length of intruder fish were 8.7 ± 2.2 g and 6.5 ± 0.44 cm, while the mean weight and length of the resident fish were 9.2 ± 2.1 g and 6.5 ± 0.43 cm. For pairing, the intruder fish were caught from their respective tanks using a net and were introduced into the resident fish tanks. To control for the handling disturbance, the resident fish were also captured and re-introduced into their own tank simultaneously with the intruder fish. The eye colours of both fish were quantified every 2 min over a 40-min pairing period, for a total of 20 observations. Concomitantly, the paired fish were videotaped for subsequent analysis of aggressive behaviour.

2.3. Aggressive behaviour, eye colour and data analysis

Aggressive interactions between the fish pairs were video-recorded during the 40-min pairing periods. The total number of attacks (biting and tail beating) was quantified from these videotapes. The dominant–subordinate relationship was evaluated by calculating the dominance index (DI = directed attack by an individual/total number of interactions in the pair) according to Bailey et al. (2000). DI values range from 0 to 1, and the greater the DI value, the higher the animal's rank with regard to dominance. An animal was considered dominant if the DI was at least 0.60 (Bailey et al., 2000).

Eye colour was quantified as the percentage of the sclera and iris area that was darkened (based on Suter and Huntingford, 2002 and Volpato et al., 2003). Fractional darkening of the iris and sclera around the pupil was observed for each fish. For quantification, the fish's eye was visually inspected, and based on a drawing that represented the circular area of the eye, it was divided into eight regions of equal area using four imaginary diameter lines. Each area was filled in with a pencil representing the status of eye darkening (dark or white) in the respective areas, which allowed us to calculate the percentage of darkened area.

The link between eye colour and social status depends on aggression intensity at the pair level, and for a better analysis of this phenomenon, pairs can be divided into two aggressiveness categories, high- and low-attack pairs (Volpato et al., 2003). In this study, we used the following approach for statistical analysis.

To enhance the normality and homogeneity, data describing the attack frequency were transformed by adding 0.5 to each value and then extracting the square root, while arcsine transformation was applied to the data describing eye colour. Normality and homoscedasticity were confirmed by the Kolmogorov–Smirnov test and the Bartlett test, respectively. We used one-way repeated measures ANOVA with two levels of repeated measures to analyse the effects of aggressiveness category (independent factor) on the response variables (attack frequency or percentage of eye darkening), with social status and time as the two levels of repeated measures. Social status in paired animals must be considered a repeated measure (see discussion in Briffa and Elwood, 2010). The ANOVA was complemented by a Newman–Keuls test. For this analysis, the aggressiveness categories and the social status after pairing were used to divide the baseline values of eye colour into the same 4 conditions of post-pairing (dominant or subordinate animal of high- or low-attack pairs). Linear models were used to assess the correlations between eye colour of the subordinate fish and

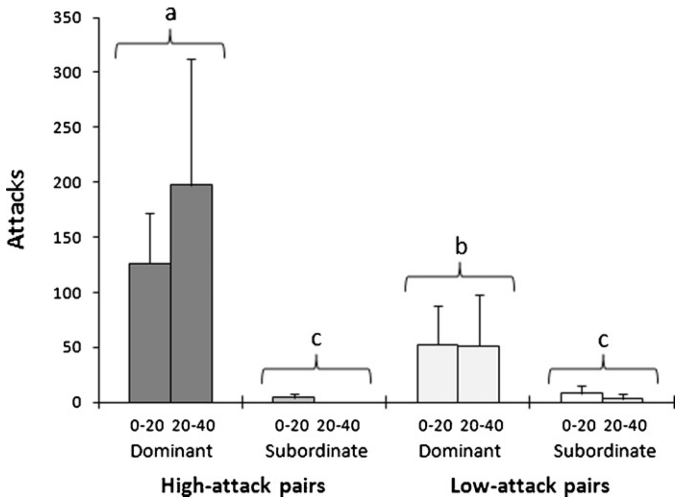

Fig. 1. Directed attacks of dominant and subordinate fish in high- and low-attack pairs in the pearl cichlid *Geophagus brasiliensis*. Aggression levels were assessed in 18 pairs of fish during a time period of 40 min, divided into two 20-min time intervals (0–20 min and 20–40 min). Pairs of fish were divided into the following two aggressiveness categories: high- and low-attack pairs (n = 9 for both categories). The different letters denote statistically significant differences when comparing the interaction between social status and aggressiveness category (one-way ANOVA with two levels of repeated measures, status and time; $F_{(1;16)} = 20.92$; $P = 0.0003$).

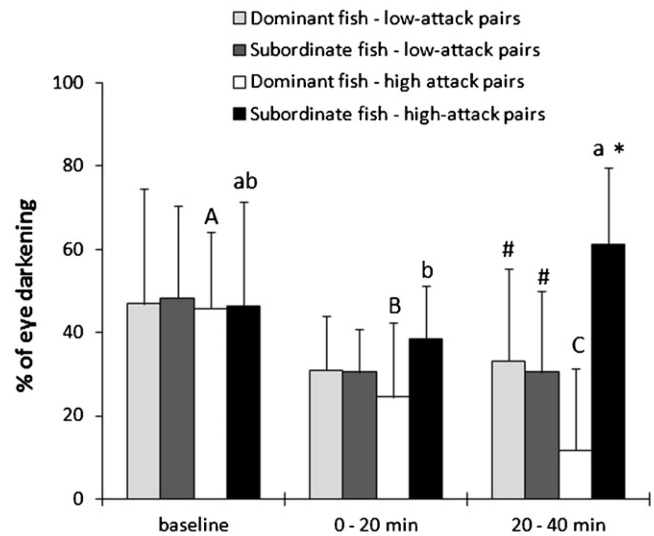

Fig. 2. The percentage of eye darkening in relation to social status and time in high- and low-attack pairs of pearl cichlids (*Geophagus brasiliensis*). A one-way ANOVA with two levels of repeated measures (status and time) revealed a significant interaction between aggressiveness categories, status and time ($F_{(2;32)} = 5.53$; $P = 0.0087$). The superscript letters indicate statistically significant differences when comparing fish of the same social status (capital letters – dominant, small letters – subordinate) between the time intervals (baseline, 0–20 min, or 20–40 min) within the high-attack pair aggressiveness category. *Statistically significant difference between subordinate and dominant animals in high-attack pairs during the 20–40 min interval. #Statistically significant difference for both dominant and subordinate fish between the two aggressiveness categories during the 20–40 min time interval.

directed attacks of the dominant toward the subordinate fish for both high- and low-attack pairs. Statistical differences were considered significant for values of $P < 0.05$.

3. Results

A dominance hierarchy was clearly established in all 18 of the pairs tested. The wide range of attack frequencies (43–474) between pairs was used to assess the relationship between attacks and hierarchical ranking, as well as the link to eye colour.

Based on the total number of aggressive interactions, the pairs were subdivided into two classes by quartile analysis. The first and second quartiles represented the low-attack pairs (43–178 attacks), and the third and fourth quartiles represented the high-attack pairs (188–474 attacks). The one-way ANOVA with two levels of repeated measures (status and time) revealed a significant interaction between aggressiveness category and status ($F_{(1;16)} = 20.92$; $P = 0.0003$). The dominant fish of high-attack pairs attacked their respective subordinate fish more often than the dominant fish of low-attack pairs, while the number of attacks by the subordinate animal toward the dominant one was not significantly different between the two aggressiveness categories (Fig. 1).

The one-way ANOVA with two levels of repeated measures (status and time) revealed significant interactions between aggressiveness category, status and time ($F_{(2;32)} = 5.53$; $P = 0.0087$). The analysis of baseline eye colour confirmed that the fish started from a statistically similar level of eye darkening. In the high-attack pairs, the eyes of dominant fish became paler over time, while the eyes of subordinate fish were darker during the later time interval (20–40 min) when compared to the earlier time interval (0–20 min). During the later pairing interval (20–40 min), the eyes of subordinate fish were darker than those of dominant fish, with the mean values higher and lower than the mean eye colour values of the subordinate and dominant animals, respectively, of low-attack pairs (Fig. 2).

Interestingly, correlation tests revealed that eye-darkening levels and received attacks were only linked in subordinate fish from the high-attack pairs (Fig. 3). There was a significant positive correlation ($R = 0.77$; $R^2 = 0.60$; $P = 0.014$) during the first time interval (0–20 min). However, the results of the later time interval (20–40 min) indicated a significant negative correlation ($R = -0.79$; $R^2 = 0.62$; $P = 0.012$).

4. Discussion

In the present study, we confirmed the association between dark eye colour and social subordination in pearl cichlids, similar to what was observed for Nile tilapia (Volpato et al., 2003) and Atlantic salmon (Suter and Huntingford, 2002). We further demonstrated that this association is dependent on attack intensity. In this context, eye colour is a visual signal that reduces intraspecific aggression. Eye colour was correlated with both contest intensity and social status, suggesting that it may be a graded signal for the communication of status, depending on the escalation level of the contest.

In all dyads tested, the dominance hierarchies remained stable throughout the observation period. These findings are supported by the analysis of the number of attacks directed and received by the animals in each pair. Accordingly, eye colour can be used as an indicator of social rank in this species. This association has also been described for salmonids (O'Connor et al., 1999, 2000; Suter and Huntingford, 2002) and for another cichlid, the Nile tilapia *O. niloticus* (Volpato et al., 2003).

An interesting fact revealed by this study is that the socially induced change in eye colour was linked to the individuals' aggression level. The subordinate fish in the high-attack pairs received more attacks, and the magnitude of eye darkening was greater than in the subordinate fish in the low-attack pairs. Moreover, eye-darkening levels were initially positively correlated with the aggression level (0–20 min), but then became negatively correlated (at 20–40 min) in the high-attack pairs. These correlations, however, were not present in the low-attack pairs. During the initiation of social interaction, fish receiving high numbers of attacks darkened their eyes rapidly and more dramatically than those receiving

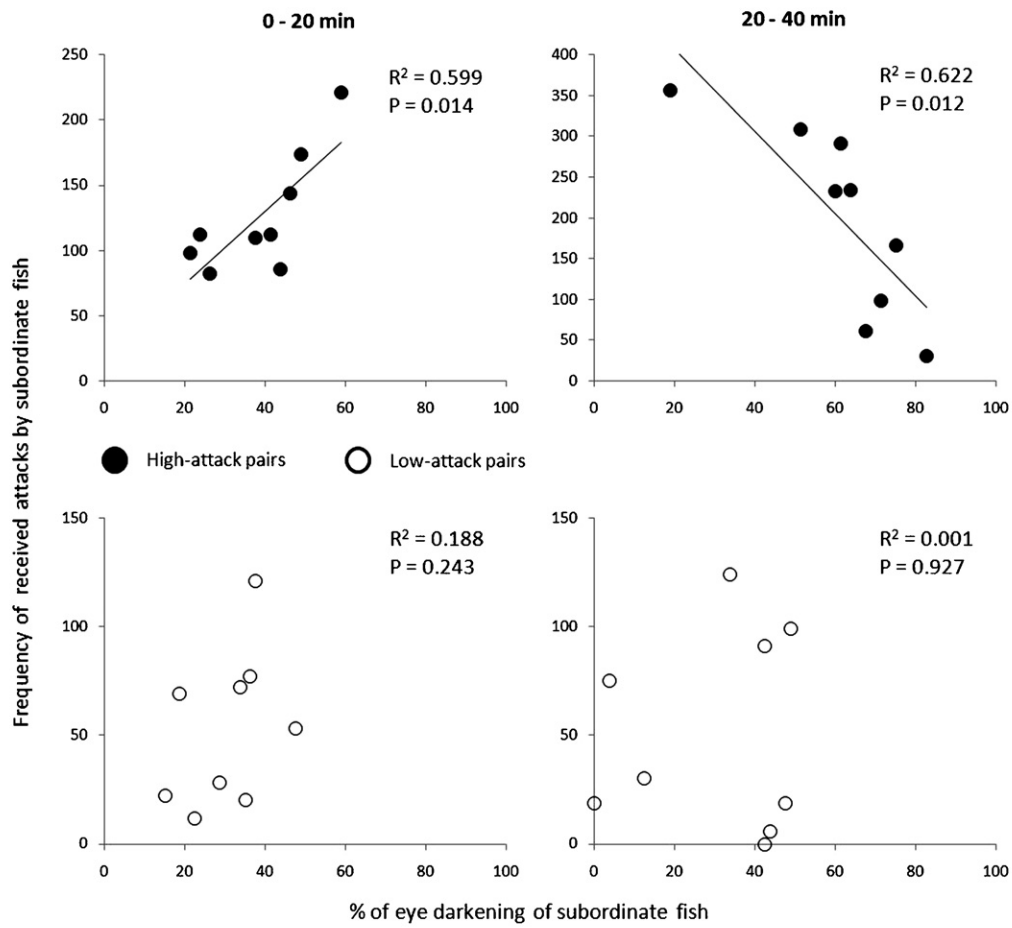

Fig. 3. Correlation between the percentage of eye darkening in the subordinate fish and the number of directed attacks by the dominant fish to the subordinate fish in high- and low-attack pairs in the pearl cichlid, *Geophagus brasiliensis*.

low numbers of attacks (positive correlation). Following eye darkening, the change in eye colour may alter the motivation of the dominant fish such that it does not attack the subordinate (negative correlation). Thus, eye darkening is a subordination signal that operates as a negative social feedback signal; the sooner the subordinate fish signals subordination through the darkening of its eyes, the less it is attacked. The rate of this negative feedback mechanism is dependent on the intensity of the contest (number of aggressive events).

Most studies examining fish colouration changes have considered body, rather than eye colour (Falter, 1987; O'Connor et al., 1999; Korzan et al., 2008; Rodrigues et al., 2009; review by Leclercq et al., 2010). Fluctuations in eye colour often correlate with shifts in body colour. In pearl cichlids, however, eye colour is independent of body stripe patterns, because horizontal, vertical, or both stripe types can develop without the occurrence of eye darkening and vice versa (unpublished data). This trend was also previously reported for Nile tilapia (Volpato et al., 2003). In the cichlid *Nannacara anomala*, medial stripe colour displays are associated with, and predicted by, tail beating, while vertical bar colour displays are associated with mouth wrestling (Hurd, 1997). These findings suggest that body colour displays are used to facilitate the transmission of assessment information within a fight. Thus, at least in cichlid species, colour patterns involving stripes and eye colours interact in a very complex manner meriting further investigation.

The pairing of individuals of aggressive fish species can result in confrontation and, consequently, social stress. Social stress is known to induce changes in the activity of the hypothalamus–pituitary–interrenal axis, which lead to increased plasma cortisol levels in fish (Pottinger and Pickering, 1992; Fox et al., 1997; Pottinger and Carrick, 2001; Barreto and Volpato, 2006; Bender et al., 2008). Social stress may be induced, e.g., by visual cues of an opponent, such as large body size (Chen and Fernald, 2011). Moreover, social stress can concomitantly increase levels of α-MSH, a hormone that modulates chromatophore dispersal, resulting in the alteration of skin colouration (Hoglund et al., 2000). It is plausible that social stress may have a similar effect on eye colour. Thus, the modulation of eye darkening in fish may be a consequence of the stress that is imposed by this social context. Further studies are needed to confirm whether these physiological mechanisms related to stress response (cortisol and α-MSH levels) are the underlying mechanism of the negative social feedback phenomenon described in this study.

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