



## Eye colour in juvenile Atlantic salmon: effects of social status, aggression and foraging success

H. C. SUTER\* AND F. A. HUNTINGFORD

*Division of Environmental and Evolutionary Biology, Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow, G12 8QQ, U.K.*

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Status-based differences in sclera colour in small groups of juvenile Atlantic salmon *Salmo salar*, held in a semi-natural environment over a 20 day period, became obvious 3 days after the start of the study and persisted for the 20 days. Dominant fish had pale sclera, and this pattern was very stable over the experimental period. In contrast, the sclera colour of subordinate fish (ranks 2–5) fluctuated from day to day. Median sclera colour of fish ranked 4–5 darkened on days they received more aggression, and sclera of rank 2 fish were lighter on days on which they initiated more attacks. Changes in sclera colour of fish ranked 2–4 were more frequent during feeding periods than non-feeding periods. This study confirms that the relationship between eye colour and status described in tanks is also seen in more natural environments, and also that colour change in juvenile salmonids is a complex response to local events.

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### INTRODUCTION

In a population where there is competition for limited resources, conflict between individuals is a common outcome (Huntingford & Turner, 1987). It makes sense to minimize energy wastage and the risk of physical damage by avoiding conflict situations with animals that are better competitors. Modifying appearance to signal status or intentions to conspecifics is one way to do this.

Some modifications of appearance may be a product of ageing, or a seasonal change, and are irreversible or last for several weeks or months; the development of red breeding colouration in the three-spined stickleback *Gasterosteus aculeatus* L. is one such case (Matsuno & Katsuyama, 1976). Other modifications may be very rapid and reversible. Rapid, reversible visual signals mediated through differential colour patterns often play an important role in the control of aggressive behaviour in fishes (Huntingford & Turner, 1987). For example, the colour of the opercular flap and iris becomes very prominent during aggressive encounters in the pumpkinseed sunfish *Lepomis gibbosus* (L.). Once dominance has been established, these features remain prominent in the dominant individual, but fade or disappear in the subordinate (Stacey & Chizar, 1977).

In salmonids, social subordination results in darkening of the skin and eyes (Keenleyside & Yamamoto, 1962; Abbott *et al.*, 1985; O'Connor *et al.*, 1999; Höglund *et al.*, 2000). O'Connor *et al.* (1999) found that the intensity of fights

\*Author to whom correspondence should be addressed. Tel.: +44 (0) 141 330 4769; fax: +44 (0) 141 330 5791; email: hayley\_suter@hotmail.com

between pairs of newly introduced juvenile Atlantic salmon *Salmo salar* L. decreased immediately after the subordinate darkened (within 4 h of introduction), indicating that darkening may act as a social signal of submission. Several studies have shown that the darkened eye and body colour of subordinate salmonids persists for several weeks following hierarchy formation, and that dominant fish can be readily identified by their lighter colour (Keenleyside & Yamamoto, 1962; Abbott *et al.*, 1985; R. W. Wilson & S. F. Owen, unpubl. data).

The studies described above have generally concentrated on colour change in relation to aggression, have taken place in tank environments and have frequently considered only pairs of fish. Also, fish are often held together for short or interrupted periods of time. While conducting a study on the foraging behaviour of Atlantic salmon parr held in small groups in an artificial stream for 20 days, it became obvious that the relationships between eye colour and behaviour were very complex. Aggression and foraging success appeared to affect eye colour in a manner that varied with individual social status.

Data collected in this study were used to examine the development of differences in eye colour following the introduction of fish into a semi-natural stream environment, and to examine factors affecting eye colour in fish of different social status on a daily basis.

## METHODS

### ANIMALS, HUSBANDRY AND EXPERIMENTAL CONDITIONS

The study fish were non-sibling offspring of wild Atlantic salmon, reared at the SOAEFD Hatchery at Almondbank, Perthshire. The fish were transferred in November 1999 to the University Field Station at Rowardennan, on Loch Lomondside, Scotland, and held in a 1 m<sup>2</sup> tank until needed for experiments. The fish were maintained under natural photoperiod and were fed commercial salmon food (Trouw) *ad libitum*. All parr were of approximately equal size and were from the upper mode of the size distribution (individuals that hatched during early 1999 and would smolt and migrate during autumn 2000) as they have been shown to maintain feeding throughout winter (Metcalfe *et al.*, 1988).

The experiment was conducted between January and March 2000, in identical sections of an outside artificial stream fed with a constant exchange of water pumped from Loch Lomond. Each section was 2.4 m long by 60 cm wide by 20 cm deep, bounded by wire mesh screens, lined with gravel, and contained 12 coloured bricks set perpendicular to the current to serve as shelters, current baffles and visual landmarks (Braithwaite *et al.*, 1996). The flume was covered with mesh lids to prevent escape and predation. The exterior flume wall was of opaque fibreglass, while the interior wall was of transparent glass surrounding a covered hide. Water velocity in the centre of the channel was 10–15 cm s<sup>-1</sup> (c. 1 body lengths s<sup>-1</sup>), a level within the preferred range of 10–12 cm fork length ( $L_F$ ) parr during autumn and winter (Rimmer *et al.*, 1984; Huntingford *et al.*, 1998; Veselov *et al.*, 1998).

Fish used in the flume were anaesthetized then weighed, their  $L_F$  measured, and individually marked with Alcian blue dye on their fins. Once marked, fish were held separately to recover from anaesthesia, then introduced to the stream sections after nightfall. Observations commenced the next morning (day 1). Five size-matched fish were used in each of the sections, and the experiment lasted 20 days. Data were collected from seven groups of fish.

Fish were fed twice daily on thawed frozen bloodworm washed through plastic tubes that passed from inside the hide, down the side of the flume, and under the fine gravel

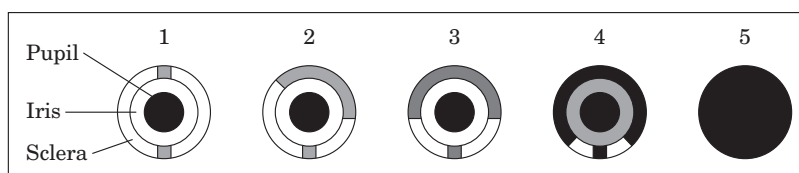


FIG. 1. Patterns of sclera colour and their designated scores. Eyes are drawn as if the fish were facing right.

substratum before emerging at the substratum surface. This method of worm release was designed to simulate natural invertebrate drift off the floor of the stream. Worms were introduced in clumps of one to five until *c.* 100 worms had been released into the stream during each feed. Each section was flanked (and thus separated) by deeper 'pool sections' that were 1.2 m long, contained fine nets, and trapped unconsumed bloodworms as they passed out of the experimental sections. The screens were cleaned daily after the second feed.

At the end of 20 days, the fish were killed using terminal anaesthesia and a blow to the head, and sex, length and mass data were collected.

### BEHAVIOURAL OBSERVATIONS

Each group of five fish was observed for *c.* 70 min a day. These observations were made during both feeding (twice daily, *c.* 20 min each; times could vary by 1–2 min) and non-feeding periods (three times daily, 10 min each). During each observation period, the identity of the initiator and recipient was recorded for all aggressive acts. An aggressive act was defined as a charge, chase or bite (Keenleyside & Yamamoto, 1962). Where a prolonged chase occurred, each burst of swimming was counted as one act. During feeding observations, a record was also made of which fish took each worm offered.

### SCORING EYE COLOUR

The eyes of the Atlantic salmon have a central black pupil surrounded by a narrow, brilliant yellow iris. A broad ring of tissue called the sclera, which can vary from cream to black (Keenleyside & Yamamoto, 1962), surrounds the iris. As the sclera gets darker, the iris fades, to the extreme stage where the entire eye appears black. A pilot study identified five clear patterns of sclera colouration. These patterns and the scores used to define them are shown in Fig. 1. The experiments were conducted during daylight hours under ambient lighting conditions. This meant that lighting could vary between observations, but also within observations as parts of the section could be in shade. To ensure that the sclera scores used were robust under different lighting conditions, the pilot study investigated whether observer perception of sclera score changed as fish moved between sunlight and shade, and whether the same patterns of sclera colour could be observed on overcast and sunny days. From these observations, scoring of sclera patterns appeared to be highly robust and unaffected by ambient lighting conditions.

Before and after each observation period, the group was scanned to identify the sclera score of each individual. Thus, the sclera colour of each individual was scanned 10 times each day, giving six scores from non-feeding periods, two pre-feeding scores and two post-feeding scores. Changes in sclera score within an observation period did occur, but were not recorded for practical reasons.

### ASSIGNING SOCIAL STATUS

Individuals within each group were assigned a social status (ranking from 1, dominant to 5, most subordinate). The number of aggressive acts received and initiated between each pair of fish in a group during 20 days of observations were totalled. The proportion of interactions won by each fish within each pairing was then calculated, and these proportions organized into an aggression matrix for each group (Martin & Bateson, 1986). The values for each fish were shuffled within the matrix until the proportions were

maximized in the bottom left of the matrix. The final order of individuals along the top of the matrix (from left to right) was used to rank the fish (1–5). Rank 1 was termed dominant, ranks 2–5 subordinate.

A variety of methods can be used to rank individuals within groups of juvenile salmonids, including food intake (McCarthy *et al.*, 1992), aggression (Adams *et al.*, 1998) and non-aggressive behaviours (Sloman *et al.*, 2000). Aggression appeared to be the primary force shaping group dynamics in this experiment and an aggression-based ranking system was therefore deemed appropriate.

Two-way ANOVAs of initial mass and  $L_F$  data (using social rank and group as factors) showed that rank was not affected by initial size (mass,  $P=0.201$ ;  $L_F$ ,  $P=0.232$ ).

#### EXAMINING RELATIONSHIPS BETWEEN SOCIAL STATUS AND COLOUR CHANGE

The first and last non-feeding sclera scores recorded for each fish on each day of the experiment were examined for a social status-based difference in sclera colour using Kruskal–Wallis analyses (adjusting for tied ranks). *Post-hoc* nonparametric multiple comparisons were made using a modified Nemenyi test that considers differences between mean ranks (Miller, 1981; Zar, 1999).

To examine daily fluctuations in sclera colour, the median basal sclera score (basal sclera score) was calculated for each individual for each day. This was defined as the median of the pre-feeding and non-feeding sclera scores recorded on that day. Post-feeding scores were excluded so that any short-term changes in sclera score attributable to the feeding experience would not affect the calculation of a basal sclera score.

The daily proportion of offered worms captured (foraging success) and the level of aggression initiated and received (acts per min) were also calculated for each fish. Basal sclera scores for 20 days were rank-transformed, and these ranks were then separately regressed against foraging success, aggression initiated and aggression received for each individual. The regression slopes calculated for each individual were used as single data points in *t*-tests. This allowed examination of relationships between social status, daily basal sclera score and aggressive and foraging experiences, while avoiding issues of pseudo-replication arising from multiple observations for each individual. A regression slope of zero indicates there is no relationship between sclera score and levels of aggression and foraging success for that fish. Two-tailed *t*-tests examined whether the average slope was significantly different from zero (regression slope data were normally distributed).

#### EFFECTS OF FEEDING

Changes in sclera colour over an observation period were examined by comparing the pre- and post-observation sclera scores for each fish and classifying them as the same or different. To examine effects of feeding, these changes were then compared for feeding and non-feeding observation periods. To avoid pseudo-replication, the proportions of changes during feeding and non-feeding periods observed over the 20 day period were calculated for each individual, and the difference between these proportions tested using paired two-tailed *t*-tests (data were normally distributed).

#### ETHICS

The experiment was carried out under a U.K. Home Office Licence (#60/2025). Fish were observed several times a day during the course of the experiment, so fish could have been removed if any kind of physical damage had been observed, or if fights had ever escalated to a point where injury could occur. This was never necessary, as overt aggression is rare once dominance hierarchies are established (Metcalf *et al.*, 1989). None of the fish sustained physical damage during the experiment.

### RESULTS

#### SCLERA COLOUR AND SOCIAL STATUS IN A SEMI-NATURAL ENVIRONMENT

How basal sclera scores of individuals of different rank changed over the course of 20 days is illustrated in Fig. 2. On the first day of the study, there was

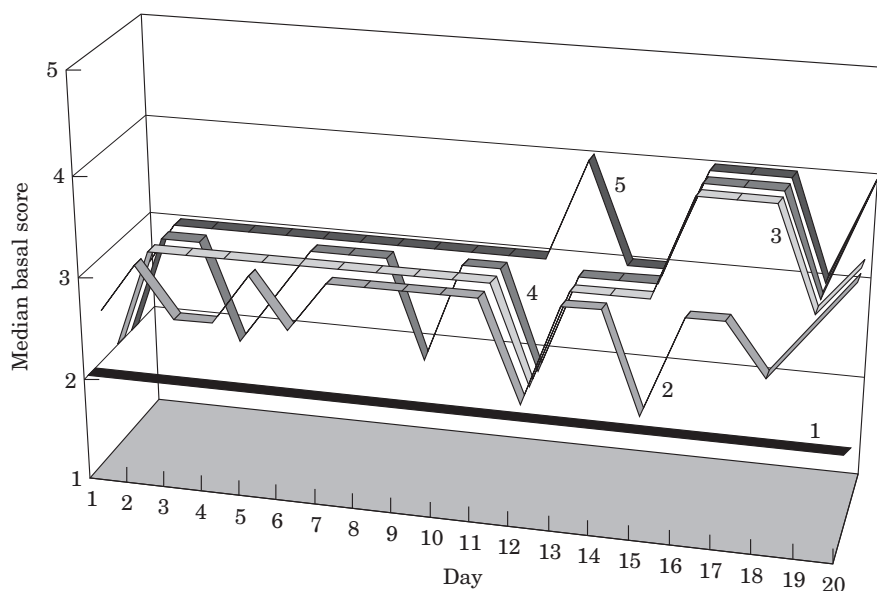


FIG. 2. Changes in the median basal sclera score of individuals of different social status over 20 days. Points represent the social rank median ( $n=7$ ) of median basal sclera scores of each individual, where the median daily basal sclera score is the median of sclera scores recorded before feeding observations and before and after non-feeding observations. Social status (numbers) is derived from aggression data collected over 20 days. The most aggressive (dominant) individual has a rank of 1.

no significant difference between the initial sclera scores of all fish based on their eventual social status (Kruskal–Wallis,  $P=0.906$ ). By the morning of day 3 after the start of the study, however, there was a significant difference in sclera score between individuals of different ranks ( $H=15.54$ , d.f.=4,  $P=0.004$ ), with the most dominant fish and the most subordinate fish having significantly different sclera scores. These differences persisted to the end of the experiment. On day 20, the final sclera colour of dominant fish was significantly lighter than that of the two most subordinate individuals (fish ranked 4 and 5).

#### DAILY FLUCTUATIONS IN SCLERA COLOUR: EFFECT OF AGGRESSION AND FEEDING

The basal sclera score of the dominant individual was very stable, while the basal sclera score of subordinate individuals fluctuated from day to day (Fig. 2). Regression analyses revealed that, on days that the two most subordinately ranked individuals were most heavily attacked, their basal sclera colour was darkest (two-tailed  $t$ -tests of individual regression slopes, rank 4:  $t=3.54$ ,  $P<0.05$ ; rank 5:  $t=3.31$ ,  $P<0.05$ ). A significant negative relationship was found between basal sclera score and levels of aggression initiated for rank 2 individuals ( $t=-2.45$ ,  $P=0.05$ ), suggesting that on days that these fish initiate more aggression, their basal sclera colour is lighter. All other relationships were non-significant.

The frequency of changes in sclera score during feeding and non-feeding observation periods were compared. The sclera was more likely to change colour during feeding than non-feeding observations (paired  $t$ -test:  $t=4.34$ ,  $n=35$ ,

$P < 0.001$ ). Repeating the  $t$ -tests for each rank separately, this relationship was found to apply only to fish ranked 2 and 3 ( $t = 2.69$ ,  $P < 0.05$  and  $t = 3.92$ ,  $P < 0.01$  respectively,  $n = 7$ ), although a similar trend was also present in the data for fish ranked 4 ( $t = 2.08$ ,  $P = 0.082$ ).

## DISCUSSION

These results support previous findings that sclera colour in Atlantic salmon can be used to differentiate between aggressively dominant and subordinate fish (Keenleyside & Yamamoto, 1962; O'Connor *et al.*, 1999, 2000), and suggest that the colour variation observed in artificial tank situations is also likely to occur within a stream environment. Status-based differences in sclera colour became obvious very soon after the start of the study. While the pale sclera colour of the dominant fish was very stable from day to day, subordinate fish experienced changes in sclera colour that were associated with changes in levels of aggression and foraging activity.

Temporal variation in subordinate colour has not been reported previously in salmonids, as darkening has represented the end point of observations. Most studies, however, have considered body rather than sclera colour. Although it is possible that fluctuations in eye colour are not always matched by corresponding shifts in body colour, O'Connor *et al.* (1999) reported a highly significant association between body and sclera colour of juvenile Atlantic salmon. Body colour was not scored during this experiment, but change in body and sclera colour did appear to be positively related. The darkest sclera score (when the eye is completely black) seemed to be associated with very dark body colour as defined by (O'Connor *et al.* (1999).

Looking at the social ranks separately, various relationships emerged between sclera colour and levels of aggression. Levels of aggression within each group varied from day to day, probably as a result of changes in individual motivational status. All subordinates had pale sclera at the start of the study, but subsequently darkened. The ranks were aggression-based, with subordinates receiving proportionally more attacks by definition. Thus, the strongest relationship that could be expected to emerge from the data would be that between levels of aggression received and darkening, particularly within the most subordinate ranks. This was found to be the case; the sclera of the two most subordinate ranks of fish (ranks 4 and 5) being darker on days they were attacked more. The sclera of rank 2 fish were lighter-coloured on days on which they initiated more attacks. These findings again illustrate that the sclera of subordinate fish did not simply darken and remain dark, but that they were responsive to daily variation in the aggressive environment. The above associations, detected on a daily basis, could be considered a conservative estimate of the associations occurring on a finer time-scale.

Status-based differences in the relationship between sclera colour and feeding activity were also apparent. The sclera colour of intermediate-ranked fish (ranks 2–4) was more likely to change during feeding than non-feeding observations, while the sclera of the most dominant and most subordinate individuals were unaffected by foraging activity. Thus, sclera changes occurred during feeding in intermediate-ranked fish, but not in fish at the extreme ends of the social scale.



Dominant sclera colour appears to remain light regardless of foraging experience, while the sclera colour of the most subordinate fish appears to remain dark.

Subordinate activity results in an increased chance of social interaction, which may lead to aggression. It makes sense to minimize interaction with the dominant (or higher ranked subordinates) during non-feeding periods, when there is little or no benefit to be had by fighting. During feeding, subordinate fish may be more active and thus involved in more social interactions that might influence sclera score. *Ad hoc* observations during the study showed that successful foraging was associated with sclera change, so changes recorded during feeding periods may not be solely due to increases in aggressive interaction.

Sclera colour was observed to change very rapidly (frequently within a minute) and often more than once during an observation period. On several occasions, subordinate fish were observed successfully feeding, and lightening, then being attacked and darkening within one observation period. Subordinate foraging activity is known to elicit attacks from dominant fish (Newman, 1956; Jenkins, 1969), but sclera lightening may also attract the attention of the dominant. Abbott *et al.* (1985) found that subordinate steelhead trout *Oncorhynchus mykiss* (Walbaum) maintained their dark body colouration when fed isolated from the dominant individual. It may be that successful foraging in full view and attack range of the dominant triggers a neural response that results in lightening of the subordinate sclera, a response that is absent if subordinates are fed in visual isolation. Clearly, experiments designed with the sole purpose of examining colour change during feeding need to be conducted. The very rapid change in sclera colour observed during successful foraging is likely to be under neural control, while the darker, basal sclera state of subordinates is more likely to be under the control of various neural and pituitary hormones (Fujii & Oshima, 1986; Höglund *et al.*, 2000). Elucidating the mechanism by which foraging success results in lightened sclera could provide an interesting comparison with mechanisms involved in translating aggressive stimuli into colour changes (Höglund *et al.*, 2000).

Groups of juvenile Atlantic salmon within streams form very stable social structures. While some fish are mobile, most maintain the same small home ranges for prolonged periods (Kalleberg, 1958). Some fish aggressively defend a territory based around a profitable feeding site, while others 'float' between the territories of more dominant individuals (Kalleberg, 1958; Puckett & Dill, 1985). Interactions between floating and territorial individuals are likely to be frequent during foraging, and the ability to communicate social status during these interactions could help to prevent unnecessary and potentially costly conflict (O'Connor *et al.*, 1999). Status signalling through body colour, however, may be disadvantageous in a stream situation, as pale individuals could be more visible to predators than their darkened, cryptic, conspecifics. Ignoring predation risk and signalling hypotheses, cryptic colouration in a natural situation may simply help subordinates to escape the attention of territory holders.

The results discussed here have demonstrated that subordinate juvenile Atlantic salmon have darker sclera than aggressively dominant individuals under semi-natural conditions. Also, under these conditions, short-term behavioural

experience can affect sclera colouration, especially in subordinate fish. Sclera darkened when subordinates were attacked more frequently, but were often observed to lighten in relation to increased foraging success. Foraging, and possible lightening, of the most subordinate fish elicited attacks from the dominant that resulted in sclera darkening. Fish of rank 2 lightened on days they initiated more aggression. The results suggest that subordinate rank and the aggressive response of the dominant affect the stability of sclera colour. Future work on the stimuli and mechanisms controlling colour change in salmonids under natural or semi-natural conditions would contribute to a better understanding of subordinate survival strategies in populations of juvenile salmonids.

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