



Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*?

KIRSTINE I. O'CONNOR, NEIL B. METCALFE & ALAN C. TAYLOR

Institute of Biomedical and Life Sciences, University of Glasgow

(Received 3 March 1999; initial acceptance 31 March 1999;
final acceptance 18 August 1999; MS. number: 6170R)

Communication by means of visual signals occurs during the competitive, aggressive and sexual interactions of many animals. Some animals such as fish are able to change their body coloration rapidly, and there is evidence that this is used as a means of signalling. However, the precise meaning of such signals is rarely understood. We examined whether (1) darkness in juvenile Atlantic salmon is associated with submission, and (2) changing to a darker colour could act as a signal to the opponent and hence induce a change in its behaviour. We found that both the sclera of the eye and the overall body coloration tended to darken in fish that were losing territorial encounters, while victors retained their original coloration. The darkening was rapid and usually occurred during a period of sustained attacks by the opponent; however, the aggression level decreased as soon as the losing fish had become darker. We suggest that the darkening of the losing fish was associated with submission and may result in a change in the behaviour of its opponent, so minimizing the potential risk of injury during unnecessarily prolonged fights.

© 1999 The Association for the Study of Animal Behaviour

Aggressive interactions are one of the most common situations in which animals are assumed to engage in signalling. Several different types of information could be conveyed in this context, including the relative social rank of a contestant and cues indicating its intent. Signals indicating status (e.g. 'badges of status'; Rohwer 1982; Roper 1986) tend to remain stable during a given encounter, whereas those conveying motivational state or intent are far more labile. Cues indicating intent allow combatants to assess their opponents continuously in order to decide whether to abandon or continue a fight (Enquist & Leimar 1983, 1987, 1990; Leimar & Enquist 1984; Enquist et al. 1990). While at first it might be assumed that transmission of such information to an opponent would be maladaptive, since individuals fighting over a resource have opposing interests in the outcome of the contest (Huntingford & Turner 1987), the contestants share a common interest in the avoidance of injury (Geist 1974; Enquist & Leimar 1990; Hurd 1997). There is therefore the potential for mutually beneficial and hence co-operative signalling between opponents to resolve disputes with minimal risk of potentially costly injuries (Hurd 1997). Other costs associated with escalated conflicts that may also be avoided include increased predation risk (Jakobsson et al. 1995) and lost foraging

opportunities (Grant 1997). Although this strategy of avoiding excessive physical contact would potentially be open to cheating, honest signalling is likely to be the evolutionarily stable strategy (van Rhijn & Vodegel 1980).

Communication of intent in a quickly developing contest requires a graded signal that can be modified rapidly, and hence visual signals are often used in this context. While these commonly take the form of changes in body posture or movement patterns, some animal groups appear to use rapid changes in body coloration. Examples are those species of fish (such as cichlids) that have the capacity to modify both the colour and the visual pattern of areas of the body within very short periods (Barlow 1963; deMartini 1985) by nervous and hormonal control of the expansion and contraction of thousands of pigment cells (chromatophores; Waring 1963; Fujii & Oshima 1986; Nelissen 1991; Hulscher-Emeis 1992). Although visual signalling is often assumed to be a principal means of communication in fish, the vast majority of studies on colour pattern variation in fish have focused on cichlids (Nelissen 1991; Hulscher-Emeis 1992). Previous studies have integrated the ethological and physiological aspects of colour change in the actor (Barlow 1963; Baerends et al. 1986; Hulscher-Emeis 1992), and several have suggested that visual signalling may modify the aggressive behaviour of the receiver (reviewed by Guthrie & Muntz 1993).

Correspondence: K. O'Connor, Fish Biology Group, Institute of Biomedical and Life Sciences, Graham Kerr Building, University of Glasgow, Glasgow G12 8QQ, U.K. (email k.oconnor@udcf.gla.ac.uk).

We studied contests in juvenile Atlantic salmon. In these young fish aggression is associated with the defence of a feeding territory rather than reproduction. There is some indication that body darkening is associated with territorial defence, as territory-holding salmon can become pale in overall coloration while fighting, but darken between bouts (Keenleyside & Yamamoto 1962). Aggressive fish will also develop vertical bands through each eye; Keenleyside & Yamamoto (1962) proposed that it would be possible to determine which was the most dominant fish in a tank since it would have the most pronounced vertical eye band. However, there has been no detailed investigation of either the factors that determine darkening, or whether it is apparently being used as a signal. Therefore we examined whether (1) darkening in juvenile Atlantic salmon is associated with submission, and (2) this darkening could act as a signal to the opponent and hence induce a change in its behaviour.

METHODS

A batch of full-sibling eggs from sea-run salmon caught in the River Almond, Perthshire, U.K., were incubated at the Scottish Office Agriculture, Environment and Fisheries Department Almondbank salmon rearing unit. We moved the eggs to the University Field Station at Rowardennan, Loch Lomond on 8 November 1996. Once hatched, the fish were kept under ambient photoperiod and temperature conditions in round tanks 1 m in diameter. These tanks received a continuous turnover of water pumped from Loch Lomond and was therefore rich in zooplankton. Once the yolk sacs of the fish were completely absorbed, we supplemented their diet with commercial salmon food (Fulmar feeds, BOCM Pauls Ltd, Glasgow, U.K.), which they received *ad libitum* from automatic feeders.

On 30 September 1997, we transferred 100 lower modal group fish (i.e. those that would delay seaward migration for at least a further 18 months; Thorpe 1977) to Glasgow University where they were kept in square tanks 1 m wide. The fish were kept at 15°C under ambient photoperiod and hand fed bloodworm (chironomid larvae species) *ad libitum*. At this stage the fish had a mean \pm SE forklength of 60.49 ± 0.75 mm ($N=80$) and weighed a mean \pm SE of 2.32 ± 0.09 g ($N=80$).

To aid further identification, we gave each fish a unique combination of marks with alcian blue dye on its pectoral, pelvic, dorsal, anal and/or caudal fins. This marking technique has no effect on the behaviour or growth of first-feeding salmon fry (Metcalfe et al. 1992).

We carried out the experiments between 28 October and 9 December 1997 (i.e. 7–9 months after first feeding), using an aquarium maintained at 15°C, with a 12:12 h light:dark regime.

Invasion Experiment

The tanks used for testing responses to territorial invasion were divided in half (10 × 10 cm) by an opaque partition, and had a water depth of 8 cm. At the centre of

the dividing partition was a circular door (6 cm diameter) which was initially kept shut. Three of the glass sides of the tank were coated in waterproof white paper leaving one side through which observations could be made. The substratum of each tank consisted of small marble chips (Esmo, 0.5 cm in diameter; Roweb, Glasgow, U.K.) which produced a topographically natural but light-coloured substratum against which the fish could easily be seen. Salmon parr in the wild will naturally come across patches of substratum of similar colour to the marble chips used in this experiment.

At 1500 hours at the start of each experimental run, we assigned fish to weight-matched pairs (mean percentage weight difference \pm SE = $8.19 \pm 7.84\%$), and placed one fish in each half of a tank. We refer to the fish placed in the left side of the tank as the 'resident', and the fish in the right side as the 'intruder'. Both sides of the tank were identical in every respect, except that the side of the door facing the intruder was marked with a red cross so that the intruder would be able to distinguish between its own familiar side of the tank and the side into which it was subsequently induced to invade (see below).

We left the fish for either 0, 1, 2 or 3 days in their respective sides of the tank before the experiment began. We varied prior residence time to investigate the effect of the duration of residency on the nature and outcome of aggressive encounters with intruding fish (unpublished data). For the present paper, we pooled the data for the different residence times.

Quantification of Body and Eye Coloration

Juvenile salmon are light brown on the dorsal and lateral surfaces down to approximately the lateral line. Below the lateral line they are light grey, shading to silver on the belly (Jones 1959). Straddling the lateral line along each side of the body are a series of clearly defined oval dark patches called 'parr marks'. There are 7–12 of these, with 11 or 12 being most frequent (Jones 1959). Dorsal to the lateral line are numerous black or dark brown oval patches. These are scattered over the entire dorsal and dorso-lateral surfaces with concentrations in several irregular bands which straddle the mid-dorsal line.

We used three areas to grade the colour of the fish (Fig. 1): (1) the parr marks; (2) the spaces between the parr marks; and (3) the oval patches straddling the mid-dorsal line of the fish. We assigned each of these areas to one of three categories according to its colour (Table 1). We also scored eye coloration. The eyes of the salmon have a central black pupil surrounded by a narrow, brilliant yellow iris. Around this iris is the broader sclera which can vary from light grey to black. We graded the colour of the sclera on a scale of 1–3 (Table 1). The intermediate sclera coloration occurs when the melanophores anterior and posterior to the pupil expand and lead to darkening of the sclera, while the sclera in front of and behind the pupil remains light grey (Keenleyside & Yamamoto 1962). All colour scoring was done by K.I.O'C. To assess the objectivity of the colour grading, the scores were compared to those obtained by five independent fish biologists asked to grade the same 10 fish using the method

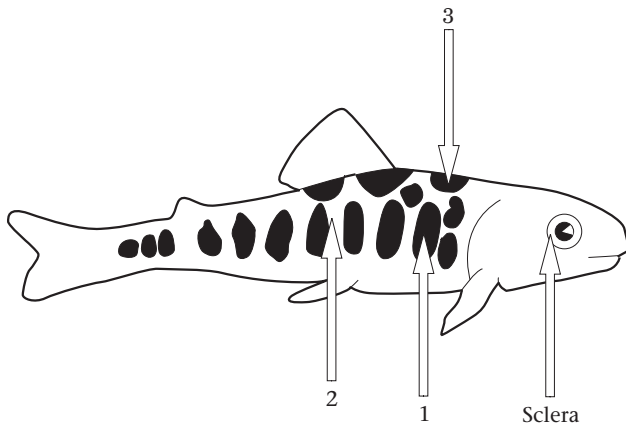


Figure 1. Areas of the body of a juvenile salmon used for scoring colour: (1) parr marks; (2) spaces between parr marks; (3) oval patches; (4) sclera or eye ring.

described. There was an 80% agreement between the score given by K.I.O'C. and those of the other five scorers, with no consistent bias being evident. Since 18 different colour grade combinations were identified during the experiment, an 80% agreement constitutes a high level of concordance, and we therefore concluded that the method provided a sufficiently accurate and objective means of scoring the colour patterns of the fish.

We colour graded both fish involved in each experiment at 4, 2 and 0 min before the start of the simulated territory invasion. We then opened the door between the two sides of the test tank and, using a transparent Perspex rod, gently induced the intruder to move into the resident's side of the tank. Once both fish were in the resident's side of the tank the door was closed. We then recorded the behaviour of the two fish continuously for 2 h. We classified the different behaviours of the fish according to a modification of the scheme outlined by Keenleyside & Yamamoto (1962). To assign dominance within the pairs of fish, we gave their behaviours point values and the fish that totalled the most points was classified as the winner of the contest. We assigned points to behaviours as follows: one point for each lateral display, where the fish expanded all its fins maximally, tensed its body and arched its tail upwards, before beating its tail slowly, irregularly and with wide amplitude; two points for each charge, which was the most direct form of attack and involved one fish swimming directly and quickly towards its opponent; and three points for each charge that culminated in the aggressor biting its

opponent. Biting involved approaching the opponent with an open mouth but closing it on contact. Bites were typically focused at the opercular flap region and did not puncture the skin.

In conjunction with recording the behavioural interactions, we scored the body and sclera colour of each fish each minute over the 2-h observation period. Unfortunately the observation time limitations meant that it was not possible to record the body postures of the fish as well.

At the end of the observation period, we left the fish for 2 h, after which we scored their colour again. The fish were then fed bloodworm and left overnight in the same section of the observation tank. Next morning they were scored for colour again before being removed and returned to the stock tank. We carried out 40 replicate territorial invasions, each with previously untested fish.

Ethical Note

The experiment was carried out under licence from the U.K. Home Office. The fish were under observation continuously during the period when the dominance status of the fish was established, so that we could intervene and remove either fish immediately if contests ever escalated to a point where injury could occur. However, this was never necessary. Interaction rates in salmon are low and rarely involve overt aggression once dominance hierarchies are established (Metcalf *et al.* 1989; see also Fig. 4 below). None of the fish sustained physical damage during the contests. In the 34 contests involving point scoring by either fish, the winner bit its opponent an average of 12 times over the 2 h of observations but bites did not puncture the skin (see above).

RESULTS

Patterns of Darkening

Prior to the territorial invasion (2 and 4 min before the partition door was opened) 75 out of 80 fish (94%) were assigned the palest possible body colour classification (1, 1, 1) and had a sclera colour grade 1. This pale coloration was therefore taken to represent the 'normal' condition. Any change in colour to a higher grade than that scored during the two preinvasion measurements we deemed a darkening. Two fish darkened both body and eye colour the instant the intruder entered the resident's side of the tank. However, as no behavioural data had been collected

Table 1. Description of the colour changes and assigned scores for the eye and three areas of the body of each fish

Score	Body area 1	Body area 2	Body area 3	Sclera
1	Light grey/cream	Cream/white	Light grey/cream	Light grey
2	Slate grey	Light brown/grey	Slate grey	Dark grey above and below the pupil, light grey in front and behind ('vertical bar')
3	Dark grey/black	Slate grey	Dark grey/black	Dark grey/black

Body areas are shown in Fig. 1.

by this time, we did not include these fish in the statistical analyses of the factors causing colour changes. Of the 40 contests that were staged, 22 resulted in both body and sclera darkening in at least one of the two fish, which indicates a highly significant association between colour changes of the two areas (chi-square: $\chi^2=21.78$, $P<0.001$). Two contests resulted only in body darkening and two only in sclera darkening. No contests involved body and sclera darkening in both fish.

Four hours after the start of the territorial invasion, seven of the fish that had darkened their body colour had returned to their original pale coloration. Next morning, 12 of the 24 were back to their normal pale body colour, while the rest were still dark.

Links Between Colour Change and Aggression

During six of the trials, neither of the fish was aggressive, and in one trial both fish obtained the same aggression score and so could not be assigned to relative dominance categories. None of the fish involved in these seven trials darkened, and all seven trials were excluded from the statistical analyses of dominance. The mean difference \pm SE in points scored between the winner and loser in the remaining trials was 65.42 ± 15.29 ($N=33$).

Of the 24 fish that developed a darker body colour, 19 were losers of the territorial contest while five were winners; thus fish winning a contest were significantly less likely to darken their body colour than those that lost (chi-square: $\chi^2=12.83$, $P<0.001$). Of the five winners that darkened, two returned to their original colour within the following 20 min, and the mean point difference between opponents \pm SE was 28 ± 14.6 , which is considerably less than the mean point difference between the opponents in the 19 contests in which the loser darkened (100.42 ± 23.18). The same trend for darkening to be associated with losing was shown with eye coloration: 19 of the 25 fish that changed sclera colour were losers while six were winners (in one fight both the winner and loser changed), so fish that won contests were less likely to darken their sclera than those that lost (chi-square: $\chi^2=9.14$, $P<0.01$).

The probability of an encounter resulting in body or eye darkening increased with the total number of points scored in the contest (logistic regressions: model χ^2_1 for body colour = 14.40, $P<0.001$; model χ^2_1 for eye colour = 20.77, $P<0.001$). The amount of aggression a fish received influenced significantly the probability that it would darken, since the more points that were scored against it the greater the likelihood that both body and sclera colour would darken (logistic regressions: model χ^2_1 for body = 26.03, $P<0.001$; model χ^2_1 for sclera = 29.28, $P<0.001$; Fig. 2). However, the number of attacks initiated by a fish had no effect on how likely it was to darken its body or sclera colour (logistic regressions: model χ^2_1 for body = 3.08, $P=0.08$; model χ^2_1 for sclera = 0.27, $P=0.60$).

We calculated an index of body darkening throughout the experiment as the sum of the mean grades awarded for each of the body areas prior to the invasion at the start of the experiment subtracted from the sum of the grades

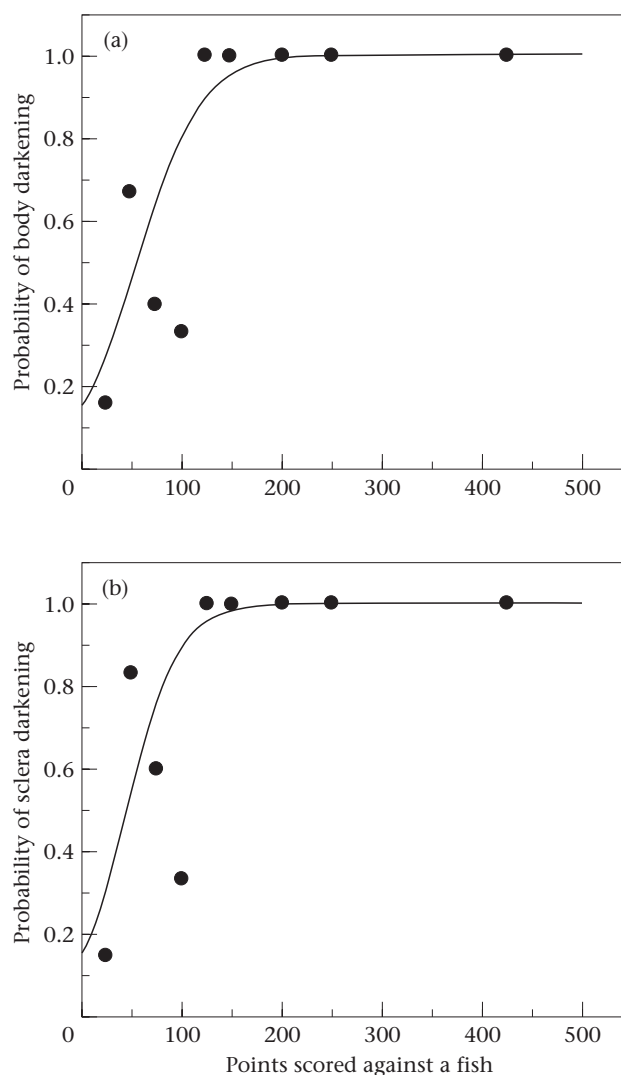


Figure 2. Relationship between points scored against a juvenile salmon and the likelihood of (a) the body and (b) the eye sclera darkening. Points were awarded for aggressive behaviours as follows: 1 point for each lateral display; 2 points for each charge; 3 points for each charge culminating in a bite. Points scored against a fish were grouped together into 25 point bands so that the nine data points on the graph represent 33 fights. Equations of the logistic regression lines are as follows (see text for statistical analysis): probability of body darkening = $a/(a+1)$, where $a=e^{(0.0315X-1.7593)}$; probability of sclera darkening = $a/(a+1)$, where $a=e^{(0.0388X-1.7264)}$.

at the end of the 2-h observation. Therefore a fish that scored 1, 1, 1 at the start and 3, 1, 3 at the end would have an index of body darkening of four (i.e. 7–3). An aggression difference score was also calculated as the difference between the points scored by a fish and its opponent. The degree of darkening of losers was inversely proportional to the signed difference in the aggression difference scores of the two fish (Fig. 3; Spearman rank correlation; $r_s = -0.67$, $N=33$, $P<0.001$). Hence the greater the extent to which a loser was attacked by the winner, the darker its final colour. However, there was no relationship between the difference in aggression difference points scored and the comparable index of body darkening in winners

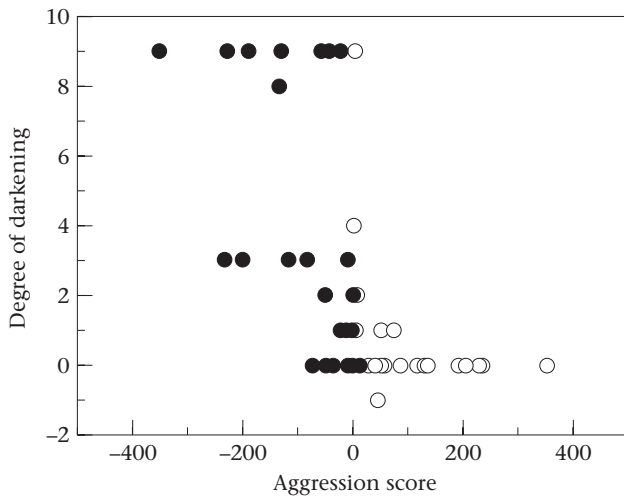


Figure 3. The relationship between net aggression difference score and index of the extent of body darkening in juvenile salmon. ●: Losers (i.e. those with an aggression difference score less than zero); ○: winners. See text for statistical analysis.

(Fig. 3; Spearman rank correlation: $r_s = -0.23$, $N=33$, $P=0.19$). Winners therefore tended to retain their initial coloration.

For those fish that darkened during the 2 h of continuous observation, there was no relationship between the number of points scored against them up to the time of the darkening and the time at which the colour change took place (linear regression: body: $r^2=0.04$, $F_{1,23}=0.97$, $P=0.34$; eye: $r^2=-0.03$, $F_{1,22}=0.95$, $P=0.34$). Thus the amount of aggression a fish was subjected to did not determine how quickly it darkened. There was also no relationship between the percentage weight difference of the two opponents and the time at which one of the fish darkened (linear regression: body: $r^2=-0.03$, $F_{1,23}=0.37$, $P=0.55$; eye: $r^2=-0.04$, $F_{1,22}=0.10$, $P=0.76$). Hence the time of darkening was not mediated by a size asymmetry. However, there was a positive relationship between the time at which the sclera darkened and when the body darkened, indicating that the two areas tended to darken simultaneously (Spearman rank correlation: $r_s=0.91$, $N=24$, $P<0.001$).

To determine whether the darkening in a loser acts as a signal to its opponent, or is merely a reaction to the aggression to which it is subjected, we examined the behaviour of the winner and loser relative to the time of the losing fish's colour change. To do this, we calculated the points scored by the winner during successive 10-min periods with respect to the time of the loser's first body or sclera darkening. The mean rate of aggression (points scored per 10-min period) against the loser increased dramatically until it first darkened its body or eye colour (Fig. 4; Spearman's rank correlation: body: $r_s=0.96$, $N=11$ time periods, $P<0.001$; eye: $r_s=0.87$, $N=11$, $P<0.001$). However, after the initial darkening of colour, the aggression rate dropped equally rapidly (Fig. 4; Spearman's rank correlation: body: $r_s=-0.86$, $N=10$, $P<0.01$; eye: $r_s=-0.87$, $N=10$, $P<0.001$). This result suggests that there is an association between the darkening of the

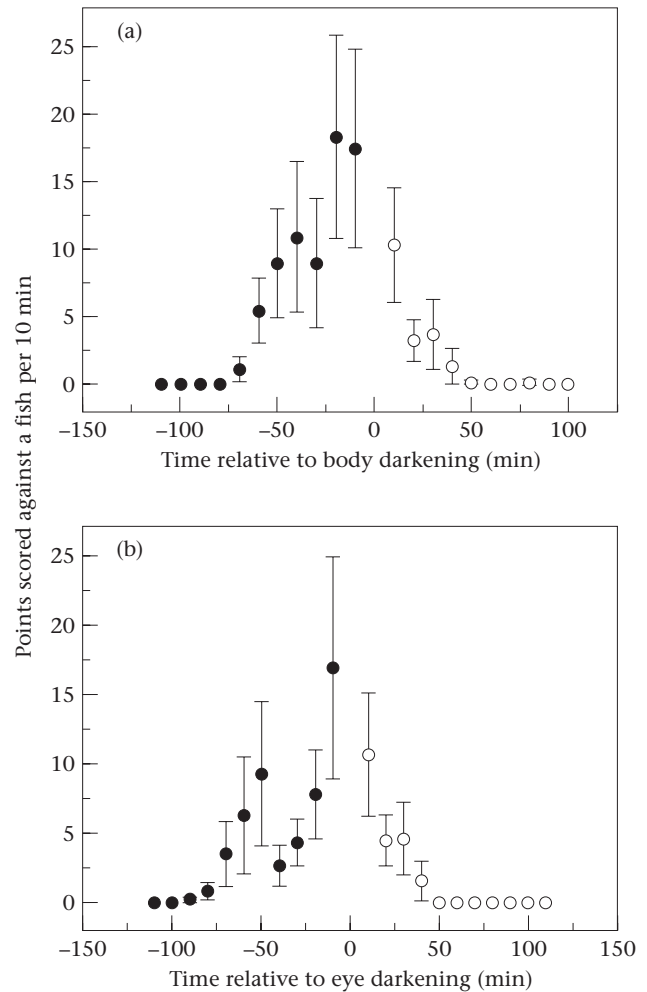


Figure 4. The relationship between the rate of incurred aggression (points per 10 min) and time of first darkening in (a) the body and (b) the eye sclera of juvenile salmon losing territorial contests. ●: Predarkening aggression rate; ○: postdarkening aggression rate. Vertical bars indicate SE.

loser and the change in the aggressive behaviour of the opponent.

There was a nonsignificant trend for the mean rate of aggression (points scored per 10-min period) by the loser to increase up to the time when it first darkened its body or eye colour (Fig. 5; Spearman's rank correlation: body: $r_s=0.58$, $N=11$ time periods, $P=0.06$; eye: $r_s=0.56$, $N=11$, $P=0.07$). As the mean rate of aggression focused at the subordinate fish by the dominant fish increased up to the point when it darkened it might have been under increasing pressure to defend itself. Thus the increase in mean aggression rate by the subordinate fish might have been a direct result of an increase in encounter rate. However, the mean aggression rate of the loser was consistently lower than that of the winning fish throughout the contest. The increase in aggression rate of the subordinate would seem to suggest that the change in behaviour of the dominant fish was in response to something other than a change in behaviour of the subordinate since just before it darkened it became more aggressive.

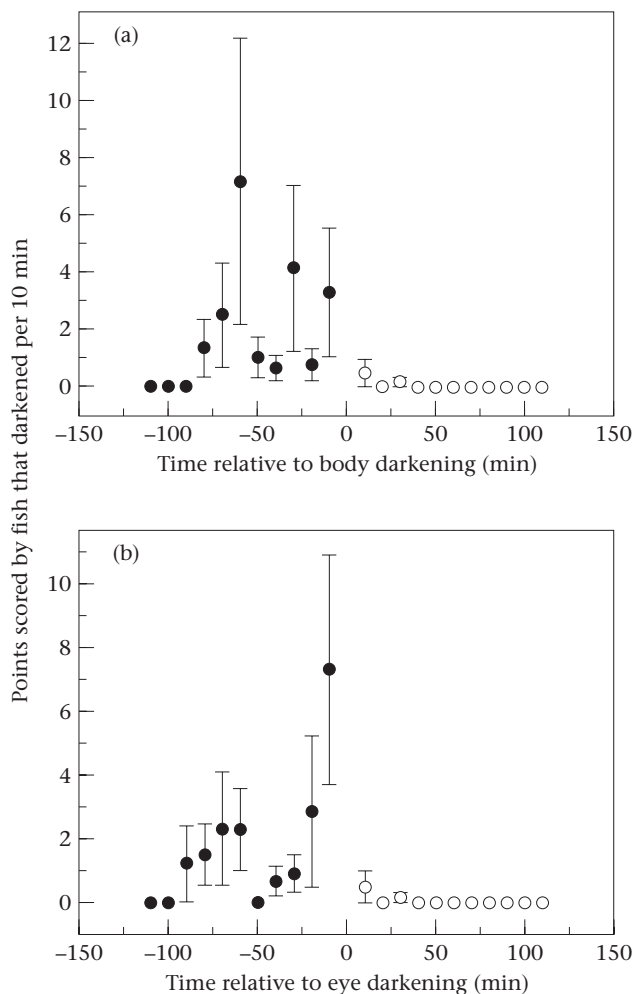


Figure 5. The relationship between the rate of aggression (points per 10 min) by the fish that darkened and time of first darkening in (a) the body and (b) the eye sclera of juvenile salmon. ●: Predarkening aggression rate; ○: postdarkening aggression rate. Vertical bars indicate SE.

DISCUSSION

Our results indicate that juvenile Atlantic salmon parr typically adopt a uniformly pale coloration when on a light-coloured substrate, and that darkening of the body and sclera are associated with an aggressive encounter with a dominant fish. A relationship between temporary changes in body colour and dominance has been observed in several other species of fish (Baerends et al. 1955; Okaichi et al. 1958; Stacey & Chiszar 1975, 1977; De Boer 1980). In contests involving two salmon, the subordinate fish was more likely to become darker than the dominant, which usually retained its normal light coloration. The more intense the fight, the greater the likelihood that one fish would darken, and the more aggression a fish received, the more likely it was to be the one that darkened. There did not appear to be a set threshold level of incurred aggression at which a darkening was triggered in the subordinate fish, but the greater the difference in aggression between the dominant and subordinate fish, the darker the subordinate became.

Darkening of the sclera and body appeared to be closely linked, since they almost always occurred simultaneously. It is unlikely that darkening simply indicates stress, since the fish became paler again while the stress of being subordinate persisted. Stress responses (i.e. elevated cortisol levels) in salmonids can persist for up to 4 weeks (Pickering & Pottinger 1989). Therefore if darkening was simply a stress response, we would expect it to persist for the remainder of each trial.

All of the above trends suggest that the sudden change to a darker colour is linked to the moment when a fish loses an aggressive interaction and becomes subordinate to its opponent. This interpretation is supported by the fact that the behaviour of the more dominant fish changed abruptly once its opponent changed colour. As a result, the number of attacks on the subordinate decreased rapidly. The change in the dominant's behaviour is probably a result of the loser darkening rather than a response to a change in behaviour of the loser, since in the time leading up to the colour change the loser tended to become increasingly aggressive, and reduced its aggression only once it had changed colour and the dominant's behaviour had changed. These results suggest that the change in behaviour of the dominant is associated with the darkening, and not with a change in the aggressive behaviour of the loser.

There are two clear hypotheses to account for this effect: darkening either makes the subordinate fish less conspicuous to the aggressor (Rasa 1969), or it is associated with, and may indeed signal, defeat. Reduced conspicuousness does not seem plausible since the substratum used in the experiment was very pale in colour. The second explanation therefore seems more likely: the darkening of the subordinate fish is associated with submission and in this way may signal its defeat. Previous studies have shown that darkened subordinate rainbow trout, *Oncorhynchus mykiss*, also change their body postures when dominant fish are present (Abbott et al. 1985). Body posturing may act in conjunction with body darkening to signal submission to the dominant fish, although we did not record postures in this study. To confirm that darkening signals submission, further research is needed. If either the colour of the fish, or their ability to darken, could be manipulated it would be possible to assess the impact of colour alone on the dominant's behaviour and in this way tease apart the influence of colour and other variables such as body posture. In addition, body and sclera could be manipulated separately to identify the signals provided by the two areas.

The social system of salmonids in streams is very stable. A minority of fish are mobile, but most maintain the same small home ranges for prolonged periods (Kalleberg 1958). Within these small home ranges, some fish aggressively defend a territory while others adopt a floating strategy, avoiding conflict by living in the interstices between the sites occupied by more dominant individuals (Kalleberg 1958; Bachmann 1984; Puckett & Dill 1985). Interactions between fish for feeding positions are therefore likely to be frequent. The balance between the value of the contested resource and the value of the future is an

important factor influencing the frequency of death or severe injury during a fight (Enquist & Leimar 1990). Although obtaining a feeding station is an important factor in determining early performance in salmonids (Elliott 1994), fish should not invest too heavily in attempting to obtain or defend a particular feeding territory at this early stage of their life history. They should therefore avoid the dangerous fights seen between combatants when a major part of a contestant's lifetime reproductive success is at stake (Enquist & Leimar 1990).

In this situation, rapid communication is paramount to avoid unnecessary and potentially costly fights. The status-signalling hypothesis proposed by Rohwer (1975) suggests that superior fighters benefit from distinctive colour markings ('badges of status') because these reduce the number of aggressive contests that are needed to maintain their dominance status, while subordinates benefit by avoiding interactions with superior individuals (Rohwer 1982; Senar & Camerino 1998). However, darkening, which could be a signal, is a trait more characteristic of subordinates than dominants in salmon, and it does not appear to prevent the onset of aggression; rather, it accompanies defeat. It is likely that darkening in subordinates receiving frequent attacks may be a result of extreme stress, which also indicates subordination to the opponent. Since subordinates did not maintain their darker coloration after the initial contest, this may carry an associated cost, such as increased conspicuousness and hence risk of predation (see Morris et al. (1995) for discussion of costs of vertical bars in swordtail fish, *Xiphophorus multilineatus*).

Classical models of animal conflicts such as the Hawk-Dove war of attrition (see Maynard Smith 1982 for a review) are probably less appropriate to contests between salmon than the sequential assessment model (Enquist & Leimar 1983, 1987, 1990; Leimar & Enquist 1984; Enquist et al. 1990). This model assumes that there is an assessment process that occurs during fights such that individuals perform behaviours that provide information to their opponents about their fighting ability. As the fight proceeds, the combatants build up an increasingly accurate profile of their opponent's capabilities as they assess asymmetries such as differences in size or strength. Eventually one contestant will judge the other to be stronger and will give up, thereby avoiding any (further) injury. In juvenile salmon, the abandonment of the fight was then accompanied, and possibly signalled, by the darkening in skin and eye colour.

The sequential assessment model predicts that subsequent fights between the same contestants will be shorter if they can remember their opponent's fighting potential. The majority of disputes among salmon over territories will be between long-term neighbours. Salmonids apparently have the capacity for individual recognition, in that they are less aggressive to familiar opponents (Johnsson 1997). It would be interesting to test whether darkening during a conflict varies according to the familiarity of the opponents, since fish may signal their submission to a familiar and more dominant individual by darkening before they have incurred the cost of being attacked (see Whitfield 1987 for a discussion of the relative roles

of the individual recognition and status-signalling hypotheses).

Acknowledgments

This work was carried out whilst K.I.O'C. was in receipt of a NERC studentship. We are grateful to John Laurie for technical assistance and BOCM Pauls Ltd. for provision of fish feed. The manuscript benefited from the comments of two anonymous referees.

References

- Abbott, J. C., Dunbrack, R. L. & Orr, C. D. 1985. The interaction of size and experience in dominance relationships of juvenile steelhead trout (*Salmo gairdneri*). *Behaviour*, **92**, 241–253.
- Bachmann, R. A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. *Transactions of the American Fisheries Society*, **113**, 1–32.
- Baerends, G. P., Brouwer, R. & Waterbolk, H. T. J. 1955. Ethological studies on *Lebistes reticulatus* (Peters). I. An analysis of the male courtship pattern. *Behaviour*, **8**, 249–334.
- Baerends, G. P., Wanders, J. B. W. & Vodegel, R. 1986. The relationship between marking patterns and motivational state in the pre-spawning behaviour of the cichlid fish *Chromidotilapia guentheri* (Sauvage). *Netherlands Journal of Zoology*, **36**, 88–116.
- Barlow, G. W. 1963. Ethology of the Asian teleost, *Badis badis*: II. Motivation and signal value of the colour patterns. *Physiological Zoology*, **11**, 97–105.
- deMartini, E. E. 1985. Social behaviour and coloration changes in painted greenling, *Oxylebius pictus* (Pisces: Hexagrammidae). *Copeia*, 966–975.
- De Boer, B. A. 1980. A causal analysis of the territorial and courtship behaviour of *Chromis cyanea* (Pomacentridae, Pisces). *Behaviour*, **73**, 1–50.
- Elliott, J. M. 1994. *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.
- Enquist, M. & Leimar, O. 1983. Evolution of fighting behaviour: decision rules and assessment of relative strength. *Journal of Theoretical Biology*, **102**, 387–410.
- Enquist, M. & Leimar, O. 1987. Evolution of fighting behaviour: the effect of variation in resource value. *Journal of Theoretical Biology*, **127**, 187–205.
- Enquist, M. & Leimar, O. 1990. The evolution of fatal fighting. *Animal Behaviour*, **39**, 1–9.
- Enquist, M., Leimar, O., Ljungberg, T., Mallner, Y. & Segerdahl, N. 1990. A test of the sequential assessment game: fighting in the cichlid fish *Nannacara anomala*. *Animal Behaviour*, **40**, 1–14.
- Fujii, R. & Oshima, N. 1986. Control of chromatophore movements in teleost fishes. *Zoological Science*, **3**, 13–47.
- Geist, V. 1974. On fighting strategies in animal combat. *Nature*, **250**, 354.
- Grant, J. W. A. 1997. Territoriality. In: *Behavioural Ecology of Teleost Fishes* (Ed. by J.-G. J. Godin), pp. 81–103. Oxford: Oxford University Press.
- Guthrie, D. M. & Muntz, W. R. A. 1993. Role of vision in fish behaviour. In *Behaviour of Teleost Fishes* (Ed. by T. J. Pitcher), pp. 112–115. New York: Chapman & Hall.
- Hulscher-Emeis, T. M. 1992. The variable colour patterns of *Tilapia zillii* (Cichlidae): integrating ethology, chromatophore regulation and the physiology of stress. *Netherlands Journal of Zoology*, **42**, 525–560.
- Huntingford, F. A. & Turner, A. K. 1987. *Animal Conflict*. London: Chapman & Hall.

- Hurd, P. L. 1997. Cooperative signalling between opponents in fish fights. *Animal Behaviour*, **54**, 1309–1315.
- Jakobsson, S., Brick, O. & Kullberg, C. 1995. Escalated fighting behaviour incurs increased predation risk. *Animal Behaviour*, **49**, 235–239.
- Johnsson, J. I. 1997. Individual recognition affects aggression and dominance relations in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, **103**, 267–282.
- Jones, J. W. 1959. *The Salmon*. London: Collins.
- Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Institute of Freshwater Research Drottningholm*, **39**, 55–98.
- Keenleyside, M. H. A. & Yamamoto, F. T. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). *Behaviour*, **19**, 139–169.
- Leimar, O. & Enquist, M. 1984. Effects of asymmetries in owner–intruder conflicts. *Journal of Theoretical Biology*, **111**, 475–491.
- Maynard Smith, J. 1982. *Evolution and Theory of Games*. Cambridge: Cambridge University Press.
- Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London, Series B*, **236**, 7–19.
- Metcalfe, N. B., Wright, P. J. & Thorpe, J. E. 1992. Relationships between social status, otolith size at first feeding and subsequent growth in Atlantic salmon (*Salmo salar*). *Journal of Animal Ecology*, **61**, 585–589.
- Morris, M. R., Gass, L. & Ryan, M. J. 1995. Assessment and individual recognition of opponents in the pygmy swordtails *Xiphophorus nigrensis* and *X. multilineatus*. *Behavioral Ecology and Sociobiology*, **37**, 303–310.
- Nelissen, M. H. J. 1991. Communication. In: *Cichlid Fishes: Behaviour, Ecology and Evolution* (Ed. by M. H. A. Keenleyside), pp. 225–241. London: Chapman & Hall.
- Okaichi, T., Kai, H. & Hashimoto, Y. 1958. A rapid colour change in the filefish. *Bulletin of the Japanese Society of Scientific Fisheries*, **24**, 389–393.
- Pickering, A. D. & Pottinger, T. G. 1989. Stress responses and disease resistance in salmonid fish: effects of chronic elevation of plasma cortisol. *Fish Physiology and Biochemistry*, **7**, 253–258.
- Puckett, K. J. & Dill, L. M. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour*, **92**, 79–111.
- Rasa, O. A. E. 1969. Territoriality and the establishment of dominance by means of visual cues in *Pomacentrus jenkinsi* (Pisces: Pomacentridae). *Zeitschrift für Tierpsychologie*, **26**, 825–845.
- van Rhijn, J. G. & Vodegel, R. 1980. Being honest about one's intentions: an evolutionary stable strategy for animal conflicts. *Journal of Theoretical Biology*, **85**, 623–641.
- Rohwer, S. 1975. The social significance of avian winter plumage variability. *International Journal of Organic Evolution*, **29**, 593–610.
- Rohwer, S. 1982. The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, **22**, 531–546.
- Roper, T. J. 1986. Badges of status in avian societies. *New Scientist*, **109**, 38–40.
- Senar, J. C. & Camerino, M. 1998. Status signalling and the ability to recognise dominants: an experiment with siskins (*Carduelis spinus*). *Proceedings of the Royal Society of London, Series B*, **265**, 1515–1520.
- Stacey, P. B. & Chiszar, D. 1975. Changes in the darkness of four body features of bluegill sunfish (*Lepomis macrochirus* Rafinesque) during aggressive encounters. *Behavioural Biology*, **14**, 41–49.
- Stacey, P. B. & Chiszar, D. 1977. Body colour pattern and the aggressive behaviour of male pumpkinseed sunfish (*Lepomis gibbosus*) during the reproductive season. *Behaviour*, **64**, 3–4.
- Thorpe, J. E. 1977. Bimodal distribution of length of juvenile Atlantic salmon (*Salmo salar* L.) under artificial rearing conditions. *Journal of Fish Biology*, **11**, 175–184.
- Waring, H. 1963. *Color Change Mechanism of Cold-blooded Vertebrates*. New York: Academic Press.
- Whitfield, D. P. 1987. Plumage variability, status signalling and individual recognition in avian flocks. *Trends in Evolution and Ecology*, **2**, 13–18.