

# The importance of being familiar: individual recognition and social behavior in sea trout (*Salmo trutta*)

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This study addressed two hypotheses: (1) that individual recognition is used to reduce the cost of contesting resources in sea trout and (2) that the hatchery environment selects against individual recognition. Predictions from these hypotheses were tested in laboratory experiments where behavior and growth were studied in juvenile sea trout. Intact groups of familiar fish were compared with groups that contained both familiar and unfamiliar individuals. In general, the results were in agreement with the first hypothesis. Familiar fish in intact groups had more stable dominance ranks, higher food intake, and better utilization of food. Familiarity also reduced the distance to the nearest neighbor. Furthermore, initiators of conflicts were more likely to win against familiar fish than against strangers. These results support game-theory-based hypotheses explaining the dear-enemy phenomenon as an effect of familiarity. A picture emerges in which familiarity stabilizes the hierarchical structure of a group and governs behavioral modifications that will promote feeding and growth, in turn leading to higher fitness. The second hypothesis, which predicted a reduced effect of individual recognition in sea-ranched trout, was not strongly supported because familiarity affected sea-ranched and wild trout similarly in most respects. However, familiarity was not beneficial for growth in sea-ranched trout, whereas it increased growth rate in wild fish. In addition, sea-ranched trout tended to maintain larger distances to their nearest neighbors than did wild trout. *Key words*: brown trout, individual recognition, *Salmo trutta*, social behavior. [*Behav Ecol* 9:445–451 (1998)]

Behavioral research is accumulating evidence for the widespread ability of animals to distinguish among conspecifics (Magurran et al., 1994). This ability can confer several advantages. Maynard Smith and Parker (1976) suggested that the evolutionarily stable strategy (ESS) in asymmetric contests will usually be to "permit the asymmetric cue to settle the contest without escalation." Individual recognition can be used as such a cue to reduce the potential fitness costs of escalated contests over resources, especially when other cues of fighting ability are unreliable (Barnard and Burk, 1979). Indeed, individual recognition has been shown to reduce contest aggression in breeding turnstone, *Arenaria interpres* (Whitfield, 1986), pygmy swordtails, *Xiphophorus nigrensis* and *X. multilineatus* (Morris et al., 1995), and rainbow trout, *Oncorhynchus mykiss* (Johnsson, 1997).

Both dominants and subordinates may benefit from stable groups through the advantages of clear hierarchical roles (Senar et al., 1990; Ydenberg et al., 1988; see also Getty, 1989). Consistent with these ideas, guppies (*Poecilia reticulata*) prefer to associate with familiar individuals rather than unfamiliar (Griffiths and Magurran, 1997; Magurran et al., 1994). Repeated interactions between familiar individuals could also facilitate the formation of cooperative partnerships (Milinski, 1991). Dugatkin and Wilson (1992) found that the tendency for bluegill sunfish (*Lepomis macrochirus*) to associate with familiar individuals was stronger after successfully foraging with that individual. Furthermore, Van Rhijn and Vodegel (1980)

suggested that recognition of individuals in a group can prevent the invasion of "signal cheaters," thereby maintaining a signal of motivation.

In this study we examined the effect of familiarity on behavior in foraging groups of sea trout. After emergence from the nest, trout fry start to establish feeding territories or form social groups, depending on population density and habitat structure (Elliott, 1994; Jenkins, 1969). Under both these conditions, selection should favor the use of individual recognition to modify behavior, thereby reducing the cost of contesting resources. In contrast, if fish cannot distinguish between familiar and unfamiliar conspecifics, no such behavioral modifications are expected (null hypothesis).

The main predictions from the hypothesis above are that aggression levels should be lower in groups consisting of familiar individuals and that there should be smaller changes in the social hierarchy compared with new groups joined by unfamiliar fish. More time could be spent feeding instead of fighting, and the growth rate should thus be higher in groups of familiar fish. Furthermore, assuming that nearest-neighbor distance decreases with increasing tolerance, familiar fish should be positioned closer together than unfamiliar individuals.

Hatchery selection alters the behavior of salmonids in multiple ways (e.g., Johnsson and Abrahams, 1991; Johnsson et al., 1996; Mesa, 1991; Moyle, 1969; Swain and Riddell, 1990). These changes have been attributed to relaxed and/or altered selection pressures in the hatchery environment (Kohane and Parsons, 1989). Hatchery trout are generally reared at much higher densities than are common in nature, and it therefore appears that it would be difficult for a fish to distinguish between thousands of conspecifics in a hatchery tank. Moreover, the reduced environmental heterogeneity characteristic of the

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**Table 1**  
Initial sizes ( $\pm$ SD) for wild and sea-ranched brown trout in three experimental series ( $n = 36$  for all groups)

Series	Wild		Sea ranched	
	Weight (g)	Length (cm)	Weight (g)	Length (cm)
1	5.6 $\pm$ 0.7	7.7 $\pm$ 0.3	6.1 $\pm$ 0.6	8.0 $\pm$ 0.2
2	6.4 $\pm$ 0.6	8.2 $\pm$ 0.2	6.9 $\pm$ 1.0	8.4 $\pm$ 0.3
3	7.4 $\pm$ 0.9	8.9 $\pm$ 0.3	8.7 $\pm$ 1.0	9.2 $\pm$ 0.3

hatchery environment should lower the potential for habitat preferences and feeding specializations. In turn, this may limit social grouping as well as cooperative partnerships based on familiarity. From this hypothesis we predicted that individual recognition effects are less pronounced in sea-ranched trout than in wild trout.

## METHODS

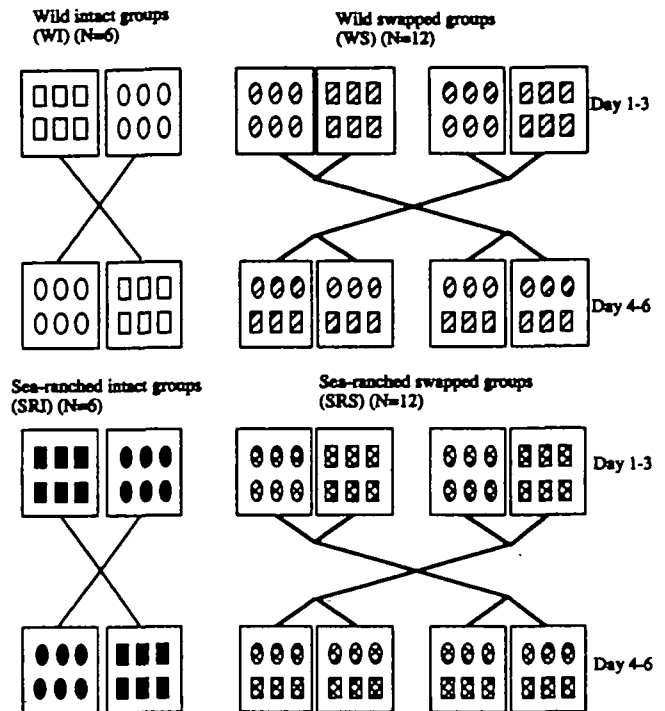
### Location and strains

The experiment was performed in September, 1995 at the fishery research station in Älvkarleby, on the east coast of Sweden, using wild and sea-ranched strains of sea trout from the river Dalälven. The "wild" strain consists of all sea trout having wild parents or sea-ranched parents spawning in the wild. The "sea-ranched" strain originates from 1967, when a large number of fish were caught and used for artificial breeding and cultivation. The juveniles of the sea-ranched strain have been raised in the hatchery until smoltification (age about 2 years) and then released in the river. An allozyme analysis revealed significant differences in gene frequencies in four of eight investigated loci between the two strains (Jansson H, Salmon Research Institute, personal communication). Furthermore, an analysis of the mtDNA (NADH-1 gene) showed that the genetic variation was significantly larger within the wild strain versus the sea-ranched strain (Öst T, Järvi T, and Petterson E, unpublished data). The wild-strain trout in this experiment were the offspring of 11 males and 11 females, artificially fertilized between 20 October and 9 November, 1994. The sea-ranched trout were obtained from six males and six females fertilized between 6 and 26 October, 1994. Both strains were cultivated at the research station under similar conditions. We used three tanks for each strain, each containing the mixed offspring from at least two females and two males.

### Experimental procedure

The experiment was performed in twelve 60  $\times$  60 cm experimental stream channels with a water depth of 15 cm. We used groundwater heated to 13°C ( $\pm$ 1°C) with a flow of 1 l/min, and simulated natural photoperiod. The channels were covered with dark plastic to avoid disturbance. At the start of the experiment, we sampled 36 wild and 36 sea-ranched trout randomly from the 6 holding tanks. After anesthetization with 2-phenoxy-ethanol (0.5 ml/l), we measured the initial body weight and total length of each individual, and then freeze-branded each fish dorsally with 1 of 12 different combinations of dots. Thereby we could separate the individuals in each channel both before and after swapping. Initial sizes are shown in Table 1. We also matched the fish by size ( $\pm$ 0.3 cm) within each stream channel and between swapped channels (Figure 1).

Immediately after handling, we placed six parr (Figure 1)



**Figure 1**

Scheme describing the principle for moving intact and swapped groups of trout during the experiment. Note that all groups are transferred to new tanks on day 4;  $N$  in this figure refers to the number of groups.

in each channel, allowing them to acclimatize for 2 days before the observations started. Systematic effects of kin discrimination (Brown and Brown, 1996) were avoided because for each strain all groups were a random mixture of offspring from all parents. Twice daily, using a funnel, the trout were fed deep-frozen chironomids (thawed but dispensed all together) equivalent to a rate of 1% dry weight per fish wet weight and day. We observed the trout twice daily (starting at 0900 and 1300 h) through a small opening in the plastic. Each observation period started 5 min before feeding and ended 10 min after feeding. Five types of well-defined agonistic interactions were registered (see below), and the initiator and winner of each conflict was identified. We also counted the number of chironomids eaten by each fish. In addition, twice a day (immediately before the first and after the second 15-min observation period) we recorded the activity and position of each fish on a map over the stream channel, the bottom of which was divided into 36 numbered, equally sized squares. The activity behavior of the individuals were scored from low to high activity, from stationary low (fish motionless at the bottom, activity score = 0) to fighting (activity score = 4). Other activity scores were stationary high (maintaining position in the water column) = 1, swimming = 2, and feeding = 3. The median score of the individuals in each replicate before transfer was compared with the median score after transfer. We used the recorded positions to analyze the distance to nearest-neighbor fish in the groups.

After 3 days, we assumed that the initial dominance rank was set and in eight groups three individuals were swapped with three fish from another group (Figure 1). Thus, in those new groups each individual had previous experience of two competitors but was unfamiliar with the other three. The other four groups were kept intact. After swapping, the trout were observed for 3 more days, following the same procedure as before swapping. However, to equalize handling, we moved all

groups to a new channel on day 4. Thereafter, the fish were anesthetized, and final fork lengths and weights were measured, and then the fish were killed. Three experimental series, as described above, were conducted on 5–10, 13–18, and 21–26 September. We studied 216 individuals in 36 groups. Four treatment groups could be compared: wild (WI) and sea-ranched (SRI) groups of fish, both kept intact during the full 6-day experiment, and wild (WS) and sea-ranched (SRS) groups (Figure 1), both swapped after 3 days. Each stream channel was used three times, with treatments randomly distributed among channels.

#### Treatment of data and statistical analysis

Interactions separated by less than 30 s were treated as a single interaction, unless they were separated by a conflict between different contestants. When comparing aggression levels among unfamiliar and familiar individuals in the swapped groups, the number of interactions between familiar individuals was multiplied by 1.5 because the probability of two unfamiliar individuals meeting was 1.5 times higher than for two familiar individuals. Aggression levels refer to the number of interactions initiated. We recorded five types of agonistic interactions: (1) display, either lateral or frontal, where one or both fish erect all fins; (2) circling, where two fish circle round each other; (3) attack, where one fish charges at the other; (4) bite; and (5) hunt, where one fish pursues the escaping combatant (see also Fernö et al., 1976; Noakes, 1980). We did not observe any serious injury to any fish during the experiments.

We calculated the cardinal dominance rank with a computer program using an iterative technique as described by Boyd and Silk (1983). The rank before swapping was based on the interactions during days 1–3, and the rank after swapping was based on the interactions during days 4–6. For statistical analysis, we used the absolute value of the change of rank for each individual.

Specific growth rates (Ricker, 1979) were calculated using the formula  $G = \log(s_1/s_0) \times 100/\text{days}$ , where  $s_0$  and  $s_1$  were the initial and final weight or length for the period  $d$  (days). Growth efficiency was estimated as specific growth rate in weight + 3 (to obtain all positive values) per amount of food taken during observations on days 1–6.

Most experimental data were either normally distributed or transformed to an approximately normal distribution. The activity data, however, could not be transformed to normality, so we used a  $G$  test on median values. Dominance rank, food intake, growth efficiency, and growth rate data were analyzed using a two-way factorial ANOVA with strain and familiarity as class variables and the effect of replicate nested within class variables (MGLH; Wilkinson, 1989). Replicate effects were considered random with respect to the main factors and are not presented. We analyzed aggression and nearest-neighbor distance data using repeated measures ANOVA with strain, familiarity, and time as class variables (SAS Institute, 1989). For repeated measurements, replicates were pooled, and degrees of freedom and  $F$  values refer to Wilk's lambda (Rao, 1973). The nearest-neighbor distance data were also analyzed using  $t$  tests based on group means. We obtained correlation coefficients using the Pearson rank correlation test (Wilkinson, 1989).

## RESULTS

### Feeding and growth

#### Growth rate

Mean growth rates ( $\pm$ SE) in weight were  $-0.36$  ( $\pm 0.09$ ) in the WI group ( $n = 36$ ),  $-0.53$  ( $\pm 0.07$ ) in the WS group ( $n = 71$ ),  $-0.69$  ( $\pm 0.11$ ) in the SRI group ( $n = 34$ ), and  $-0.54$  ( $\pm 0.07$ ) in the SRS group ( $n = 69$ ). Overall, wild trout lost less weight than sea-ranched trout ( $F_{1,174} = 5.0$ ,  $p = .026$ ). There was no significant effect of familiarity between intact and swapped groups ( $F_{1,174} = 0.005$ ,  $p = .95$ ), but wild trout in the intact groups performed best, which was reflected in a significant interaction between familiarity and strain ( $F_{1,174} = 5.3$ ,  $p = .022$ ). Mean growth rates in lengths were  $0.12$  ( $\pm 0.02$ ) in the WI group ( $n = 36$ ),  $0.09$  ( $\pm 0.02$ ) in the WS group ( $n = 71$ ),  $0.07$  ( $\pm 0.03$ ) in the SRI group ( $n = 34$ ), and  $0.06$  ( $\pm 0.02$ ) in the SRS group ( $n = 69$ ), respectively. Overall, wild fish grew significantly faster than sea-ranched fish ( $F_{1,175} = 5.7$ ,  $p = .018$ ), but there was no significant effect of familiarity between shifted and intact groups ( $F_{1,175} = 0.5$ ,  $p = .49$ ) or strain by familiarity interaction ( $F_{1,175} = 0.5$ ,  $p = .50$ ).

Food intake

The mean change in number of chironomids eaten (after minus before the swap) by each treatment group were  $-1.3$  ( $\pm 2.5$ ) in the WI group ( $n = 36$ ),  $-7.3$  ( $\pm 2.3$ ) in the WS group ( $n = 71$ ),  $-1.3$  ( $\pm 2.5$ ) in the SRI group ( $n = 34$ ), and  $-5.4$  ( $\pm 1.7$ ) in the SRS group ( $n = 70$ ). Familiarity affected food intake significantly, as food intake declined less in intact groups than in swapped groups, both for wild and sea-ranched trout ( $F = 8.4$ ,  $p = .004$ ). There was no significant difference between the strains ( $F = 0.400$ ,  $p = .53$ ) or strain by familiarity interaction ( $F = 0$ ,  $p = .991$ ). Time had a strong effect on food intake ( $F_{3,300} = 7.76$ ,  $p < .0001$ ), with low intakes during day 1 and day 4, the first day after swapping.

#### Food intake

Growth efficiency

Growth efficiencies were  $0.48$  ( $\pm 0.14$ ) in the WI group ( $n = 36$ ),  $0.24$  ( $\pm 0.05$ ) in the WS group ( $n = 71$ ),  $0.44$  ( $\pm 0.10$ ) in the SRI group ( $n = 34$ ), and  $0.34$  ( $\pm 0.06$ ) in the SRS group ( $n = 69$ ). Fishes in intact groups had a better growth efficiency reflecting in a significant effect of familiarity ( $F_{1,174} = 6.3$ ,  $p = .013$ ), whereas we found no effect of strain ( $F_{1,174} = 0.2$ ,  $p = .66$ ) or strain by familiarity interaction ( $F_{1,174} = 0.93$ ,  $p = .34$ ).

#### Growth efficiency

Nearest-neighbor distance

The repeated-measurement ANOVA showed a time-dependent effect of treatment ( $F_{3,187} = 3.8$ ,  $p = .0015$ ) and strain ( $F_{3,185} = 5.2$ ,  $p = .0002$ ) on nearest-neighbor distance (Figure 2a). Furthermore, a  $t$  test based on group means (for days 4–6) showed that nearest-neighbor distance tended to be smaller in intact than in shifted groups ( $t = 1.69$ ,  $df = 34$ ,  $p = .10$ ) whereas no significant difference was detected between the wild and sea-ranched strain.

#### Nearest-neighbor distance

Within swapped groups, the difference in distance between familiar and unfamiliar individuals were compared after the shift (for days 4–6). Familiar individuals were positioned  $1.8 \pm 0.4$  cm closer together than unfamiliar fish (matched  $t$  test on group means;  $t = 15.5$ ,  $n = 24$ ,  $p = .0001$ ). This effect of familiarity was not significantly different between wild and sea-ranched trout ( $2.8 \pm 0.4$  cm versus  $0.8 \pm 0.8$  cm, respectively). For descriptive data, see Figure 2b.

Agonistic interactions

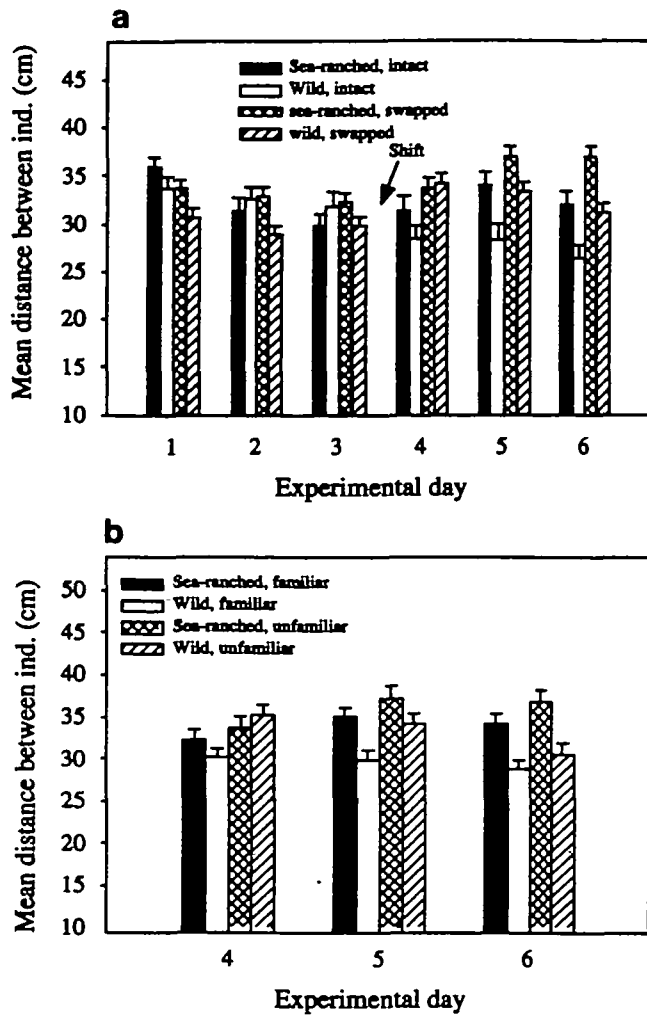
Cardinal dominance rank

Mean absolute changes in dominance ranks were  $4.13$  ( $\pm 0.75$ ) in the WI group ( $n = 36$ );  $4.39$  ( $\pm 0.53$ ) in the WS group ( $n = 71$ );  $2.75$  ( $\pm 0.64$ ) in the SRI group ( $n = 34$ ) and  $4.95$  ( $\pm 0.54$ ) in the SRS group ( $n = 69$ ). Dominance rank was thus more stable in intact groups ( $F_{1,174} = 4.7$ ,  $p = .031$ ), but there was no difference between the strains ( $F_{1,174} = 0.7$ ,

#### Agonistic interactions

#### Cardinal dominance rank

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**Figure 2**  
Nearest-neighbor distances (a) during days 1–6 in the four treatment groups of trout and (b) after swapping in familiar and unfamiliar individuals in the swapped groups.

$p = .41$ ), and no interaction between strain and familiarity ( $F_{1,174} = 2.1, p = .15$ ).

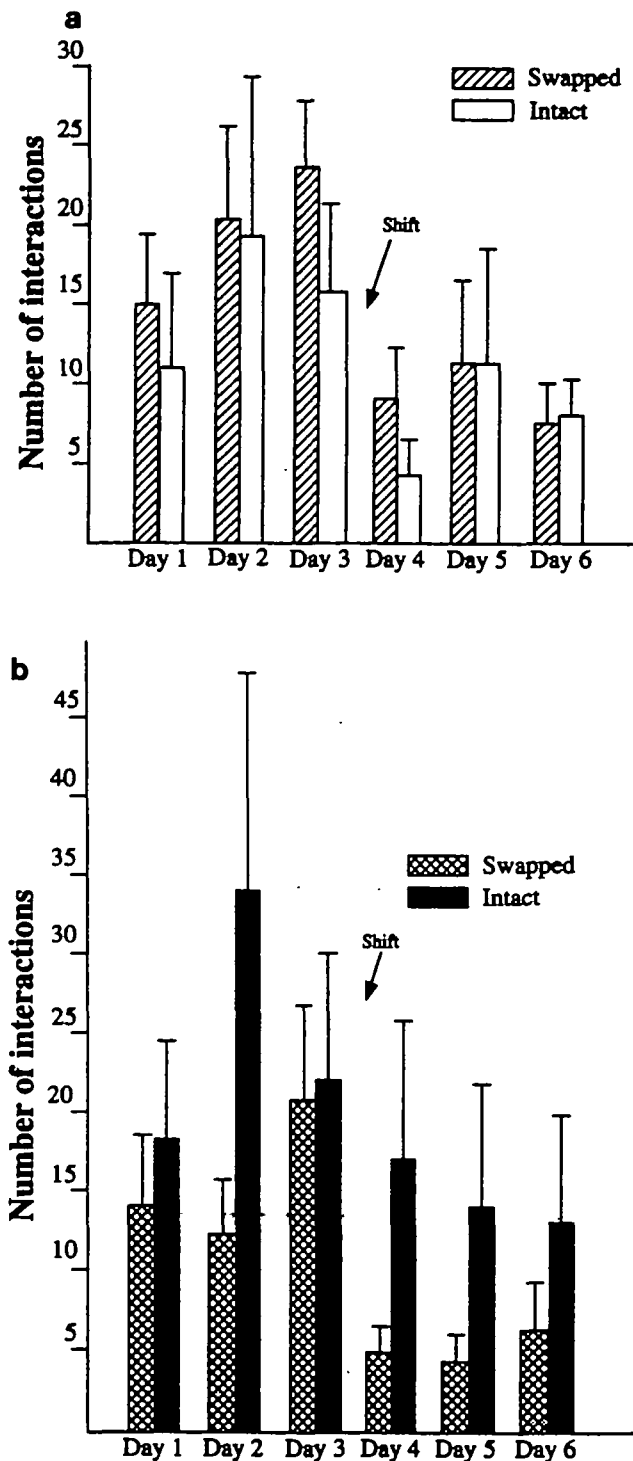
#### Aggression levels

Aggression levels (Figure 3a,b) changed significantly with time ( $F_{5,200} = 4.98, p = .0003$ ), generally being lower after swapping. The temporal change in aggression was not different between the two strains ( $F_{10,400} = 0.76, p = .67$ ) but differed between swapped and intact groups ( $F_{10,400} = 2.20, p = .017$ ), being lower in intact groups on day 4 ( $F_{1,204} = 5.41, p < .005$ ).

Furthermore, within the swapped groups, aggression levels were higher in the wild strain ( $F_{4,560} = 2.48, p = .043$ ) than in sea-ranched fish. There was no overall difference in aggression between familiar and unfamiliar individuals ( $F_{4,560} = 0.26, p = .90$ ).

#### Familiarity and the probability of winning interactions

Within swapped groups, the initiators won, 191 of 200 (96%) of interactions initiated against familiar individuals, but were significantly ( $G$  test,  $df = 1, \chi^2 = 4.03, p = .045$ ) less likely to win against unfamiliar fish [182.7 of 202.0 (90%) conflicts won; the number of observations adjusted for the probabilities of encounter familiar and unfamiliar individuals]. The wild and sea-ranched strains did not differ in this respect (heterogeneity  $G = 0.31, df = 1, ns$ ).



**Figure 3**  
Mean number of agonistic interactions in (a) WI and WS groups and (b) SRI and SRS groups of trout.

#### Type of interactions used

Within shifted groups, the frequencies of the five types of agonistic interactions (display, charge, circle, chase, and bite) differed between unfamiliar and familiar fish ( $G = 11.95, p < .02, df = 4$ ), mainly because circling was used more frequently in contests between unfamiliar fish (10 observations) than between familiar fish (1 observation, adjusted for unequal encounter probability).

**Table 2**  
Summary of effects of familiarity and domestication on growth and behavior in juvenile brown trout

Variable	Effect of familiarity	Effect of domestication
Weight growth rate	Increasing in wild trout	Decreasing
Length growth rate	—	Decreasing
Food intake	Increasing	—
Growth efficiency	Increasing	—
Dominance rank	Stabilizing	—
Aggression level	Decreasing, especially in wild trout, time dependent	Decreasing in shifted groups
Probability of winning initiated conflict	Increasing	—
Activity	Decreasing in wild trout	—
Nearest-neighbor distance	Decreasing	Increasing, time dependent

#### Level of activity

There was no overall difference in activity between swapped and intact groups ( $G = 2.47$ ,  $df = 1$ , ns). However, the activity differed between the WI and WS groups ( $G = 4.27$ ,  $df = 1$ ,  $p < .04$ ). In WI groups, the activity tended to decrease after transfer (in 5 out of 6 replicates), whereas there was an opposite trend in WS groups (activity decreased in 4 out of 12 replicates). For sea-ranched trout, there was no difference in activity between intact and swapped groups.

#### Correlations

In all groups, dominance index was positively correlated with food intake [ $r_p$  (all groups pooled) = .42,  $p < .001$ ]. Moreover, food intake in all groups was positively correlated with growth rate in weight [ $r_p$  (all groups pooled) = .34,  $p < .001$ ].

#### DISCUSSION

The present experiment was designed to test two hypotheses. The first was that sea trout use individual recognition as a cue to reduce the cost of contesting resources. Our results, summarized in Table 2, show that familiarity has numerous effects on the behavior of sea trout. Most of these effects are consistent with our predictions.

Intact groups had a more stable social hierarchy, as shown by smaller changes in the rank of individuals. In addition, trout in intact groups maintained a similar food intake after swapping, whereas feeding decreased considerably in the swapped groups. A possible explanation for this is that from day 4, the WS and SRS groups were partly composed of unfamiliar individuals, and a new dominance hierarchy had to be established; therefore, less time could be spent searching for food. The low food intake during day 1 and day 4, the first day after swapping, probably reflects acclimation after transfer to new tanks and may partly explain why mean growth rates were negative in the experiment. Not only did fish in intact groups eat more food, they were also more efficient in utilizing it for growth. This novel result may be explained by a less stressful situation in the more socially stable intact groups. Social conditions have previously been shown to affect digestive efficiency. Abbott and Dill (1989) showed that subordinate steelhead trout (*Salmo gairdneri*) grew less well than dominants eating the same amount of food. Furthermore, we found significantly lower aggression in intact groups on day 4. Because aggression is energetically costly (Chellappa and Huntingford, 1989; Thorpe et al., 1995), it is possible that increased aggression in the swapped, more socially turbulent groups increased energy expenditure, in turn reducing food utilization efficiency.

Although the effect of familiarity on aggression appeared to be highly time dependent in the present study, our results

are generally in agreement with previous studies (Johnsson, 1997; Morris et al., 1995; Whitfield, 1986). However, Olsén et al.'s (1997) study on sea trout revealed no significant effect of familiarity on aggression. Still, there was a tendency for higher aggression among unfamiliar contestants in their data.

Furthermore, trout in the WI group lost less weight than trout in the other groups, whereas we found no effect of familiarity on the growth of SRI groups. Dominance, food intake, and growth were positively correlated, and high growth rate will increase fitness through higher reproductive success and survival (Huntingford and Turner, 1987; Metcalfe et al., 1995). It thus appears that familiarity stabilizes hierarchical groups and governs behavioral modifications that will be beneficial for the fitness of individuals in such groups.

The present study shows that the initiator of a conflict is more likely to win against a familiar opponent than against a stranger. This is the first empirical support of the hypothesis proposed by Ydenberg et al. (1988). They presented a model based on the asymmetric war-of-attrition model (e.g., Parker, 1984), suggesting that familiarity affects an individual's estimate of the likelihood of role mistakes, where a role mistake is the probability that an individual incorrectly judges its role as a winner or loser. Our results suggest that familiarity perfects knowledge about an opponent's fighting ability, which should reduce conflict costs.

Mean distance to nearest neighbors, as well as aggression, has previously been shown to be reduced among kin (Brown and Brown, 1996). These results have been explained by Hamilton's (1964) model for kin selection: by biasing social behavior toward kin, an individual can maximize its genetic fitness by including the fitness of relatives (inclusive fitness). However, in this study we showed that familiarity can generate similar changes in spatial distribution, as nearest-neighbor distance was reduced between familiar individuals within shifted groups. Moreover, there was a time-dependent effect of familiarity with an overall tendency for nearest-neighbor distance to be lower in intact groups than in shifted groups. This finding, which is consistent with the results from a shoaling study on fathead minnows by Chivers et al. (1995), may indicate a higher tolerance among familiar neighbors as predicted by the "shepherd hypothesis" (Rower and Ewald, 1981). Another, not mutually exclusive, possibility is that decreased distance functions as an antipredator adaptation, analogous to schooling, by diluting individual risk and/or confusing predators (Mathis and Smith, 1993; Pitcher and Parrish, 1993). The present study was conducted in stream tanks with a "plain" habitat structure, so extrapolation to natural streams should be made cautiously. However, it is possible that group stability reduces spacing, thereby increasing the carrying capacity of natural streams.

Our second hypothesis, that the hatchery environment se-

lects against individual recognition, predicted a reduced effect of familiarity in sea-ranched trout. The results yielded no strong support for this hypothesis because familiarity affected sea-ranched- and wild trout similarly in most respects (see Table 2). However, familiarity was not beneficial for growth in weight in sea-ranched trout, but it increased growth rate in wild fish. This may be linked to the fact that familiarity reduced the general activity (which should reduce energetic costs; Brett, 1995) in wild fish but not in sea-ranched fish.

Because the sea ranched trout were descended from fewer families ( $6 \times 6$ ) than the wild trout ( $11 \times 11$ ), kin relatedness was lower in the wild strain. Thus, the kin selection hypotheses would predict larger nearest-neighbor distances in the wild fish (Brown and Brown, 1996). Moreover, hatchery densities are generally much higher than natural densities which could select for increased neighbor tolerance. Despite these predictions, sea-ranched trout tended to maintain larger distances to their nearest neighbors than did wild trout (Figure 9a), perhaps because clustering is an antipredator strategy that may be less favored in the predator-free hatchery environment (Johnsson and Abrahams, 1991; Johnsson et al., 1996). Alternatively, social tolerance may be reduced by hatchery selection, as suggested by several studies (Mesa, 1991; Moyle, 1969; Swain and Riddell, 1990). In this study, however, aggression levels were not higher in the sea-ranched strain. This could be a consequence of the larger distance between sea-ranched fish, reducing the scope for agonistic interactions. The tendency for larger distance between sea-ranched trout could also be a consequence of larger optimal territory sizes resulting from higher optimal feeding rates favored by hatchery selection.

Is individual recognition really needed to explain the effects of familiarity found in the present study? For variables such as growth and food intake, we cannot exclude the possibility that the intact groups may experience some general "familiarity" in the group as a whole, for example, through olfaction, which could reduce stress and enhance growth. For some of the behavioral interactions, a kind of "semi-individual" recognition is theoretically possible: a fish may match the smell from the encountered individual against a memory template, consisting of previously encountered smells. In a natural stream, however, selection favoring group recognition through olfaction should be limited because it only works when the recipient is downstream from the signaler. Moreover, the trout in our study won initiated conflicts more often against familiar opponents, strongly suggesting that they can distinguish and remember individual fighting ability.

In summary, our results suggest that individual recognition allows familiarity to develop, which reduces turbulence and aggression in hierarchical groups or among territory neighbors. This will increase the food intake and utilization of food for growth, in turn leading to higher fitness. Thus, selection for the ability to distinguish among conspecifics may be expected both in territorial and group-living animals.

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