

# The benefits of genetic diversity outweigh those of kin association in a territorial animal

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The theories of kin selection and heterogeneous advantage have been central to studies of altruistic behaviour and the evolution of sex over the last 35 years. Yet they predict diametrically opposite effects of genetic diversity on population density. Close relatives gain inclusive fitness advantages by preferentially associating with and behaving altruistically towards one another. However, heterogeneous advantage, which predicts competition to be highest when genetic diversity is low, suggests that benefits will be greater for individuals in groups of non-kin. Here we test how these two processes balance and affect the productivity of populations of animals in natural habitats. We report from a study of juvenile Atlantic salmon in the wild that heterogeneous advantage outweighs the benefits of kin-biased behaviour, resulting in a 1.8-fold higher population biomass and significantly better condition of individual fish.

**Keywords:** kin selection; genetic diversity; competition; population density; *Salmo salar*

## 1. INTRODUCTION

The theory of kin selection is based on Hamilton's (1964) model for the evolution of social behaviour, which states that individuals can maximize their own fitness by the mechanism of inclusive fitness. This mechanism occurs when individual animals reduce aggression towards or actively assist kin, resulting in an increase in the fitness of both the individual and of the kin. This is because individuals have many genes in common with their close relatives, and can increase the chances of these genes being propagated to the next generation both through their own offspring and those of their kin. A prerequisite to individuals accruing advantages through kin selection is interaction between relatives, which usually involves kin aggregation.

The question of how relatedness influences the patterns of interaction between territorial animals has focused on studies of salmonid fishes. Preferential association among kin has also been documented in amphibians (e.g. Blaustein & Waldman 1992). Many salmonid fish are ideal study species because, as juveniles, they are territorial and experience intense intraspecific competition for several months after hatching. During this critical period juveniles must obtain a territory on the river substratum if they are to survive (Elliott 1987). Among territory holders, weaker individuals are 'thinned out' as the fish grow and the need for space increases. Losers tend to die *in situ* rather than move downstream (Egglshaw & Shackley 1982; Elliott 1987).

The opportunity exists for relatedness to influence both their initial choice of neighbouring territory holders, as well as subsequent growth and survival. First, salmon are among siblings as they disperse from their nests and have the option of segregating by family as they take up territories in streams (Jenkins 1969; Dill 1977; Elliot 1994). Indeed, many salmonid species are known to prefer water scented with the odour of siblings (Brown &

Brown 1996; Olsén 1999), although evidence for fish using this discriminatory ability in a naturalistic setting is equivocal (Fontaine & Dodson 1999; Mjølnerød *et al.* 1999). Second, juvenile salmonid fishes held in uniform laboratory environments with their siblings are less aggressive than non-kin and, as a consequence, grow faster and realize higher densities (Brown & Brown 1993). The implications of these laboratory experiments are that, in suitable habitats, individual salmon associating with their kin may benefit directly by increased growth, which correlates with fitness (Hutchings & Jones 1998; Einum & Fleming 2000) and indirectly by higher survival (through increased size-dependent densities) of their neighbouring kin (Grant & Kramer 1990).

The theory of heterogeneous advantage predicts that competition intensifies when genetic diversity is low and, therefore, diametrically opposes the predictions of kin association. Several mechanisms may lead to heterogeneous advantage. First, if different genotypes have different ecological needs they may use a homogeneous resource in different ways (Young 1981). Second, mixtures may exploit a spatially heterogeneous environment more fully than homogeneous groups (Bell 1985). Third, in temporally heterogeneous habitats, mixtures may be more likely than homogeneous groups to produce genotypes that are better suited to the environment (Williams 1975). Furthermore, mixtures may be more resistant to pathogens because there should be a greater chance of there being a resistant genotype present (Wolfe 1985). Evidence for heterogeneous advantage in animals has come from laboratory studies of *Trilobium* beetles (Jasienski *et al.* 1988) and *Drosophila* (Pérez-Tomé & Toro 1982; Fowler & Partridge 1986).

It seems that there is strong evidence from laboratory studies to support both kin selection and heterogeneous advantage, despite the fact that these two mechanisms oppose one another. However, it remains to be seen how the trade-off between these two theories is balanced in the wild. Are the advantages of reduced competition for resources among groups of unrelated

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conspicuous overridden by the advantages of decreased aggression and increased growth among groups of kin? To answer this question we studied juvenile Atlantic salmon (*Salmo salar*), which have been shown to benefit from kin association in simple laboratory environments, but tested them in a natural stream habitat, which offered opportunities for heterogeneous advantages to be expressed.

## 2. MATERIAL AND METHODS

Wild, adult Atlantic salmon were caught by the Conon and Alness District Salmon Fishery Board (CADSFB) at the Black Water fish trap on the River Conon, Scotland. The eggs of one female were fertilized with the milt of one male in order to produce a family of full-sibling offspring. Eight different families were produced in this way. Eggs from each family were incubated at the CADSFB hatchery in a common water supply.

Homogeneous groups (full siblings) were formed by taking 1000 juveniles from each family ( $n=8$ ) and heterogeneous groups were formed by mixing together 1000 of the remaining juveniles from each of the eight families and splitting this mixture into eight equal-sized groups. In this way the genotypes sampled in the two treatments were the same and explanations such as heterozygote advantage could be disregarded when interpreting the results of the experiment (Pérez-Tomé & Toro 1982).

The 16 groups of juvenile salmon were released on 29 April 1999, at the stage before they had started to feed exogenously, into a tributary of the River Conon (Loch nan Eun Burn) that did not naturally contain salmon due to an obstruction to migrating adults. Each group was released at a different location ( $> 100$  m apart) within the stream. This distance between locations was chosen in order to ensure low interference between groups from dispersing fish based on models of existing data (Crisp 1995; K. Martin-Smith and J. D. Armstrong, unpublished data). Heterogeneous and homogeneous groups were alternated as the stream's altitude increased in order to eliminate the possibility of environmental clines influencing the results. The salmon were poured slowly into the flow of the stream from a bucket. A stream length of 20 m was stocked at a density of  $25 \text{ fish m}^{-2}$ . This is a very high density in salmon and was chosen because it was expected that any difference in production between treatments should be easier to detect under strong competition (Martin *et al.* 1988). Furthermore, high densities of fish with strong prior residence advantage would be expected to repel any fish attempting to immigrate strongly (Cutts *et al.* 1999).

The young salmon were allowed to grow during the summer before the populations were resampled by electric fishing on 23 and 24 September 1999. Nets were positioned in order to prevent the escape of fish from the sampled sections (the central 10-m length of each stocked section) during fishing. Each section was fished three times. The number of juvenile salmon captured during each separate fishing attempt was noted. The fork length and wet weight of each individual fish was also measured. The maximum-likelihood method (Riley *et al.* 1993) used data collected from each of the three separate fishings for calculating the density (number of fish per square metre) of juvenile salmon at each site. Eight homogeneous and seven heterogeneous groups were compared in the analyses, as the relocation posts of one heterogeneous group could not be relocated.

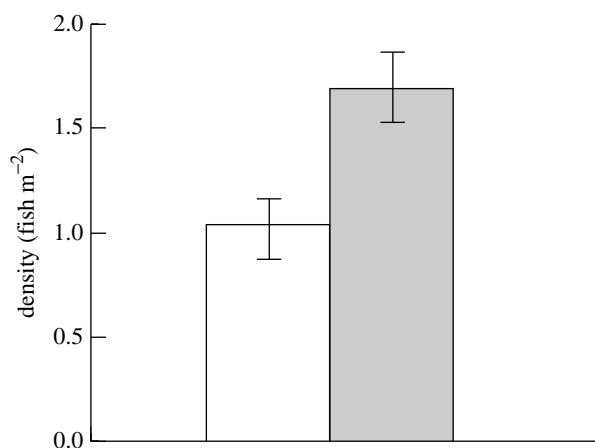


Figure 1. Densities (mean  $\pm$  s.e.) of wild juvenile Atlantic salmon raised in homogeneous groups (full siblings, white bars) ( $n=8$ ) and heterogeneous groups (mixture of full siblings, shaded bars) ( $n=7$ ).

## 3. RESULTS

At resampling, the density of mixed-family (genetically heterogeneous) groups was significantly greater (almost double) (figure 1) than that of single-family (genetically homogeneous) groups (two-tailed  $t$ -test of density assuming unequal variances,  $t_{12}=3.02$  and  $p < 0.05$ ). However, there was no significant difference in their mean lengths ( $t_{13}=0.23$  and  $p=0.82$ ) between the treatments. At the end of the experiment, the mean fork length and wet weight of salmon from the homogeneous groups were  $x \pm \text{s.e.} = 67.11 \pm 0.71$  mm ( $n=8$ ) and  $3.46 \pm 0.11$  g ( $n=8$ ), respectively. The respective mean fork length and wet weight of salmon from the heterogeneous groups were  $x \pm \text{s.e.} = 66.89 \pm 0.69$  mm ( $n=7$ ) and  $3.49 \pm 0.11$  g ( $n=7$ ). Biomass, the product of weight and density, was significantly higher in the heterogeneous groups (two-tailed  $t$ -test of biomass,  $t_9=3.01$  and  $p < 0.05$ ).

The ratio of weight to length ( $w:l^3$ ) is commonly used as an index of the physical condition of fish (Bolger & Connolly 1989). The mean condition index of the salmon was significantly higher in the mixed relatedness groups than in the homogeneous groups ( $t_{13}=2.18$  and  $p < 0.05$ ) (figure 2).

One possible explanation for the difference in density between the homogeneous and heterogeneous groups is that a small number of families performed poorly. If this had been the case, the variation in performance would have been much greater among the single-family (homogeneous) groups than among the mixed-family (heterogeneous) groups. We can discount this possibility as the variance in density between the homogeneous groups was not significantly different from that between the heterogeneous groups (variance ratio  $F$ -test,  $F_{7,6}=0.73$  and  $p=0.34$ ). The between-group variance in biomass did not differ significantly between the two treatments ( $F_{7,6}=0.35$  and  $p=0.09$ ).

The sites stocked out with kin and mixed groups did not differ significantly in gradient ( $t_{11}=1.30$  and  $p=0.242$ ), mean water depth ( $t_{11}=0.14$  and  $p=0.892$ ), mean stream width ( $t_{11}=0.84$  and  $p=0.418$ ) or percentage habitat composed of riffle ( $t_{11}=0.04$  and  $p=0.973$ ).

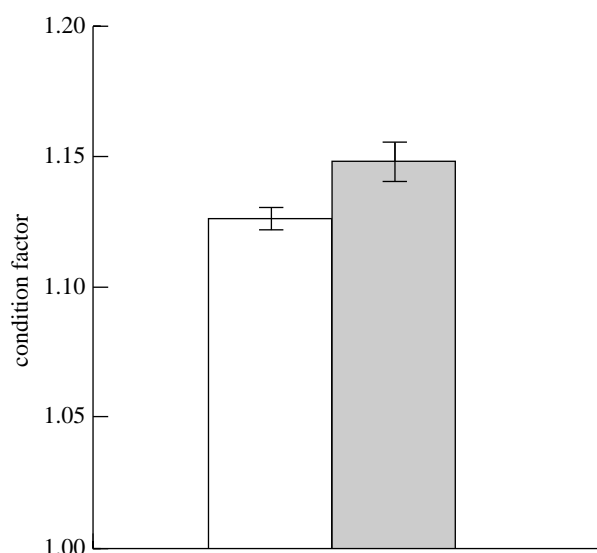


Figure 2. Condition factors of wild juvenile Atlantic salmon raised in homogeneous groups (full siblings, white bars) and heterogeneous groups (mixture of full siblings, shaded bars). Means of the condition factor for each group (s.e.) are given for the homogeneous ( $n=8$ ) and heterogeneous ( $n=7$ ) treatments.

#### 4. DISCUSSION

The results of this field experiment showed that heterogeneous advantage outweighed the benefits of kin association for juvenile salmon in a natural habitat both at an individual level, as shown by the differences in the condition indices, and at a population level, as shown by the differences in density. These results may explain why studies have failed to find evidence of kin aggregating in natural populations (Fontaine & Dodson 1999; Mjølnerød *et al.* 1999), despite the apparent advantages of such behaviour being implicit from the results of laboratory studies.

The mechanisms by which heterogeneous advantage is achieved by territorial animals such as salmon are not clear. It is known that different individual salmon can use their environment in different ways (Armstrong *et al.* 1999). However, because they are territorial, they do not have the opportunities for sharing space that are evident in less aggressive animals. It is possible that some different families of salmonid fishes tend to specialize in different microhabitats (McLaughlin *et al.* 1999). It would be interesting to investigate the possibility that the balance point between kin selection benefits and heterogeneous advantage may therefore be influenced by habitat heterogeneity.

The results suggest an ecological advantage of avoiding relatives for individual juvenile salmon. It is also possible that parents gain an ecological advantage by producing genetically diverse progeny, as these offspring may realize higher densities than juveniles of low genetic diversity. Decreased competition among genetically diverse siblings is a mechanism for maintaining genetic recombination in parents that reproduce sexually. The low intensity of competition among genetically heterogeneous progeny may also be one advantage to parents reproducing sexually rather than asexually (Maynard Smith 1978; Barton & Post 1986). Heterogeneous advantage may also play a role in the maintenance of genetic variability in

natural populations. If the fitness of a genotype is frequency dependent so that its fitness decreases as its relative abundance increases, then mixtures of genotypes could be more stable than homogeneous groups (Ayala & Campbell 1974; Lewontin 1975; Bell 1985).

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