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ORIGINAL ARTICLE

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Do dominants have higher heterozygosity? Social status and genetic variation in brown trout, *Salmo trutta*

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Abstract A key question of evolutionary importance is what factors influence who becomes dominant. Individual genetic variation has been found to be associated with several fitness traits, including behaviour. Could it also be a factor influencing social dominance? We investigated the association between social status and the amount of intra-individual genetic variation in juvenile brown trout (*Salmo trutta*). Genetic variation was estimated using 12 microsatellite loci. Dominant individuals had higher mean heterozygosity than subordinates in populations with the longest hatchery background. Heterozygosity–heterozygosity correlations did not find any evidence of inbreeding; however, single-locus analysis revealed four loci that each individually differed significantly between dominant and subordinate fish, thus giving more support to local than general effect as the mechanism behind the observed association between genetic diversity and a fitness-associated trait. We did not find any significant relation between mean d^2 and social status, or internal relatedness and social status. Our results suggest that individual genetic variation can influence dominance relations, but manifestation of this phenomenon may depend on the genetic background of the population.

Keywords Dominance status · Aggression · Microsatellites · Heterozygosity · Genetic background

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Introduction

Dominance hierarchies are common in many species, and dominant individuals are often expected to enjoy higher fitness than subordinates (Huntingford and Turner 1987). For example, juvenile salmonid fish with high social status may have higher survival (Elliot 1994) and faster life history strategy with higher growth rate, earlier migration and earlier maturation compared with individuals having low social status (Metcalfe et al. 1989). A key question of evolutionary importance is what factors influence who becomes dominant? A series of studies conducted in Atlantic salmon (*Salmo salar*) have shown that early territory establishment and high standard metabolic rate are important predictors of dominance status (Metcalfe et al. 1989, 1995). Interestingly, there are also indications that early feeding salmon fry are more heterozygous (allozymes; Metcalfe 1998; Borrell et al. 2004). As early feeding fish generally have higher standard metabolic rates and are more dominant (Metcalfe et al. 1995; Cutts et al. 1998), it seems possible that dominants and subordinates may also differ in the amount of intra-individual genetic variation. In a previous study, we found that salmon fry with less genetic variation behaved less aggressively than fry with more genetic variation (Tiira et al. 2003). These

results suggest that one important and yet undiscovered factor influencing dominance can thus be the amount of genetic variation. Are individuals with high social status genetically more variable compared to subordinates?

Highly polymorphic microsatellite loci are efficient genetic markers for estimating genetic diversity and especially for describing recent inbreeding and outbreeding events (Pemberton et al. 1999; Tsitrone et al. 2001). Studies using microsatellite heterozygosity (*H*), mean d^2 (a squared difference in repeat number in a locus) and internal relatedness (IR; an estimate of parental genetic similarity) have all found correlations with several fitness traits such as survival, reproductive success and disease susceptibility (*H*: Hedrick et al. 2001; Slate et al. 2000; Slate and Pemberton 2002; mean d^2: Coulson et al. 1998; Slate et al. 2000; Rossiter et al. 2001; IR: Amos et al. 2001; Bean et al. 2004). However, studies connecting intra-individual genetic variation and individual social status are scarce (Höglund et al. 2002; Tiira et al. 2003).

In this study, we measured a short-term dominance hierarchy in groups of four trout and analysed the amount of genetic variation in the same individuals using 12 microsatellite loci. Our null hypothesis was that genetic variation does not have any influence on the social status of an animal, and thus, the dominant and subordinate juvenile brown trout (*Salmo trutta*) do not differ in the amount of genetic variation. The alternative hypothesis was that individual genetic variation does affect the social status of an individual. Our study fish originated from nine populations, which are reared in hatcheries for conservation and supplementary stocking purposes. These populations differed in their hatchery history and were grouped into three different categories based on the length of the hatchery rearing. Hatchery practises can dramatically affect the genetic composition of the population through founder effects, inbreeding and selection (Allendorf and Phelps 1980; Ryman and Ståhl 1980; Nielsen 1998; Primmer et al. 1999; Altukhov et al. 2000), and these changes can sometimes be seen already after one generation (Crozier 1998).

The two main genetic explanations for finding associations between selectively neutral microsatellites and fitness traits are identity disequilibrium (Charlesworth 1991; David et al. 1995) and linkage disequilibrium (Bierne et al. 1998). In identity disequilibrium (general effect), there is correlation between the homozygosity of different loci, whereas in linkage disequilibrium (local effect), neutral markers are associated (through genetic linkage) with genes affecting the fitness-associated traits. As factors promoting these events (e.g. non-random mating, small effective population size, partial inbreeding; Bierne et al. 1998; Avise 1994; David et al. 1995; Hansson and Westerberg 2002) are common in hatchery populations (Allendorf and Phelps 1980; Ryman and Ståhl 1980; Nielsen 1998; Primmer et al. 1999; Altukhov et al. 2000), the background of the populations becomes especially relevant when the populations are predisposed to variable lengths of hatchery environment. We found higher heterozygosity levels with dominants compared to subordinates; however, this was observed only in populations having longer hatchery histories. This finding adds an important new factor to the traits shown to influence dominance and highlights the importance of preserving genetic variation in populations. In addition, our results underline the importance of the genetic background of the study population in exploring associations between genetic diversity and fitness.

Materials and methods

Study fish

We used juveniles from nine brown trout populations originating from different parts of Finland (Table 1, see Lahti et al. 2001 for a map of locations). Each population was given a score indicating the length of the hatchery background, which was used in later analyses. Populations in the group 'hatchery' have the longest hatchery background, with all parents being from first- to third-generation hatchery stocks (Table 1). Populations included in the 'mixed' group consisted of crosses between hatchery and wild-caught parents, and the 'wild' group was produced by crosses between wild-caught fish (Table 1). Earlier research showed that the hatchery background did not have an effect

Table 1 Hatchery history of the brown trout populations

Score	Parents	Source river of the population	Background and number of parents (H, W)
1 Hatchery	All parents from hatchery stocks	Luutajoki (R)	1st H generation, 100 (males + females)[a]
		Iijoki (S)	3rd H generation, 26 males, 44 females
		Ingarskila (S)	1st H generation, 197 males, 293 females[b]
2 Mixed	Part of the parents originate from hatchery stocks, part from nature	Isojoki (S)	129 W males, 130 3rd H generation females
		Rautalampi (L)	160 W males, 130 H females
		Kuusinkijoki (L)	Parents from H and W, 15 males, 25 females
3 Wild	All parents from the wild	Kemijoki (R)	20 males, 26 females
		Vuoksi (L)	39 males, 12 females
		Ounasjoki (R)	60 males, 60 females

The background of the parents is indicated with W when the parents originated from the wild and H when the parents are of hatchery origin. The number of parent fish used in fertilisation producing the offspring is indicated in the last column. The number of hatchery generations is given when the information was available. Migratory form of the population: resident, sea-run and lake-run

H, Hatchery, *W* wild, *R* resident, *S* sea-run, *L* lake-run

The numbers of individuals used to fertilize the present parent fish were 24 males and 8 females[a] and 26 individuals[b]

on the aggressiveness of these populations (Lahti et al. 2001). The populations were brought to the facilities of the Saimaa Fisheries Research and Aquaculture in Enonkoski, eastern Finland, from other hatcheries as eyed-stage eggs, and thereafter, the fish were raised under similar conditions. Detailed information on the hatchery and growing conditions is given in Lahti et al. (2001).

Behavioural observations

Detailed methodology of behavioural trials and, for determination, the dominance ranks are given in Lahti et al. (2001). In short, eight replicate trials, each containing a group of four individually marked, size-matched 0+ (yearling) fish, were conducted for each population. From each population, 32 individuals were used in the trials. The trials were conducted in ten aquaria (40 cm×25 cm, water depth 30 cm), and observations on aggressive behaviour and dominance ranks were made twice a day in conjunction with feeding. Dominance ranks of the four fish were determined exclusively on the basis of their aggressiveness, and the dominant fish was removed at the end of each day until all the fish had been given a rank (see Lahti et al. 2001 for further details). Aggressiveness has been used as an indicator of dominance in several studies (Holtby et al. 1993; Nakano 1995) and is considered as a reliable measure of dominance in salmonid species (Metcalfe et al. 1989; Bailey et al. 2000).

At the end of each observation day, the dominant individual in each trial was determined based on the number of performed aggressions. An individual was regarded as dominant, if it (1) performed most aggressions towards other fish and also responded aggressively in a situation where aggressions were directed towards itself, or (2) if it could perform aggressions towards others without receiving any. In the rare cases when the fish classified dominant under (1) and (2) was not the same individual, the one that performed most aggressions towards the other fish was classified as dominant (see Lahti et al. 2001 for further details).

Microsatellite analysis

In total, 230 individuals scored for dominance in behavioural trials were analysed for polymorphism at 12 microsatellite loci (Table 2). In addition, we also analysed 156 fish from these populations to produce for reliable estimates of the genetic parameters at the population level. DNA was salt-extracted from approximately 1 mm^3 of adipose/dorsal fin according to the method of Aljanabi and Martinez (1997). Markers were divided into two groups, and end-labelled fluorescent primers (FAM, HEX or NED) were ordered so that loci labelled with the same dye colour

Table 2 Analysis conditions for the 12 microsatellite loci and diversity indices for a larger (N=386) sample of trout from the same nine populations

Microsatellite locus	Panel	Source species	Fluoroscent label	Primer amount (pmol)	PCR annealing temperature (°C)	Size range (bp)	Number of alleles	H	Mean d^2	V	Number of fish analysed
BS131[a]	2	*Salmo trutta*	HEX	3	50	130–212	16	0.76	6.1	399.23	362
MST15[b]	1	*Salmo trutta*	NED	2	58	190–230	7	0.63	7.1	826.06	362
MST60[b]	1	*Salmo trutta*	NED	3	55	85–120	4	0.34	3.5	706.12	346
MST73[b]	1	*Salmo trutta*	NED	2	58	130–170	5	0.49	3.6	747.28	366
MST85[c]	2	*Salmo trutta*	NED	3	55	130–220	15	0.68	2.4	352.32	346
One9[d]	1	*Onchorhynchus nerka*	HEX	3	55	182–220	7	0.48	6.2	752.74	308
Ssa85[e]	1	*Salmo salar*	FAM	3	60	90–130	4	0.56	2.0	378.98	373
Ssa197[e]	1	*Salmo salar*	HEX	6	60	100–180	11	0.55	9.59	1814.1	348
Ssa407[f]	2	*Salmo salar*	FAM	3	60	200–310	53	0.86	2.6	372.82	366
Ssa408[f]	2	*Salmo salar*	HEX	4	58	212–210	40	0.82	5.1	355.10	308
SSOSL417[g]	1	*Salmo salar*	NED	3	52	160–210	15	0.70	16.4	931.38	380
Strutta58[h]	2	*Salmo trutta*	FAM	3	54	100–200	32	0.81	7.7	645.51	348

The number of alleles is indicated as overall number of alleles in nine populations
H Proportion of heterozygous individuals, V locus-specific variance of mean d^2
[a]Estoup et al. (1998)
[b]Estoup et al. (1993)
[c]Presa and Guyomard (1996)
[d]Scribner et al. (1996)
[e]O'Reilly et al. (1996)
[f]Cairney et al. (2000)
[g]Slettan et al. (1995)
[h]Poteaux (1995)

had non-overlapping size ranges (Table 2). The general protocol for 10-μl polymerase chain reactions (PCR) reactions of the seven loci included in panel 1 was as follows: 1% of the extracted DNA solution, 2–4 pmol of each primer 200 μM dNTP, 10 mM Tris–HCl (pH 8.3), 50 mM KCl, 1.5 mM $MgCl_2$ and 0.25 U AmpliTaq DNA polymerase (Applied Biosystems). PCR amplification of loci in panel 2 included 0.1 U of BioTaq DNA polymerase (Bioline) instead of AmpliTaq and PCR buffer containing 1.5 mM $MgCl_2$, 160 mM ($(NH_4)_2SO_4$), 670 mM Tris–HCl, 0.1% Tween-20). The PCR profile used for all the 12 markers was as follows: 94°C for 3 min, followed by 34 cycles of 94°C for 30 s, marker-specific annealing temperature (Table 2) for 30 s and 72°C for 30 s, with a final 72°C extension of 5 min. All reactions were carried out either on PTC100, PTC200 (MJ Research) or Mastercycler gradient (Epperdorf) thermal cyclers. Following PCR, samples were pooled and electrophoresed using an ABI377 sequencer (see Primmer et al. 1999 for more details). Genotypes were scored with the Genotyper 2.5 programme (Applied Biosystems) using locus-specific macros made by C.R.P. and K.T., followed by manual corrections. Individuals scored for less than eight loci were excluded from the final analysis. GENEPOP3.1b was used to conduct exact tests for Hardy–Weinberg equilibrium and for genotypic linkage.

The genotypes of two tetranucleotide loci, namely, Ssa407 and Ssa408, included alleles that differed by only two base pairs in size, i.e. not in accordance with changes solely in repeat unit number. Closer examination of the sequences of these loci (Genbank accession numbers AJ402724 and AJ402725) revealed that they included short dinucleotide stretches [$(CA/GT)_{4–5}$], which may have also been length-polymorphic. For the calculation of d^2-based measures, the allele lengths that differed by only 2 bp were adjusted to the length of the nearest 'in-frame' repeat number observed in the population. In cases where there were two equidistant in-frame allele sizes, one of the two was chosen randomly.

Estimates of genetic variation

Three parameters were used to quantify the amount of intra-individual genetic variation:

1. Observed heterozygosity (H)—the number of heterozygous loci divided by the total number of loci analysed
2. Mean d^2—the squared difference in repeat units between the two alleles within loci, averaged over all loci (Coulson et al. 1998)
3. Internal relatedness (IR)—an estimate of parental similarity

$$\mathrm{IR} = \left(2\mathrm{h} - \sum \mathrm{f}_1\right) / \left(2\mathrm{N} - \sum \mathrm{f}_1\right)$$

where h is the number of the homozygous loci, N is the number of the loci and f_1 is the frequency of the allele in that locus (Amos et al. 2001).

Statistical analyses

Only the fish ranked as dominants (rank 1) and subordinates (rank 4) were used in the analyses because the differences are most likely to appear between the dominants and the subordinates. Initial mixed-model ANOVAs using population origin (nested within hatchery history) as a random factor and rank and hatchery history as fixed factors did not find significant population effects or rank × population interactions on H, mean d^2 or IR. Consequently, we ran the final models by using rank and hatchery history as fixed factors. All linear modelling was done using Proc Mixed in SAS (Littell et al. 1996).

The significance of differences in genetic diversity indices (allelic richness, mean d^2, IR) and observed and expected heterozygosity between populations with different hatchery history were calculated using a permutation scheme whereby the group-specific genetic diversity indices (averaged over samples and loci) were compared to groups where individuals had been allocated at random. The one-tailed P value of the tests was calculated as the proportion of 10,000 randomised data sets giving a genetic diversity index larger than the observed value. Estimation of genetic diversity indices and subsequent statistical significance was done using Fstat v2.9.3.2 (Goudet 1995).

To investigate which of the two possible mechanisms, identity or linkage disequilibrium, is behind the observed connection between genetic diversity and dominance, we performed two further analyses. If heterozygosity is correlated between independent loci, then heterozygosity carries an inbreeding signal, and the mechanism behind the observed result would most likely be identity disequilibrium (i.e. general effect; Balloux et al. 2004; Pemberton 2004). This was studied by dividing the markers randomly in two groups and calculating the heterozygosity for these two groups. Correlation between the heterozygosity of the two groups was calculated, and this procedure was repeated 1,000 times (heterozygosity–heterozygosity correlation).

To investigate whether the result would originate from one single locus, we analysed locus-specific heterozygosity

Table 3 ANOVA tables for the effects of dominance rank and hatchery history on heterozygosity, mean d^2 and internal relatedness (IR)

Source	*df*	Heterozygosity		d^2		IR	
		F	*P*	*F*	*P*	*F*	*P*
Rank	1,108	4.08	**0.046**	0.71	0.402	2.748	0.100
Hatchery history	2,108	0.72	0.488	4.18	**0.018**	0.396	0.674
Rank × hatchery	2,108	3.17	**0.046**	2.23	0.112	2.515	0.086

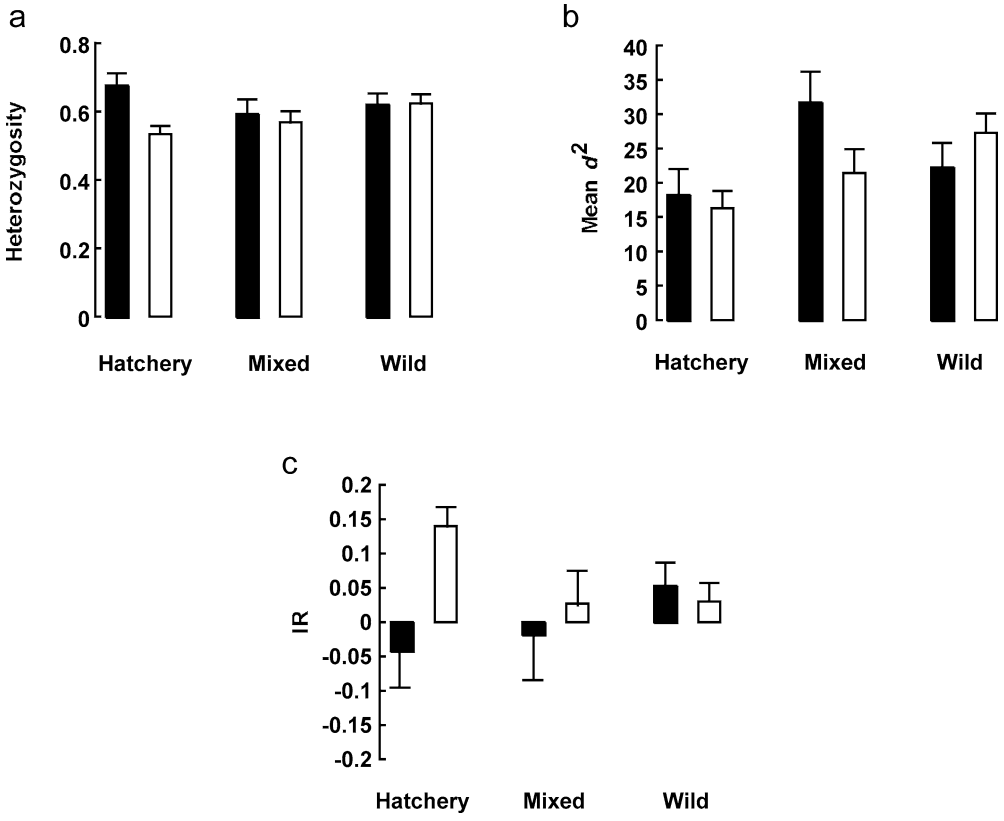

Fig. 1 Mean (±SE) heterozygosity (**a**), mean d^2 (**b**) and IR (**c**) of dominant (*black bars*) and subordinate brown trout (*white bars*) in the different hatchery history groups

as a binary variable with generalised linear models (Proc Genmod in SAS; Allison 1999) using rank, hatchery history and their interaction as fixed factors. If the effect originates from one or few loci, then these are most likely linked with fitness loci in the local chromosomal vicinity of the markers (local effect; Hansson et al. 2004).

Results

Dominant trout were more heterozygous than subordinates (Table 3; Fig. 1). However, a significant rank × hatchery interaction indicated that the difference in heterozygosity originated mainly from the hatchery group, whereas there were no differences in the two other categories between the dominant and subordinate fish (Table 3; Fig. 1). A posterior comparison was performed in order to investigate in detail whether the difference originates only from the hatchery group. Dominant fish indeed had higher heterozygosity compared with subordinates only in the hatchery group ($F_{1,44}$=11.71, p=0.001; mixed: $F_{1,25}$=0.23, p=0.639; wild: $F_{1,39}$=0.01, p=0.934). The hatchery history groups did not differ in heterozygosity. No difference was found in mean d^2 or IR values between the dominants and subordinates; however, hatchery fish had lower d^2 than wild and mixed groups (Table 3; Fig. 1b,c).

A number of significant deviations from Hardy–Weinberg equilibrium were observed at 5% significance

Table 4 Diversity indices calculated for 12 microsatellite loci in a larger sample (N=386) of the same brown trout populations

Population	Hatchery background	N	Allelic richness	H	Mean d^2	IR
Luutajoki	Hatchery	36	4.60	0.60	17.73	0.017
Iijoki	Hatchery	48	7.55	0.64	19.32	0.041
Ingarskila	Hatchery	46	6.71	0.59	28.79	0.096
		Average	6.29	0.61	21.95	0.051
Isojoki	Mixed	44	5.00	0.57	16.77	−0.023
Rautalampi	Mixed	38	7.39	0.61	27.80	0.05
Kuusinkijoki	Mixed	47	5.14	0.52	26.82	0.071
		Average	5.84	0.57	23.80	0.033
Kemijoki	Wild	47	8.11	0.65	29.84	0.034
Vuoksi	Wild	32	7.64	0.67	31.37	0.025
Ounasjoki	Wild	48	8.10	0.63	22.06	0.02
		Average	7.95	0.65	27.75	0.026

H Proportion of heterozygous individuals in each population

Table 5 Mean coefficients (r±SD) of heterozygosity–heterozygosity correlation in fish originating from different background (a) and in subordinates in hatchery group and all subordinates in the data (b)

	Mean r (±SD)
a. Background	
Wild	−0.108 (0.094)
Mixed	0.015 (0.108)
Hatchery	0.027 (0.088)
b. Subordinates	
Hatchery group	−0.125 (0.112)
Wild, mixed and hatchery groups	−0.050 (0.084)

Correlation coefficients were obtained by dividing the 13 markers randomly into two groups and calculating the heterozygosities for these groups. The correlations between the heterozygosities of these groups were calculated, and this procedure was repeated 1,000 times

level, but the deviations remained significant only in two populations after Dunn–Sidák correction: Kuusinkijoki (mixed) and Ingarskila (hatchery) had significant heterozygote deficiencies at 5% level. The number of significant genotypic disequilibrium events from the total of 198 pairwise locus tests were 21 for wild, 11 for mixed and 15 for hatchery group. After correction for multiple tests, only one event remained significant (Ounasjoki, group wild). When the genetic diversity indices of larger background populations of hatchery, wild and mixed were compared (386 individuals in total), mixed populations had significantly lower allelic richness (Table 4; P=0.034) and lower observed heterozygosity (Table 4; P=0.014) than wild populations. Allelic richness of wild populations was also higher than that of hatchery populations; however, this difference was not statistically significant (Table 5, P=0.081) There were no differences in mean d^2 or IR among the hatchery groups (Table 4, P>0.49).

The heterozygosities calculated for two randomly chosen groups of loci did not correlate significantly (Table 5). The single-locus analyses revealed several significant effects: in the loci MST60 (χ^2=4.71, df=1, P=0.03) and Ssa197 (χ^2=5.11, df=1, P=0.024), dominants were more heterozygous. Furthermore, the loci MST15 (χ^2= 7.18, df=2, P=0.028) and Ssa85 (χ^2=6.29, df=2, P=0.043) showed significant rank × hatchery background interactions. In both cases, dominant hatchery fish were more heterozygous than subordinates or fish from the other hatchery groups. However, after correction for multiple tests, none of these effects remained significant.

Discussion

The results of the present study enable the question of what factors affect individual dominance to be addressed. Our results suggest that individual genetic variation can be an important factor affecting the dominance status of the fish. We found microsatellite heterozygosity to be associated with a fitness-related behavioural trait; dominant juvenile brown trout had higher levels of heterozygosity than those ranked as subordinates. This finding is consistent with our earlier study with landlocked salmon (*Salmo salar*), where we found that fish with higher genetic diversity behaved more aggressively than fish with less genetic diversity (Tiira et al. 2003). In addition, studies conducted with inbred lines of mice have shown that inbreeding decreases aggressiveness and competitive ability (Eklund 1996; Meagher et al. 2000). In these studies, the fitness of inbred male mice was reduced through effects on competitive ability (Meagher et al. 2000). The results of the present study, however, differ significantly from the mouse studies because in our study, the amount of genetic variation influenced an individual's social status in the absence of evidently inbred individuals.

The genetic variability in the present study was determined on the basis of neutral genetic markers. As already mentioned in the introduction, the two explanations for the positive associations between heterozygosity assessed with neutral microsatellite markers and fitness-related traits are linkage disequilibrium (local effect) and identity disequilibrium (general effect; Charlesworth 1991; David et al. 1995; Bierne et al. 1998; Hansson and Westerberg 2002). If inbreeding, and thus general effect, would have been behind the observed association between microsatellite heterozygosity and dominance, we should have found a significant heterozygosity–heterozygosity correlation in our data (Balloux et al. 2004). As we did not find such a correlation, the most likely explanation for our result is the local-effect hypothesis with linkage disequilibrium. Through linkage disequilibrium, neutral microsatellites can mark large fragments of the chromosome and thus co-segregate with fitness-associated genes (Bierne et al. 1998). Indeed, our single-locus analyses showed a significant effect for four individual loci (two for rank and two for the interaction between rank and hatchery background). Although none of them remained significant after correction for multiple tests, several of these are likely to be genuine as all the significant results were in the same direction as the main result. Hence, the local-effect hypothesis gained more support as a mechanism for association between neutral markers and fitness traits from our data than the general-effect hypothesis, although the evidence for the local effect was not very strong. The general effect has gained more empirical support than the local effect (Slate et al. 2000; Höglund et al. 2002; but see Bean et al. 2004); however, according to Hansson et al. (2004), linkage disequilibrium may be more common than generally has been thought. Recent theoretical study also suggests that the ability for heterozygosity measured at a small number of loci to accurately reflect level of individual inbreeding is extremely low (Balloux et al. 2004). Therefore, it is clear that the local-effect hypothesis should be considered as a potential factor explaining genetic-diversity–fitness associations.

An important result in this study is the effect of the population background on detecting the association

between neutral genetic variation and dominance. Populations with a longer hatchery history showed a clear difference between dominants and subordinates in genetic diversity as compared to populations with a shorter hatchery history. Similarly, in the previous study where we also found a positive association between aggressiveness and genetic variation, the fish used in the experiment were of second hatchery generation (Tiira et al. 2003). Small and newly founded populations, and events such as inbreeding, bottlenecks and strong selection, which can generate both local and general effect, are not rare in hatchery stocks (Allendorf and Phelps 1980; Ryman and Ståhl 1980; Nielsen 1998; Primmer et al. 1999; Altukhov et al. 2000). Therefore, it may be that artificial breeding can increase the chance of both identity and linkage disequilibrium and also increase the chance of finding genetic-diversity–fitness association in these populations. However, small population sizes, inbreeding, bottlenecks and strong selection are common phenomena in the wild as well. Therefore, correlations between neutral marker heterozygosity and fitness can be also expected to be found in the wild. Indeed, several studies have found significant heterozygosity–fitness correlations in natural populations (Coltman et al. 1998; Coulson et al. 1998, 1999; Slate et al. 2000). However, in the light of the present results, the strength of these effects in natural populations may depend on the population's genetic history.

Of the genetic indices studied, only heterozygosity (*H*) was significantly associated with dominance. While *H* simply indicates the number of heterozygous loci, internal relatedness (IR) is a measure of how related individuals' parents are (Amos et al. 2001). Mean d^2, on the other hand, is based on long-term mutational differences of parental alleles and is suggested to be sensitive to population admixture and recent inbreeding events (Coulson et al. 1998). Recent studies using theoretical analysis (Tsitrone et al. 2001) or a very large number of microsatellite loci have suggested that heterozygosity (and also IR) would be most effective in detecting inbreeding and heterosis (Amos et al. 2001; Hedrick et al. 2001; Slate and Pemberton 2002). Our results thus support the finding that heterozygosity outperforms mean d^2 in most cases. The reason for not finding an association between dominance and IR may be that IR is particularly good in detecting inbreeding effects as it measures parental similarity, and in our populations, direct inbreeding did not seem to be a major factor.

Our result is based on an experiment, which was conducted in hatchery environment among only few fish, and the situation can be different in the wild (Höjesjö et al. 2002). Metcalfe et al. (1990) separates absolute status and relative status in fish dominance hierarchy. Absolute status is the fish's ability to dominate in a larger group, whereas relative status is the ability to dominate in smaller groups. In our experiment, the dominance rank determined among four fish clearly described the relative status. Thus if the situation or context will change, the relative status of the fish may well change, too. However, the relative status assessed in our experiment appears to be rather stable. The stability of a dominance hierarchy was tested in an experiment where we repeated the behavioural experiment after 8 months using the same fish (125 fish out of 319) and the same group constitutions as in the first experiment (Tiira et al., submitted). The stability of the linear dominance hierarchy was good; the later dominance rank of the fish (measured 8 months after the first rank) was significantly dependent on the first rank.

Assuming that the local-effect hypothesis is the mechanism for the observed association between genetic variation and dominance, the next interesting question to address is which genes are in linkage disequilibrium with the used markers? On the basis of earlier research (Metcalfe et al. 1995; Cutts et al. 1998), we could speculate that genes affecting metabolic rate or hormonal control of behaviour and growth may be involved. It is also notable that higher heterozygosity might be associated with bold behaviour under predation threat, as dominant and more aggressive individuals are generally more willing to take risks. These are hypothetical associations, however, and require further testing.

Finally, we can ask what the ecological implications of this study are. Preserving a sufficient amount of genetic variation in a population has been an important conservation goal for a long time (Frankham et al. 2002), as inbreeding depression can cause severe effects on individual and population fitness (Maynard Smith 1956; Saccheri et al. 1998). In this study, there was no indication of inbred individuals; nevertheless, the difference in social status between individuals with differing amounts of genetic variation was clear. Considering the magnitude of the effect that social status may have on the later life history and fitness in salmonids (Metcalfe et al. 1989) and other species (Clutton-Brock et al. 1986; Pusey et al. 1997), the importance of genetic variation is clearly emphasized. Rather than having drastic effects directly on viability or fertility, the effect of individual genetic variation can be more subtle through behaviour on competitive ability, but may finally result in large effects on fitness.

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