

BOTH MALE AND FEMALE SEXUAL ORNAMENTS REFLECT OFFSPRING PERFORMANCE IN A FISH

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Secondary sexual characters are often expressed in both sexes (mutual ornamentation), but are less often studied simultaneously. We studied the adaptive signaling function of male and female ornamentation in a mutually ornamented fish, the whitefish *Coregonus lavaretus*. In an experimental design in which nongenetic environmental effects were minimized, we found that highly ornamented females, males, and their parental combinations had offspring with better swimming performance and predator-avoidance ability than less ornamented individuals or combinations. Furthermore, highly ornamented females had larger offspring that also had higher yolk volume than less ornamented individuals. Offspring swimming performance was not dependent on offspring size and was only weakly affected by yolk volume, which suggest that swimming performance and measured morphological traits are independent fitness measures. In conclusion, mutual ornamentation of whitefish may signal the quality of individuals in both sexes, which may indicate ongoing directional selection for these ornamental traits. However, offspring fitness traits were also dependent on parental combination, which suggests that genetic compatibility effects may weaken the directional selection and the indicator value of the ornamentation.

KEY WORDS: Breeding tubercles, compatible genes, genetic quality, offspring fitness, performance, sexual selection.

Sexual selection theory has successfully explained the evolution of elaborate sexual ornamentation in males (Trivers 1972; Zuk et al. 1990; Clutton-Brock and Vincent 1991; Andersson 1994; Sheldon et al. 1997; Amundsen 2000; Candolin 2003; Sheldon et al. 2003; Tregenza et al. 2006), but the effects of sexual selection on female ornaments have received much less attention (Amundsen 2000; Clutton-Brock 2007, 2009). Female ornamentation is conventionally considered as a genetically correlated response to selection for male ornamentation (e.g., Lande 1980) or similar selection pressures in both sexes (Kraaijeveld et al. 2007). However, recent studies have

shown that elaborate ornamentation of females may also be under direct sexual selection by males (Jones and Hunter 1993; Amundsen et al. 1997; Jones and Hunter 1999; Amundsen and Forsgren 2001) or under selection via reproductive competition (Watson and Simmons 2010a,b). The resources allocated to ornamentation may constrain female fecundity (Fitzpatrick et al. 1995; LeBas et al. 2003; Chenoweth et al. 2006), which may lead to selection for dishonest female signaling (Funk and Tallamy 2000; Bonduriansky 2001). Thus, whether female ornamentation honestly signals individual genetic quality is largely unknown.

The majority of studies demonstrating fitness benefits of males mating with highly ornamented females, have been correlative, rather than experimental (Doutrelant et al. 2008). Roulin et al. (2000, 2001) performed cross-fostering experiments in the barn owl (*Tyto alba*) and found that the offspring antibody response toward a nonpathogen antigen was positively correlated to plumage spottiness of the mother, but not the father. These authors concluded that although the most likely explanation for their finding was additive genetic effects, maternal environmental effects could not be ruled out. In other studies, female ornaments have been demonstrated to reflect, for example, individual differences in fecundity (Amundsen 2000; LeBas et al. 2003), hatching success of the offspring (Komdeur et al. 2005), temporal changes in female reproductive status (Clutton-Brock 2007), offspring survival (Domb and Pagel 2001), or condition and sprint speed (Weiss et al. 2009).

In many species elaborated ornamental traits are expressed in both sexes (mutual ornamentation) (Kraaijeveld et al. 2007). Numerous studies have demonstrated that sexually monomorphic characters can be a consequence of mutual sexual selection (Johnstone et al. 1996; Kraaijeveld et al. 2007). If both sexes prefer the same ornamental trait, this can lead to assortative mating (pairing of individuals with similar ornamental traits) or directional mate preferences (both sexes prefer to pair with highly ornamented mates (Hill 1993; Andersson et al. 1998; Jawor et al. 2003). On the other hand, as highly ornamented individuals may not always have genotypes of highest genetic compatibility, genes that are good for some parental combinations may not be good for another (e.g., Mays Jr. and Hill 2004). Roberts and Gosling (2003) demonstrated that these two separate mate choice criteria (good genes vs. compatible genes) may act simultaneously. Selection for compatible genes can constrain directional selection on indicator (ornamental) traits (Colegrave et al. 2002), and partly explain why the association between ornamental traits and offspring fitness is usually relatively weak (Møller and Alatalo 1999).

Although a growing number of studies have offered correlative evidence that female ornamentation is often linked to some component(s) of fitness, carefully designed experiments are needed to clarify evolutionary mechanisms of mutual ornamentation (Kraaijeveld et al. 2007). Mating systems with external fertilization and no parental care are ideal model systems for this purpose (Simmons 2005). Whitefish *Coregonus lavaretus* do not provide paternal care and females produce large numbers of eggs that are externally fertilized. Both sexes in many populations develop a distinct breeding ornamentation, that is, keratinized epidermal tubercles prior to the spawning period (Wiley and Collette 1970; Wedekind et al. 2001, 2008). It has been suggested that the primary function of breeding tubercles in whitefish is to maintain contact between individuals during spawning, but the conspicuous white color and hardness of these ornaments may enable tubercles

to also be used as visual, tactile, and hydrotactile signals (Wiley and Collette 1970). Previous studies have demonstrated that the size and/or number of the male breeding tubercles in different fish species are linked to individual condition (Wedekind 1992; Rudolfsen et al. 2008), male dominance (Kortet et al. 2004a), parasite resistance (Kortet et al. 2004b), embryo mortality (Wedekind et al. 2001), and offspring first-feeding success (Huuskonen et al. 2009). It is not known whether breeding tubercles are energetically (or otherwise) costly to produce (Wedekind et al. 2008, but see Kortet et al. 2003). However, it has been demonstrated that honest ornamentation does not always need to be costly (Berglund et al. 1997; Maynard Smith and Harper 2003).

Here we studied whether male and female ornamentation could signal potential genetic differences in offspring swimming performance, a behavioral trait that indicates offspring posthatching fitness in the nature. Furthermore, we examined whether offspring swimming performance is related to their predator-avoidance ability. Such performance skills of newly hatched fish larvae are crucial factors determining subsequent growth and survival of individuals (Fuiman and Cowan Jr. 2003; Huuskonen et al. 2009), and are therefore strongly linked to fitness. We crossed 10 males and 10 females in all possible combinations (North Carolina II design) (Lynch and Walsh 1998), and partitioned fitness variation among good genes, compatible genes, and maternal environmental effects. Although North Carolina II breeding design is probably the best alternative for this purpose it has certain limitations and not even this breeding design can fully separate maternal genetic and maternal environmental effects. Thus, for the simplicity we assumed that maternal genetic effects equal paternal genetic effects.

Materials and Methods

ARTIFICIAL BREEDING EXPERIMENT

Parental fish originated from the River Oulujoki (Finland) anadromous whitefish population (65°1'N, 25°28'E). The fish were caught on their way to their spawning grounds in the Merikoski rapids from October 22 to 24, 2008 using long-handled dip nets and were maintained in single-sex tanks in a hatchery. On 27 October, we stripped eggs from 10 haphazardly selected, ovulating females (mean total length 41.4 cm ± 0.40 SEM) and distributed their eggs into Petri dishes (Table S1). We collected sperm from 10 haphazardly selected males (mean total length 38.8 cm ± 0.45 SEM) and used 30 µl of milt to fertilize the egg batches in all possible crosses (North Carolina II design: Lynch and Walsh 1998) resulting in 100 sib groups. Same volume of eggs was taken from each family (about 300 eggs/family). All families were randomly divided into two replicates and the eggs were incubated in 600 L cooled and aerated tanks in nonchlorinated tap water at 4°C until hatching in March 2009. All eggs were incubated

in identical (35 mm × 70 mm × 70 mm) incubating containers. Dead eggs were counted and removed weekly. To measure the size of the breeding tubercles of the parental fish, we made plaster casts immediately after fertilization following procedures in Wedekind et al. (2001), and the average cast depth (with 0.01 mm accuracy) of ten tubercles in the middle row anterior to anal fin was measured by a dial indicator (Mitutoyo Co., Aurora, IL).

SWIMMING PERFORMANCE

After hatching whitefish larvae were kept in their incubating containers, where their family-specific hatching times and density differences were observed. As the swimming performance trials were conducted approximately seven days after hatching (during February 2009), the pre-experiment mean density of offspring remained approximately the same in all families. To determine the swimming performance of larvae, we constructed a simple swimming tube system with gravity-driven flow (Huuskonen et al. 2009) (Fig. 1). Water flowed from the container into a tube (diameter 9 mm) at a constant velocity of 6.2 cm s⁻¹. This corresponds to 4.8 body lengths s⁻¹ in the tested larvae, which had a mean total length of 12.8 mm. In the experiments, individual larvae were forced to swim against a current at 6°C water temperature, and their fatigue time was recorded as the time at which they drifted against a net placed at the rear end of the tube and could not continue swimming within 10 s. From each family, five randomly selected individuals were used in the experiments. After the experiments, the larvae were killed in an overdose of tricaine methanesulfonate (MS-222, Sigma[®], Sigma Chemical Co., Perth, Australia) and preserved in a solution of 70% ethanol and 1% neutralized formalin. The larvae were measured for total length (TL), and the length (l) and height (h) of yolk were also measured for the calculation of yolk volume (V) by the equation for a prolate spheroid: $V = 0.5236 * l * h^2$ (Blaxter and Hempel 1963).

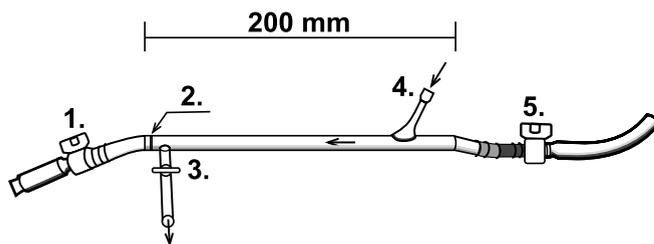


Figure 1. Swimming tube system used in offspring swimming performance trials. The system consisted of aquarium pump (not shown), which lifted water into 10 L plastic container at the height of 60 cm, where the water flowed into a tube (diameter 9 mm). The velocity of the water was adjusted by means of two taps (1, 5). Experimental fish were placed inside the swimming tube via the side duct (4) and removed from the tube via the removal tap (3) after the fish had exhausted and drifted against the net (2).

PREDATOR-AVOIDANCE ABILITY

One-year-old Arctic charr (*Salvelinus alpinus*) were used as a novel predator in the trials. Experimental predator fish were obtained from Lake Keskijärvi aquaculture station 6 weeks prior to trials and maintained in a 360 L aquarium (length × width × height 110 cm × 55 cm × 60 cm) with constant water flow. The fish were fed on commercial dry food (BioMar, Aqualife, Denmark) by an automated feeding system. In addition, to train the feeding skills of the predators, they were fed on newly hatched whitefish larvae 3–5 times/week during 4 weeks before the trials. Larvae originated from the same parental fish as offspring used in actual experimental trials, but the larvae had been incubated in warmer water (at 6°C) to decrease the development time of the embryo. Before the trials, five randomly selected predators (mean total length 120 ± 1.3 mm SEM) were captured from the maintenance aquarium and placed into 80 L experimental aquarium (length × width × height 59 cm × 41 cm × 33 cm). Then three whitefish larvae were picked from the selected families and placed in the experimental aquarium. Prior to offspring sampling, whitefish families were ranked according to their swimming performance. Then systematic sampling was applied (every fifth family was selected), so that the total number of selected families was 20. The predator-avoidance time of the offspring was determined by measuring the time from the start of the experiment to the moment when 2 of 3 offspring had been predated. We used this procedure as our preliminary trials showed that the predator behavioral response to only one prey item was significantly weaker than when several larvae were placed to aquarium simultaneously. Six sequential replicates were made, so that the total number of offspring used per family was 18. All five predators were changed before each six replicate ($n = 30$ predators in total) to avoid satiation. According to our preliminary tests, one predator fish could eat approximately 30–40 larvae within a few minutes. As the total number of whitefish larvae/replicate was 60 (of which 40 were eaten) and five predators were used in each replicate, the mean number of larvae per predator was only 8. We also randomized the order of families in each six replicates. Thus, it is likely that predator satiation did not affect our results.

STATISTICAL ANALYSES

General linear mixed effect models (LME) with restricted maximum likelihood (REML) were used to analyze the parental effects on offspring swimming performance, size (total length) and yolk volume. Female and male identity and their interaction were used as random factors in the models. The significance of random factors was tested using likelihood ratio (G^2) statistics (Sokal and Rohlf 1995; Quinn and Keough 2002). Additive and nonadditive genetic effects on offspring swimming performance were calculated as 4 × the sire, dam and sire × dam components of variance (Lynch and Walsh 1998). Maternal environmental effects were

estimated as the difference between the variances associated with dam and sires (dam minus sire). Because additive genetic variances cannot be reliably estimated for traits with strong maternal effects (Shaw and Byers 1998), additive and nonadditive effects for offspring yolk volume and total length were not determined. The correlations between tubercle size and three fitness parameters (i.e., offspring swimming performance, total length and yolk volume) were studied using Pearson product moment correlations. Because even relatively weak ornamentation–fitness correlations may have significant evolutionary consequences (e.g., Alatalo et al. 1998), we further divided both sexes to two classes (small tubercles, ST vs. large tubercles, LT) to improve the probability of detection of these potential weak fitness benefits (c.f. Alatalo et al. 1998). The mean tubercle size value was used as a separator between classes. We expected that offspring fitness is higher in highly tubercled parents than in less ornamented individuals. Therefore, the effect of the ornamentation on offspring swimming performance was tested in sex-specific directed analyses of covariance (ANCOVAs) (see Rice and Gaines 1994; Wedekind et al. 2001 for details), with the male or female tubercle class as the fixed factor and the offspring yolk volume as a covariate. Directed tests have greater power than conventional two-tailed tests and they can treat noncompliance with H_0 in the unexpected direction, which is not possible in one-tailed tests (Rice and Gaines 1994). The effects of ornamentation on offspring total length and yolk volume were tested in directed analyses of variance (ANOVAs) with the male or female tubercle class as the fixed factor. Similar analyses were used to test the effect of different male–female combinations (i.e., ST ♂/ST ♀, ST ♂/LT ♀, LT ♂/ST ♀, and LT ♂/LT ♀). Following Moran (2003), we did not use Bonferroni corrections in our tests. As in ecological (and behavioral) studies measured parameters often have high variability (such as swimming ability of the whitefish larvae) and subsequently low statistical power, highly significant P -values of the statistical tests

are rare (Moran 2003). In addition, Bonferroni corrections only examine individual P -values of each test, while ignoring the number of statistical tests that are significant. As the aim of the present work was to study the fitness benefits of mate choice, which are often weak (see above), we decided not to correct our P -values to improve the detection probability of these weak effects. The fulfillment of the assumptions of tests was ensured graphically and with Levene's tests according to Quinn and Keough (2002). Normality was assessed using Shapiro–Wilk statistics and when needed, a natural logarithm transformation was applied to satisfy the requirement of normal distribution. Statistical analyses were performed using the SPSS 16.0 statistical package (SPSS Inc., Chicago, IL).

Results

SWIMMING PERFORMANCE

No correlation was found between swimming performance and total length of the offspring (Pearson, $r = -0.044$, $P = 0.664$, $n = 100$). The correlation between swimming performance and offspring yolk volume tend to be weakly negative (Pearson, $r = -0.180$, $P = 0.074$, $n = 100$) (Fig. 2). In offspring swimming performance, all three effects (male, female, and male \times female) were statistically significant (Table 1, Table S1). Dam, sire and dam \times sire effects explained 18.0% of the phenotypic variation in swimming performance. Maternal (genetic and environmental) effects accounted for 29.6% of the variation. The relatively small difference between male and female components of variance (2.9%) indicates that these maternal effects are largely genetic (additive). Additive sire effects accounted for 18.0% and nonadditive effects accounted for 24.4% of the phenotypic variation. Swimming performance was significantly higher in offspring of more ornamented females and males than in less

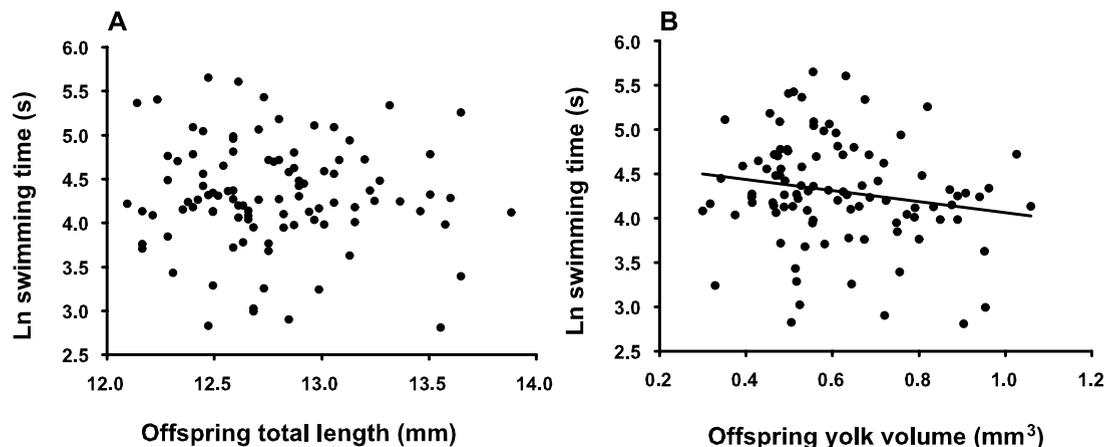


Figure 2. The association between swimming performance and total length (A) and between swimming performance and yolk volume (B) of the whitefish larvae.

Table 1. Statistics of general linear mixed models (with REML method) for three offspring fitness measures. Female, male, and the interaction between female and male were used as random factors in the models.

Fitness measure	Effect	Log likelihood	G^2	P	% of variance
Swimming time	Female	1580.1	24.98	<0.001	7.4
	Male	1574.0	12.78	<0.001	4.5
	Female × male	1571.2	7.21	0.007	6.1
	Residual	1567.6			82.0
Total length	Female	2683.7	133.41	<0.001	42.5
	Male	2621.6	9.21	0.002	2.1
	Female × male	2643.8	53.66	<0.001	12.8
	Residual	2617.0			42.6
Yolk volume	Female	-333.5	141.29	<0.001	38.4
	Male	-400.0	8.12	0.004	3.3
	Female × male	-370.3	67.71	<0.001	11.8
	Residual	-404.1			46.5

ornamented individuals (directed ANCOVA, $F_{1,99} = 4.095$ and 3.305 , $P = 0.029$ and 0.045 , respectively) (Fig. 3A). Furthermore, the effect of female–male (tubercle) combination was significant (directed ANCOVA $F_{3,99} = 2.720$, $P = 0.031$) (Fig. 3B). Tukey's posthoc tests revealed that offspring swimming performance was higher in the large–large combination than in the small–small combination ($P = 0.035$). All other paired comparisons were insignificant (Tukey's test, $P > 0.05$). The effect of covariate (yolk volume) was significant in females and female–male combinations ($P = 0.021$ and 0.038 , respectively), but not in males ($P = 0.131$). The correlation coefficient between tubercle size and offspring swimming performance was not significant in either sex (Pearson, $n = 10$, $r = 0.131$, $P = 0.718$ and $r = 0.321$, $P = 0.365$ for males and females, respectively). Furthermore, there was no correlation between parental body size (total length) and tubercle size (Pearson, $n = 10$, $r = -0.054$, $P = 0.881$ and $r = -0.032$, $P = 0.930$ for males and females, respectively) (Table S1).

TOTAL LENGTH AND YOLK VOLUME

All three effects (male, female, and male × female) were statistically significant for offspring total length and yolk volume (Table 1, Table S1). Dam, sire, and dam × sire effects explained 57.4% and 53.5% of the phenotypic variation in offspring total length and yolk volume, respectively. The relatively large difference between female and male effects in offspring total length and yolk volume (Table 1) suggests that maternal environmental effects may explain most of the variation in these fitness measures. The offspring of the more ornamented females were longer and had larger yolk volume than those of less ornamented individuals (directed ANOVA, $F_{1,99} = 10.833$, $P < 0.001$, $F_{1,99} = 9.450$, $P = 0.002$, respectively, Fig. 3C, E). In males no difference between ornament groups were found (directed ANOVA, $F_{1,99} = 1.290$,

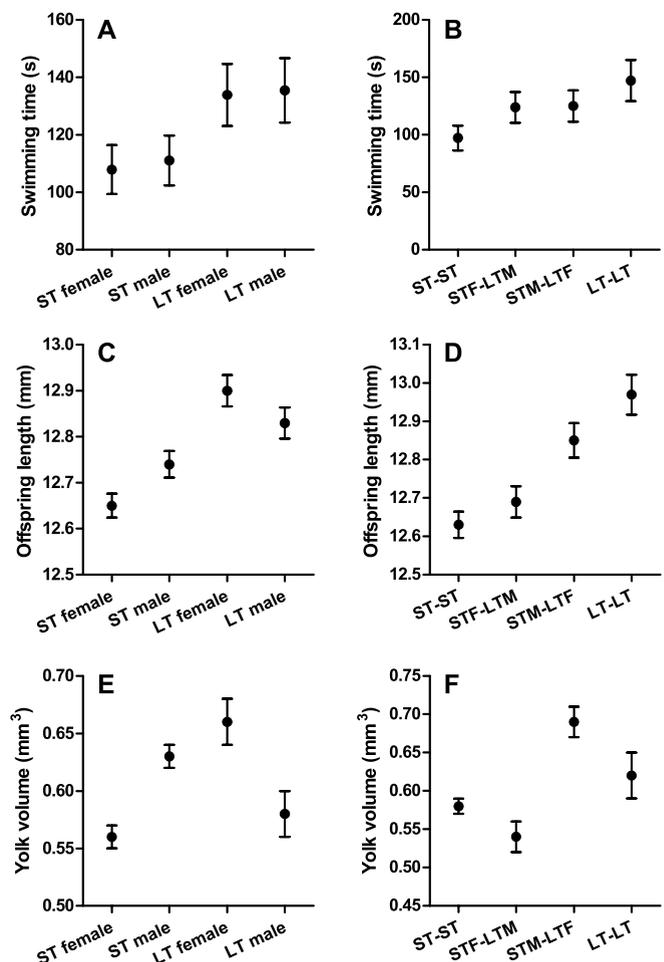


Figure 3. Swimming performance ($s \pm SEM$, $n = 500$) (A, B), total length ($mm \pm SEM$, $n = 500$) (C, D) and yolk volume ($mm^3 \pm SEM$, $n = 492$) (E, F) of the offspring of females and males with large and small tubercles and various parental tubercle combinations. ST = small tubercles, LT = large tubercles, F = female, M = male.

$P = 0.162$, $F_{1,99} = 2.413$, $P = 0.078$ for offspring total length and yolk volume, respectively). The effect of the female–male (tubercle) combination was significant for both offspring total length (directed ANOVA, $F_{1,99} = 4.095$, $P = 0.006$) and yolk volume (directed ANOVA, $F_{1,99} = 4.119$, $P = 0.006$) (Fig. 3D, F). The highly ornamented female–male combination had the largest offspring. Tukey posthoc tests revealed that they differed statistically from the small–small combination ($P = 0.011$), but not from the other two combinations ($P > 0.05$). The yolk volume was largest in the large tubercle female–small tubercle male combination, which differed from small–small (Tukey’s test, $P = 0.041$) and large tubercle male–small tubercle female groups ($P = 0.010$). The correlations between tubercle size and offspring total length or yolk volume were not statistically significant (Pearson, males: $n = 10$, $r = 0.134$, $P = 0.711$ and $r = -0.584$, $P = 0.076$; females: $n = 10$, $r = 0.233$, $P = 0.517$, $r = 0.291$, $P = 0.414$, respectively) (Table S1).

ASSOCIATION BETWEEN SWIMMING PERFORMANCE AND PREDATOR AVOIDANCE BEHAVIOR

We found a statistically significant positive correlation between offspring swimming performance and their mean predator-avoidance time (Pearson, $r = 0.210$, $P = 0.022$, $n = 119$). When family-specific ($n = 20$) mean avoidance time was calculated over all six replicates the positive correlation was stronger, but only marginally significant (Pearson, $r = 0.396$, $P = 0.084$, $n = 20$), due to lower statistical power.

Discussion

We found that highly ornamented whitefish females, males, and their parental combinations produced offspring with better swimming performance (indicating better predator-avoidance ability), than did the less ornamented individuals or combinations. Furthermore, highly ornamented females had larger offspring, which had higher yolk volumes than less ornamented females (see also Bang et al. 2006; Kekäläinen et al. 2010). Even if we cannot make a clear distinction between maternal genetic and maternal environmental effects, our results suggest that mutual ornamentation in this species may indicate the genetic quality of individuals in both sexes.

Nearly all of the natural mortality in fish populations takes place in early life stages, mainly due to predation or starvation (Fuiman and Magurran 1994; Fuiman and Cowan Jr. 2003). Thus, variation in performance during the first days after hatching probably has a high evolutionary significance (e.g., Elliot 1989). In an earlier study, we have shown that male ornamentation predicts offspring feeding success in whitefish (Huuskonen et al. 2009). Together with the present study, our results suggest that parental ornamentation indicates offspring performance both in early feed-

ing and predator avoidance. Because both of these skills are highly dependent on locomotion, swimming ability is vital for larval survival (Fuiman and Cowan Jr. 2003). However, also individual size is an important factor affecting larval survival (Kraak and Bakker 1998). Larger body size provides larvae a competitive advantage over smaller individuals (Einum and Fleming 1999; Eilertsen et al. 2009) resulting in higher growth and survival rates, particularly in poor growth environments (Einum and Fleming 1999), which are typical during natural (spring) hatching periods of whitefish larvae. Growth and development of newly hatched fish larvae are highly dependent on yolk reserves (Kamler 2008). Offspring with larger yolk volumes have more time to initiate external feeding before exhaustion compared to individuals with smaller reserves. In the present study, the larger size and yolk volume among the offspring of highly ornamented females indicates that these offspring may, in addition to better swimming and predator avoidance ability, also have higher competitive ability and better ability to resist unfavorable feeding conditions. Offspring swimming performance was not associated with offspring total length and the correlation between swimming performance and yolk volume was weak. Therefore, offspring swimming performance and offspring total length/yolk volume can be regarded as relatively independent measures of fitness in the present study.

The mutual sexual selection hypothesis proposes that monomorphic secondary sexual characters are used as mate choice or status signals in both sexes and that the most ornamented individuals are of highest quality and obtain the highest mating success (Johnstone et al. 1996; Johnstone 1997; Kraaijeveld et al. 2007). Therefore, the observed association between mutual breeding tubercle ornamentation and offspring fitness suggests that mutual sexual selection may have important role in whitefish mating. The evolution of mutual mate choice requires (1) high variance in individual quality among potential mates of both sexes, (2) high mate encounter rates (low reproduction constraints), and (3) that investing in mating with one partner reduces the ability to invest in other matings (Kraaijeveld et al. 2007; Lihoreau et al. 2008). All of these requirements are fulfilled in whitefish. We found that individual variation in offspring swimming ability was high in both sexes. As the whitefish is a group spawner, mate encounter rates do not limit sexual selection (Wedekind et al. 2001; Rudolfsen et al. 2008). In such mating systems, the mating opportunities of males often exceed the number of eggs they can fertilize and thus male reproductive success is restricted by the limitations of sperm (Cornwallis and O’Connor 2009).

Although breeding tubercles have been demonstrated to have a clear signaling function in spawning and prespawning behavior in other species (Kortet et al. 2004a; Jacob et al. 2009), their exact role in whitefish mating remains to be confirmed (Wedekind et al. 2008). Because mutual mate choice is common in various fish species (e.g., Rowland 1982; Kraak and Bakker 1998;

Amundsen and Forsgren 2001; Werner and Lotem 2003; Wong et al. 2004), our results, together with the facts above suggest that the mutual ornamentation of whitefish could have evolved through mutual mate preferences. Alternatively, mutual breeding tubercle ornamentation may result from reproductive competition in both sexes, that is, mutual ornaments can function as badges of status or weapons in both sexes (Watson and Simmons 2010a,b). Therefore, secondary sexual traits can be under intrasexual selection, which may promote directional selection on ornamental traits even without ornament-based mating preferences (Watson and Simmons 2010b). However, as the mechanism maintaining whitefish breeding ornamentation remained unclear we cannot theoretically rule out the possibility that female ornaments are just a genetically correlated response to selection for male ornamentation. On the other hand, genetic correlation hypothesis may not explain why we found female ornamentation to be linked to several offspring fitness traits. In any case, although our study clearly suggests that female breeding tubercles can have independent signaling function, additional studies are required to confirm our results.

One of the predictions of the mutual sexual selection hypothesis is that selection for the same secondary sexual traits in both sexes should result in assortative mating (MacDougall and Montgomerie 2003; Siefferman and Hill 2005). If ornamental showiness of both males and females is positively associated with some aspect of individual quality, directional mate preferences should lead to directional selection for these ornamental traits (Kraaijeveld et al. 2007; Baldauf et al. 2009). Thus, both sexes may prefer to pair with highly ornamented partners, which would leave less ornamented individuals to pair among themselves (McLain and Boromisa 1987). We found that the offspring of highly ornamented parental combinations have higher fitness than when one or both parents are less ornamented. This indicates that in the present population, breeding ornamentation of whitefish may be under directional selection.

However, our results show that the effect of parental combination was significant for all three fitness measures (offspring swimming performance, size, and yolk volume). This indicates that the fitness of the offspring is also dependent on the genetic compatibility of the parental fish (Zeh and Zeh 1996; Johnsen et al. 2000; Tregenza and Wedell 2000; Roberts and Gosling 2003; Rudolfsen et al. 2005). When both selection mechanisms (good genes and compatible genes) operate simultaneously, selection for genetic compatibility can weaken directional selection on ornamental traits (Colegrave et al. 2002). This should further undermine the correlation between ornamental expression and genetic quality (Rudolfsen et al. 2005). This may be the case with whitefish, because in both sexes we detected only a relatively weak correlation between breeding ornamentation and offspring fitness, although highly ornamented individuals or combinations

had higher fitness than less ornamented fish on average. Alternatively, potential undetected violations of the assumptions of the Pearson correlation analysis caused by low sample size ($n = 10$ males and females), may have led to underestimation of the strength of the association in one or more ornament–fitness correlations. However, fitness benefits do not necessarily need to be large to have important evolutionary consequences. For example Møller and Alatalo (1999) found that the viability-based sexual selection is widespread across taxa, but that the fitness benefits of mate choice are relatively minor: the average correlation coefficient between male traits and offspring fitness (survival) was 0.122. As pointed out by Alatalo et al. (1998) even relatively weak fitness benefits can maintain the honesty of sexual signaling and may have considerable consequences on an evolutionary time scale (Møller and Alatalo 1999). Furthermore, these minute benefits and trade-offs between different mate choice criteria (Roberts and Gosling 2003; Mays Jr. and Hill 2004; Neff and Pitcher 2005) may explain how genetic variation in sexually selected traits is maintained (i.e., may resolve the lek paradox). Further experimental studies controlling for the confounding nongenetic effects are required for a more comprehensive understanding of the evolution of mutual ornamentation.

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Supporting Information

The following supporting information is available for this article:

Table S1. Total length, body mass, the mean size of the breeding tubercles and the mean values of the three offspring fitness measures in 20 parental fish.

Supporting Information may be found in the online version of this article.

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