Experimental evidence for paternal effects on offspring growth rate in Arctic charr (*Salvelinus alpinus*)

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Sexual selection theory predicts that females should choose males that signal viability and quality. However, few studies have found fitness benefits among females mating with highly ornamented males. Here, we use Arctic charr (*Salvelinus alpinus*), a teleost fish with no parental care, to investigate whether females could gain fitness benefits by mating with highly ornamented and large-sized males. Carotenoid-based coloration signalled by males during spawning is believed to be an indicator of good genes for this species. Paternal effects on offspring size (body length and dry body mass) were examined experimentally by crossing eggs and sperm *in vitro* from 12 females and 24 males in a split-brood design and raising larvae to 30 days past hatching. We clearly demonstrated that there was a relationship between offspring size and paternal coloration. However, a negative interaction between paternal length and coloration was evident for offspring length, indicating that positive effects of paternal coloration were only present for smaller males. Thus, the red spawning coloration of the male Arctic charr seems to be an indicator of good genes, but the effect of paternal coloration on offspring length, an indicator of 'offspring quality', is size dependent.

Keywords: good genes; carotenoid coloration; female choice; fitness; body length; body mass

1. INTRODUCTION

Signals are actions or structures that increase an individual's fitness by altering the behaviour of other organisms detecting them (Endler *et al.* 2000). Certain signals serve as interspecific deterrents, warning potential predators off a venomous or foul-tasting prey, while others are used mainly for intraspecific signalling. The differences between the sexes in coloration or morphology, in addition to differences in gonads and genitalia, are called secondary sexual characters. Secondary sexual characters may be in the form of elaborate plumage, colourful scales and fins, heavy antlers or horns, tusks or body size (Andersson 1994). They all serve as important signals in attracting sexual partners and deterring sexual competitors (Andersson 1994).

Most secondary sexual characters are believed to be handicaps (Zahavi 1975), reducing a male's chance of survival. Although such traits may be directly opposed by natural selection (Moen *et al.* 1999), they are favoured by the female through sexual selection (Andersson 1994). Bright colours and noisy vocalization might draw the unwanted attention of predators to the displaying individual. Yet, the traits may act as strong signals of viability, as any male that can successfully forage and

escape predation despite such handicaps might indeed be worthy of the female's favour. Other characters are so costly to produce and maintain that only resourceful, high-quality males can afford them (Maynard Smith 1985).

Females choosing males based on their secondary sexual characters might receive direct benefits such as food or protection, or indirect benefits such as good genes (Hamilton & Zuk 1982; Sheldon *et al.* 1997; Barber *et al.* 2001). An example of the latter is found in grey tree frogs (*Hyla versicolor*). Here, females mated with males that produced long courtship calls sired offspring of better quality when compared with females mated with males that produced shorter calls (Welch *et al.* 1998). Further support for the idea that secondary sexual characters can be regarded as indicators of good genes is the correlation between the expression of male secondary sexual characters and offspring viability documented in meta-analysis (Møller & Alatalo 1999). Yet, the variation in offspring viability explained by variation in male ornaments was rather small, only 1.5 per cent (Møller & Alatalo 1999). However, even such small effects on offspring fitness might favour females with a preference for highly ornamented males (Møller & Alatalo 1999). Good genes might, for example, provide offspring with resistance to parasites, as hypothesized by Hamilton & Zuk (1982). Offspring may also inherit other potentially fitness enhancing morphological traits, including body size (Trivers 1972; Sheldon *et al.* 1997; Schousboe *et al.* 2004). Maternal effects on offspring quality have been demonstrated in a variety of species. In fact, several studies have revealed that females adjust their reproductive effort in accordance with

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0884> or via <http://journals.royalsociety.org>.

male attractiveness (Burley 1986; Cunningham & Russell 2000; Sheldon 2000; Saino *et al.* 2002). In experimental studies, *in vitro* fertilization provides a powerful method of controlling for non-genetic benefits and maternal effects on offspring quality.

The Arctic charr (*Salvelinus alpinus*) is a salmonid where dominant males establish and defend territories (Fabricius & Gustafson 1954). No parental care is given and the eggs are hidden in rocks and gravel, and thereafter left unguarded as they develop over winter (Sigurjónsdóttir & Gunnarson 1989). During the breeding season, displaying males aggregate and fish coloration intensifies (Klemetsen *et al.* 2003). Additionally, the size (length) of a male may reflect an individual's dominance within a hierarchy (Noakes & Balon 1980), with differently sized males adopting different reproductive strategies (e.g. Archer 1988; Andersson 1994; Taborsky 1998). The larger males may monopolize females by chasing away subordinate males, but the spawning areas of Arctic charr offer no form of protection for mating pairs. Consequently, during spawning acts between a female and a guarding male, non-guarding and subordinate males may intrude the spawning area and release their milt (Fabricius 1953; Sigurjónsdóttir & Gunnarson 1989). Experimental studies have shown that male Arctic charr are likely to respond and change their social status within a hierarchy depending on the state of their competitors (Strøm 2007), which means that a male's social status within the hierarchy is plastic and depends on both the state of itself and its competitors.

The red colour of the male Arctic charr, acquired partly through feeding on carotenoid-carrying crustaceans (Klemetsen *et al.* 2003), may be a way of displaying individual health status. Carotenoids are naturally occurring pigments that usually appear as red, orange or yellow, and they are responsible for many sexually dichromatic traits. Females of several vertebrate species have been shown to prefer males with bright carotenoid-based coloration (Møller *et al.* 2000). However, vertebrates can only obtain carotenoids by ingesting them (McGraw *et al.* 2003). A number of health benefits have been attributed to carotenoids, including their importance in activating the immune system (Chew 1993) and their ability to absorb free radicals (Olson & Owens 1998). Rather than functioning specifically for the immune system, carotenoids used for ornamentation may depend on the capacity to absorb and/or transport carotenoids; coloration may thus reflect an individual's nutritional condition rather than immune capacity (McGraw *et al.* 2005; Fitze *et al.* 2007). Consequently, individuals with low nutritional condition and those that are mounting strong immune responses will appear more drab, suggesting that coloration is reflecting health, condition and high immunocompetence. Using carotenoids for colourful signals is thus costly, as the already limited supply of carotenoids, once deposited in fat, skin or proteinaceous structures such as feathers and scales, is left unavailable to the immune system (Olson & Owens 1998). Consequently, a sick or weakened male would not benefit from prioritizing costly signals over his own health.

The present study represents a confirmatory (Anderson *et al.* 2001) experimental study to investigate paternal effects on offspring length and body mass in Arctic charr. By using a split-brood design, we control for potential

confounding maternal effects. If paternal coloration reflects the underlying genetic quality, then offspring sired by two differently coloured males should differ in quality (Taborsky 1998). We expect that females mating with the most colourful male will gain advantages for her offspring, as this will result in larger offspring compared with mating with the less colourful male. As body size in males is an important determinant of dominance and potentially covaries with the underlying genetic quality (Archer 1988; Reynolds & Gross 1992; Andersson 1994), paternal length was included as a potential covariate in the present study.

2. MATERIAL AND METHODS

(a) Field protocol

Sexually mature Arctic charr ($n_{\delta}=24$ and $n_{\text{♀}}=12$) were caught in Lake Fjellfroskvatn (69°4' N, 19°20' E) after dark by netting at a known spawning ground in late September 2002. The fish were quickly removed from the nets and kept in submerged holding cages awaiting further handling. The fish were sacrificed by a blow to the head, dried with an absorbent paper towel to prevent water from mixing with the gametes (Liljedal *et al.* 1999) and stripped of gonadal products with gentle bilateral pressure to their abdomens. Gametes were stored in airtight plastic containers in a refrigerator at approximately 4°C awaiting further handling.

(b) Experimental protocol

(i) Colour sampling

The fish were photographed in a dark room (standardized light conditions) using a digital camera (Sony Digital Handycam DCR-VX1000E) to record their spawning coloration for later analysis. Digital photographs of adult fish were analysed according to Skarstein & Folstad (1996) using the software application PHOTOSHOP (Adobe Systems 2000). Red/green/blue values were used to calculate hue, saturation and brightness using the same software (Skarstein & Folstad 1996). Relatively little variance was found in the values for all colour measurements. The coefficient of variation (CV) for hue was estimated to be 0.10 (mean = 44.04, s.d. = 4.37, range = 34–50, $n=24$), saturation had an estimated CV of 0.08 (mean = 85.38, s.d. = 6.72, range = 73–94, $n=24$), whereas brightness had too little variation to be included in any further analyses (CV < 0.01, mean = 99.50, s.d. = 0.51, range = 99–100, $n=24$). Hue is reported on an inverted scale, which means that low values of hue represent a high degree of coloration. While hue can be said to be a qualitative measure of colour, saturation can be said to be a quantitative measure representing the density of pigmentation. Saturation is therefore more likely to represent the amount of carotenoid-based pigmentation of the skin. Red coloration in fish may also be caused by pteridines, which have similar spectral properties as carotenoids, but in contrast to carotenoids, pteridines are not extracted in acetone (Grether *et al.* 2001). We tested for the presence of pteridines, which may bias the results in our study population, but as skin samples became colourless after extraction in acetone we conclude that this was not the case.

(ii) Fertilization

The sperm samples were paired in order of collection to minimize the difference in storage time between the two

semen samples. The amount of sperm used from each male was adjusted according to recorded spermatocrite levels, so that an approximately equal number of sperm was used in each fertilization (Liljedal *et al.* 1999; Skarstein *et al.* 2004). Two males were used for every female in the experiment; each male fertilizing the same number of eggs, resulting in two batches of eggs with different fathers per female. These maternal half-sibling batches were kept separated during the rest of the experiment. Each male and female was randomly assigned to each other. The sperm was placed in a plastic container, mixed with 50 ml of lake water for 5 s and poured over the eggs. The water was later topped off to give a total volume of approximately 250 ml. The same procedure was used for all the batches. After fertilization, eggs were kept cool in a refrigerator overnight, after which dead eggs (presumably unfertilized) were removed and the remaining eggs were placed in perforated containers in running water.

(iii) Hatching

Batches of eggs, i.e. each female–male combination, were separately cultured in plastic containers with circulating unfiltered water placed at random in holding racks in two 350 l plastic tanks at 6°C. The development of the eggs was monitored on a daily basis. When all the eggs in each container had developed visible eyespots, dead eggs were removed and discarded. Eggs were considered dead when they turned partially or completely white. When the first hatchlings appeared, 10 eggs were chosen at random from each batch and raised separated from the rest of the batch. This was done to ensure that potentially density-dependent factors were kept at constant levels in all containers. Each collection of eggs was divided between two rearing tanks and kept at a constant density of five larvae per container. Eggs and larvae were inspected daily and dead eggs or larvae were immediately replaced with live ones from the original tanks ($n_{\text{larval}\delta} = 10$ and $n_{\text{larva}} = 10 \times 24 = 240$). This only happened twice and in two different batches.

(iv) Morphological characteristics

Thirty days after all 10 eggs had hatched, fish larvae were culled using benzocaine and the length of the larvae (including caudal fin) was measured to the nearest 0.01 mm using a digital slide calliper (mean = 21.48, s.d. = 0.97, range = 17.67–24.13, $n = 240$) to estimate the growth rate. The larvae were later dried for 48 hours at 50°C, after which they were stored at 20°C for one day and their body mass was recorded to the nearest 0.01 g (mean = 12.97, s.d. = 1.98, range = 9.24–16.77, $n = 240$; METTLER TOLEDO AT261 DeltaRange). Paternal length was measured on the same photographs as used to measure coloration. Each fish was lying on a grid (known width and height), which was used to assess length to the nearest 0.50 cm. The CV for paternal length was estimated to be 0.09 (mean = 26.50, s.d. = 2.35, range = 20–31, $n = 24$).

(c) Statistical procedures

(i) Predictor variables: paternal characteristics

The three paternal characteristics were all correlated: (i) saturation and hue (Pearson's product–moment correlation, $r = -0.58$ [95% confidence intervals: $-0.79, -0.22$], d.f. = 22), (ii) saturation and length ($r = 0.40$ [$-0.01, 0.69$], d.f. = 22), and (iii) hue and length ($r = -0.55$ [$-0.78, -0.19$], d.f. = 22). Since hue, which is measured on an inverted scale, and saturation may measure two different

aspects of paternal coloration, we chose to perform separate analyses with each of them as predictors. Consequently, the different analyses presented below cannot be regarded as completely independent.

(ii) Linear mixed-effect models: larval length and body mass as responses

Statistical analyses were carried out using the software application R (R Development Core Team 2006). Linear mixed-effect (LME) models (Pinheiro & Bates 2000) using the *lme* function in the *nlme* library in R (Pinheiro *et al.* 2007) were used to analyse the effects of saturation, hue and paternal body length on larval body length and body mass. Saturation, hue and paternal length were applied as fixed effects, whereas female identification was included as a random effect (Pinheiro & Bates 2000). The effect of tank has been found unimportant in previous analyses of the data (see Eilertsen 2005 for additional details). Consequently, we did not include tank as a random effect. Our predictions can be tested statistically by estimating the effects of paternal coloration (saturation or hue) on larval body mass and body length. Consequently, paternal coloration was kept in all candidate models based on our *a priori* expectations (e.g. Anderson *et al.* 2001; Burnham & Anderson 2002). Thus, we started with a model containing paternal coloration, paternal body length (covariate) and the two-way interaction between them. From this model, we formed a pool of candidate models where the covariate and the interactions were removed sequentially (see appendix I, table AI.1 of the electronic supplementary material). Akaike's information criterion (AIC) was used to assess the fit of several candidate models (e.g. Anderson *et al.* 2000; Burnham & Anderson 2002), and we always selected the model with the smallest AIC value as the most parsimonious model (i.e. a Δ_i equal to zero; see table AI.1 of the electronic supplementary material for a presentation of the candidate models). Paternal coloration was centred (subtracting the average value) in order to make the intercept biologically valid. The intercept now represents the predicted value for a father with an average value of coloration instead of the predicted value at zero coloration. Following Pinheiro & Bates (2000), maximum-likelihood (ML) fitted models were used when models were compared (see table AI.1 of the electronic supplementary material), whereas a restricted ML (REML) fitted model was used for parameter estimation (table 1). All statistical tests in the present study were two-tailed, and the null hypothesis that the coefficients equal zero was rejected at the α -level of 0.05. Test statistics and *p*-values are provided, but effect sizes (means and differences between means) were the main consideration in the study (Anderson *et al.* 2001).

3. RESULTS

Adding paternal length to the models, i.e. increasing the complexity of the selected model, was not justified in the analyses of larval body mass as a function of hue, whereas the main effect of paternal length was justified in the analyses of saturation (see appendix I of the electronic supplementary material). In these analyses, we found support for our prediction that the secondary sexual traits included in the present study, i.e. saturation and hue, had a statistically significant effect on body mass of the larvae (table 1b; figure 1a,b). Moreover, in the analysis of saturation, we selected a model that included the

Table 1. LME models relating paternal coloration (saturation and hue) to larval (a) body length and (b) body mass. (The coloration variables were centred (subtracting the average), which makes the intercept biologically meaningful (it represents the predicted value for the mean value of coloration keeping other predictors at zero). See appendix I of the electronic supplementary material and main text for details on the model selection procedure applied. The models used for inference were fitted using REML (see text for additional details).)

parameter	saturation		hue			
	value	(95% CI)	d.f.	p-value	value	(95% CI)
(a) body length (mm)						
fixed effects						
intercept	21.853	(19.833, 23.873)	225		21.564	(18.873, 22.255)
coloration	0.275	(0.041, 0.510)	225	0.022	-0.282	(-0.573, 0.010)
paternal length (cm)	-0.012	(-0.085, 0.062)	225	0.752	0.037	(-0.024, 0.098)
coloration × paternal length	-0.010	(-0.018, -0.001)	225	0.026	0.010	(<0.001, 0.020)
random effects: females ^a (♀)						
among ♀ st. dev.	0.668	(0.430, 1.040)		$n_{\text{larvae}} = 240$	0.691	(0.445, 1.075)
within ♀ st. dev. (residual)	0.667	(0.609, 0.732)		$n_{\text{♀}} = 12$	0.670	(0.610, 0.734)
(b) body mass^b (g)						
fixed effects						
intercept	11.570	(9.526, 13.984)	225		12.952	(11.907, 13.997)
coloration	0.033	(0.004, 0.062)	225	0.025	-0.088	(-0.139, -0.036)
paternal length (cm)	0.052	(-0.014, 0.119)	225	0.124	-	-
random effects: females ^a (♀)						
among ♀ st. dev.	1.807	(1.184, 2.757)		$n_{\text{larvae}} = 239$	1.828	(1.999, 2.789)
within ♀ st. dev. (residual)	0.833	(0.759, 0.913)		$n_{\text{♀}} = 12$	0.835	(0.761, 0.916)

^a Female (♀) random terms involved only the constant term (i.e. random intercepts fitted per female).

^b One outlying observation (standard residual value ≥ 5.3 in both analyses) was excluded from the analyses of body mass (figure 1b). This exclusion did not affect the results notably; in fact, this exclusion made the estimate more conservative.

Figure 1. (a) Contour plot of larval body mass as a function of saturation and paternal length, and (b) scatter plot of larval body mass as a function of hue. The lines show predicted larval body mass from the same model as in [table 1b](#) except that paternal coloration was not centred. In (b), a considerable difference in the variance between the 12 females, i.e. the groups of observations represented by different points, is revealed, which was the reason why LME models were applied in the data analyses (see main text). One outlier, shown in parenthesis in (b), was removed in both analyses of larval body mass (see [table 1](#) for details).

Figure 2. Contour plot showing larval body length as a function of paternal coloration ((a) saturation and (b) hue) and paternal length. The lines show predicted larval body length from the same model as in [table 1a](#) except that paternal coloration was not centred, whereas points show data on paternal characteristics (coloration and length) for each of the 12 females in the data.

main effect of paternal length. This clearly showed that including paternal length in this analysis did not alter any conclusion regarding the effect of saturation. Saturation was, in fact, statistically significant as opposed to paternal length, which did not reach statistical significance. In both analyses of larval body length, however, we selected a model including coloration, paternal length as well as the interaction between the two (see [table AI.1b](#) of the electronic supplementary material). Larval body length was positively associated with saturation ([table 1a](#), main effect of saturation). However, in this analysis, we also found a negative interaction between saturation and paternal length, proving that the positive relationship between saturation and larval length was only apparent for smaller males ([table 1a](#), coloration $\times$ paternal length). Consequently, there are no positive effects between saturation and larval length for larger males ([figure 2a](#)). We found the opposite relationships with approximately similar effect sizes for hue (hue is on an inverted scale), but these relationships were weaker ([table 1b](#); [figure 2b](#)).

Alternative and simplified analyses that solely focus on ranked paternal coloration generally lead to similar conclusions regarding the main effect of paternal coloration on larval length (results in appendix II of the electronic

supplementary material versus [table 1](#)). These analyses must, however, be viewed with caution as: (i) the interactions between paternal coloration and length were not taken into account, and (ii) the information available on paternal coloration was reduced to a two-levelled factor ('low' versus 'high') in these analyses (see appendix II of the electronic supplementary material for details).

4. DISCUSSION

When controlling for maternal effects our results showed that males with a high degree of coloration produced larvae with higher body mass compared with less colourful males. Thus, early growth in Arctic charr seems to be determined not only by the amount of resources in the yolk sac, but also by the genetic contribution of the father. For larval body length, the results are a bit more complicated: (i) for smaller males, we found the same results as above, i.e. more intensely coloured males produced larger offspring, but (ii) for larger males, we found no relationship between coloration and offspring length. The latter result suggests that fitness benefits of female preference for brightly coloured males can interact with other fitness-enhancing traits, such as male body size.

Maternal effects have been demonstrated in a variety of species, such as plants (*Senecio* spp.; Kirk *et al.* 2005), arachnids (e.g. Beckerman *et al.* 2006), insects (Spitzer 2004; Pertoldi *et al.* 2005; Steigenga *et al.* 2005), frogs (*Rana sylvatica*; Rasanen *et al.* 2005), fishes (*S. alpinus*; Jónsson & Svavarsson 2000; Valdimarsson *et al.* 2002), birds (*Taeniopygia guttata castanotis*; Forstmeier *et al.* 2004), large terrestrial herbivores (Festa-Bianchet & Jorgenson 1998; Jones *et al.* 2005; Kruger *et al.* 2005; Safari *et al.* 2005), seals (*Phoca vitulina*; Ellis *et al.* 2000) and humans (*Homo sapiens*; e.g. Korpelainen 1999; Lummaa & Clutton-Brock 2002; Lummaa 2003). Such widespread female effects on offspring are probably explained by females' effect on offspring, not only by their genetic contribution, but also by altering the amount of resources made available to the developing foetus (see Hansen & Olafsen (1999) for a review in marine fishes). This obvious connection might explain the large number of studies on maternal effects in a number of species, including Arctic charr (Jónsson & Svavarsson 2000; Valdimarsson *et al.* 2002). In Arctic charr, resources are deposited in the yolk sac and are closely related to egg size. Egg size, in turn, varies between females (Jónsson & Svavarsson 2000; Valdimarsson *et al.* 2002).

To our knowledge, there are few studies that have demonstrated paternal effects on offspring development. Yet, in Trinidadian guppies (*Poecilia reticulata*), parental size has been shown to influence offspring growth (Reynolds & Gross 1992). This study did not however, control for female bias in reproductive output. Paternal effects on morphological traits of offspring have, on the other hand, been demonstrated in several species, including pink salmon (*Oncorhynchus gorbuscha*; Funk *et al.* 2005), brown trout (*Salmo trutta*; Chevassus *et al.* 2004; Petersson & Jarvi 2007; Wedekind *et al.* 2008), haddock (*Melanogrammus aeglefinus*; Rideout *et al.* 2004), fruitflies (*Drosophila melanogaster*; Mignon-Grasteau *et al.* 2004), ant queens (*Formica truncorum*; Bargum *et al.* 2004) and humans (Schousboe *et al.* 2004). However, only three previous studies have documented that male secondary characters predict early growth rate in offspring. In one of these, Sheldon *et al.* (1997) demonstrated paternal effects on fledgling condition (body mass corrected for body size) in collared flycatchers (*Ficedula albicollis*). The magnitude of the paternal effects was positively correlated with the size of a condition-dependent male secondary sexual character. Yet, a negative correlation between offspring growth rate and the expression of paternal sex traits has been documented in sticklebacks (*Gasterosteus aculeatus*; Barber *et al.* 2001) and in one study of brown trout (Wedekind *et al.* 2008). In the stickleback study, females mating with highly ornamented males gained parasite-resistant, yet slow-growing, offspring, indicating a trade-off in resource allocation between somatic growth and the immune system (Barber *et al.* 2001). Additionally, the number of surviving juveniles was negatively associated with paternal redness in brown trout (Wedekind *et al.* 2008). Contrary to Wedekind *et al.* (2008), this present study suggests that the spawning coloration of the father has a positive effect on offspring. The differences in the size of the larvae between batches of maternal half-siblings may be a sign of paternal-induced differences in larval growth rate, i.e. the rate and efficiency with which the resources in the yolk sac is allocated into larval tissue. Thus, benefits of females mating with larger males probably have

only indirect (i.e. genetic) benefits to females (e.g. Wedekind *et al.* 2001; Sheldon *et al.* 2003; Evans *et al.* 2004).

Paternal spawning coloration had a positive effect on offspring body mass and body length in the present study, and this finding is in accordance with the good gene hypothesis. We did, however, not record individual hatching dates and one might argue that our results are explained by variation in hatching dates. However, while most studies use the time from fertilization to hatching as the measure for developmental rate (Valdimarsson *et al.* 2002), Balon (1985) pointed out that 'hatching is not an instantaneous event but a process that occurs at a different developmental state in different individuals and is influenced by many epigenetic and environmental stimuli'. That is, those larvae that hatch early are often less developed than larvae that hatch later. Consequently, the time from fertilization to hatching might therefore be a poor indicator of developmental rate. We measured the effect of paternal coloration at the end of the yolk sac stage when density-dependent competition for food was not an important factor.

Given no parental care (Sigurjónsdóttir & Gunnarson 1989), the contribution of the male Arctic charr to its offspring is purely genetic. The red spawning coloration of male charr thus seems to be an indicator of good genes. The rate of growth may be positively correlated with individual fitness in interspecific competition as the species exhibits ontogenetic niche shifts partly related to size and partly to developmental rate (Klemetsen *et al.* 2003). There is usually a correlation between the size of the fish and the amount of food eaten, with the larger fish eating the most food (Huntingford *et al.* 1993). In Arctic charr, size appears to be the primary determinant of dominance, and size alone could predict the outcome of most aggressive or defensive interactions (Noakes & Balon 1980). Increased size is therefore likely to be an advantage when the fish starts to feed. Our results support the hypothesis that in species with no parental care, indirect (i.e. genetic) benefits of mate choice are likely to be of major importance (Andersson 1994; Sheldon 2000). Our results indicate that the selection pressure on each trait will depend on how females weigh these desirable qualities (i.e. paternal coloration versus size) under different conditions. In conclusion, male Arctic charr may signal their quality through coloration, and females mating with highly ornamented males gain fitness benefits for their offspring through enhanced offspring growth—especially among smaller males.

This experiment was performed in accordance with the legal requirements of Norway.

The present study was funded by the Department of Biology, Faculty of Science, University of Tromsø, Tromsø, Norway. We wish to thank Dahnah Urbach, Andreas Palmén, Jonas Sjögren, Asle Lilletun, Marika Ljetoff and John A. Henden for assisting us during the preparation and completion of the fieldwork and/or for valuable discussions during the process of writing this study. We also wish to thank Torkild Tveraa and Per Fauchald for their valuable discussion on the statistical analyses applied. Finally, we wish to thank the two anonymous referees for their constructive remarks and comments, which have improved the manuscript.

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