WILEY-
BLACKWELL

Nordic Society Oikos

Sexual Dichromatism and the Immunocompetence Handicap: An Observational Approach Using Arctic Charr
Author(s): Frode Skarstein and Ivar Folstad
Source: *Oikos*, Vol. 76, No. 2 (Jun., 1996), pp. 359-367
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3546208
Accessed: 08/10/2008 11:51

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=black.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.

Blackwell Publishing and *Nordic Society Oikos* are collaborating with JSTOR to digitize, preserve and extend access to *Oikos*.

http://www.jstor.org

OIKOS 76: 359–367. Copenhagen 1996

Sexual dichromatism and the immunocompetence handicap: an observational approach using Arctic charr

Frode Skarstein and Ivar Folstad

Skarstein, F. and Folstad, I. 1996. Sexual dichromatism and the immunocompetence handicap: an observational approach using Arctic charr. – Oikos 76: 359–367.

Secondary sexual characters may signal parasite resistance because the development of such traits can have costs to immune functioning. Here we show that expression of red coloration in the salmonid Arctic charr is a sexually dimorphic character that reveals information of potential importance in sexual selection. Intensity of the carotenoid dependent coloration is in both sexes negatively related to lymphocyte counts. A causal mechanism for this relationship could be reduced availability of carotenoids for immunological application created by increased carotenoid requirements for ornamental development. Alternatively, if more ornamented individuals also have lower intensities of infection, the observed relationship might be explained by healthy individuals being both bright and having low antigen stimulation of lymphocyte transformation and proliferation. Parasite intensities also show relationships with intensity of coloration, and this is used to evaluate the latter explanation.

F. Skarstein and I. Folstad, Dept of Ecology/Zoology, Inst. of Biology and Geology, Univ. of Tromsø, N-9037 Tromsø, Norway (frodes@ibg.uit.no).

Sexual differences in breeding ornamentation are known from a large variety of animal species (Andersson 1994), ranging from the extreme example of the peacock's tail to the more subtle differences in color and morphology within many vertebrate species. Interpreting this gradient of sexual differences as the result of variance in the strength of sexual selection presumes that mainly one sex is selective in mate choice. In general, the sex with the lowest potential reproductive rate is expected to be more choosy (Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992), but depending on the costs involved in mate search, any sex may gain fitness advantages by assessing the quality of potential mates. Consequently, in some species choosiness may occur in both sexes (Parker 1983), producing bisexual ornamentation without clear sexual dimorphism. Under such a scenario, ornaments may reveal information about individual qualities in both sexes.

In "good gene" models of sexual selection it is assumed that individuals can assess heritable qualities of potential mates and thus increase the genetic quality of their offspring. This fitness advantage has been hypothesized to fuel the evolution of quality signalling traits, such as costly secondary sexual characters (e.g., Zahavi 1975, 1977). As an explicit case of "good gene" models, Hamilton and Zuk (1982) suggested that parasite resistance is an important genetic quality revealed in secondary sexual ornaments. Heritability of parasite resistance and thus variation in expression of sexual ornaments will be maintained despite directional selection exerted through mate choice because of the particular ability of parasites to rapidly co-evolve with their hosts (but see Atkinson 1991). Given a positive parent-offspring correlation in genetic resistance, mate choice based on signals of parasite resistance will give fitness benefits in the form of parasite resistant offspring.

Parasites can specifically influence the development and maintenance of secondary sexual characters through two different mechanisms. First, in cases where the acquisition of important metabolites for ornamental

Accepted 6 December 1995

ISSN 0030-1299

development, like carotenoids, results in increased exposure to pathogens, ornaments may reveal an individual's ability to tolerate parasite exposure (Folstad et al. 1994). Second, since development and maintenance of secondary sexual characters may impose costs to immunity, they may honestly signal parasite resistance (Folstad and Karter 1992; see also Wedekind 1994). Genetic resistance to parasites will in both cases influence establishment rates and pathogenicity of parasites and thus modify expression of secondary sexual characteristics.

The Arctic charr, *Salvelinus alpinus* (L.) has several qualities making it an interesting species for studies on signals of potential importance in sexual selection in general, and more specifically, for testing hypothesis related to signals of parasite resistance. First, both sexes develop bright, carotenoid based (Scalia et al. 1989), red abdominal coloration during the spawning period, making it a bisexually ornamented species. Second, neither sex shows parental care after spawning (Fabricius 1953), and both sexes receive nothing but gametes when they reproduce. This suggests that any mate choice in this species may, in addition to potential direct benefits from avoiding contact-transmitted diseases and gamete quality and quantity (Skarstein and Folstad 1995, Folstad and Skarstein in press), be for "good genes". Third, the species is polygamous, with males usually fertilizing eggs from several females (Fabricius 1953, Fabricius and Gustafson 1954). Females are also observed spawning with several different mates, although not as frequently as males (Fabricius and Gustafson 1954). This variation in number of mates within both males and females suggests that sexual selection may be at work in both sexes. Fourth, since Arctic charr may be reproductively active for over fifteen years (Johnson 1980), benefits of current ornamentation should be carefully balanced against costs to future reproduction. Subsequently, age-specific variation in spawning coloration should be low compared to species with shorter life expectancies. Fifth, several carotenoid rich crustaceans are intermediate hosts for parasites harbored by Arctic charr. This link between colorants for ornamentation and parasitic transmission propagules might increase the homogeneity in exposure (Folstad et al. 1994), reducing the problem of distinguishing between unexposed and resistant individuals (Read 1990, McLennan and Brooks 1991). Last, Arctic charr are commonly infected with easily identified parasites with similar transmission routes, but with large species specific variation in pathogenicity.

In this study, we investigated three a priori predictions: First, since individual female Arctic charr have a lower potential reproductive rate than individual males, males are expected to be the most ornamented sex (Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992). Second, if immunological costs are associated with development of breeding ornamentation, a negative relationship between level of immunocompetence and degree of ornamentation should be expected (Folstad and Karter 1992). Third, parasites are expected to show a relationship with intensity of coloration. More precisely, the pathogenic parasites should have intensities negatively associated with color intensities because of their detrimental effects on their hosts (Hamilton and Zuk 1982, Folstad et al. 1994). The low pathogenic parasites, on the other hand, inflict less harm on their host and should therefore not necessarily have intensities related to coloration. However, those weakly pathogenic parasites transmitted through foods containing metabolites necessary for developing ornaments should have intensities positively related to coloration (Folstad et al. 1994).

Materials and methods

Sampling

Sexually mature Arctic charr, 22 males and 38 females, were caught on a spawning ground in Lake Fjellfrøsvatn, northern Norway. This occurred on three consecutive nights during the short spawning period in mid-September. The spawning ground was identified with the help of local knowledge, presence of redds (i.e., marks from finished spawnings) and occurrence of large numbers of ripe males and females.

The between-sample variation of the effect stress may have on labile characters, such as coloration and immunological parameters, caused by netting was reduced by setting and emptying the nets so that fishing time of each net, which was the maximum time a fish could spend in the net, spanned from between one to three h. This variation was due to differences in size of catches, producing differences in handling time.

Photographic equipment and picture analysis

Immediately after collection, each fish's abdomen was photographed under identical light conditions with Kodak 64 ASA EPR Ectachrome film. The pictures of the individual abdomens were later digitized using Kodak's Photo-CD system, making them available for evaluation with the computer application Adobe Photoshop (Macintosh version 2.5) to produce numerical estimates for the three color properties hue, value and chroma. Hue represents the wavelength of a color, while value and chroma can respectively be understood as the darkness and saturation of a color (Smithe 1975). The more commonly used and readily understood terms darkness and saturation will be used instead of value and chroma. For each fish, the average intensity for each of the three color properties was measured, based on all pixels enclosed by an area within the pentagon obtained by drawing lines between the four paired fins and the point where the two gill opercula meet. Mean intensity of the three color parameters with standard deviation are given in Table 1.

The three color parameters hue, darkness and saturation have usually been fused to produce an index appropriate to the investigated coloration (e.g., Burley et al. 1991). However, each of these color properties might vary with regard to parasite levels independently of each other, and thus be of separate importance in the complete spawning coloration (Wedekind 1992). Therefore hue, darkness and saturation were treated as separate components of the breeding ornamentation. As we evaluate ornaments in the context of metabolic costs, a dark or saturated coloration was considered more ornamented than a light or unsaturated coloration because of the higher density of metabolic colorants, just as redder hues were considered more ornamented.

Immunology

Blood samples were collected from the caudal vessel of each fish using 2-ml heparinized vacutainers. Blood smears were fixed and stained for identification of lymphocytes and erythrocytes according to Rowley (1990). These blood smears were later used to determine the lymphocyte/erythrocyte ratio by taking the average of lymphocyte and erythrocyte counts from two independent areas on the smear. Hematocrit (i.e., the percentage of red blood cells in a blood sample) for each fish was determined by centrifuging a portion of the blood sample in a capillary tube for three min at 11500 rpm with a Compur Mini Centrifuge. Then, by multiplying hematocrit value by the lymphocyte/erythrocyte ratio, an estimate for the level of circulating lymphocytes in each fish was obtained.

Morphometric and parasitological data

Body length and ungutted weight were measured and each fish was aged using the number of growth zones on the otoliths (Grainger 1953). Sex was determined by investigation of gonads. A condition factor was calculated using the formula: weight (g)/length (cm)^b, where b is the regression coefficient when regressing log weight on log length of males and females separately (Bolger and Connolly 1989). Mean length, age, condition factor and weight with standard deviation are presented in Table 1. Macroparasites were recorded during investigation of the eyes, gills, outside and inside the gastrointestinal tract, swim bladder and kidney tubules. Eight groups of parasites were identified, namely the digeneans *Phyllidostomum umblae*, *Diplostomum* spp. and *Crepidostomum* spp. (Thomas 1958, Bortz et al. 1988), the cestodes *Diphyllobothrium* spp., *Eubothrium salvelini* and *Cyathocephalus truncatus* (Chubb et al. 1987), the nematode *Cystidicola farionis* and finally the crustacean *Salmincola* sp. Terminology describing parasite populations follows Margolis et al. (1982).

Table 1. Arithmetric means with standard deviation (SD) for length, age, weight, condition factor and the color properties hue, darkness and saturation (all given as log-Munsell values), grouped by sex. For length, age, weight and condition factor the mean and SD of the raw data is used, while for the color parameters the mean and SD is calculated from the log-transformed intensities. For the three color parameters, $N = 20$ males and 33 females. All other parameters $N = 22$ males and 38 females.

	Males		Females	
Parameter	Mean	SD	Mean	SD
Length (cm)	20.8	1.35	20.8	1.41
Age (yr)	5.8	0.96	5.7	0.69
Weight (g)	125.1	32.43	136.2	31.58
Condition factor	0.85	0.03	0.97	0.03
Log hue	0.99	0.06	1.03	0.03
Log darkness	0.95	0.04	0.97	0.02
Log saturation	0.90	0.04	0.88	0.02

Statistical analysis

Statistical analyses were done using Statsoft Statistica (Macintosh version 3.0a). All color, lymphocyte and parasite parameters were log-transformed to meet the assumption of normality for the parametric statistics used. Distributions were tested for normality using the Kolmogorov-Smirnov two-sample test. When controlling for age or condition, correlation of residuals of regression were used (Kleinbaum et al. 1988). Transformations were unable to conform *C. truncatus* intensities to the assumptions of parametrical analysis and consequently, Kendal's rank analysis and partial rank order coefficients analyses were used (Siegel and Castellan 1988).

Results

Effect of sampling time

No significant relationship was found between intensity of either hue, darkness or saturation and fishing time of nets ($\tau = 0.08$, $P = 0.4$; $\tau = 0.06$, $P = 0.5$; and $\tau = -0.05$, $P = 0.58$, respectively, $N = 53$) or between lymphocyte levels and fishing time ($\tau = -0.10$, $P = 0.29$, $N = 55$).

Sexual differences

There was a positive relationship between the three color parameters, i.e., individuals with redder hues also tended to be darker and more saturated (t ranged between 0.56 and 0.66, $N = 53$, P always < 0.0001). Males differed significantly from females with respect to all three color properties (hue: $t = -3.52$, $P < 0.001$; darkness: $t = -2.21$, $P < 0.02$ and saturation: $t = -1.82$, $P = 0.038$, one-tailed t-test, see Fig. 1). That is, males had redder hues and were darker and more saturated. Neither weight, length nor age differed significantly between the sexes.

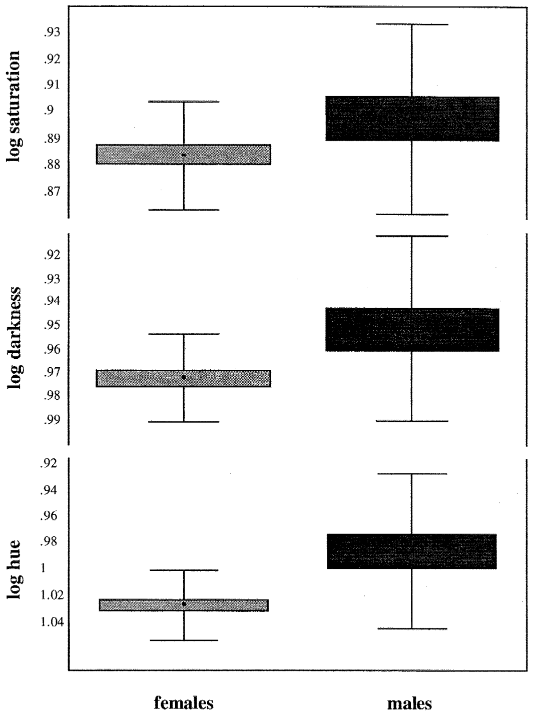


Fig. 1. Box and whiskers plot with mean, standard error and standard deviation, of the sex difference in the three color parameters hue, darkness and saturation ($t = -3.52$, $P < 0.001$; $t = -2.21$, $P < 0.02$; and $t = -1.82$, $P = 0.038$, respectively, one tailed t-test). Hue and darkness intensities are plotted on inverse axes as the Munsell system assigns lower numerical values to intensities which in this study are considered as more ornamented, that is, darker, more saturated and with redder hues. Sample size: 20 males and 33 females.

Lymphocytes and ornamentation

Significant negative relationships were found between levels of lymphocytes and degree of coloration in both sexes (Table 2). In males hue, darkness and saturation showed significant negative correlations with lymphocyte levels (Table 2 and Fig. 2). Among females, only darkness and saturation showed a significant negative relationship with levels of lymphocytes (Table 2). In females, but not males, all the three color properties were also positively related to the condition factor. However, after controlling for condition factor, both darkness and saturation still showed a significant negative relationship to lymphocyte counts (Table 2).

Parasites and ornamentation

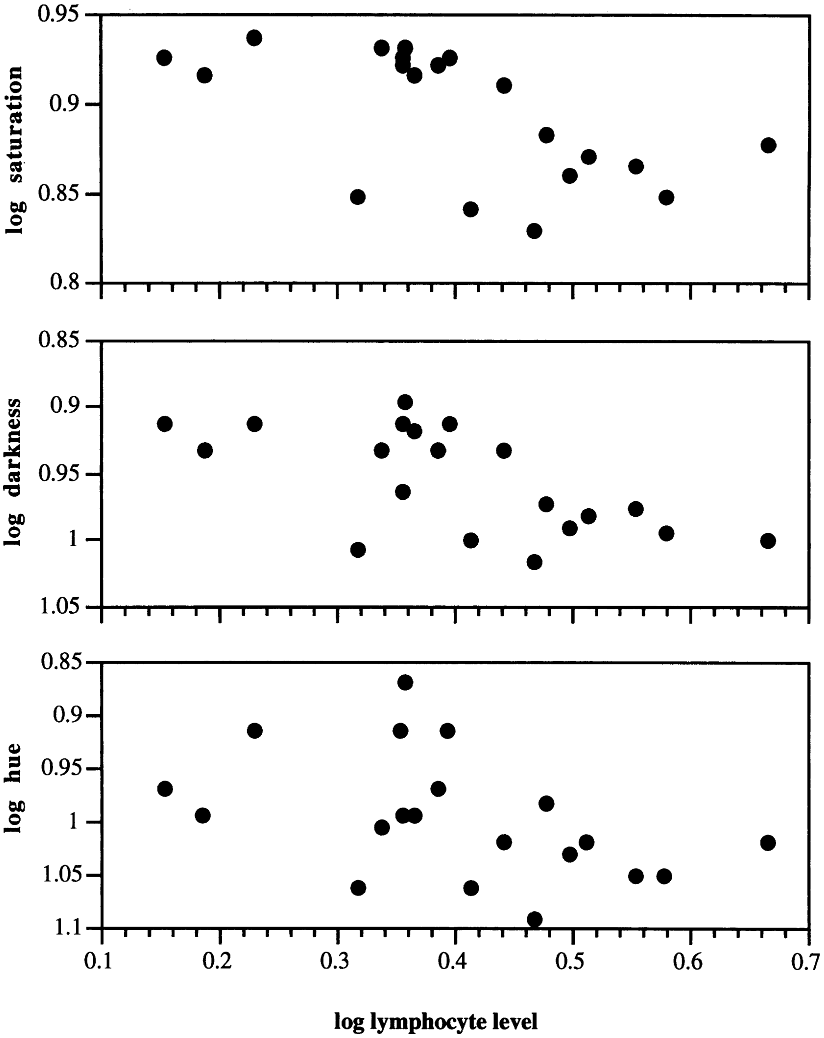
Prevalence (i.e., percentage of infected individuals) and arithmetic mean intensity of the log-transformed data with standard deviation (SD) of the different parasite groups are given in Table 3.

Males. Intensities of the intestinal digenean *Crepidostomum* spp. were positively correlated to both hue and darkness, and intensities of the eyefluke *Diplostomum*

Table 2. Parasite and immunological correlates to the three color properties, both before and after the effect of relevant confounders were removed. *Diplostomum* spp. intensities were related to age in both sexes, and consequently, age was controlled for. Among females, hue, darkness and saturation were related to the condition factor, therefore the color properties were controlled for regarding this confounder. The numbers in parentheses are the results after removing the effect of the relevant confounder. All relationships between lymphocyte counts and intensities of coloration were negative, while all relationships between intensities of *Diplostomum* spp. and *Crepidostomum* spp. and coloration were positive. (n.s. denotes "not statistically significant".)

	Males ($N = 20$)			Females ($N = 33$)		
Parameter	Hue	Darkness	Saturation	Hue	Darkness	Saturation
Lymphocyte counts	$r^2 = 0.19$, $P < 0.005$	$r^2 = 0.40$, $P < 0.0003$	$r^2 = 0.36$, $P < 0.005$	n.s. (n.s.)	$r^2 = 0.15$, $P < 0.03$ ($r^2 = 0.15$, $P < 0.03$)	$r^2 = 0.17$, $P < 0.02$ ($r^2 = 0.14$, $P < 0.03$)
Crepidostomum spp.	$r^2 = 0.25$, $P < 0.03$	$r^2 = 0.21$, $P < 0.04$	n.s.	$r^2 = 0.12$, $P < 0.05$ (n.s.)	n.s. (n.s.)	$r^2 = 0.18$, $P < 0.014$ ($r^2 = 0.11$, $P < 0.05$)
Diplostomum spp.	$r^2 = 0.22$, $P < 0.04$ ($r^2 = 0.23$, $P < 0.03$)	n.s. (n.s.)	n.s. (n.s.)	$r^2 = 0.17$, $P < 0.02$ ($r^2 = 0.20$, $P < 0.01$)	n.s. (n.s.)	n.s. (n.s.)

Fig. 2. Relationship between intensities of the three color properties and lymphocyte counts in males. Hue and darkness intensities are plotted on inverse axes as the Munsell system assigns lower values to intensities which in this study are considered as more ornamented, that is, darker, more saturated and with redder hues. Sample size: 20 males.



spp. were positively correlated to hue (see Table 2). None of the other parasite intensities were related to color intensities in males. *Diplostomum* spp. intensities were also positively related to age. Nevertheless, after controlling for age, the positive relationship between *Diplostomum* spp. intensities and hue remained significant (Table 2). No significant relationship was found between the potential confounder condition factor and intensities of *Crepidostomum* spp.

Females. Intensities of *Crepidostomum* spp. were positively correlated to hue and saturation, and *Diplostomum* spp. intensities were positively correlated to hue (see Table 2). We also found negative association between *C. truncatus* intensities and darkness levels ($\tau = 0.23$, $P = 0.063$, $N = 33$). Condition factor was positively related to coloration, and when partialling out the effect of this confounder, the level of significance increased to $P < 0.05$ ($\tau_{xy.z} = 0.24$, $N = 33$). Moreover, intensities of *C. truncatus* were positively related to age, and after controlling for age the relationship between *C. truncatus* intensities and darkness levels became significant ($P < 0.025$, $\tau_{xy.z} = 0.26$, $N = 33$). In females, intensity of the three color properties were positively related to condition factor, therefore relationships between parasite intensities and color intensities were calculated for a given condition (see Table 2). None of the other parasite intensities were related to coloration in females. *Diplostomum* spp. intensities were positively related to age. However, after controlling for age, the positive relationship between *Diplostomum* spp. intensities and hue remained significant (Table 2). No significant relationship was found between the potential confounder condition and intensities of *Crepidostomum* spp.

Interrelationships between parasite intensities

Among the parasites investigated, only intensities of *Phyllidostomum umblae* and *Eubothrium salvelini* were correlated to each other ($r = 0.30$, $P < 0.02$, $N = 60$, both sexes pooled).

Table 3. Prevalence (percentage of infected individuals) and arithmetic mean intensity with standard deviation (SD) calculated from the log-transformed data of the different parasite groups. ($N = 60$.)

Parasite group	Prevalence (%)	Mean intensity (log-transformed)	SD
Salmincola sp.	30	−0.30	0.01
Cystidicola farionis	78	1.41	0.52
Crepidostomum spp.	83	1.37	0.69
Diplostomum spp.	100	4.69	0.45
Cyathocephalus truncatus	37	0.32	0.06
Phyllidostomum umblae	100	4.37	0.59
Diphyllobothrium spp.	100	3.20	0.82
Eubothrium salvelini	78	0.43	0.2

Discussion

As opposed to age, length and weight, all three color properties differed significantly between the sexes. Males have redder, darker and more saturated ornamentation than females. This observation is as expected from the sexual difference in potential reproductive rates (Clutton-Brock and Vincent 1991, Clutton-Brock and Parker 1992). In addition, the ornament reveals information that could potentially be of use in mate choice. Both factors are indicative of sexual selection's involvement in the evolution of the trait. However, if sexual selection elaborates on a character, the homologous character in the opposite sex may show a correlated response (Lande and Arnold 1985, Lande 1987), producing sexual elaboration without bisexual selection. Yet, if the trait is costly, uncoupling and degeneration of the trait in the choosier sex would be expected to occur (Lande and Arnold 1985). The correlations between coloration and both parasite intensities and lymphocyte counts suggest that coloration may impose costs on both sexes, disfavoring the explanation based on correlated responses. Although only indicative evidence exists, it seems likely that sexual selection may be involved in the evolution of Arctic charr spawning coloration.

The concept of immunocompetence is elusive, and a measure like the number of circulating lymphocytes can only assess a limited aspect of host immune function. However, lymphocytes do play several important functions in the immune response, permitting such crucial processes as antibody formation, immunological memory and interleukin secretion (Post 1987). Accordingly, the level of circulating lymphocytes in blood may indicate a fish's ability to defend itself against pathogens (Pickering 1986). In this study we document a negative relationship between intensity of ornamentation and levels of circulating lymphocytes. Similar relationships have been found in birds (Gustafsson et al. 1994, Saino and Møller 1994, Zuk et al. 1995). If more ornamented individuals also have lower intensities of infection, the observed relationship might be explained by healthy individuals being both bright and having low antigen levels available to stimulate lymphocyte transformation and multiplication. In the present study, however, highest parasite intensities were, with the exception of the parasite *C. truncatus* in females, found in the more ornamented individuals. Thus, an explanation based on general health as a determinant of both coloration and lymphocyte levels, although parsimonious, seems insufficient to account for the observed negative correlation between intensity of coloration and our estimate of immunocompetence.

The above explanation would suffice if lymphocyte levels depend mainly on current infection levels. However, host decisions might alter lymphocyte levels independent of antigen-stimulated effects on lymphocyte populations. Thus, an alternative interpretation of the negative correlations between intensity of coloration and our measure of immuncompetence may stem from immunosuppressive effects of sex hormones necessary for ornament development (Folstad and Karter 1992). Such a dual effect may arise if sex hormones allocate limited amounts of energy or metabolites between immune functioning and ornament development (Wedekind and Folstad 1994). In species where carotenoid-dependent coloration is commonly used as sexual signals, carotenoids may be of limited availability in the environment (Hill 1992). The use of carotenoids in secondary sexual characters may on the one hand increase the bearer's attractiveness towards potential mates, while on the other hand such use channels carotenoids away from important immunological functions. These immunological functions may be served both directly (Chew 1993) or indirectly through provitamin-A activity (Deuel 1957, Bauernfeind et al. 1981) and may, among a multitude of effects, cause increased size and activity of lymphocyte populations (Bendich 1989). Consequently individuals may, depending on immune system efficiency, distribute their limited amounts of metabolites (i.e., carotenoids) between ornamental and immunological uses in a manner that maximizes their lifetime reproductive success (Wedekind and Folstad 1994). The development of secondary sexual characters in salmonids is stimulated by several androgen hormones (Leatherland et al. 1982), which in both male and female Arctic charr also show distinct titer peaks during the spawning period (Mayer et al. 1992). Consequently, in the arctic charr, sex hormones may mediate both immunological functioning and ornamental development and this may explain why more ornamented individuals have lower immunocompetence.

Established parasites affect host immune responses and vice versa, a relationship influenced by and influencing parasite pathogenicity. Additionally, differential immune responses among hosts may affect parasite establishment and cause variation in number of parasites per host even under equal parasite exposure. These interactions may cause a complicated relationship between parasite intensities observed in hosts and ornamental development compromising immune responses. Observational studies of relationships between expression of ornamentation and parasite intensities have given equivocal results (Read 1990). Also in our study, which only investigates three components of the Arctic charr's complex breeding ornamentation, intensity of coloration is not related to all parasite intensities (i.e., those of *Diphyllobothrium* spp., *Eubothrium salvelini*, *Cystidicola farionis*, *Phyllidostomum umblae* and *Salmincola* sp.). There are however, parasite species (i.e., those of *Diplostomum* spp., *Crepidostomum* spp. and *C. truncatus*) that show intensities related to sexual ornamentation.

Intensities of *Diplostomum* spp. show a positive correlation with fin size, a sexually dimorphic character, in male three-spined sticklebacks (Brønseth and Folstad, unpubl.). *Diplostomum* spp. intensities also show a positive correlation with red coloration in both male and female Arctic charr. Because of the metacercaria's site-specificity in the eye of Arctic charr, *Diplostomum* spp. infections are not thought to cause significant harm (Bouillon and Curtis 1987) and should consequently have little effect on lifetime reproductive sucess of Arctic charr. Infections of *Diplostomum* spp. may possibly accumulate in the host with age, indicating that age could be of importance in causing the relationship between parasite intensity and coloration. However, after controlling for age, the correlation remains significant, suggesting that age is of minor importance in the relationship between parasite intensity and coloration. *Crepidostomum* spp. infections are also not believed to be pathogenic (Thomas 1958), and their intensities also show a positive relationship with color intensity. The positive relationship that both *Diplostomum* spp. and *Crepidostomum* spp. intensities show with intensity of coloration can be explained by reduced immune responses in the more ornamented individuals. Alternatively, intensity of coloration could be expected to correlate with *Crepidostomum* spp. intensities from the coupling between metabolites necessary for character development and parasite exposure in the more ornamented individuals. That is, individuals that develop intense, carotenoid based breeding ornamentation could be impelled to increase their carotenoid rich prey consumption containing transmission propagules of *Crepidostomum* spp. with a resulting increased exposure to this parasite. In the case of *Crepidostomum* spp. the two explanations (i.e., increased exposure or reduced immune response) are not mutually exclusive, and may be operating simultaneously.

To appreciate the positive correlations between color and parasite intensities in the context of the Hamilton and Zuk (1982) hypothesis, where the most elaborately ornamented individuals should have heritable resistance, one must view them in the light of costs to immune function. Immunosuppression by hormones necessary for ornamental development may produce a degree of trait expression which signals the effectiveness of the carrier's immune system. Therefore, individuals with good parasite resistance will experience less cost with immunosuppression and the concomitant increase in parasite intensities and/or pathogenicity, and can express more elaborate ornamentation. Also, recognizing the cost of eliminating infections might help explain the adaptiveness of moderate responses to infectious organisms (Benhke et al. 1992). Thus, ability to co-exist with pathogens might not always result in parasite-free individuals, but may be expressed through high tolerance. High-quality individuals may consequently have lower costs for a given parasite burden than low-quality individuals. Therefore, individuals whose mate choice is based on characters positively correlated with intensities of low pathogenic parasites may, given the conditions of the parasite–host system under study, be mating with parasite tolerant partners.

The cestode *C. truncatus* has attracted attention because of its apparent pathogenicity in salmonid hosts (Vik 1954, Amin 1977, Reimchen 1982), manifested through lesions and mucosa damage at the site of attachment (Asia 1971), local swelling, perforations (Vik 1954) and damage to ovaries (Senk 1956), resulting in higher mortality (Huitfieldt-Kaas 1927) and host growth retardation (Wisniewski 1933). Such pathogenicity may constrain the development of ornamentation in infected fish, and in this way, cause the observed negative correlation between darkness and intensity of *C. truncatus*. Curiously, this relationship was only found in females.

The manner in which intensities of *C. truncatus* are associated with coloration may point to which mechanisms (i.e., increased exposure or susceptibility) are causing the positive correlation between degree of color and intensities of *Crepidostomum* spp. These two parasites share the crustacean *Gammarus* spp. as one of their intermediate hosts. If the positive correlations between degree of coloration and intensity of *Crepidostomum* spp. infection are the result of increased transmission because of the increased consumption of intermediate hosts, one would also expect the relationship between color and *C. truncatus* to be positive. Moreover, there should be a positive relationship between the intensity of the two parasite species. In the current study, however, no support for these predictions is found. Consequently, the positive correlations between parasite intensities and degree of coloration seem to be the result of increased susceptibility which is also the most parsimonious explanation.

It has been suggested that by basing mate choice on carotenoid-dependent coloration, individuals will mate with partners with good foraging efficiency and predator avoidance (Endler 1983). Elaborating on this, Lozano (1994) suggests that such mate choice for good carotenoid foragers would also obtain matings with individuals healthy from the immunological benefits of carotenoids. As a reasonable prediction from this body of theory, one would expect a positive relationship between intensity of coloration and lymphocyte levels, since individuals better at obtaining carotenoids should have carotenoids available for both ornamentation and immune defense. However, the observed negative relationship between lymphocyte counts and intensity of coloration suggests that intensity of coloration could reveal inherent qualities of the immune system, rather than just reflecting an individual's excess of carotenoids.

In conlusion, if the immunological implications of ornamentation suggested in this study should prove to be of a more general nature, increased susceptibility to parasites and parasite pathogenicity may be found as the proximate cost ensuring honesty in signal systems within sexual selection.

Acknowledgements – We thank Anders Pape Møller, Andrew Read, Arne Skorping, Claus Wedekind and Marlene Zuk for valuable comments on earlier drafts of this paper. Victor Apanius and Torfinn Brønseth were important sources of inspiration during the writing of the manuscript. Finally, we would like to thank Rune Knudsen for providing vital knowledge about the Arctic charr in lake Fjellfrøsvatn and Nancy Peterson for her language corrections.

References

Amin, O. M. 1977. Helminth parasites of some south-western Lake Michigan fishes. – Proc. Helminthol. Soc. Wash. 44: 210–217.

Andersson, M. 1994. Sexual selection. – Princeton Univ. Press, Princeton, NJ.

Asia, E. 1971. Infestione da *Cyathocephalus truncatus* Pall. (Cestoda: Cyathocephalidae) in una popolazione di *Tinca tinca* L. del Lago Trasimeno. – Atti. Soc. Ital. Sci. Vet. 25: 470–471.

Atkinson, D. 1991. Sexual showiness and parasite load: correlations without parasite coevolutionary cycles. – J. Theor. Biol. 150: 251–260.

Bauernfeind, J. C., Adams, C. R. and Marusich, W. L. 1981. Carotenes and other vitamin A precursors in animal feed. – In: Bauernfeind, J. C. (ed.), Carotenoids as colorants and vitamin A precursors. Academic Press, London, pp. 563–743.

Behnke, J. M., Barnard, C. J. and Wakelin, D. 1992. Understanding chronic nematode infections: evolutionary considerations, current hypothesis and the way forward. – Int. J. Parasitol. 22: 861–907.

Bendich, A. 1989. Carotenoids and the immune response. – J. Nutr. 119: 112–115.

Bolger, T. and Connolly, P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. – J. Fish Biol. 34: 171–182.

Bortz, B. M., Kenny, G. E., Pauley, G. B. and Blundt-Milam, A. H. 1988. Prevalence of two site-specific populations of *Diplostomum* spp. in eye infections of rainbow trout, *Salmo garidneri* Richardson, from lakes in Washington State, USA. – J. Fish Biol. 33: 31–34.

Bouillon, D. R. and Curtis, M. A. 1987. Diplostomasis (Trematoda: Strigeidae) in Arctic Charr (*Salvelinus alpinus*) from Charr lake, Northern Labrador. – J. Wildl. Dis. 23: 502–505.

Burley, N., Tideman, S. C. and Halupa, K. 1991. Bill colour and parasite levels of zebra finches. – In: Loye, J. E. and Zuk, M. (eds), Bird-parasite interactions. Oxford Univ. Press, Oxford, pp. 359–376.

Chew, B. P. 1993. Role of carotenoids in the immune response. – J. Dairy Sci. 76: 2804–11.

Chubb, J. C., Pooland, D. W. and Veltkamp, C. J. 1987. A key to the species of the cestodes (tapeworms) parasitic in British and Irish freshwater fishes. – J. Fish Biol. 31: 517–543.

Clutton-Brock, T. H. and Vincent, A. C. J. 1991. Sexual selection and the potential reproductive rates of males and females. – Nature 351: 58–60.

– and Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. – Q. Rev. Biol. 67: 437–456.

Deuel, H. J. 1957. The lipids, their chemistry and biochemistry, vol III: biochemistry. – Wiley, New York.

Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. – Environ. Biol. Fish. 9: 173–190.

Fabricius, E. 1953. Aquarium observations on the spawning behaviour of the char, *Salmo alpinus*. – Inst. Freshwater Res. Drottningholm Rep. 34: 14–48.

– and Gustafson, K. J. 1954 Further aquarium observations on the spawning behaviour of the char, *Salmo alpinus* L. – Inst. Freshwater Res. Drottningholm Rep. 35: 58–104.

Folstad, I. and Karter, A. J. 1992. Parasites, bright males and the immunocompetence handicap. – Am. Nat. 139: 603–622.

– and Skarstein, F. In press. Is male need for germline control creating avenues for female choice? – Behav. Ecol.

– , Hope, A. M., Karter, A. and Skorping, A. 1994. Sexually selected colour in male sticklebacks; a signal of both parasite exposure and parasite resistance? – Oikos 69: 511–515.

Grainger, E. H. 1953. On the age, growth, migration reproductive potetntial and feeding habits of the Arctic char (*Salvelinus alpinus*) of Frobisher Bay, Baffin Island, Canada. – J. Fish. Res. Board Can. 10: 326–370.

Gustafson, L., Nordling, D., Andersson, M. S., Sheldon, B. C. and Qvarnström, A. 1994. Infectious diseases, reproductive effort and the cost of reproduction in birds. – Philos. Trans. R. Soc. Lond. B 346: 323–331.

Hamilton, W. D. and Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? – Science 218: 384–387.

Hill, 1992. Proximate basis of variation in carotenoid pigmentation in male house finches. – Auk 109: 1–12.

Huitfieldt-Kaas, A. 1927. *Cyathocephalus truncatus* Pall. als ursache von Fisch-Epizzotien. – Nytt Mag. Naturvidensk. 65: 143–151.

Johnson, L. 1980. The Arctic charr, *Salvelinus alpinus*. – In: Balon, E. K. (ed.), Charrs, salmonid fishes of the genus *Salvelinus*. Junk, The Hage, pp. 15–98.

Kleinbaum, D.G., Kupper, L.K. and Muller, K.E. 1988. Applied regression analysis and other multivariate methods. 2nd ed. – PWS-Kent, Boston.

Lande, R. 1987. Genetic correlations between the sexes in the evolution of sexual dimorphism and mating preferences. – In: Bradbury, J. W. and Andersson, M. B. (eds), Sexual selection: testing the alternatives. Wiley, New York, pp. 83–94.

- and Arnold, S. J. 1985. Evolution of mating preferences and sexual dimorphism. - J. Theor. Biol. 117: 651-664.

Leatherland, J. F., Copeland, P., Sumpter, J. P. and Sonstedard, R. A. 1982. Hormonal control of gonadal maturation and development of secondary sexual characteristics in Coho Salmon, *Onchorhynchus kisutch*, from Lakes Ontario, Erie, and Michigan. - Gen. Comp. Endocrinol. 48: 196-204.

Lozano, G. A. 1994. Carotenoids, parasites, and sexual selection. - Oikos 70: 309-311.

Margolis, L., Esch, G. W., Holmes, J., Curtis, A. M. and Scad, G. A. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of The American Society of parasitologists). - J. Parasitol. 68: 131-133.

Mayer, I., Schmitz, M., Borg, B. and Schultz, R. 1992. Seasonal endocrine changes in male and female Arctic charr (*Salvelinus alpinus*). I. Plasma levels of three androgens 17α-hydroxy-20β-dihydroprogesterone, and 17β-estradiol. - Can. J. Zool. 70: 37-42.

McLennan, D. A. and Brooks, D. R. 1991. Parasites and sexual selection: A macroevolutionary perspective. - Q. Rev. Biol. 66: 255-286.

Parker, G. A. 1983. Mate quality and mating decisions. - In: Bateson, P. (ed.), Mate choice. Cambridge Univ. Press, Cambridge, pp. 141-166.

Pickering, A. D. 1986. Changes in blood cell composition of the brown trout, *Salmo trutta* L., during the spawning season. - J. Fish Biol. 29: 335-347.

Post, G. 1987. Textbook of fish health. - T.F.H. Publ., Neptune City, USA.

Read, A. 1990. Parasites and host sexual behaviour. - In: Barnard, C. J. and Behnke, J. M. (eds), Parasitism and host behaviour. Taylor and Francis, London, pp. 117-157.

Reimchen, T. E. 1982. Incidence and intensity of *Cyathocephalus truncatus* and *Schistocephalus solidus* infection in *Gaserosteus aculeatus*. - Can. J. Zool. 60: 1091-1095.

Rowley, A. F. 1990. Collection, Separation and Identification of Fish Leucocytes. - In: Fletcher, J. S., Anderson, D. P. and Roberson, B. S. (eds), Techniques in fish immunology. SOS Publ., Fair Haven, pp. 113-135.

Saino, N. and Møller, A. P. 1994. Secondary sexual characters, parasites and testosterone in the barn swallow, *Hirundo rustica*. - Anim. Behav. 48: 1325-1333.

Scalia, S., Isaksen, M. and Francis, G.W. 1989. Carotenoids of the Arctic charr, *Salvelinus alpinus* (L.). - J. Fish Biol. 34: 969-970.

Senk, O. 1956. *Cyathocephalus truncatus*, Pallas - Its influence on the reproductive organs of trout (*Salmo trutta* Fario). - Veterinaria (Sarajevo) 5: 607-615.

Siegel, S. and Castellan, N. J. 1988. Nonparametric statistics for the behavioral sciences. 2nd Ed. - McGraw-Hill, Mexico.

Skarstein, F. and Folstad, I. 1995. On sperm and immunocompetence handicap. - Poster presentation, VI Congr. European Soc. Evol. Biol. Edinburgh.

Smithe, F. B. 1975. Naturalist's color guide. - American Museum of Natural History, New York.

Thomas, J. D. 1958. Studies on *Crepidostomum metoecus* (Braun) and *C. farionis* (Müller), parasitic in *Salmo trutta* L. and *S. salar* L. in Britain. - Parasitology 48: 336-352.

Vik, R. 1954. Investigations on the pseudophyllidean cestodes of fish, birds and mammals in the Anoya water system in Trøndelag. I *Cyathocephalus truncatus* and *Schistocephalus solidus*. - Nytt Mag. Zool. 2: 5-51.

Wedekind, C. 1992. Detailed information about parasites revealed by sexual ornamentation. - Proc. R. Soc. Lond. B 247: 169-174.

- 1994. Handicaps not obligatory in sexual selection for resistance genes. - J. Theor. Biol. 170: 57-62 (1994).

- and Folstad, I. 1994. Adaptive or non-adaptive immunosuppression by sex hormones? - Am. Nat. 146: 657-659.

Wisniewski, L. W. 1933. *Cyathocephalus truncatus* Pallas. I. Die Postembryonalentwicklung und Biologie. II Allgemeine Morphologie. - Bull. Acad. Pol. Sci. Math. Nat. B 3: 237-252, 311-327.

Zahavi, A. 1975. Mate selection - a selection for a handicap. - J. Theor. Biol. 53: 205-214.

- 1977. The cost of honesty. - J. Theor. Biol. 67: 603-605.

Zuk, M., Johnsen, T. S. and Maclarty, T. 1995. Endocrine-immune interactions, ornaments and mate choice in red jungle fowl. - Proc. R. Soc. Lond. B. 260: 205-210.