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Maintenance of Genetic Variation in Sexual Ornamentation

Role of Precopulatory and Postcopulatory Sexual Selection

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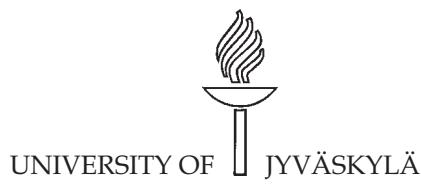## Role of Precopulatory and Postcopulatory Sexual Selection

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Role of Precopulatory and Postcopulatory Sexual Selection

UNIVERSITY OF JYVÄSKYLÄ

Cover picture: Breeding ornamentation of male minnow (Phoxinus phoxinus)

ABSTRACT

Kekäläinen, Jukka
Maintenance of genetic variation in sexual ornamentation – role of precopulatory and postcopulatory sexual selection
Jyväskylä: University of Jyväskylä, 2010, 52 p.
(Jyväskylä Studies in Biological and Environmental Science
ISSN 1456-9701; 216)
ISBN 978-951-39-4130-7
Yhteenveto: Seksuaaliornamenttien geneettisen muuntelun säilyminen – parittelua edeltävän ja sen jälkeisen seksuaalivalinnan merkitys
Diss.

According to the lek paradox, secondary sexual ornaments are under strong directional selection, which should deplete additive genetic variation of these traits. I studied the signalling content of male and female secondary sexual ornaments and the potential factors that may help to maintain the genetic variation of these traits and thus contribute to the resolution of the lek paradox. The results of my thesis are based on three fish species, the Eurasian minnow (*Phoxinus phoxinus*), the Arctic charr (*Salvelinus alpinus*) and the whitefish *Coregenus lavaretus*. In minnows, multiple sexual ornamentation of the males signalled dominance status, courtship activity, parasite resistance and condition of the individuals. Females differed in their ornament-based mating preferences on these traits. In whitefish, the ornamentation of both sexes predicted genetic differences in offspring post-hatching performance, and female ornamentation was positively associated with the size of the offspring and their yolk reserves. However, offspring fitness was also dependent on the parental genetic combination. In the Arctic charr, the intensity of the male breeding colouration was positively associated with their sperm quality (velocity) and potentially also with offspring viability. On the other hand, it could not be ruled out that the cryptic female choice criteria are at least partly inconsistent (non-directional) with the criteria used in pre-copulatory mate choice. My results on charr major histocompatibility complex genes also show that the superiority of the heterozygote individuals may lead to disassortative mating, where females prefer to pair with genetically dissimilar males. All of these factors (varying female preferences, selection on compatible or dissimilar genes and non-directional cryptic female choice) may weaken the directional selection on ornamental traits and thus maintain the genetic variation of the traits. Together, they may provide light on a way towards the resolution of the lek paradox.

Keywords: *Coregenus lavaretus*; genetic benefits; lek paradox; *Phoxinus phoxinus*; *Salvelinus alpinus;* sexual ornamentation; sexual selection.

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I-VI. I participated in the planning of each of the six papers and I was responsible for analysing the data and writing articles I-V. I participated data collecting and statistical analyses of the paper VI.

I   Kekäläinen, J., Valkama, H., Huuskonen, H. & Taskinen, J. 2010. Multiple sexual ornamentation signals male quality and predicts female preference in minnows. Ethology 116: 895-903.

II   Kekäläinen, J., Leppänen, H.-R., Huuskonen, H., Valkama, H. & Taskinen, J. 2010. The information content of multiple sexual ornaments in the mate choice of minnows. Submitted manuscript.

III   Kekäläinen, J., Vallunen, J. A., Primmer, C. R., Rättyä, J. & Taskinen, J. 2009. Signals of major histocompatibility complex overdominance in a wild salmonid population. Proceedings of the Royal Society B 276: 3133-3140.

IV   Kekäläinen, J., Huuskonen, H., Tuomaala, M. & Kortet, R. 2010. Both male and female sexual ornaments reflect offspring performance in a fish. Evolution 64: 3149-3157.

V   Kekäläinen, J., Rudolfsen, G., Janhunen, M., Figenschou, L., Peuhkuri, N., Tamper, N. & Kortet, R. 2010. Genetic and potential non-genetic benefits increase offspring fitness of polyandrous females in non-resource based mating system. BMC Evolutionary Biology 10: 20.

VI   Janhunen, M., Rudolfsen, G., Kekäläinen, J., Figenschou, L., Peuhkuri, N. & Kortet, R. 2009. Spawning coloration and sperm quality in a large lake population of Arctic charr (Salmonidae: *Salvelinus alpinus* L.). Biological Journal of the Linnean Society 98: 794-802.

INTRODUCTION

Most of the species-specific characteristics are adaptations that help the performance of organisms in their environment via natural selection. Elaborate secondary sexual ornaments of males contradict this general view since they often have negative impacts on survival. Darwin (1871) resolved the contradiction with his theory of sexual selection, which states that secondary sexual traits have evolved because they produce fitness advantages in reproduction. According to this theory, the reduced survival probability of highly ornamented males is more than compensated for because females prefer to mate with them (inter-sexual selection) and/or because such males are efficient competitors in order to achieve mating opportunities (intra-sexual selection). Thus, sexual signals often have a dual function both in female choice and male-male competition (Berglund et al. 1996, Alonzo-Alvarez et al. 2004).

The signalling content of secondary sexual ornaments can be divided into two classes, namely direct and indirect benefits. Direct benefit models propose that females base their choice on the male's resources, such as nuptial gifts, territory quality and parental care (Trivers 1972, Forsgren et al. 1996, Oneal et al. 2007). Instead, models of indirect benefits predict that female choice is based on genetic benefits and thus fitness benefits for the offspring (e.g. Fisher 1930, Zahavi 1975). Although the relative importance of these alternative explanations for the evolution of ornamental traits has been under considerable debate, both of them may act together (e.g. Oneal et al. 2007).

The evolution of animal signalling systems requires that signals must alter the behaviour of the other organism, i.e. receivers must respond to the signals. This in turn requires that the signal receiver should benefit from assessing the signal rather than ignoring it. In other words, signals must be honest. If the signal is not honest, the receiver should evolve to ignore the signal, which means that signalling is no longer beneficial to the signaller either and the whole signalling system should disappear. Therefore, in order to understand the evolution of animal communication, we must understand the factors that maintain the honesty of signalling.

1.1   What maintains the reliability of sexual signalling?

In many species, the only contribution of males to reproduction is to produce sperm to fertilize the eggs, which often means that the reproductive investments of the females are higher than the males. Therefore, females are expected to benefit if selectively reproducing only with high quality (i.e. highly ornamented) males. Instead, males often maximize their fitness by mating as frequently as possible. Thus, if there were no constraints, poor and high quality males could equally benefit from producing a similar "high quality" signal (Searcy & Nowicki 2005, see also Maynard-Smith & Harper 2003). However, if all of the males, regardless of their quality, produce a similar signal, such a signal is inevitably uninformative with respect to male quality. In this case, females should be selected to ignore the signal and males should cease to produce it. Therefore, some mechanism must sustain the honesty of signalling. A potential solution to the dilemma is that the signals are costly (Zahavi 1975, Grafen 1990). Signals are reliable if the costs increase with the expression of the signal and if high quality individuals pay lower relative costs of signalling than lower quality individuals or if higher quality signallers have greater marginal fitness returns from an incremental increase in the signal (Getty 2002).

Sexual signalling of animals is mostly based on visual, chemical, acoustic, tactile or behavioural cues or, as in some cases, nuptial gifts. A vast number of species mainly rely on colour signals, which often consist of various carotenoid pigments. Since animals cannot synthesize these pigments, they must acquire carotenoids from food (Fox 1976), which makes carotenoid-based ornaments energetically costly to produce (Kodric-Brown 1998). Along with secondary sexual characters, carotenoids are also important for the immune system (Lozano 1994), suggesting that there should be a trade-off in carotenoid allocation between maintaining health and elaborate ornamentation (Blount et al. 2003). Thus, higher quality, i.e. healthier, males should be able to allocate a higher proportion of pigments to ornamental display. For this reason, carotenoid-based ornaments are believed to be reliable indicators of health and the phenotypic quality of the individual (e.g. Goodwin 1984, Badyaev & Hill 2000). However, a signal does not necessarily need to be energetically costly to be honest. For example, dark melanin pigments are synthesised from amino acids as a by-product of metabolism (Fox 1976), which makes them a much cheaper signal than carotenoids (Badyaev & Hill 2000). However, despite the low energetic costs, some other mechanism can maintain the reliability of melanin ornamentation. Melanin pigments have been demonstrated to reflect, for example, the competitive ability and dominance status of individuals, i.e. they act as status signals (Kodric-Brown 1998, McGraw et al. 2003, see also Roulin 2004, McGraw 2005, Wedekind et al. 2008a for other fitness benefits of melanin). Melanin ornamentation can be costly because the reliability of status signals is continually tested by competitors (Berglund et al. 1996, Tarof et al. 2005). If only the dominant males are able to pay the cost of increased

aggressiveness from the other males, dishonest signalling is prevented (social control hypothesis: Rohwer 1975, Candolin 1999, 2000a, b).

In many animal species sexual signals consist of several different signal components (multiple cues: Candolin 2003), which can be grouped into 1. informative cues or 2. uninformative cues. Informative cues provide information about mate quality (see above), for example, whereas uninformative cues are unreliable indicators of quality and can increase the fitness of the receiver, decrease it (through intersexual conflict: Holland & Rice 1998, see also Leonard & Hedrick 2009) or be selectively neutral. Thus, not all of the signals (or signal components) are beneficial to the receiver. The evolution of uninformative signal components can be understood if they produce indirect fitness benefits through other signal components or if they are the remnants from past selection. Uninformative cues can produce fitness benefits to the receiver if they facilitate, for example, the detection of some other signal components and thus reduce mate choice errors or costs related to the choice. Therefore, sexual signals can evolve without being attractive to females if they expose cues that are informative about male quality or, in other words, if they amplify previously recognized differences in male quality ("amplifier" hypothesis: Hasson 1989, 1990, 1997, Ljetoff et al. 2007). For example, energetically cheap melanin ornaments are not necessarily attractive to females by themselves, but they can accentuate the patterns of the carotenoids, making them more conspicuous and thus improving the females' ability to discriminate between males (Brooks 1996). Therefore, melanin ornamentation may coevolve with the preferred ornament, without having an independent signalling function in the mate choice.

On the other hand, several studies have demonstrated that different females can base their mating preferences on different male ornamental traits (e.g. Brooks & Endler 2001, Coleman et al. 2004, see also Hunt et al. 2005), and that females show temporal variations in mating preferences (e.g. Jennions & Petrie 1997, Cotton et al. 2006). These observations suggest that the existence of multiple male traits can be explained by multiple female mating preferences (Brooks & Endler 2001). The demonstration of multiple mating preferences can be difficult since it requires experimental manipulation of male traits and intensive monitoring of females throughout the mate choice process (Coleman et al. 2004). Thus, variation in female preferences may prove to be more common than is currently assumed. The important, but rarely studied, consequence of multiple female preferences is that they may reduce the strength of sexual selection on individual male traits. Therefore, this preference variation may have important evolutionary consequences, as it may be one important mechanism of maintaining the variation in secondary sexual characters.

1.2 Sexual selection for attractive genes and good genes

Despite it being commonly accepted that secondary sexual traits evolved through sexual selection, the exact evolutionary mechanism behind their existence is still under debate. Two main genetic hypotheses exist: runaway selection ("sexy son" hypothesis: Fisher 1930) and the handicap theory ("good genes" hypothesis: Zahavi 1975). Although these hypotheses have traditionally been referred to as alternative evolutionary mechanisms, Kokko et al. (2002) showed that this dichotomy may be unnecessary. In either case, according to Fisher's theory, secondary sexual traits are under strong female preference and females tend to pair with males who have the strongest expression of the trait. Females who mate with these males will have male offspring that inherit the "attractive" genes of their fathers, whilst female offspring will inherit their mother's preference genes for mating with the elaborately ornamented males. Thus, male ornaments would have been evolved together with the females' preference for ornaments, at an ever-increasing speed. Female preference supposedly originally arose because, early on, male traits were positively associated with survival, but female preference remained because the genes for preference hitchhiked with the genes producing male attractiveness traits.

The handicap theory predicts that ornaments have evolved because they help females to detect differences between males in genetic quality. For example, Hamilton & Zuk (1982) suggested that sexual ornamentation signalled the genetic ability of the males to resist predominant parasite species (see also Folstad & Karter 1992). This theory predicts that the secondary sexual ornaments of the males act as handicaps which reduce their survival and that only the high quality males can survive despite the costs of elaborate signalling. In this case, females that mate preferentially with the handicapped males will mate with the individuals with good genes. In general, female choice will be favoured by selection if the fitness advantage from superior genes outweighs the cost of handicaps. The basic requirement of this theory is that there must be variation in male genetic quality, i.e. heritability of fitness. In addition, the ornamental trait must capture additive genetic variation among individuals (Rowe & Houle 1996, Tomkins et al. 2004, Neff & Pitcher 2005).

Good gene models assume that certain genes increase the fitness of the offspring despite the structure of the remaining genome, i.e. that the same high quality males are good mates for all females (Colegrave et al. 2002, Neff & Pitcher 2005). Therefore, there should be a strong directional selection on male traits since all of the females are expected to prefer highly ornamented males. This should deplete additive genetic variation in male traits and exhaust genetic variation in viability (Tomkins et al. 2004, Kotiaho et al. 2008). However, it has been demonstrated that despite the directional selection, genetic variance remains (Houle 1992, Pomiankowski & Møller 1995, but see Blows et al. 2004, Hine et al. 2004). This raises a well-known paradox, a lek paradox: what

maintains additive genetic variation in fitness-related traits? Several hypotheses have presented (e.g. Hamilton & Zuk 1982, Kotiaho et al. 2001, Tomkins et al. 2004, Kotiaho et al. 2008, Radwan 2008), but no general agreement has been reached.

1.3 Sexual selection for genetic compatibility (compatible genes)

Increasing numbers of studies suggest that, in addition to good genes, mate choice is often based on genetic compatibility between male and female genomes (Zeh & Zeh 1996, 1997, Tregenza & Wedell 2000, Colegrave et al. 2002, Mays & Hill 2004, Neff & Pitcher 2005, Kempenaers 2007). The genetic compatibility hypothesis predicts that individual females (or males) differ in their mate preferences because the genetic quality of the potential mate depends on the interaction between male and female genotypes (non-additive genetic variation). Thus, a "compatible gene" cannot go to fixation because it is only beneficial in combination with another gene (Kempenaers 2007). Although non-additive variation can theoretically be under directional selection, this may happen only under specific circumstances (Lynch & Walsh 1998). Thus, directional selection on non-additive genetic benefits might be rare. However, Neff & Pitcher (2008) demonstrated that non-additive genetic variation can sometimes (mainly in small populations) be "inherited" from parent to offspring, which suggest that directional mating preferences can occasionally produce non-additive genetic benefits (see also Reid 2007, Fromhage et al. 2009). However, the predominant view is still that sexual selection for genetic compatibility cannot be based on quality indicators, but that it requires direct assessment of the mates (Zez & Zeh 1997, Tregenza & Wedell 2000, Colegrave et al. 2002).

The fitness effects of genetic compatibility can arise via two mechanisms: 1. interactions between genes in different loci (epistasis) or 2. genetic interactions within a locus (overdominance). Epistasis means that the effect of a particular genotype on the phenotype is dependent on the genetic background of the individual, i.e. the phenotypic effect of one locus depends on the genotype at one or several other loci (Carlborg & Haley 2004). In other words, the phenotype of a given genotype cannot be predicted by the sum of its component single-locus effects (Philips 1998). In overdominance, the fitness of the heterozygote genotype is higher than that of either of the homozygote genotypes within a locus (Doherty & Zinkernagel 1975). This should lead to negative assortative (disassortative) mating where different females are expected to pair with different males in order to produce genetically compatible (heterozygote) offspring. For example, *aa* females are expected to mate with *AA* males, whereas *AA* females should pair with *aa* males. Instead, *Aa* individuals could mate with any other individual, since in all cases half of the offspring are heterozygotes (and half are homozygotes).

One of the model gene groups with the greatest potential for studying sexual selection for genetic compatibility is the major histocompatibility complex (MHC) genes (Potts & Wakeland 1990, Apanius et al. 1997, Edwards & Hedrick 1998, Penn & Potts 1999, Sommer 2005, Piertney & Oliver 2006). The primary role of the MHC is to encode molecules that recognize foreign proteins, present them to T-cells and initiate an immune response (Langefors et al. 2001, Piertney & Oliver 2006). The crucial function of MHC molecules in the adaptive immune response suggests that pathogens and parasites are the most important agents of selection for MHC polymorphism (Landry & Bernatchez 2001, Wegner et al. 2003a, b, 2004, Froeschke & Sommer 2005, Harf & Sommer 2005, de Eyto et al. 2007, Turner et al. 2007). On the other hand, MHC genes are also closely linked to individual recognition, which suggests that MHC genes have an important function in mate choice. The reason why MHC genes are linked to genetic compatibility is the observation that MHC heterozygosity is often associated with increased fitness (Tregenza & Wedell 2000). This is also supported by the fact that many small and isolated natural populations show strong homozygote deficiencies, which may, for example, indicate that disassortative mating is common.

1.4   Simultaneous selection for good genes and compatible genes

Many studies have proposed that female choice yields genetic benefits either in the form of good or compatible genes (e.g. Pryke et al. 2010), but only a very few studies have investigated both of these genetic mechanisms simultaneously. Roberts & Gosling (2003) studied the relative importance of good genes and compatible genes in mate choice decisions by female mice. Females were allowed to choose between males that differed in scent-marking rate (good gene indicator) and in the degree of MHC-dissimilarity (compatible gene trait). The results showed that females base their choice on both traits simultaneously but that the relative importance of the traits varies depending on the available variation in the traits. Since it is often impossible to optimize both traits simultaneously, the females are expected to face a trade-off when choosing between different mate choice criteria. Neff & Pitcher (2005) proposed that two types of mating systems define a continuum. In a population where good gene (additive) effects dominate, females are expected to base their choice on good genes. Similarly, if compatible gene (non-additive) effects dominate, directional selection on indicator traits should be weak and selection on genetic compatibility should dominate. By using the model developed by Colegrave et al. (2002), Neff & Pitcher (2005) demonstrated that natural selection may lead to an evolutionarily stable strategy, where both mate choice criteria coexist. This requires that both additive and non-additive effect variations are present at intermediate levels. Then, natural selection may lead to two different equilibrium conditions (evolutionarily stable strategy, ESS): 1. a mate choice that optimally trades off fitness benefits from both good genes and compatible

genes, or 2. two alternative strategies in which some females choose males for good genes and other individuals rely on compatible genes. In the latter case, ESS is stable if the abundance of different female types fluctuates (negative frequency-dependent selection). The alternative scenario is that the population cycles between a state where additive genetic variation is abundant, and a state where most of the genetic variation is non-additive. This should lead to temporal fluctuations in the prevalence of mating types.

According to the lek paradox, directional selection on male traits should erode additive genetic variation in the traits, in which case the benefits of choice should disappear. But how strong is directional selection on male traits? The abovementioned results demonstrate that when both mate choice mechanisms operate simultaneously, selection for genetic compatibility can weaken the directional selection on ornamental traits. In addition, the narrow-sense heritability of fitness (ratio of the additive genetic variance to the total phenotypic variance: V_A/V_P) seems to be low, which also indicates that the potential fitness benefits of female choice on good genes may be minor (but still important in the evolutionary time scale) (Alatalo et al. 1998, Møller & Alatalo 1999, Puurtinen et al. 2009). If directional selection on ornamental and associated fitness traits proves to be weak, female choice may not be strong enough to deplete the additive genetic variance in these traits. Therefore, it is not even clear whether the lek paradox actually exists (Ritchie 1996, Kotiaho et al. 2008).

1.5 Genetic benefits and post-copulatory sexual selection

Sexual selection for genetic benefits does not end with copulation (e.g. Wedekind 1994). Female choice continues after copulation in a form of cryptic female choice, i.e. the ability of the females to bias the fertilization success of the copulating males (Birkhead & Pizzari 2002). As well as pre-copulatory female choice, its post-copulatory analogue can result in directional or non-directional selection. In directional cryptic female choice, females bias the paternity towards the males they preferred in pre-copulatory selection (Pizzari & Birkhead 2000, Evans et al. 2003). In non-directional cryptic female choice, females selectively favour the sperm of more compatible (or less incompatible) males. The existence of pre-copulatory sexual selection for genetic compatibility may require that females know both their own genotype as well as the genotypes of their potential mates, which may often be an unrealistic assumption. Thus, it is possible that cryptic female choice could often be the only mechanism enabling mate choice for compatible genes (Zeh & Zeh 1997, Jennions & Petrie 2000, Puurtinen et al. 2009, but see Olsén et al. 1998, Carroll et al. 2002). This suggests that post-copulatory sexual selection for genetic compatibility may be highly dependent on the occurrence of polyandry (when a female mates with several males) or, to be precise: sperm competition (Colegrave et al. 2002).

Sperm competition refers to the competition between the sperm of different males to fertilize the eggs of the female (Parker 1970). The simultaneous occurrence of sperm from several males enables the female to directly assess the compatibility of potential mates at the gametic level (e.g. Zeh & Zeh 1997, Martin-Villa et al. 1999, Birkhead 2000, Pitnick & Brown 2000, Birkhead & Pizzari 2002). In externally fertilizing fish, an important component of cryptic female choice is ovarian fluid (Turner & Montgomerie 2002, Urbach et al. 2005, Nordeide 2007, Liljedal et al. 2008, Rosengrave et al. 2008). Ovarian fluid is the liquid matter that surrounds the eggs in the female gonads and which is released with the eggs during spawning. Earlier studies have demonstrated that ovarian fluid can affect the various sperm characteristics, mainly sperm longevity, swimming speed and the proportion of motile sperm in the ejaculate (Litvak & Trippel 1998, Lahnsteiner 2002, Turner & Montgomerie 2002, Elofsson et al. 2003). This suggests that cryptic female choice in externally fertilizing fish species could be mainly dependent on female-specific variations in ovarian fluid composition (Rosengrave et al. 2008).

Several hypotheses have been proposed to explain the evolution of polyandry. In addition to genetic incompatibility avoidance, there are several other genetic hypotheses. Two of them, the "sexually selected sperm hypothesis" ("sexy sperm hypothesis") and the "intrinsic male-quality hypothesis" ("good sperm hypothesis") are directly comparable to the pre-copulatory "sexy son" and "good genes" hypotheses. According to the sexy sperm hypothesis, sperm competition allows females to mate with males who have high fertilization efficiency and thus produce male offspring that are successful in sperm competition (Keller & Reeve 1995). The good sperm hypothesis predicts that males who are more successful in sperm competition produce more viable offspring than their less successful counterparts (Madsen et al. 1992, Yasui 1997, Fisher et al. 2006). Furthermore, sperm competition can also produce fitness benefits by increasing offspring diversity or reducing the costs of mate choice errors ("bet-hedging" hypothesis) (Zeh & Zeh 2001).

As mentioned above, post-copulatory sexual selection can either favour the same traits as pre-copulatory sexual selection or it can operate in different directions (Danielsson 2001, Birkhead & Pizzari 2002). The phenotype-linked fertility hypothesis states that male sexual ornaments have evolved as reliable signals of male fertilization ability (Sheldon 1994). Therefore, males who are successful in obtaining matings (i.e. are favoured in pre-copulatory sexual selection) are expected to produce sperm that are also successful in post-copulatory sexual selection. This hypothesis has been under intensive study in recent years, but these studies have yielded contradictory results (e.g. Pizzari et al. 2004, Malo et al. 2005, Parker et al. 2006, Rogers et al. 2008). Thus, the idea is currently under debate.

1.6   Could males also be choosy?

A quick look at the sexual selection literature (and above) reveals that the term "mate choice" is almost invariably used as a synonym for "female choice". Is there any possibility that males could sometimes be choosy? Although the conditions for the evolution of male choice may be more restricted than the evolutionary prerequisites for female choice (Servedio & Lande 2006, Servedio 2007, Candolin & Salesto 2009, Barry & Kokko 2010), the answer clearly seems to be positive. Male choice can evolve when females differ in their ability to produce offspring, when male mating and/or parental care is costly and when the fertilization opportunities of males exceed the number of eggs they can fertilize (Parker 1983, Johnstone et al. 1996, Kokko & Monaghan 2001, Cornwallis & O'Connor 2009). These requirements are expected to be readily fulfilled in mating systems where males can copulate with several females, which often leads to sperm limitation and the costly production of ejaculates (Dewsbury 1982, Nakatshuru & Kramer 1982, Pitnick 1996, Olsson et al. 1997, Preston et al. 2001, Cornwallis & O'Connor 2009).

Although ignored in many studies, secondary sexual characters of females are common in many species (Clutton-Brock 2007, 2009). Female ornamentation is conventionally considered as a genetically correlated response to selection for male ornamentation (e.g. Lande 1980) or to similar selection pressures in both sexes (Kraaijeveld et al. 2007). On the other hand, many studies have demonstrated that female ornamentation can be under the direct sexual selection by males (Jones & Hunter 1993, Amundsen et al. 1997, Jones & Hunter 1999, Amundsen & Forsgren 2001) and also under selection via reproductive competition (Watson & Simmons 2010a, b). However, the exact signalling content of female ornamentation is often unclear. In particularly, it is not known whether female ornaments can be honest indicators of genetic quality (Fitzpatrick et al. 1995, see also Berglund et al. 1997, LeBas et al. 2003). This is because the resources that females invest in their sexual ornamentation are often believed to reduce the resources they can invest in offspring. Despite this trade-off, females can be expected to invest in secondary sexual characters if the fitness benefits of investing in both ornamentation and offspring exceed the fitness benefits of the strategy where females only invest in offspring (no ornamentation). This would mean that ornamented females might sacrifice part of their fecundity if some other fitness component, such as increased quality of the offspring, compensates for their reduced fecundity. However, it should be mentioned that this trade-off may only be present if sexual ornaments are energetically costly to produce. As mentioned above, not all honest ornaments are energetically costly because some other mechanisms can also maintain the reliability of signalling (Berglund et al. 1997, Maynard-Smith & Harper 2003, chapter 1.1).

Mate choice is commonly assumed to be a one-sided process where one sex (usually the female) chooses and other (usually the male) is just a passive

object of the selection (Cunningham & Birkhead 1998, Bergstrom & Real 2000). However, this is often an overly simplistic view. In many species, elaborate ornamental traits are expressed in both sexes (mutual ornamentation: Rowland 1982, Verrel 1995, Saether et al. 2001, Kraaijeveld et al. 2007). Thus, it seems likely that mutual ornaments function as mate choice or status signals in both sexes (mutual sexual selection).

1.7 Aims of the study

The aim of my thesis was to study the information content of secondary sexual ornaments in different fish species with a non-resource-based mating system and no parental care. More specially, I investigated whether secondary sexual ornaments of males and females indicate the potential genetic quality of the individuals ("good genes"). Since good gene models of sexual selection predict that directional selection on ornamental traits should erode the variation of fitness-related traits, I tried to find potential explanations for why the variation in these traits does not seem to disappear.

In first two papers, I studied whether the multiple sexual ornaments of male minnows indicate male dominance status and courting activity (I), as well as parasite resistance and condition (II). The main aim in both studies was to investigate the relative importance of different "good gene" indicators (colouration, breeding tubercles and odour) in determining female mating preference. In study III, I studied the mechanisms that maintain genetic variability of the major histocompatibility complex (MHC) genes in a natural Arctic charr population. Since MHC heterozygote individuals can recognize a wider range of pathogens, selection should favour the production of heterozygote offspring. Thus, the aim of this paper was also to test whether sexual selection for genetic compatibility could play a role determining female mating preferences in nature. In study IV, I studied whether the mutual ornamentation of whitefish is linked to offspring post-hatching performance. The aim of the study was to compare the relative importance of good gene and compatible gene effects on offspring fitness variation. In the last two studies (V and VI), I studied cryptic female choice in the Arctic charr. The aim of these studies was to test the "phenotype-linked fertility hypothesis" and to find out whether females could gain genetic benefits from polyandrous mating.

2   METHODS

2.1 Study species

The results of my thesis are based on studies on three fish species: Eurasian minnow (*Phoxinus phoxinus*) (I and II), Arctic charr (*Salvelinus alpinus*) (III, V, VI), and whitefish *Corefonus lavaretus* (IV). All of these species develop breeding ornamentations during their spawning seasons which have been linked to various fitness traits (minnow: Müller & Ward 1995, Jacob et al 2009, Arctic charr: Skarstein & Folstad 1996, Måsvær et al. 2004, whitefish: Wedekind et al. 2001, 2008b, Huuskonen et al. 2009). Furthermore, all of these species have a non-resource-based mating system, all of them produce a relatively large number of externally fertilized eggs and they do not provide parental care for their offspring. Thus, females of these species should not gain any direct material benefits from mating, which suggests that the sexual ornamentation of the males should mainly reflect genetic (indirect) benefits.

The Eurasian minnow is a small (5-7 cm) cyprinid fish that lives in relatively cold and well-oxygenated running and still waters. Prior to spawning, the males develop a conspicuous breeding colouration with a bright red, carotenoid-based abdomen colour, red lips (Tack 1940, Müller & Ward 1995, 1998) and a dark lateral skin with a metallic green appearance. In addition, secondary sexual characters include breeding tubercles on the head (e.g. Jacob et al. 2009). Male minnows are capable of rapidly changing their colouration (ephemeral colour change), which occurs more often during agonistic interactions between males and when courting the females. Therefore, the signalling system of male minnows is an ideal model system for studying multiple sexual signals. Secondary sexual characters of the females are less developed, but they can sometimes be conspicuous, particularly in large females.

The Arctic charr is a salmonid fish with the most northerly distribution of any freshwater fish species in the world. It is a diverse species, with several ecotypes and morphotypes that differ in their migration behaviour, nutrition

and morphology. As with minnows, Arctic charr develop a carotenoid-rich orange-red spawning colouration, which is also present in the females. Arctic charr have a lek-like breeding system where both sexes mate with several other individuals (e.g. Figenschou et al. 2004). During egg release, one large male is usually in close contact with the female (Sigursjónsdóttir & Gunnarson 1989) and generally fertilizes the largest proportion of the eggs (Blanchfield & Ridgway 1999). However, several smaller males are also usually present in the vicinity of the female and these sneaky males fertilize a proportion of the eggs, leading to intense sperm competition between the males (Rudolfsen et al. 2006).

Departing from the abovementioned species, the whitefish is a silvery layered salmonid fish that does not develop a breeding colouration. Instead, the males, and in many populations also the females, develop keratinized epidermal tubercles prior to the spawning season (Wiley & Collette 1970, Wedekind et al. 2001, Wedekind et al. 2008b) that are distributed over the entire lateral sides of the fish and are also present on the head. The primary function of these tubercles is believed to be in the maintenance of contact between individuals during spawning, but they can also act as visual, tactile and hydrotactile signals in mate choice (Wiley & Collette 1970).

2.2 Male dominance, courtship and female mate preference

Male dominance and courtship behaviour was studied in minnows (I) in two sequential (10 min) experiments. In the first experiment, the aggressive behaviour of two size-matched males was observed when only these two fish were present in the experimental aquarium. In the second experiment, a sexually active, gravid female was added to the same experimental aquarium with the males and, in addition to aggressive behaviour, the courting activity of the males was also observed. The primary aim of this procedure was to study the effect of female presence on male behaviour and their visual signalling (colouration).

Female preference towards the males was studied in two separate experiments. In study I, the females were allowed to choose between two males in a three-part glass aquarium when only visual cues were present. In this visual preference experiment the same males as in the abovementioned dominance and courtship trials were used. Therefore, the females were allowed to directly observe the behaviour of males during male-male competition and thus could gather information from the male behaviour and sexual signalling patterns, which was expected to facilitate later visual mate preference of the females. In study II, female preference behaviour was studied when only olfactory signals were present. Again, the females were allowed to gather information from the potential mates during 10 min in the same aquarium with the two size-matched males. Then, all of the fish were placed into the mate choice fluviarium (Hirvonen et al. 2000). Water flowed from two (left and right) male compartments (100 ml min^{-1}) through the fluviarium so that females were

able to smell but not see the males; furthermore, all visual and olfactory contacts between the males were prevented. In both tests, female behavioural preference towards the male signals was followed for 10 min by measuring the time the female spent on each male's side in the experimental aquarium/fluviarium.

2.3   Artificial fertilization and offspring fitness measurements

In study IV, artificial fertilization was used to study whether male and female ornamentation of the whitefish signalled potential genetic differences in the post-hatch size (body length and yolk volume) and performance (swimming and predator avoidance ability) in the offspring. A total of 10 females and 10 males were haphazardly selected and stripped for their gametes. The parental fish were then crossed in all possible combinations to produce 100 sibling groups (North Carolina II breeding design). All of the families were randomly divided into two replicates (ca. 150 eggs/replicate) and the eggs were incubated in 600 l cooled and aerated tanks in non-chlorinated tap water at 4 ºC until the time of hatching. About seven days after hatching, five haphazardly selected offspring from each of the 100 families were placed into a 9 mm diameter swimming tube with gravity-driven flow (6.2 cm s^{-1}), as described in Huuskonen et al. (2009). The fish were forced to swim against a current at 6 ºC water temperature and their time to fatigue 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. After the experiments, the larvae were killed in an overdose of tricaine methanesulphonate (MS-222, Sigma®, Sigma Chemical Co., USA). The total length of the larvae was measured, and the length and height of the yolk were also measured to calculate yolk volume (V) using the equation for a prolate spheroid:

V = 0.5236 × length × height^2 (Blaxter & Hempel 1963).

After the swimming experiments, the 100 families were ranked according to their mean swimming performance and then 20 families (every fifth) were systematically selected for the predator avoidance experiment. In these experiments, three whitefish larvae were picked from the selected families and placed in the experimental aquarium with five haphazardly selected predators (one-year-old Arctic charr). The predator-avoidance time of the offspring was determined by measuring the time from the start of the experiment to the moment when two out of three offspring had been predated. Six sequential replicates were made for all families. To avoid satiation, all of the predators were changed after each replicate.

General linear mixed effect models (LME) with restricted maximum likelihood (REML) were used to analyse the parental effects on offspring size and swimming performance. Female and male identity and their interactions

were used as random factors in the models. The significance of random factors was tested using likelihood ratio (G^2) statistics (Sokal & Rohlf 1995, Quinn & Keough 2003). The relative importance of good genes and compatible genes (additive and non-additive genetic effects) were calculated as 4 x the sire, dam and sire x dam components of variance (Lynch & Walsh 1998). The maternal environmental effects for swimming performance were estimated as the difference between the variances associated with dam and sires (dam minus sire).

In study V, artificial fertilization was used to investigate the potential fitness benefits of polyandry (sperm competition of two males) in the Arctic charr. A total of 10 small (mean total length 50.5 cm, range 46.6-53.6 cm) and ten large (mean total length 60.1 cm, range 55.7-70.2 cm) males and three females (50.8, 55.3 and 57.9 cm) were randomly selected from a common brood stock for the experiment. The eggs of each female were stripped and divided into 30 equally large batches (approximately 100 eggs/batch) of which 10 were fertilized with the sperm of small males, 10 with the sperm of large males and 10 with the sperm of both small and large males simultaneously (sperm competition treatment). To exclude material benefits (sire environmental effects), the same volume of spermatozoa was used in each fertilization. In other words, the total volume of spermatozoa/male in the sperm competition trials was only half of the volume used in the single male trials. All egg batches were randomly divided into two independent containers where they were incubated until time of hatching.

The number of dead eggs was counted and removed weekly until all of the fish had hatched (V). Total mortality of the embryos was defined as the percentage of offspring remaining from the initial number of eggs. After hatching, a haphazard sample of 20 (10 × 2) offspring from each of the single male batches and 40 (20 × 2) offspring from the sperm competition batches were collected. Due to the high mortality among one female's eggs, the offspring of only two females were sampled for further analyses. All of the offspring were killed by an overdose of tricaine methanesulphonate (MS-222), photographed and their body mass was individually measured to 1 mg precision. The total length of the fish to the nearest 0.01 mm and the size of the yolks were measured from the digital images using Image-Pro Plus 3.0 graphic software (Media Cybernetics, Inc., Silver Spring, MD, USA). The volume of the yolk was again calculated according to Blaxter & Hempel (1963).

2.4 Ornament measurements

In study I, the intensity of male colouration, i.e. darkness (lightness) of the lateral and redness (hue) of the ventral skin, was visually ranked by two independent observers. Since minnows are capable of altering their colour signalling within seconds, visual colour ranking was considered to be the best method of estimating individual colour differences. The colouration of each

male was ranked four times: before the experiments and after each of the three experiments (chapter 2.2). Both colour traits were ranked using a scale of 0-4, where rank 0 means a totally pale colouration and rank 4 means a maximal dark lateral or red ventral colouration. The mean values of the ranks of the two observers were used in the statistical analyses.

In study II, all of the males were photographed after the female odour preference experiments under standardized lighting conditions with a Sony DSC-F828 digital camera. The digital photographs were further analysed using the graphical user interface developed at the InFotonics Center, University of Eastern Finland. The colouration was measured using HSL (hue, saturation, lightness) colour coordinates from two standardized areas: a rectangle with the four corners defined by the origins of the pectoral fins and the end of the gill covers, and a rectangular area between the ventral fins.

The same graphical user interface was also used to study the association between breeding colouration (HSL) and parasite abundance on naturally spawning male minnows (II) and to investigate the breeding colouration intensity of the Arctic charr (VI). In study VI, mean numerical RGB (red, green, blue) values were calculated from two specified ventral areas (Fig. 1. in VI). Then, red intensity was calculated according the formula:

I_R = red/(red+green+blue) (Liljedal et al. 2008).

The arc-sine square-root transformed I_R values were used in statistical analyses.

In order to measure the size of the breeding tubercles of the whitefish (IV), plaster casts were made from the lateral side of the parental fishes, as described by Wedekind et al. (2001), and the average cast depth (with 0.01 mm accuracy) of 10 tubercles in the middle row anterior to the anal fin was measured using a dial indicator (Mitutoyo Co., Aurora, IL).

2.5 Parasite abundance, condition and mortality

Diphyllobothrium cysts from the body cavity and muscles of the Arctic charr were counted and the thickness of the belly flap was measured for charr over 300 mm using a micrometer (Mitutoyo Co., Aurora, IL) (III). The mortality of Arctic charr under gill-netting stress was estimated by calculating the total numbers of dead and alive individuals found from the gill-nets. To avoid any time effects on mortality, the gill nets were examined once a day, approximately at the same time every day.

In naturally spawning male minnows (II), all parasite fauna of the body cavity and eyes were determined. Also, the condition factor of the males was determined using the equation:

$K = 1000 \times$ fish weight (g)/(body total length (mm))^b,

where b is the slope of a regression of $\log_{10}$ (weight) on $\log_{10}$ (length) of the males (Bolger & Connolly 1989).

2.6 Sperm motility analyses

Spermatocrit (the percentage of a given volume of semen that is occupied by cells) of Arctic charr (V, VI), was measured by centrifuging a homogenized proportion of the milt in a capillary tube for 3 min at 11,500 rpm (5396 g) using a mini-centrifuge (Compur-electronic Gmbh). Sperm velocity and the percentage of motile sperm cells of Arctic charr (V, VI) were determined using computer-assisted sperm analysis (CASA). Sperm activity was initially video-recorded for 40 s after activation, that is, from the precise moment the subsample of pure milt was exposed to 4.5 µl ovarian fluid (2 ovarian fluid:1 water -mixture) of the females on a cooled (ca. 5 °C) microscope slide (Leja Products BV, Nieuw-Vennep, The Netherlands). Recordings were made using a CCD B/W video camera (Sony XC-ST50CE PAL, Tokyo, Japan) attached to a negative phase-contrast microscope (Olympus CH30, Tokyo, Japan) with a ×10 magnification objective. Video recordings were later analysed using the HTM-CEROS sperm tracker software (CEROS v.12, Hamilton Thorne Research, Beverly, MA, USA). The variables measured included: average path velocity (VAP), straight line velocity (VSL) and curvilinear velocity (VCL) (Rurangwa et al. 2004). The velocity estimates were based on the mean velocity of all motile cells (i.e. those that exceeded the pre-determined threshold values of VAP > 10 µm s^{-1} and VSL > 20 µm s^{-1}) recorded at 10, 20, 30 and 40 s after activation. The average values of the replicated measures for each male were used for statistical analyses. The percentage of motile cells 40 s after activation was used as an estimate of sperm longevity (VI).

2.7 MHC and microsatellite analyses

In study III, DNA was extracted from tissue samples as described in Vähä et al. (2007). Arctic charr MHC II B sequence specific primers MHC-int-F and MHC-int-R were designed using the program PRIMER3 (Rozen & Skaletsky 2000). The MHC-int-F-primer had a 40 bp 'CG clamp' added to the 3'-end to prevent total denaturation of the samples (Sheffield et al. 1989) in denaturing gradient gel electrophoresis (DGGE) (Myers et al. 1987). The 25 µl PCR mixture contained approximately 100 ng of DNA, 0.75 U of BioTaq polymerase (Bioline), 12.5 pmol of each primer, 1× PCR reaction buffer, 60 pmol of $MgCl_2$ and 6.25 pmol of dNTPs. The PCR program consisted of an initial 2 min denaturation at 95 °C, followed by 30 cycles of denaturation for 1 min at 94 °C, annealing for 1 min at 56 °C and extension for 1 min at 72 °C. The final extension was for 10 min at 72 °C.

Denaturing gradient gel electrophoresis was performed using 9.5 µl of the PCR product in 9 % 19:1 acrylamide:bisacrylamide gels containing 1× TAE buffer and a gradient of urea and formamide (Hayes et al. 1999). The gels were cast with a gravitational gradient maker and DGGE was performed in a DGGE system buffer tank (C.B.S. Scientific Inc.) filled with 0.5× TAE and heated to 60 °C. The gels were stained with ethidium bromide for 10 min after electrophoresis and the stained DNA was visualized using a BioRad ChemiDoc XRS imaging system, after which the individuals were genotyped by eye. The genotypes of 14 individuals from the Peltojärvi population were confirmed by sequencing directly from both DGGE PCR products and full-length PBR fragments cloned to pGEM-T plasmids (Promega Corporation), according to manufacturer's instructions.

The level of neutral microsatellite variation in the studied fish was ascertained using 11 microsatellite markers. Polymerase chain reaction was carried out on two 10 µl multiplexes using the QIAGEN Multiplex PCR Kit, according to the manufacturer's instructions, with the annealing temperature of the recommended PCR program set to 56 °C. The forward primer for each locus was end labelled with a fluorescent dye and a GTTT tail was added to each reverse primer to ensure the addition of an A-overhang to each PCR fragment by Taq polymerase (Brownstein et al. 1996). The microsatellites were genotyped using the same methods as described in Vähä et al. (2007).

3   RESULTS AND DISCUSSION

3.1   Information content of secondary sexual ornamentation

3.1.1 Social status and courting activity

The signals used during aggressive male-male interactions are expected to be important cues in female choice since the reliability of such traits is continually tested by competitors and thus cannot be faked without incurring high costs (Berglund et al. 1996, Hoi & Griggio 2008). Although high dominance status of the male has occasionally been shown to reduce female fitness through sexual conflict (e.g. by overriding female preference) (Arnqvist 2004, Wong & Candolin 2005), high male status can also produce various direct benefits to females, for example, in the form of high quality resources (e.g. breeding sites) or reduced mating costs (e.g. risk of injuries or death) (Le Boeuf & Mesnick 1990, Andersson et al. 1994). Furthermore, social status can also indicate the genetic quality of a male (e.g. Cox & Le Boeuf 1977, Rantala & Kortet 2004).

In male minnows, dominant males courted the females more actively and had a redder and/or darker skin colouration than the subordinate males (I). These results suggest that both ornament traits either signal the dominance status or courting activity of the males, or both. Several studies have demonstrated that male ornaments often have a dual function in both male-male competition and female choice (e.g. Kodric-Brown 1996, Tarof et al. 2005, Griggio et al. 2007, Hoi & Griggio 2008, see also Candolin 2004), which suggests that this could also be the case in minnows. The results of study I also show that the darkness difference between subordinate and dominant males increased in the presence of a female, which suggests that male-male competition may increase the honesty of signalling and thus facilitate female choice (Candolin 1999, 2000a). Instead, the carotenoid-based red colouration was found to be a more stable indicator of male quality, which suggests that carotenoid ornaments may, besides being positively associated with dominance status, also signal a different aspect of male quality or signal quality over longer time

scales. Although the results of study I demonstrate that melanin-based ornaments may have their own signalling function, the possibility that they mainly act as an amplifier of carotenoid ornamentation could not be ruled out (Brooks & Caithness 1995, Brooks 1996).

3.1.2 Health and condition

Hamilton & Zuk (1982) proposed that females would mate with highly ornamented males because elaborate male ornaments act as honest signals of male resistance ability against concurrent parasite species. In paper II, this hypothesis was tested in minnows. In support of the hypothesis, males with a more saturated (redder) belly colouration had fewer *Philometra ovata* (Nematoda) parasites than their less ornamented counterparts. This parasite species can severely impair the fitness of its host, for example, by causing parasitic castration, chronic inflammation and tissue necrosis (Moravec 2006, Saraiva et al. 2008), and by increasing the predation risk of the host individuals (Saraiva et al. 2008). Therefore, the saturation of belly colouration may be an honest signal of the health status and overall quality of the male in the studied minnow population.

Since the sexual signalling system of the minnow contains several signalling components and different signals can have different signalling functions, the potential signalling content of the breeding tubercles and the quality (hue) of the belly colouration were also studied. The results of the paper show that both of these traits were associated with the condition factor of the males: redder (lower hue) and more tubercled males were in better condition than their less ornamented counterparts. Thus, different ornaments and even the different components of the same ornamental trait (belly colouration) may have different signalling functions (Wedekind et al. 1998, Candolin 2003, Grether et al. 2004). Interestingly, a similar phenomenon was also previously found in another cyprinid fish, the roach (*Rutilis rutilus*). The lateral breeding tubercle ornamentation of the male roach was associated with parasite resistance (Taskinen & Kortet 2002) and front head breeding tubercles were associated with condition (Kortet & Taskinen 2004). Together, these studies support the multiple messages hypothesis of sexual ornamentation (Møller & Pomiankowski 1993, Johnstone 1997, Ligon et al. 1998, Marchetti 1998, Candolin 2003). According to this hypothesis, receivers evaluate all signals together in order to estimate the general quality of the mate, or different receivers base their choice on different aspects of mate quality, i.e. different signals (Wedekind 1992, Candolin 2003).

3.1.3 Offspring performance

The association between secondary sexual traits and survival of the offspring has previously been demonstrated in numerous studies (see e.g. Møller & Alatalo 1999), but less is known about whether sexual ornamentation can indicate the physical performance of offspring, such as locomotor or predator

avoidance ability. The results of paper IV indicate that in a mutually ornamented fish species (whitefish), both male and female secondary sexual ornaments (size of the breeding tubercles) are positively associated with offspring post-hatching swimming performance, which was in turn positively associated with offspring predator avoidance ability. Furthermore, highly ornamented females produced larger offspring that also had greater yolk reserves than less ornamented individuals. Since the vast majority of the total mortality in many fish populations takes place in the early life stages, mainly due to predation and starvation (Fuiman & Magurran 1994, Fuiman & Cowan 2003), variations in this post-hatching performance probably have a high evolutionary significance (Elliot 1989).

The mutual sexual selection hypothesis predicts that selection for the same ornamental traits in both sexes should result in assortative mating (MacDougal & Montgomerie 2003, Sieferman & Hill 2005). When mutual ornamentation is positively associated with some aspects of individual quality, directional selection for the mutual ornamentation may lead to a situation where both sexes prefer to pair with highly ornamented partners, which would leave less ornamented individuals to pair among themselves (McLain & Boromisa 1987). As an indirect support of this view, the offspring swimming performance was, on average, better in highly ornamented parental combinations than when both parents were less ornamented.

Together, the results of paper IV suggest that mutual sexual selection may have an important role in whitefish mating and that mutual ornamentation may have evolved through mutual mate preferences. However, the exact signalling function of breeding tubercles in whitefish mating is currently unclear. Thus, it is possible that the breeding tubercles are also (or solely) used in reproductive competition in both sexes (Watson & Simmons 2010a, b). In other words, breeding tubercles may act as badges of status or weapons in intra-sexual contests, which may promote directional selection on ornamental traits even without ornament-based mating preferences.

3.1.4 Sperm quality and offspring survival

The phenotype-linked fertility hypothesis predicts that females gain direct benefits from mating with highly ornamented males because these individuals are also highly fertile males. The theoretical basis of this hypothesis rests on the observation that both primary and secondary sexual traits (carotenoid-based ornaments) are often promoted by the same sex hormones, the androgens (Folstad & Skarstein 1997, Hillgarth et al. 1997). Thus, the expression of carotenoid colour traits is expected to be directly associated with the males' capacity for sperm production. A positive correlation between the traits may arise either because intense secondary sexual ornamentation may signal low overall immune activity within the body and reduced exposure of "nonself" sperm cells to autoimmune attack (Folstad & Skarstein 1997, Liljedal et al. 1999) or because intense ornamentation may indicate high body supplies of

antioxidants, which may reduce the susceptibility of sperm to oxidative stress (Greco et al. 2005).

The results of paper VI give support to the phenotype-linked fertility hypothesis. This paper shows that the carotenoid-based abdominal colouration (red intensity) of the Arctic charr males was positively associated with their sperm swimming velocity. Sperm velocity has been shown to be the most important factor predicting the paternity of males during sperm competition and in monogamous matings (Lahnsteiner et al. 1998, Froman et al. 1999, Levitan 2000, Kupriyanova & Havenhand 2002, Gage et al. 2004, Liljedal et al. 2008). Interestingly, the results of paper V demonstrate that male sperm velocity of the Arctic charr is positively associated with not only paternity, but also with offspring survival. Thus, these results are in line with the good sperm hypothesis which predicts that the sperm which are more successful in competition for fertilizing the eggs are also more effective in producing viable offspring. In both studies (V and VI), the experimental fish originated from the same Lake Inari population, but they represented different hatchery generations (V: F_4, VI: F_1 and F_2). Thus, the results of these studies are not necessarily directly comparable. However, when viewed together, they indicate that male secondary sexual ornamentation may signal both sperm velocity and offspring viability. This may in turn mean that Arctic charr females bias paternity towards the highly ornamented males (directional cryptic female choice) (Pizzari & Birkhead 2000, Evans et al. 2003). However, since the nature of the association between primary and secondary sexual traits in the fourth hatchery generation (V) is unknown, further studies are needed to test this hypothesis.

3.2 Potential factors maintaining the variation of ornamental traits

Directional female mating preferences on male viability traits should rapidly exhaust the additive genetic variability of male traits and drive them to fixation (Tomkins et al. 2004). For example, studies on *Drosophila serrata* have demonstrated that sustained sexual selection can reduce genetic variation in male traits in the direction of sexual selection (Blows et al. 2004, Hine et al. 2004). As a result, females will no longer gain benefits from discriminating between males based on these traits, which in turn should lead to the disappearance of female mating preferences. Thus, it is paradoxical why females of many species still show preferences for male ornamental traits. Numerous studies have presented potential resolutions to this question (lek paradox), but an unequivocal answer remains to be found. The potential explanations can be divided to two classes (Tomkins et al. 2004). The fluctuating selection hypothesis argues that the optimal phenotype will vary in space or time, for example, because of continually evolving parasites (Hamilton & Zuk

1982) when genetic variation is maintained by cycles of host–parasite co-evolution. The mutation–selection balance hypothesis assumes that continuously accumulating mutations generate new genetic variation as quickly as directional selection reduces it (Rowe & Houle 1996, Tomkins et al. 2010). In the following chapters, I present some potential factors that may contribute to the maintenance of variation in secondary sexual traits. They partly support the fluctuating selection hypothesis, but also give some other insights to this long-lasting dilemma.

3.2.1 Sexual selection for multiple sexual signals

Papers I and II indicate that secondary sexual traits of male minnows consist of multiple signals which can contain visual (carotenoid and melanin colouration), olfactory, tactile (breeding tubercles) and behavioural (courtship behaviour) components (chapters 3.1.1 and 3.1.2). Furthermore, even the same ornamental trait can include several signal components (e.g. hue and saturation of the carotenoid traits). Female minnows were observed to have behavioural preferences towards the more colourful males when only visual cues were present (I). The selected males were both redder and darker (50 % of trials), only redder (25 %), only darker (19 %) or darker but less red (6 %). Thus, some females may have a primary preference for red carotenoid ornaments, whereas other individuals may have a preference for the dark melanin ornaments. Although the possibility that melanin traits are just amplifiers of carotenoid ornaments could not be ruled out, these results may indicate that different females have differential ornament preferences (Brooks & Endler 2001). Paper II demonstrates that within male pairs (pale vs. saturated colouration) females preferred the odour of individuals with a saturated (i.e. redder) belly colouration. Although no evidence was found for female odour preferences for the other traits (belly hue and breeding tubercle number), these traits signalled male condition (chapter 3.1.2). Thus, it is possible that in more natural conditions (e.g. when visual and tactile signals are also present), female mating decisions may rest on multiple cues or females may utilize different cues in different situations or mating seasons.

One important consequence of varying preferences is that it could contribute to the maintenance of variation in secondary sexual ornaments and fitness related traits (Candolin 2003, Lehtonen et al. 2010). Preference variation can act either within individuals (individuals show temporal variation in mating preferences) or between individuals (different individuals differ in their preferences). Female preferences can change, for example, depending on her age, current condition and the environmental conditions (Jennions & Petrie 1997, Cotton et al. 2006, Bleay & Sinervo 2007, Milner et al. 2010, see also Holveck & Riebel 2010). Temporal changes in mating preferences may be more common than has traditionally been believed. In fact, a recent meta-analysis suggested that mate preference behaviour is one of the least repeatable behavioural traits (Bell et al. 2009). Thus, strong directional selection on ornamental traits could be an artefact, resulting in short-term studies that

cannot capture fluctuations in selection gradients (Bro-Jørgensen 2010). When different genotypes are superior in different environments, i.e. when there is a strong genotype-by-environment interaction, selection on individual ornamental traits can, in fact, be rather weak (Danielson-François et al. 2006, Bussiére et al. 2008, Bro-Jørgensen 2010). Thus, dynamic variation in selection pressures may effectively prevent the erosion of additive genetic variation in ornamental traits and explain the evolution and maintenance of multiple sexual signals.

In addition to temporally fluctuating mating preferences, between-individual variations in mating behaviour could also maintain variations in sexual traits (Jennions & Petrie 1997, Widemo & Sæther 1999, Murphy & Gerhardt 2000, Brooks & Endler 2001, Coleman et al. 2004). Brooks & Endler (2001) found that female guppies vary in their responsiveness, discrimination between males and mate preferences. Thus, no universally attractive male phenotype was found for all females. Even if some ornamental traits are generally not preferred, they could still be maintained by frequency-dependent selection, if at least a minor proportion of females prefer these traits (Partridge & Hill 1984, Partridge 1988, Brooks & Endler 2001, see also Kokko et al. 2007). Therefore, it is possible that the complex sexual signalling system of male minnows has evolved as a result of multiple female preferences, which in turn may contribute to the maintenance of additive genetic variation in individual traits. In addition, it seems plausible that temporal variations in female preferences may also have an important role in the evolution of this multiple signalling system. However, long-term studies are needed to confirm this hypothesis.

3.2.2 Sexual selection for genetic compatibility

The mate choice for genetic compatibility (non-additive genetic benefits) differs radically from traditional good gene models of sexual selection. When mate choice is based on compatibility, different individuals are expected to differ in their mating preferences (Tregenza & Wedell 2000). Thus, the mate choice for non-additive genetic benefits should not exhaust additive genetic variance in fitness and associated ornamental traits (Krüger et al. 2001, Reinhold 2002, Hoffman et al. 2007, Lehmann et al. 2007, Reid 2007, Fromhage et al. 2009, Neff & Pitcher 2008, 2009). In paper III, major histocompatibility complex heterozygote Arctic charr individuals were observed to be superior over the both homozygote genotypes (overdominance). More specifically, heterozygote individuals had fewer *Diphyllobothrium* parasites, were in better condition and had higher survival rates under stress than either of the homozygotes. These results suggest that overdominance can be an important evolutionary mechanism contributing to MHC polymorphism in the wild, but because heterozygosity cannot be directly inherited by the offspring, it is inevitability non-additive. When non-additive genetic benefits are large, directional selection

on ornamental traits should be weak. In support of this view, my preliminary analyses showed that the secondary sexual ornaments (belly colouration) of the Arctic charr were not associated with MHC genotype (unpublished data). Therefore, MHC related mate choice in this Arctic charr population may be mainly based on genetic compatibility. However, it is possible that secondary sexual ornaments of the Arctic charr indicate some other aspects of genetic quality, i.e. some "good genes" other than the MHC genes. Thus, good genes and compatible genes can act together and the final mating decision could be a result of their interaction (Roberts & Gosling 2003).

Paper IV shows that both mate choice criteria really could act together. The results of this paper suggest that although secondary sexual ornamentation indicates offspring fitness (chapter 3.1.3), fitness is also dependent on the parental combination (Zeh & Zeh 1996, Johnsen et al. 2000, Tregenza & Wedell 2000, Rudolfsen et al. 2005). Furthermore, the correlation between breeding ornamentation and offspring fitness was relatively weak, although highly ornamented males, females and their combinations had higher quality offspring than their less ornamented counterparts, on average. Therefore, when both selection mechanisms act together, the directional selection on ornamental traits may be weak (Colegrave et al. 2002) and the indicator value of ornamentation relatively low. However, as pointed out by Alatalo et al. (1998), even relatively weak fitness benefits can maintain the honesty of sexual signalling. In addition, the fitness benefits of mate choice do not need to be large to be important in the evolutionary time scale (Møller & Alatalo 1999).

3.2.3 Post-copulatory sexual selection

The fact that female choice often continues after copulation in a form of cryptic female choice has been largely ignored in sexual selection studies (Birkhead & Pizzari 2002). Since cryptic female choice criteria are not necessarily consistent with the criteria used in pre-copulatory mate choice, our current understanding of the strength of directional sexual selection may not always be valid. Several studies have found that sperm velocity in ovarian fluid and male fertilization ability are strongly dependent on male-female interactions (Prout & Clark 1996, Wilson et al. 1997, Urbach et al. 2005, Rosengrave et al. 2008), suggesting that non-directional cryptic female choice may be widespread (Birkhead & Pizzari 2002). Thus, apparently strong directional pre-copulatory mating preferences may be revealed as being much weaker when both pre- and post-copulatory sexual selection processes are viewed together.

Even though indirect support for the phenotype-linked fertility hypothesis and thus directional cryptic female choice was found (V, VI), it was not possible to rule out the possibility that female Arctic charr also use post-copulatory sexual selection to bias paternity towards unrelated or genetically compatible males (Bilde et al. 2007, see also Konior et al. 2005). In fact, since the genetic variability of many natural Arctic charr populations is extremely low (III, Conojeros et al. 2008), incompatibility avoidance can be an important mechanism explaining the polyandry of Arctic charr. However, as pointed out

by Ivy (2007), the evolution and maintenance of polyandry are most easily explained if females gain both additive and non-additive genetic benefits, rather than just one. Together, these observations again suggest that directional post-copulatory sexual selection may occur (V, VI), but cryptic female choice for compatibility may weaken the indicator value of ornamentation and thus maintain additive genetic variation in secondary sexual traits. Further studies utilizing breeding designs that can partition fitness variations among both good genes and compatible genes (e.g. North Carolina II) are required in order to determine the generality of these findings.

4 CONCLUSIONS

Good gene models of sexual selection propose that females selectively mate with highly ornamented males because these traits are honest indicators of male genetic quality (Zahavi 1975). The basic assumption of these models is that the same high quality, i.e. highly ornamented, males are good mates for all females (Colegrave et al. 2002, Neff & Pitcher 2005). This should lead to directional selection on male ornamental traits, which in turn should deplete additive genetic variation in male traits and exhaust genetic variation in viability (Tomkins et al. 2004, Kotiaho et al. 2008). However, a vast number of studies have demonstrated that despite directional mating preferences, this variation does not disappear. This observation is the basis of one of the major, unresolved questions in evolutionary biology, the lek paradox: why do females of many species still prefer to mate with highly ornamented males even though the signalling value of secondary sexual traits should have disappeared? The aim of this thesis was to study the signalling content of secondary sexual ornaments and to discover potential factors that may maintain genetic variability and the information content of these traits.

In papers I and II, on minnows, I show the multiple sexual ornamentation of the males' signal dominance status and/or courtship activity (I), parasite resistance and condition (II), all of which, in addition to direct benefits, can also indicate indirect benefits, i.e. the genetic quality of the individuals. In whitefish, female ornamentation was positively associated with the size of the offspring and their yolk reserves (IV). Furthermore, the ornamentation of both sexes (i.e. mutual ornamentation) predicted genetic differences in the post-hatching performance of the offspring. Moreover, in the Arctic charr, the intensity of male breeding colouration was positively associated with their ejaculate quality (sperm cell velocity), and seemingly also with their offspring viability (V, VI). Together, these studies suggest that male (and female) ornamentation is a reliable indicator of various fitness benefits in the studied fish species. However, they also indicate that directional selection on ornamental traits may not be strong enough to exhaust the additive genetic variation in these traits.

I found several potential mechanisms that may weaken the directional selection on ornamental traits. In minnows (I, II), I showed that females probably vary in their ornament-based mating preferences and that individuals may additionally show temporal variation in their preferences. This variation should weaken the directional selection on each individual signal component. Directional selection on ornamental traits can also be weak if the fitness of the offspring is mainly dependent on the genetic compatibility of the parents. The simplest mechanism driving the genetic compatibility effects is overdominance (III), where the fitness of the heterozygote individuals is higher than that of either of the alternative homozygote genotypes. In this scenario, the directional selection on any ornamental trait should be weak because individual males and females are expected to mate disassortatively (with different mates), depending on their own genotype. As demonstrated in paper IV, both good genes and compatible genes may have simultaneous effects on offspring fitness. The results of this paper suggest that simultaneous selection for genetic compatibility weakens the directional selection on ornamental traits and thus also the indicator value of ornamentation. In papers V and VI, I studied the potential mechanism for genetic compatibility selection, post-copulatory sexual selection (cryptic female choice). Interestingly, although cryptic female choice is often referred to as a mechanism for the incompatibility avoidance of gametes, the results of these papers indicate that it may also be directional, favouring the same, brightly coloured males as pre-copulatory sexual selection. However, it also seems likely that non-directional cryptic female choice (genetic compatibility) plays an important role in determining the paternity of males under sperm competition. If post-copulatory sexual selection is non-directional or only weakly directional, it may contribute the maintenance of variation in secondary sexual traits.

Taken together, in line with good gene models of sexual selection, I found that secondary sexual ornaments signal various fitness benefits. Despite the fact that this should lead to strong directional selection on ornamental traits, the results of my thesis also suggest that the directional selection on these traits may be too weak and too variable to deplete the additive genetic variation in these traits. Thus, these results might also provide light on a way towards the resolution of the lek paradox.

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in Peltojärvi! I still wonder how we (Jouni R. and I) managed to squeeze into it with all of our equipment.

YHTEENVETO (RÉSUMÉ IN FINNISH)

Seksuaaliornamenttien geneettisen muuntelun säilyminen – parittelua edeltävän ja sen jälkeisen seksuaalivalinnan merkitys

"Hyvät geenit" -hypoteesin mukaan naaraiden odotetaan pariutuvan sekundaarisilta seksuaalipiirteiltään (ornamenteiltaan) koreiden koiraiden kanssa, koska koiraiden ornamentit ovat usein yksilöiden geneettisen laadukkuuden rehellinen signaali. Naaraiden oletetaan suosivan parinvalinnassaan tiettyjä laadukkaita koirasgeenejä, koska niiden uskotaan lisäävän jälkeläisten kelpoisuutta riippumatta muun perimän rakenteesta. Toisin sanoen hypoteesi olettaa tiettyjen laadukkaiden (koreiden) koiraiden olevan hyviä pariutumiskumppaneita kaikille naarasyksilöille, minkä tulisi johtaa voimakkaaseen, koiraiden sekundaarisia seksuaalipiirteitä suosivaan suuntaavaan valintaan. Suuntaavan valinnan puolestaan oletetaan johtavan koiraiden ornamenttien ja niiden heijastamien kelpoisuusetujen additiivisen geneettisen muuntelun häviämiseen. Useissa tutkimuksissa on kuitenkin havaittu, että suuntaavasta valinnasta huolimatta ornamenttien geneettinen muuntelu on usein varsin runsasta. Tämä havainto on pohjana yhdelle evoluutiobiologian keskeiselle ratkaisemattomalle arvoitukselle, ns. soidinparadoksille: mikä ylläpitää ornamenttien ja niiden heijastamien kelpoisuusetujen geneettistä muuntelua? Paradoksille on olemassa lukuisia vaihtoehtoisia ratkaisuehdotuksia, mutta yksiselitteistä vastausta ei ole löydetty. Väitöskirjani tavoitteena on tutkia koiraiden ja naaraiden seksuaaliornamenttien informaatiosisältöä sekä potentiaalisia ornamenttien geneettistä muuntelua ylläpitäviä tekijöitä.

Väitöskirjani osatutkimukset perustuvat kolmeen Suomessa esiintyvään kalalajiin: mutu (*Phoxinus phoxinus*), nieriä (*Salvelinus alpinus*) ja siika *Coregenus lavaretus*. Kaikilla lajeilla tavataan kutuaikaisia seksuaaliornamentteja ja kaikkien pariutumisjärjestelmä perustuu geneettisiin hyötyihin (engl. non-resource based mating system). Lisäksi kaikkien lajien naaraat tuottavat suuria määriä ulkoisesti hedelmöitettäviä munia, joista ei huolehdita hedelmöityksen jälkeen (ei vanhempien hoivaa). Näiden parinvalinnan ominaispiirteiden takia seksuaaliornamenttien voidaan olettaa heijastavan lähinnä geneettisiä (epäsuoria) kelpoisuusetuja.

Muduilla havaitsin koiraiden eri seksuaaliornamenttien (kutuvärityksen värikylläisyys ja –sävy sekä kutukyhmyt) signaloivan yksilöiden sosiaalista asemaa, kosiskeluaktiivisuutta, loisvastustuskykyä ja kuntoa. Siioilla molempien sukupuolten ornamentit (kutukyhmyt) heijastivat poikasten kuoriutumisen jälkeistä uinti- ja pedonvälttämiskykyä. Lisäksi siialla naaraan ornamenttien koko korreloi positiivisesti poikasten yksilökoon sekä poikasten ruskuaisvarastojen koon kanssa. Nieriällä koiraiden kutuvärityksen intensiteetti ilmensi koiraiden sperman laatua (siittiöiden uintinopeutta) ja mahdollisesti myös poikasten eloonjäämistodennäköisyyttä. Siten osatutkimuksieni tulokset

osoittavat, että tutkittujen kalalajien koiraiden ja naaraiden seksuaaliornamentit voivat olla luotettava yksilöiden kelpoisuuseduista kertova indikaattori.

Toisaalta tutkimukseni osoittavat, että tietyt ennen pariutumista ja sen jälkeen ilmenevät mekanismit voivat heikentää ornamentteihin kohdistuvaa suuntaavaa valintaa. Muduilla havaitsin, että naaraiden koiraiden ornamentteja kohtaan osoittamat parinvalintapreferenssit eroavat eri naarasyksilöiden välillä ja mahdollisesti myös ajallisesti kullakin naarasyksilöllä. Tulokset viittaavat siihen, että mikään yksittäinen koirasfenotyyppi ei ole paras lisääntymiskumppani kaikille naaraille tai kaikissa tilanteissa. Siten suuntaava valinta kutakin yksittäistä ornamenttia kohtaan voi olla suhteellisen heikko. Suuntaavaa valintaa heikentää myös tilanne, jossa poikasten kelpoisuus on riippuvainen naaraiden ja koiraiden geneettisestä yhteensopivuudesta. Yksinkertaisimmillaan tämä voi tarkoittaa ns. ylidominanssia (engl. overdominance), jossa genotyypiltään heterotsykoottisten yksilöiden kelpoisuus on suurempi kuin kummallakaan vaihtoehtoisista homotsygoottisista genotyypeistä. Luonnonvaraisella nieriäpopulaatiolla tehty tutkimukseni osoittaa, että major histocompatibility complex –geeneiltään heterotsykootit yksilöt voivat olla loisvastustuskyvyltään, kunnoltaan ja eloonjäämistodennäköisyydeltään homotsykootteja laadukkaampia. Tässä tapauksessa ornamenttipiirteisiin kohdistuva suuntaava valinta on oletettavasti heikko, koska suotuisa, poikasten kelpoisuuden maksimoiva koirasgenotyyppi riippuu naaraan omasta genotyypistä (ja päinvastoin). Siten kaikki yksilöt eivät todennäköisesti voi suosia samoja geenejä kantavia yksilöitä, kuten "hyvät geenit" –hypoteesi olettaa. Siioilla tehty tutkimukseni osoittaa, että eri parinvalintamekanismit (hyvät geenit ja yhteensopivat geenit) voivat kuitenkin vaikuttaa samanaikaisesti. Tämä todennäköisesti heikentää ornamenttien kohdistuvaa suuntaavaa valintaa sekä ornamenttien ja poikasten kelpoisuuden välistä korrelaatiota.

Parittelua edeltävän seksuaalivalinnan ohella myös sen jälkeinen, ns. naaraan piilovalinta on tärkeä, joskin suhteellisen vähän tutkittu seksuaalivalinnan komponentti. Nieriällä tehdyt tutkimukseni osoittavat, että vaikka naaraiden piilovalinnan on usein oletettu olevan lähinnä sukusolujen geneettisen yhteensopivuuden testaamiseen kehittynyt mekanismi, piilovalinta voi myös suosia samoja koiraiden ominaisuuksia (ornamentteja) kuin parittelua edeltävä seksuaalivalinta (suuntaava piilovalinta). Toisaalta on todennäköistä, että nieriänaaraiden piilovalinta toimii samanaikaisesti myös geneettisesti yhteensopimattomien geenikombinaatioiden syntyä kontrolloivana mekanismina. Koska monien luonnonvaraisten nieriäpopulaatioiden geneettinen muuntelu on hyvin vähäistä, geneettisen yhteensopimattomuuden välttämismekanismit voivat olla erittäin merkittävä evolutiivinen tekijä naaraiden polyandrian (naaras parittelee usean koiraan kanssa) kehittymisen taustalla. Siten havainnot viittaavat siihen, että suuntaavaa naaraiden piilovalintaa voi nieriöillä esiintyä, mutta piilovalinta geneettisen yhteensopivuuden varmistamiseksi voi heikentää ornamentteihin kohdistuvan suuntaavan valintapaineen voimakkuutta ja siten ylläpitää ornamenttien geneettistä muuntelua.

Yhteenvetona esitän, että kaikki edellä esitetyt mekanismit (naaraiden valintapreferenssien vaihtelu, valinta geneettisen yhteensopivuuden varmistamiseksi ja ei-suuntaava piilovalinta) todennäköisesti heikentävät ornamentteihin kohdistuvaa suuntaavaa valintaa ja siten ehkäisevät ornamenttien ja niiden indikoivien kelpoisuusetujen geneettisen muuntelun häviämistä. Siten väitöskirjani tulokset voivat osaltaan helpottaa soidinparadoksin ymmärtämistä ja mahdollisesti auttaa sen ratkaisussa.

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