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Arms races, ornaments and fragrant genes: The dilemma of mate choice in fishes

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ABSTRACT

Female preference for secondary sexual male ornaments that are handicapping survival has been an evolutionary puzzle since Darwin. The Hamilton-Zuk hypothesis assumes that costly ornaments can be produced only by those males that carry the genes for resistance against the current infectious disease. I review studies in fishes that indeed bright colors can only be displayed by males in good health and females prefer healthy males by choosing the brighter ones. On the other hand, female vertebrates from fish to humans smell out partners that provide the complementary genes of the major histocompatibility complex (MHC) to help them producing offspring with the optimal number of different MHC alleles. In sticklebacks females have a two-step choice. Using smell they approach a male that offers the optimally complementary number of MHC alleles. When they can see the male, they accept it only when it is bright and thus offers in its complementary set of alleles the specific MHC allele providing resistance against the current disease as revealed by the male's sexual ornamentation.

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1. Introduction

Male secondary sexual ornaments such as bright colors, long feathers, songs, etc, that handicap survival, had been a challenge for Darwin (1871) theory of natural selection. He rescued his theory by assuming that females prefer such bright males because of their esthetic sense and called the process sexual selection (see West-Eberhard, this issue). The first experimental proof for this assumption of sexual selection came only in 1982 by Andersson elongating the tail of male African widow birds and found that females preferred the elongated males. For an experimental proof in fish it took another 10 years, showing that mate choice of female sticklebacks is influenced by male red coloration, an ornament but also a reliable indicator of immune defence (Milinski and Bakker, 1990). Darwin (1871, Chapter XII, *The descent of man*) had noticed that 'the male stickleback has been described as 'mad with delight', when the female comes out of her hiding place and surveys the nest which he has made for her'. Darwin did, however, not discuss how this female esthetic sense or, in other words, the preference for ornamented mates could evolve. Fisher (1930) idea of a runaway

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process that because of a strong genetic co-variation between the male trait and the female preference for it can drive both the trait and the preference for it with "ever increasing speed" (p. 152) was supported mathematically by Lande (1981). Evidence for the runaway process is scarce, the first was provided on fish by Bakker (1993). Daughters and sons of red sticklebacks were tested to both female preference for redness and male red coloration: the two traits showed positive genetic correlation.

2. The Hamilton-Zuk good genes hypothesis

With his idea of the handicap principle Zahavi (1975) proposed an alternative to Fisher's idea. Females prefer handicapped males because they must have good genes for being able to survive despite their handicap. Maynard Smith (1976) criticized Zahavi's hypothesis because the indirectly preferred good gene would go quickly to fixation in the population. Then the handicap does not reveal anything to be preferred and should disappear. Hamilton and Zuk (1982) proposed a way out of this dilemma (see also West-Eberhard, this issue). They assumed that females need to select the males that carry *genes for resistance* against the currently prevailing disease A, to which the offspring would be exposed, too. Instead for doing a medical health test they prefer the male that can afford to display long feathers, bright colors loud songs and energetic dances—this male must be healthy and thus most probably carries the needed immunogene. Before this immunogene reaches fixation, the next disease B can spread because the population has become resistant to A to some extend. Now a different immunogene proving resistance against B is needed and females find it by again preferring bright males that that are now likely to carry resistance genes against B. This leads to cycling of both parasites and immunogenes, which never become fixed because of a Red Queen dynamic (Van Valen, 1973; Lively and Dybdahl, 2000)—the handicap continues to reveal health and good genes for resistance. Experimental support for the Hamilton-Zuk hypothesis was provided early in 1990 in stickleback fish (Milinski and Bakker, 1990), followed by supporting evidence for birds (Møller, 1990; Zuk et al., 1990).

3. Stickleback fishes in the Red Queen scenario

In wild caught stickleback males the brightness of their red breeding coloration correlated positively with their condition factor, an established measure of the health condition of bony fishes (Fig. 1a) (Milinski and Bakker, 1990). Thus, a male's brightness reveals its health condition. When gravid females were offered the choice between two neighboring displaying males in separate and visually isolated tanks, they preferred the redder of the two, even though males had only slightly different redness (Fig. 1b). This shows that by preferring the redder male females actually preferred the one with better health condition. To turn this into a decisive experiment, the choice was repeated with other females either under white light or under green light, which prevented the females to see differences in redness. The actually redder males were no longer preferred under green light showing that females take redness into account and not any correlated male trait.

After the redder male in each pair had been exposed to a mild, but condition reducing infection with the parasite *Ichthyophtyrius multifiliis* and had recovered after the tiny white cysts had dropped off the fish, the formerly redder males had reduced brightness and condition (Fig. 2a and b) and were no longer preferred (Fig. 2c and d). Thus, the expression of the male ornament reveals health, is important for female mate choice and is reduced by parasitization. Similar results were found in guppies (Houde and Torio, 1992). Barber et al. (2001) showed that the offpring of redder male sticklebacks resist parasites better than offspring of dull males when the

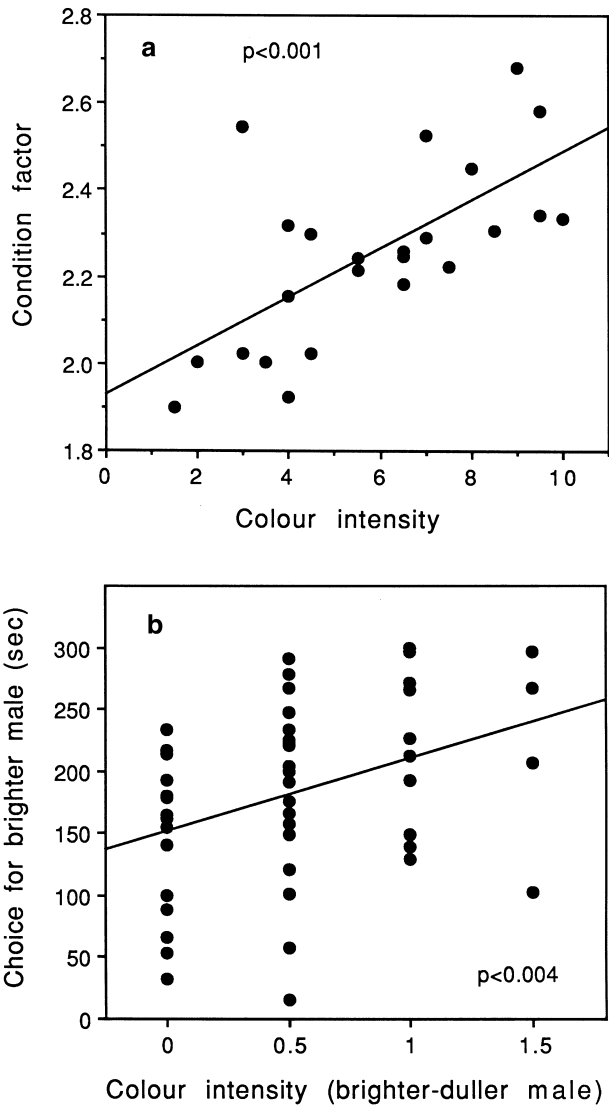

Fig. 1. (a) Correlation between the intensity of red breeding coloration and the condition factor of 24 reproductive male sticklebacks. (b) Correlation between the difference in color intensity of 12 pairs (brighter–duller male) and active female choice for the brighter male (measured in seconds, max. 300 s) by different females, one on each day. The pooled regression is significant (after Milinski and Bakker, 1990).

mother was the same by splitting clutches. Møller (1990) found in barn swallows that offspring of long-tailed males had fewer mites, compared to cross-fostered offspring of short-tailed males in the same nest. So the advantage is due to "good" resistance genes, but what is the nature of these immunogenes?

4. Olfactory mate choice aims at an optimal number of different genes of the major histocompatibility complex (MHC) for the offspring

To allow for choice among males carrying different immunogenes, these genes have to be highly polymorphic and each gene version, i.e. each allele, needs to provide resistance only to one or very few infectious diseases. The genes of the major histocompatibility complex (MHC, called human leucocyte antigen (HLA) in humans) of the adaptive immune system are the most polymorphic genes in vertebrates with more than 1000 alleles for a single locus, e.g. in humans (Janeway et al., 2005). The MHC is highly conserved in jawed vertebrates from the sharks onward. All functional