

THE ADVANTAGES OF BEING RED: SEXUAL SELECTION IN THE STICKLEBACK

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Male three-spined stickleback develop a conspicuous red breeding coloration. The intensity of red correlates positively with physical condition and decreases by parasitization. In some populations, the male's red coloration functions in male-male competition through intimidation of rival males either directly or via associated characters. A comparison of the function of red in male-male competition among populations and among stickleback species suggests that the signalling of red coloration in dominance contests is a derived function. The primary function probably is to determine female choice. Recent experimental manipulation of red coloration showed that ripe female sticklebacks base their mate choice on the intensity of the male's red coloration. In sequential choice situations, choice is based on the attractiveness of the present and previously encountered males.

HANDICAPS

In most animal species it is the male sex which possesses conspicuous secondary sexual characters. A typical example is the conspicuous nuptial coloration of the three-spined stickleback (*Gasterosteus aculeatus* L.) with the orange/red throat and forebelly and the blue eyes. The female stickleback looks inconspicuous and is, in contrast to the male, adapted to a life as a potential prey of various predators. The pronounced secondary sexual characters of the male must be a true handicap under the risk of predation, which has been experimentally proven (Moodie, 1972). What are then the advantages of such a conspicuous nuptial coloration that the stickleback has developed and maintained against the pressure of natural selection?

SEXUAL SELECTION

Since Darwin (1871) the answer to this is unequivocal: sexual selection. In species in which the males have a higher potential reproductive rate than the females, we can expect strong competition to occur among males for breeding sites and access to females, and females to be selective in their choice of mates (Clutton-Brock and Vincent, 1991). Darwin distinguished these two selection processes for explaining the occurrence of exaggerated secondary sexual traits in males: the sexual ornaments either enhance the male's competitive ability for gaining access to

females (intra-sexual selection) or make him more attractive to females (inter-sexual selection). Both selection regimes give more ornamented males a reproductive advantage relative to males with less elaborate traits. There exist examples of male ornaments that have been evolved via either intra- (e.g. horns in fungus beetles, Conner, 1989) or inter-sexual selection (e.g. the peacock's train, Petrie *et al.*, 1991). However, in most cases one cannot exclusively ascribe the conspicuous sexual ornaments of males to one of the two kinds of sexual selection. As a rule intra- and inter-sexual selection act both on the males' sexual ornaments and it is often difficult to separate their respective contributions (Harvey and Bradbury, 1991).

STICKLEBACK REPRODUCTION

The three-spined stickleback is a small fish of the northern hemisphere which reproduces in fresh or brackish water and shows a conspicuous sexual dimorphism in the coloration during the breeding season. In the beginning of the reproductive season the male settles a territory in which he builds a nest. In the nest he tries to collect clutches of several females, thereafter the male cares for eggs and young for about ten days (Wootton, 1976). Three-spined sticklebacks are highly polygynous; a male stickleback may collect as many as 20 clutches of eggs from different females in a single breeding cycle (Kynard, 1978). In addition, he may complete several breeding cycles during a single season (Wootton, 1976).

INTRA-SEXUAL SELECTION: DUMMIES

Darwin's hypothesis of intra-sexual selection did not encounter much opposition of his contemporaries. Research on intra-sexual selection in the stickleback can be traced back to the classical investigations of the late Niko Tinbergen on sign stimuli in the forties (ter Pelkwijk and Tinbergen, 1937; Tinbergen, 1948, 1951). Experiments with dummies of male sticklebacks, which were presented inside the territory of a male, showed the aggression-releasing effect of a red throat. Crude dummies with a red throat elicited more attacks of the territory owner than more realistic but nonred dummies did. The results were that clear-cut, that a quantitative analysis was considered superfluous. Nevertheless, in 1949 such an analysis was made by Collias while being a guest in Tinbergen's laboratory in Leiden, and the results were only recently published (Baerends, 1985; Collias, 1990). His data affirmed the statements of Tinbergen. Yet this was not that self-evident, because several other researchers failed to find evidence for the aggression-releasing effect of a red throat (reviewed in Rowland and Sevenster, 1985). Rowland for instance found in 1982, that when he simultaneously presented a dummy with and one without a red throat and belly, the grey dummy was significantly more often the target of aggression of the territory owner.

How to explain this discrepancy? Tinbergen and co-workers made their dummies out of wax and the belly was painted red by applying shellac mixed with a red powder (P. Sevenster, pers. comm.). A direct comparison of the remainder of probably the only dummy left from that time (present at the zoological laboratory in Leiden) and a Rowland dummy revealed a striking difference between the red colour of Rowland's plastic dummies and Tinbergen's red shellac. Rowland's red colour

appears stronger, mainly due to a difference in contrast with the body colour, in hue (Rowland's red is less orange than Tinbergen's colour) and to some extent in colour intensity. Although the colours on the remainder of the Tinbergen dummy may have faded somewhat, in any case they have originally contrasted less strongly with the body colour than in Rowland's dummies (P. Sevenster, pers. comm.; G.P. Baerends, pers. comm.). The strong red of the Rowland dummy may rather have an intimidating effect on the territory owner than an aggression-releasing effect and his results can be explained from this perspective (Rowland, 1982, in press).

INTRA-SEXUAL SELECTION: DOMINANCE

It is obvious that an aggression-releasing effect of a red throat cannot account for the evolution of the red throat and must be a side-effect; it may be rather disadvantageous to its bearer to provoke aggression of rivals. Yet male-male competition may have played a role in the evolution of the male's red breeding coloration, namely through its intimidating effect on rivals. An advantage of a red throat in intra-sexual selection is indicated by its association with the probability to win in male-male competition when new territories are being settled (Bakker and Sevenster, 1983; Bakker, 1986, in press). In the laboratory we can simulate such a situation by introducing two reproductive, isolated males into a tank which is unfamiliar to both and just large enough for the settlement of one territory. After a short and intense fight one of the males will usually dominate the other. The dominant male will start nest building, while the inferior male will remain quiet at the water surface or hidden between plants and will be attacked by the dominant male upon movement.

When dominance tests are carried out with inexperienced males that are introduced simultaneously, experiential and prior residence effects on the outcome of the dyadic combat are ruled out. Under these conditions, dominance ability was positively correlated with the degree of red breeding coloration (Bakker and Sevenster, 1983) suggesting that red, or a trait that correlates with red, intimidates the opponent. The red coloration was quantified on a four-point scale increasing from hardly any red to much red. An intimidating effect of red breeding coloration is only conceivable if this signal is uncheatable and somehow related to fighting ability. The positive correlation between the intensity of red and a male's physical condition make these likely (Milinski and Bakker, 1990; Figure 1).

A behaviour-genetic analysis of variation in dominance ability based on two-way selection experiments showed that this variation could partly be attributed to genotypic variation (Bakker, 1985, 1986, in press). Within each generation of the high and low dominance lines all possible pairwise combinations of males were tested. The criterion of selection was based on the number of tests that each male had won. In each generation, the response to two-way selection for dominance, i.e. for low and high dominance, was determined from the outcome of dominance tests between males of the high and low lines. Selection for low and high dominance ability produced significant divergence between the two lines by the third generation. Dominance tests between males of either selection line and males of an unselected control line in the second generation, suggested that the divergence between the high and low lines was due to a decrease in the dominance ability of low line males rather

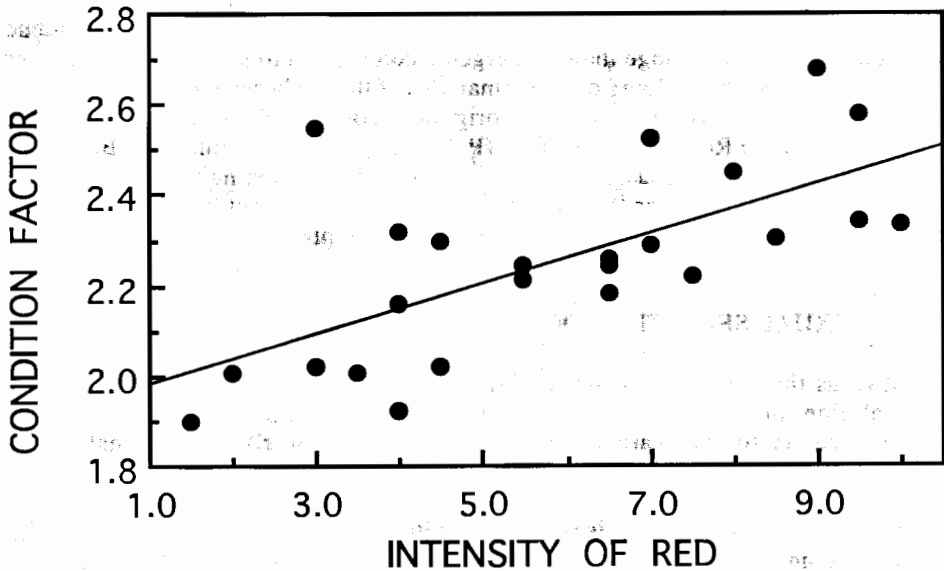


Figure 1 The correlation between the intensity of red breeding coloration and the condition factor. $r^2 = 0.44$, $F = 17.27$, $df = 1,22$, $P < 0.0004$ (after Milinski and Bakker, 1990).

than an increase in that of the high line males. This asymmetry in the response to two-way selection suggests that in nature high dominance abilities had been favoured.

As a rule, artificial selection does not only change the trait chosen as the criterion of selection. An array of other traits that are genetically correlated with the selected trait will also be affected by the applied selection regime. An analysis of these correlated responses of selection for dominance ability revealed an interesting change in the degree of red coloration. The degree of red coloration of males of the low dominance line was on average less than that of high line males or control line males (Bakker, 1986; Figure 2). The latter two did not differ significantly as to their red coloration. Notice also the difference in the degree of red coloration of all males, irrespective of their origin, after presentation of a rival male (Figure 2A) and after presentation of a ripe female (Figure 2B); both stimuli were confined in a glass tube and offered inside the territory. Females made males flush most strongly. We will come back to this point later on.

Three-spined sticklebacks exhibit two contrasting life-history patterns. Anadromous populations overwinter in estuarine or coastal marine habitats and migrate to fresh or brackish water in the spring to reproduce, while freshwater populations reside permanently in rivers, streams, or lakes. The only population that has been studied in which coloration played a prominent role in determining dominance relationships was a freshwater population (Bakker and Sevenster, 1983; Bakker, 1986). Studies in which the degree of red coloration was not correlated with dominance happened all to have used males from anadromous populations (FitzGerald and Kedney, 1987; Rowland, 1989).

To investigate whether this discrepancy could really be ascribed to a different function of red in freshwater and anadromous populations, we compared dominance

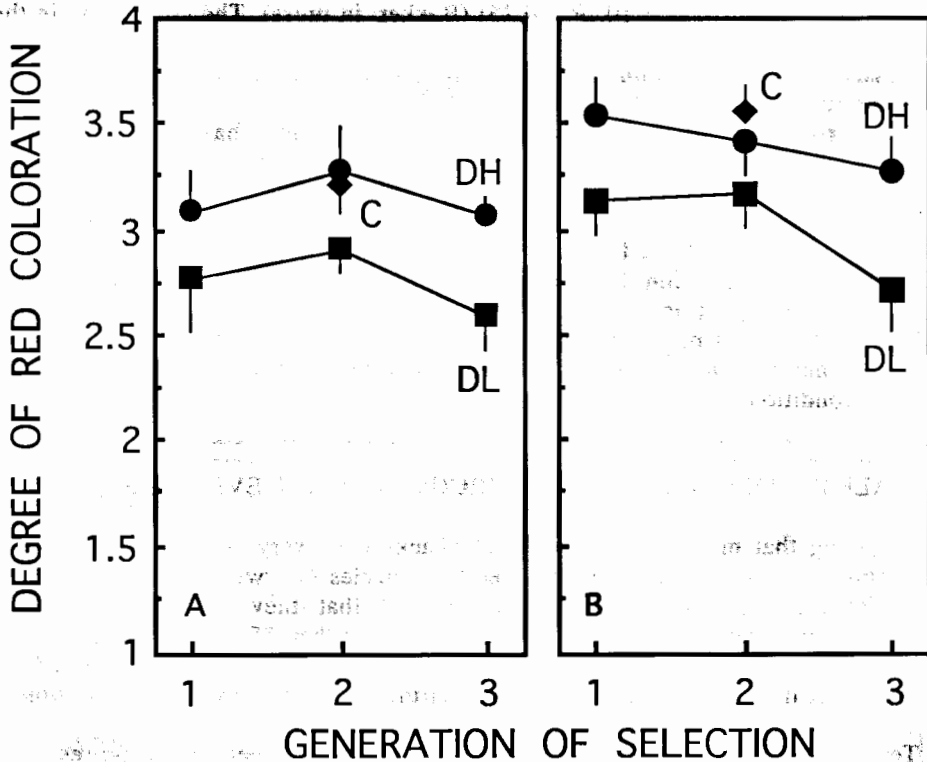


Figure 2 The average (\pm SE) degree of red breeding coloration of males in three successive generations selected for low (DL line, squares) and high (DH line, circles) levels of dominance ability, and in the second generation of the control (C, diamonds) line; (A) after presentation of a male in a tube, and (B) after presentation of a ripe female in a tube (after Bakker, 1986).

abilities between laboratory-bred males from wild-caught parents of a Dutch anadromous and a Dutch freshwater population. Laboratory-reared anadromous males tended to be slightly, but significantly brighter than laboratory-reared freshwater males, suggesting a genetic basis to the difference (Bakker, in press). Based on our earlier established positive correlation between the degree of red and dominance in the freshwater population, we expected greater dominance of the anadromous males. In dominance tests between males of the two populations, their dominance ability was, however, less than that of their freshwater counterparts. Isolated males from the freshwater population displayed greater dominance ability under various circumstances (Bakker, in press).

Within each population dominance ability was measured by making all pairwise comparisons of relative dominance among a group of individually isolated males. The males can then be arranged in a linear order of dominance based on the probability of winning the dominance contests. There existed a significant positive correlation between the degree of red coloration and dominance ability in the freshwater population ($r_s = 0.72$, $N = 10$, $P < 0.02$) but not in the anadromous

population ($r_s = 0.20$, $N = 10$, $P > 0.25$) (Bakker, in press). The correlation in the freshwater population was not attributable to particular males. Body size and aggressiveness were both uncorrelated with dominance ability in these populations (Bakker, in press).

Comparisons of anadromous and freshwater populations have the potential to provide insight into the directions of evolutionary change, because freshwater populations are thought to have been derived from the marine form (Bell and Foster, in press). In addition, phylogenetic studies suggest that the evolution of colour patterns in the stickleback family, the Gasterosteidae, is more strongly correlated with inter-sexual selection than with intra-sexual selection (McLennan *et al.*, 1988; McLennan, 1991). It is thus possible that in anadromous populations, nuptial coloration functions primarily to determine patterns of mate choice (inter-sexual selection) and that the signal function of this coloration in dominance contests is a derived condition.

FEMALE PREFERENCE FOR RED: CIRCUMSTANTIAL EVIDENCE

Considering that male three-spined sticklebacks have very conspicuous breeding colorations among European freshwater fish species (Darwin himself mentioned the stickleback as an example) and the fact that they have been used as experimental animals in ethological studies for more than 55 years, makes it rather surprising that, apart from circumstantial evidence which has been disregarded for a long time, it was only recently proven that the male's red breeding coloration is of crucial importance in female choice.

Ter Pelkwijk and Tinbergen (1937) noticed already that there was little response of ripe females to male dummies that lacked a red throat and belly. The importance of a red throat in inter-sexual selection is also suggested by the fact that males flush their red colours more strongly when given a sight of a ripe female than when given a sight of a rival male, as was indicated before in the results of the dominance selection lines (Figure 2). In an early experiment on sexual selection, Semler (1971) showed that females from a population polymorphic for male breeding coloration preferred red males over non-red males. Female preference for artificially coloured (with nail-polish or lipstick) non-red males over non-manipulated controls indicated that the females were responding to the red coloration alone. However, Semler's experimental design did not exclude effects either of red on male-male competition or of the paint itself. We applied Semler's recipe for a different purpose, but the paint came off during the experiments and the fish seemed to be adversely affected (Bakker and Sevenster, 1983). An interesting example of the various circumstantial evidence for the functioning of the male's red breeding coloration in female mating choice was given by Cronly-Dillon and Sharma (1968). Outside the reproductive season males and females have a similar visual sensitivity for red (Figure 3A). However, during the reproductive season the females' visual sensitivity for red increases and reaches a higher level than that of males (Figure 3B). These diverse, but consistent indications point to the role of inter-sexual selection in the evolution of the red coloration of male sticklebacks. This role is probably even greater than that of intra-sexual selection.

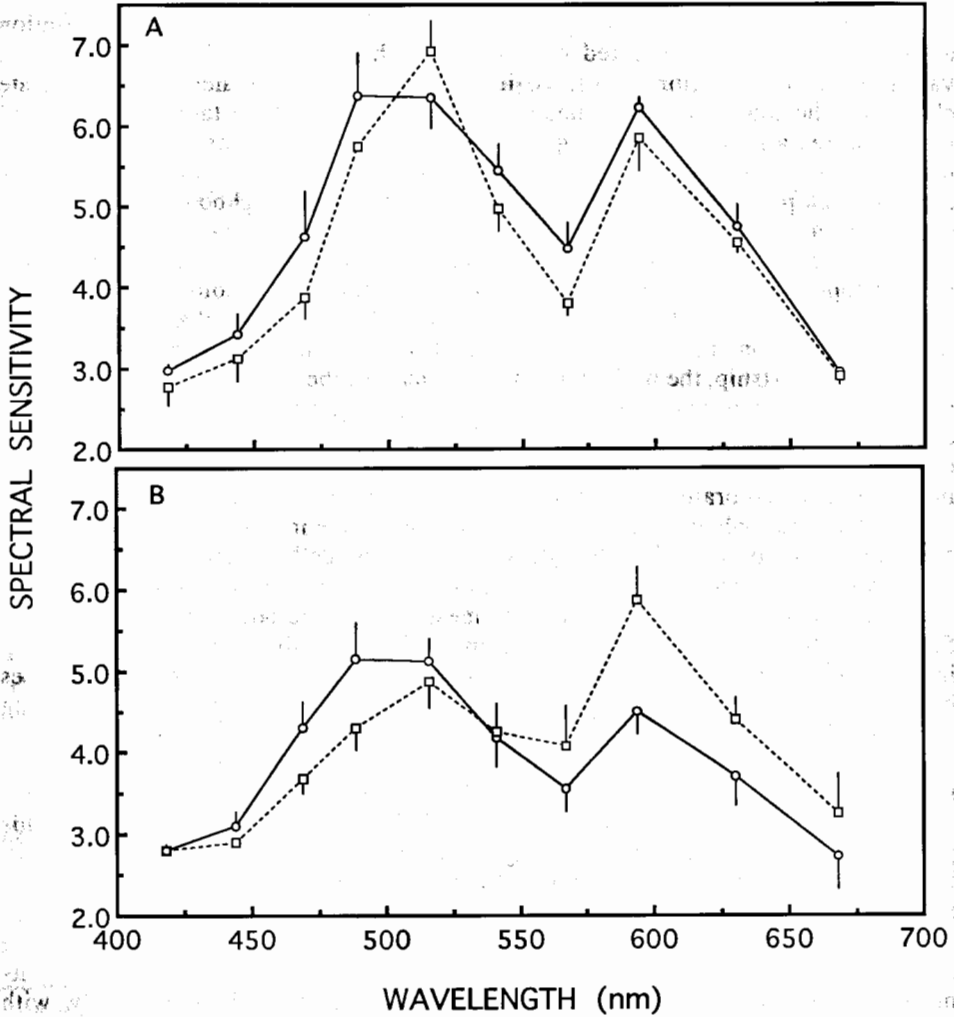


Figure 3 Spectral sensitivity (optomotor response + or - SD) of female (squares, dotted line) and male (circles) sticklebacks outside (A) and during (B) the breeding season (after Cronly-Dillon and Sharma, 1968).

FEMALE PREFERENCE FOR RED: GREEN LIGHT EXPERIMENTS

Recent experiments gave conclusive evidence that female sticklebacks base their mate choice almost exclusively on the intensity of the male's red breeding coloration (Milinski and Bakker, 1990). Unlike correlative studies on female preference for exaggerated male traits (which form the great majority of studies on sexual selection; exceptions e.g. Andersson, 1982; Møller, 1988; Hill, 1991), we ruled out the influence of confounding variables by experimental manipulation of the preferred male trait.

We did our experiments with wild-caught fish. The males showed great variation as to the intensity of their red coloration which was positively correlated with variation in the condition factor. To investigate whether females base their mate choice on the intensity of the males' breeding coloration the tanks of individual males were arranged according to increasing intensity of coloration, and neighbouring males were defined as pairs for presentation to ripe females. In a separate tank positioned centrally in front of each pair of neighbouring tanks a cell containing a single gravid female was placed and her choosing between the two males was registered. Females were previously selected for their readiness to spawn, i.e. to adopt and maintain the head-up courtship posture while pointing towards one of the two males. In order to be able to exclude the possibility that female choice would be based on some character correlated with the intensity of red, such as the intensity of courtship, the well-known zigzag dance of the stickleback, we carried out the choice experiments under two different lighting conditions. Under the first condition, choice experiments were carried out in normal white light. The other condition was such that females were almost unable to judge differences in the intensity of red coloration. This was achieved by green illumination.

In order to test whether the courtship behaviour of the males differs between light conditions, we confronted each male singly with the cell containing a ripe female under both green and white light. The number of zigzags of the male's courtship display, which is regarded as a reliable measure of male courtship intensity (e.g. Sevenster, 1961), was counted during a standard period of time. The males' courtship intensity did not differ significantly in the two light situations and differences between pair members did not change significantly either between the lighting conditions.

Although the experiment was designed so that the males of each pair were very similar in the intensity of red coloration (see above), under white light there was a significant preference by the females for the brighter male in each pair, this preference being intensified as the difference in coloration increased (Figure 4A). Under green light the trend in favour of the brighter males was not significant any more (Figure 4B). The slope of the regression under white light was significantly greater than that under green light. This inevitably leads to the conclusion that the females based their choice primarily on differences in male red coloration. This makes functional sense because colour intensity correlated significantly with condition (for definition see Milinski and Bakker, 1990) whereas courtship intensity did not correlate significantly with condition. The conclusion that female choice was based mainly on colour cues was affirmed by partial correlations under white light.

FEMALE CHOICE AND PARASITES

Among the good-genes models of the evolution of exaggerated characters by female choice, the Hamilton and Zuk host-parasite model from 1982 attracted considerable attention, because it offers a plausible explanation for a sustained heritability of fitness. Hamilton and Zuk interpret many of the male's exaggerated sexual ornaments as signals indicating parasite resistance. According to their model, these signals are "revealing handicaps", that is, they give females a chance to detect whether a potential mate is parasitized (for instance because he is less brightly coloured) or not.

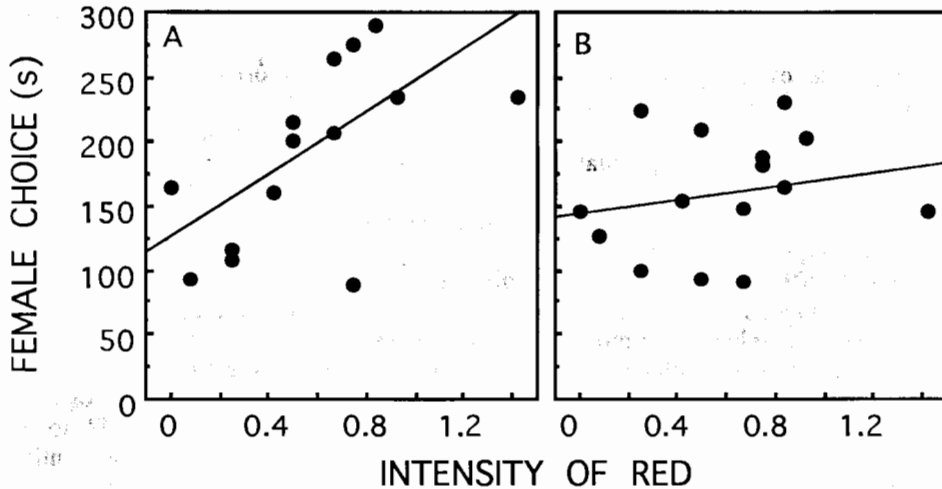


Figure 4 Average active female choice for the brighter male as a function of the difference in the intensity of red coloration of pairs of reproductive males under white (A) and green (B) light (after Milinski and Bakker, 1990).

The intensity of red breeding coloration in sticklebacks is a revealing handicap, because it correlates positively with a male's physical condition. It is also a revealing handicap in the sense of Hamilton and Zuk (1982) as suggested by the following experiment. In order to investigate whether parasites influence both the males' red breeding coloration and the result of active female choice, we infested the brighter male of each pair from the previous mentioned experiment with the ciliate *Ichthyophthirius multifiliis*, a serious and widespread fish disease known as 'white-spot'. Our fish were only mildly infected and recovered within a week. To prevent reinfection, the tanks of all fish (including control fish) were treated with an anti-white spot solution. The fish continued to court stimulus females. Four of the six students who had scored the males' red coloration before parasitization were asked to repeat their estimation of pair differences. They were not informed about the prior parasitization of half of the males. Again we submitted the remaining pairs of males to female choice experiments with new ripe females under white and green light.

Parasitization caused a significant decrease of the intensity of the males' red coloration. Parasitization also caused a significant decrease of the difference in condition factor and this was probably the cause of the reduction in colour intensity. The females significantly decreased their prior preference for the formerly brighter males under white light, but under green light the males' parasitization had no significant effect on female choice. This implies that the females detected the prior parasitization of the males by their decreased intensity of red breeding coloration, which is a necessary condition for coloration to be judged as a revealing handicap.

MECHANISM OF SEQUENTIAL FEMALE CHOICE

The empirical evidence for the evolution of male sexual ornaments by female choice is bound to simultaneous choice situations in which a direct comparison facilitates the preference for the more ornamented male. In nature, simultaneous choice is restricted either to situations in which males are displaying in a common area, a lek, or to cases in which females use acoustical male ornaments for choosing among spread out males. In most of the remaining cases the female must visit males sequentially and compare the present male with what she has stored in her memory of those met previously. This appears to be a more difficult task than that of simultaneous choice. It is, however, a prerequisite for the application of models of sexual selection to most territorial species.

Male three-spined sticklebacks claim a territory of up to several m^2 at the start of the breeding season. The distance between the males and also vegetation often forces a female to compare potential mates sequentially under natural conditions if she is able to do so. Therefore the three-spined stickleback seems to be an ideal species to study sequential female choice.

Male three-spined sticklebacks with varying degrees of breeding coloration were caught from a Swiss freshwater population and placed individually into tanks. After several weeks most males had a complete nest built in a Petri dish provided close to the backwall and courted vigorously. Out of nine males which could easily be categorized as either dull, medium or bright according to the intensity of their red breeding coloration, we used five different combinations of three males, one of each colour type, for sequential presentation to ripe females. Females caught from the same population were used in experiments when they were ready to spawn as judged from their colour and the extension of their bellies and from the opening of their cloacae.

A cell containing a single gravid female was placed in front of a male's tank and the duration of her head-up display, which correlates positively with her probability to spawn with that male (McLennan and McPhail, 1990), was measured during a standard period of time. Half of 28 females were presented to the males in the order: dull, medium, dull, pause of 30 min, bright, medium, bright. The other half saw the males in the reverse order (Figure 5). Each female was used only once.

Each female saw each male twice and the position of each type of male in the order of presentation was the same averaged over all females. Therefore we can compare the duration of head-up display each type of male received per presentation to a female with that of the other two. The duration of the females' head-up posture increased with the intensity of the males' brightness (Bakker and Milinski, 1991; Figure 6). This result demonstrates the females' ability to prefer the brighter male also when they see only one male at a time. Thus female sticklebacks are able to exert sequential mate choice. The result does not prove, however, that the females have actually compared the different males with each other, but can be the consequence of comparing each male with an internal order of standards. Since the probability to spawn with a given male depends on the female's duration of head-up posture (McLennan and McPhail, 1990) she would not need to have an additional rule for continuing to sample further males.

The probability to spawn with a given male may not only depend on its rank in the female's internal standards but could also be influenced by the brightness of the previous male. The female may rate a male higher when the previous male was duller

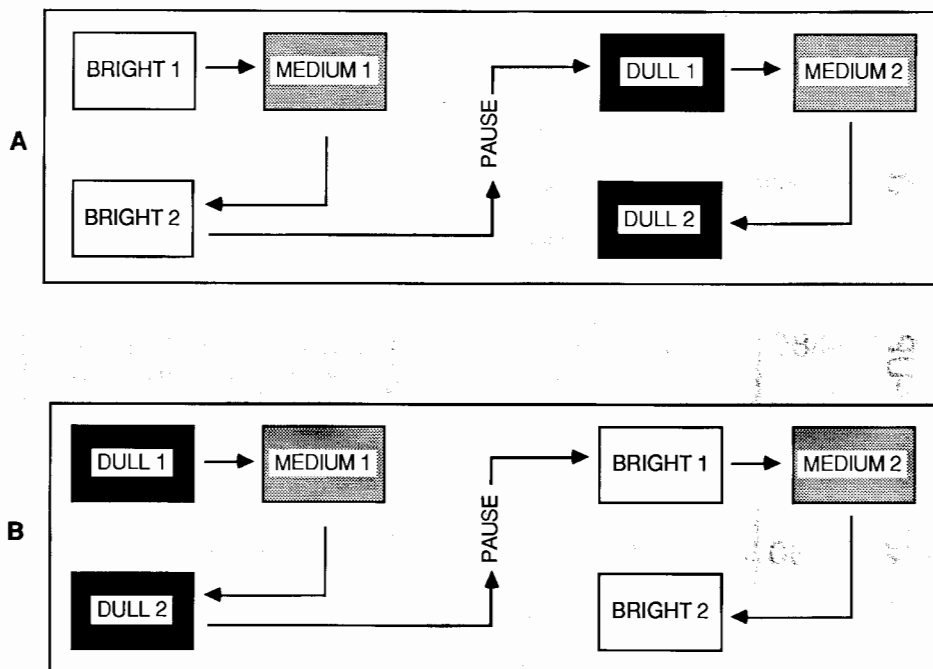


Figure 5 Order of presentation of males of 3 different colour types, i.e. dull, medium, bright, to (A) females starting with a bright male, (B) females starting with a dull male.

and vice versa. Hence we would expect that the duration of the head-up posture is longer during the second presentation than during the first one with a given colour type when the male met before the second presentation is duller. Vice versa we would expect that this duration is shorter when the male in between is brighter. In our experimental design this means that for females starting with a dull male we expect for the duration of the head-up posture the following inequalities: dull 1 > dull 2, medium 1 > medium 2, bright 2 > bright 1. Similarly, for females starting with a bright male we expect: bright 2 > bright 1, medium 2 > medium 1, dull 1 > dull 2. Each of the observed six inequalities (three for females starting with a dull male, and three for females starting with a bright male) was tested with a 1-tailed Wilcoxon matched-pairs signed-ranks test with $N = 14$ and the six probabilities were combined with a Fisher combination test; the probability of that inequality which was in variance with our hypothesis was entered as $1-P$. A potential habituation effect by which the second presentation of each color type is expected to score lower than the first one is compensated for by this procedure, i.e. three of the predicted inequalities would be in the same direction and the other three would be in opposite direction of a potential habituation effect. The combined probability supports our hypothesis of a previous male effect at the 1% level of significance (Bakker and Milinski, 1991).

Our finding of the females' ability for exerting sequential mate choice and of the 'previous male effect' concerns the mechanism of female mate choice, the existence of which is a necessary prerequisite of most models of sexual selection. It broadens

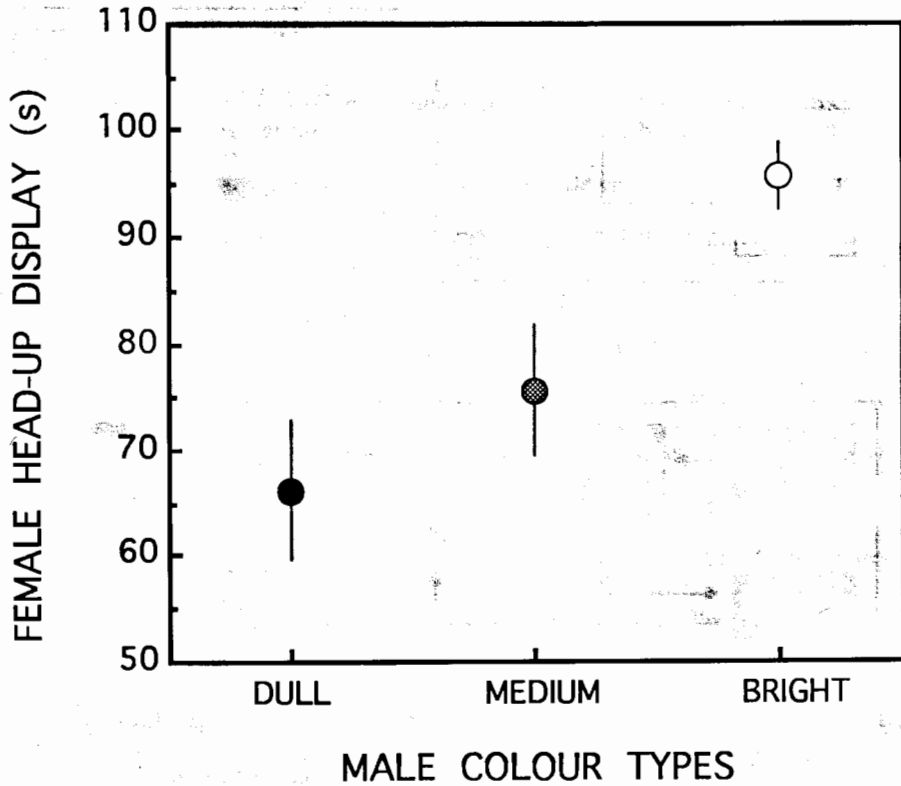


Figure 6 Average (\pm SE) duration of the female head-up display directed at dull, medium, or bright males. $P < 0.0001$ after Page test for ordered alternatives (after Bakker and Milinski, 1991).

the application of these models to species in which females can choose a potential mate only by visiting a number of males sequentially.

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