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Male–male competition facilitates female choice in sticklebacks

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In many species, secondary sexual characteristics are used in both male–male competition and in attracting females. This suggests that social control of deception could contribute to the maintenance of honest sexual signalling. In the three-spined stickleback *Gasterosteus aculeatus*, male red breeding coloration plays a dual role in sexual selection by functioning as both a threat signal in male–male competition and as a cue for female choice. To investigate whether male competition determines the level of signalling, the expression of red coloration and courtship activity were recorded both before and after male interactions. The results show that male competition influences signal expression by increasing the difference between males in signalling level. This in turn facilitates female choice and induces a preference for dominant males. Since a preference for dominant males may benefit females both directly and indirectly in this species with exclusively paternal care, male–male competition seems to increase the honesty of signalling and, thus, facilitates female choice in relation to male quality. This may increase the intensity of sexual selection and promote the evolution of breeding aggregations.

Keywords: male–male competition; sexual signalling; female choice; nuptial coloration; three-spined stickleback

1. INTRODUCTION

Sexual selection has traditionally been partitioned into competition for mates and mate choice, often referred to as intra- and intersexual selection (Darwin 1859, 1871; Andersson 1994). These two mechanisms usually occur together in species with one sex competing to be chosen by the other sex. Often males are the more competing sex and females the choosier one, owing to higher potential reproductive rates of males and, thus, male-biased operational sex ratios (the ratio of males to females ready to mate; Emlen & Oring 1977) (Clutton-Brock & Parker 1992; Kvarnemo & Ahnesjö 1996).

Most studies investigating sexual selection have focused on only one or other of the mechanisms (reviewed by Andersson 1994), whereas their relative contributions to sexual selection have rarely been addressed (but see Kodric-Brown 1996; Forsgren 1997). The importance of investigating their relative contributions is, however, emphasized by the finding that, in many species, the same secondary sexual characteristics are used both in male–male competition and as cues for female choice (reviewed by Berglund *et al.* 1996). If the traits are flexible, male–male competition may then change the expression of traits that females use as criteria for mate choice. For example, in several species of poeciliid fish, females base their mate choice on the males' dark vertical bars which intensify during male–male interactions (Franck 1964; Zimmerer & Kallman 1988; Morris *et al.* 1995). Similarly, male barn swallows, *Hirundo rustica*, adjust their song quality to the presence of other males (Galeotti *et al.* 1997).

Whether changes in trait expression due to male–male competition affect female choice has not been studied. If signalling is costly under male–male competition in terms of fights and the costs decrease with the quality of the male, male–male competition could increase the honesty of signalling and, thus, facilitate female choice. This may often be the case as dominant males probably pay lower costs of signalling than subdominant males and dominance often correlates with direct benefits, such as nest defence (Bisazza *et al.* 1989) and male genetic quality (Montgomerie & Thornhill 1989; Alatalo *et al.* 1991). On the other hand, if dominance does not correlate with male quality (see Forsgren 1997), male–male competition could instead decrease the honesty of signalling and hamper adaptive female choice.

In the three-spined stickleback *Gasterosteus aculeatus*, females base their mate choice mainly on the intensity of the males' red breeding coloration (reviewed by Rowland 1994). Red coloration is a flexible trait that also acts as a threat signal in male–male interactions by intimidating or provoking males, depending on the context in which they are given (Bakker & Sevenster 1983; Rowland 1984; Rowland & Sevenster 1985; Bakker & Milinski 1993; Bakker 1994; Rowland *et al.* 1995; Baube 1997). Signal expression during interactions could thus reflect social dominance and the resource-holding power of a male. Such characteristics probably correlate with male quality in terms of parental ability or male viability and genetic quality, as the stickleback male cares for the offspring alone for up to two weeks by oxygenating and defending them against conspecific and heterospecific egg predators.

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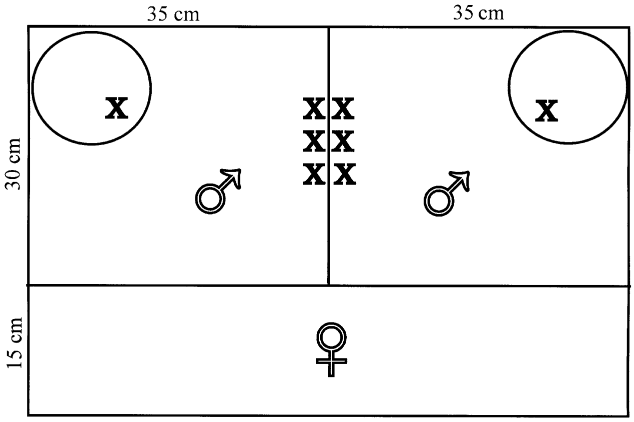

Figure 1. Experimental aquarium. The crosses indicate the positions of the artificial plants in the nesting dishes and at the border between the male territories after the white sheet had been removed.

Females could thus benefit both directly and indirectly by basing their mate choice on traits determined through male–male competition. This paper investigates whether male–male competition affects signal quality, i.e. red coloration and courtship activity, and, thus, facilitates female choice.

2. METHODS

Three-spined sticklebacks were collected from the littoral of the Baltic Sea in south-western Finland by fry traps before the start of the breeding season (early May) in 1997. Sexes were housed in separate holding aquaria at 15 °C under a 18 L:6 D cycle for one week at a density of ten fish per 125-litre aquarium. They were fed twice daily in excess with dried Tubifex worms and frozen chironomid larvae. Breeding behaviour was discouraged by the lack of suitable nesting materials.

To determine the effect of male–male competition on signal expression and female choice, four sequential experiments were conducted determining (i) trait expression in the absence of male competition, (ii) female choice in the absence of male competition, (iii) trait expression in the presence of male competition, and (iv) female choice in the presence of male competition.

The experimental aquarium (70 cm × 45 cm × 30 cm, L × W × H) was divided into two male sections, with a female section in front of them (figure 1). A white sheet separated the two male sections and prevented visual contact between the males. Olfactory contact was minimized by securing that the partitioning sheet was tightly fitted to the aquarium so that there was no water flow between the two sections. In both male compartments there was a nesting dish filled with 1 cm of sand, an artificial plant and tufts of *Cladophora* as nesting material. White curtains with small viewing holes reduced external disturbances.

Two size-matched males (±0.5 mm) with hints of nuptial coloration were placed in the experimental aquarium, one male into each male section. If both males did not build a nest within two days, they were replaced with a new male pair to ensure that both males were in the same breeding condition. The day after both males had completed a nest and developed red ventral coloration, a dummy female (54 mm standard length, SL) in a head-up posture (indicates readiness to spawn) was placed in the centre of the female section so that both males could see it. By using a dummy female it was possible to eliminate any confounding effects of female behaviour on signal intensity. During a 5-min-long female exposure, the males' courtship activity was determined by counting the number of leads to the nest and the total time spent courting and orientated towards the female. The coloration of the males was measured immediately after the female exposure. Males were dip-netted and photographed under standardized conditions (corresponding to the method used by Frischknecht (1993)). They were individually placed in a small glass box (6 cm × 3 cm × 6 cm) containing water and a black sponge that fixed them in place and served as a non-reflective background. The glass box was then placed in a fixed position in a large dark box containing a digital camera (Kodak DC 50). The left lateral side of the males was photographed. The only light source was a lateral flash. To make sure that the conditions were constant, there were three plastic strings of red, blue and green colours on the front side of the box that served as colour references in the analyses. The photographing procedure took less than 1 min and the males did not have time to fade. The extent and quality of the red coloration were later determined from the digital images using image analysis software (MCID-M4, Imaging Research Inc.). Areas that ranged in colour from yellow through red to purple were selected (hue 1–50 and 340–359, saturation 0–0.631 and intensity 0.157–0.663) and their size and mean colour quality were recorded. Both absolute and relative sizes (percentage of total lateral area) of the red areas were used in the analyses, but, since the results were the same, only relative sizes are presented.

Two hours after photographing, when the males had resumed normal activities, their attractiveness to females was determined. A glass box (15 cm × 8 cm) containing a gravid female ready to spawn was placed in the centre of the female section. The female could thus see both males, but the males could not see each other. The female presentation lasted for 5 min, after 1 min of acclimatization and the time that the female spent in a head-up posture towards each male was recorded. The procedure was repeated for two additional females (50–57 mm SL), separated by 30 min. The total time that the three females spent with each male was summed and divided by three to obtain the mean time that the females spent with each male. Females were considered to have a preference for one of the males when the mean time that they spent in contact with each male differed by at least 10%. Mating preference determined by a 10% difference has been found to reflect mate choice for several species, including sticklebacks, when actual mating is allowed (reviewed in Godin & Briggs 1996).

To investigate whether male contest affects trait expression and female choice, the white sheet between the two males was removed and replaced with a row of artificial vegetation. The males could then freely interact but still had a boundary that divided the aquarium into two equal-sized territories. In the field, males may nest as close as 20 cm (U. Candolin, personal observation) and the territory sizes corresponded to those under natural conditions. In all cases, both males continued to care for and defend their nests. The males were left for one day to become habituated to each other, after which the procedures from the foregoing day for the interacting males were repeated: the males' courtship activity with a dummy female was recorded, the males' nuptial coloration was photographed and, finally, female choice was determined by sequentially presenting three new gravid females to the males.

The values reported are means ± s.e. All data sets were tested for normality and homogeneity of variances. Nineteen pairs of males were tested, each with six new females.

Table 1. *Signal expression of the two males (A and B) when separated and when competing*

(Male A is the male with the larger red area when separated repeated measures ANOVA was used for analysis with male (M) as factor and competition (C) as repeated measure. When analysing the difference between the two males in time spent courting during competition, a paired t-test had to be used, as there was no difference in activity between the paired males when separated. $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$.)

variable	male	separated (mean ± s.e.)	competing (mean ± s.e.)	male ($F_{1,36}$)	competition ($F_{1,36}$)	$M \times C$ ($F_{1,36}$)
red area						
relative size (%)	A	11.60 ± 1.1	13.70 ± 1.4	9.94^{**}	0.52	17.15^{***}
	B	9.10 ± 1.2	6.00 ± 1.3			
hue	A	27.90 ± 1.06	31.48 ± 2.25	0.32	3.58	0.50
	B	28.03 ± 0.94	29.67 ± 1.08			
saturation	A	0.22 ± 0.00	0.22 ± 0.01	1.21	0.01	0.08
	B	0.22 ± 0.00	0.22 ± 0.00			
intensity	A	0.46 ± 0.01	0.43 ± 0.01	0.70	5.82^{*}	0.77
	B	0.46 ± 0.01	0.45 ± 0.01			
courtship						
leads (number per 5 min)	A	26.10 ± 2.18	22.65 ± 2.14	29.60^{***}	49.44^{***}	35.05^{***}
	B	23.95 ± 2.20	0.37 ± 0.16			
time courting (s)	A	300.00 ± 0.00	167.20 ± 15.0		paired $t_{18}=2.48^{*}$	
	B	300.00 ± 0.00	93.00 ± 20.5			

3. RESULTS

Before each pair of males was allowed to interact, there was a small difference between them in the size of their red areas (table 1). However, after allowing the males to interact, the difference increased (table 1): males with an initially larger red area increased their area, while males with an initially smaller red area decreased their area (table 1). For only two pairs did the relationship between the males shift so that the male with the initially larger red area had the smaller area during interaction. There was a positive correlation in the area of red before and after interaction (figure 2), both for males with the initially larger ($r^2=0.50$, $F_{1,17}=17.60$ and $p=0.001$) and smaller red areas ($r^2=0.60$, $F_{1,17}=25.13$ and $p<0.001$). Interaction thus amplified the differences between males but generally did not shift the relationship between males.

After interaction, the males were also brighter than prior to interaction (see table 1; a low value of intensity indicates brightly coloured fish as red colour pigments reduce the amount of light reflected compared to the otherwise silvery skin of sticklebacks). However, the mean hue, saturation and intensity of the red areas did not differ between the two males (table 1).

Before interaction, there was no difference in the courtship activity of the males, but both males courted for the full 5 min. During interaction, males decreased their courtship activity but to different degrees. The male with the larger red area reduced his courtship activity less than the male with the smaller red area and, thus, performed more leads and spent more time courting than the competitor (table 1). The reduction in courtship may result from both males spending time chasing and/or avoiding each other.

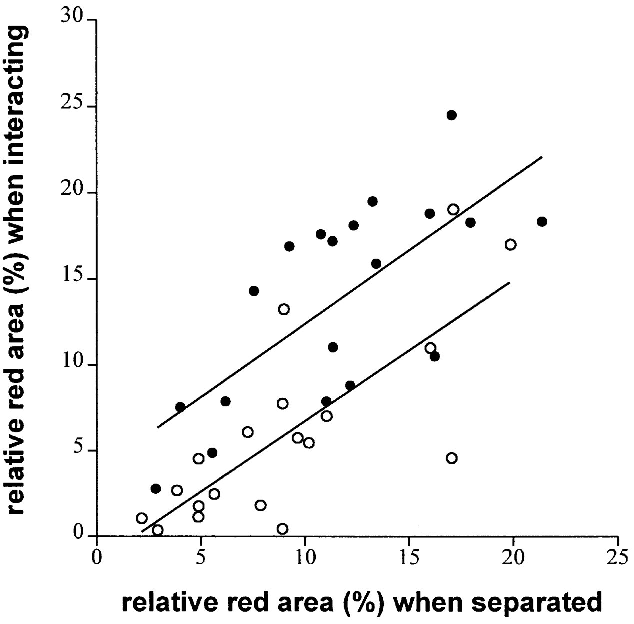

Figure 2. The relationship between relative red area of males when separated and interacting. Filled circles are the males with the initially larger red area ($y=3.87+0.85x$) and open circles are the males with the smaller area ($y=1.5+0.82x$).

Females changed their mate preference for seven out of the 19 male pairs (37%) when the males were interacting. In five of these cases (26% of all pairs), the females had preferred the male with the slightly smaller red area when the males were separated and, in two of these cases (11% of all pairs), the relationship between the males shifted. For the rest of the male pairs ($n=12$; 63%), females increased the time spent with the male that they had already preferred when the males were separated (time spent with the preferred male when the males were separated, 251.7 ± 13.3 s, and time spent with the preferred male when the males were interacting, 290.4 ± 3.9 s; paired $t_{11}=3.20$ and $p=0.008$). Under interaction, females always preferred the male with the larger red area. The initial difference in red area between the two males was smaller within pairs where females changed their mate preference ($28.8 \pm 5.7\%$, $n = 7$) than within pairs where females did not change their mate preference ($55.2 \pm 8.3\%$, $n = 12$; $t_{17} = 2.24$ and $p = 0.039$).

Female mate preference was associated with the size of the red areas of both separated (relative red area of preferred males, $11.7 \pm 1.3\%$, and relative red area of unpreferred males, $8.0 \pm 1.0\%$; paired $t_{18} = 3.21$ and $p = 0.005$) and interacting males (relative red area of preferred males, $13.7 \pm 1.4\%$, and relative red area of unpreferred males, $6.0 \pm 1.3\%$; paired $t_{18} = 4.95$ and $p < 0.001$) and with the courtship activity of competing males (frequency of leads of preferred males, $10.4 \pm 2.2\%$, and frequency of leads of unpreferred males, $3.4 \pm 1.3\%$; paired $t_{18} = 2.23$ and $p = 0.039$; time spent courting of preferred males, 167.0 ± 15.0 s, and time spent courting of unpreferred males, 93.0 ± 20.5 s; paired $t_{18} = 2.48$ and $p = 0.023$).

4. DISCUSSION

The difference between males in red area and courtship activity increased under male contest competition. This in turn facilitated female choice. It increased the preference for the male with larger trait expression when the difference between the males in trait expression had already been large prior to interaction, but led to changed female choice for 37% of the male pairs when the initial difference had been small and females may have been less able to discriminate between the males. The increased difference in trait expression was most likely directly due to male interaction. Female mate preference prior to interaction does not seem to explain the increased difference, as the preferred male reduced his trait expression for seven out of the 19 pairs when separated, which is not expected if prior encounters with responsive females had induced the difference.

Male–male competition seems to have facilitated female choice in relation to male quality. Red coloration and perhaps also courtship activity reflects male dominance under competition (Bakker & Sevenster 1983), and dominance probably correlates with overall male quality, i.e. with the ability to rear offspring to independence successfully and with general viability and genetic quality. This suggests that male–male competition is an important component for females, facilitating choice and assessment. Facilitated choice may decrease assessment errors and costs of careful mate choice, such as predation risk, lost time and energy and lost mating opportunities and, thus, increase the intensity of sexual selection. These benefits of male contest could have contributed to the evolution of a female preference for males that nest in aggregations, which in turn may have promoted the evolution of male breeding aggregations. The characteristic of stickleback males nesting in aggregations (Moodie 1972*a*,*b*; Kedney *et al.* 1987) has previously been explained, with benefits of combined efforts in the defence of nests against raiding shoals of females and non-territorial males (Whoriskey & FitzGerald 1994). However, it seems probable that the same promoting effect of facilitated female choice on the evolution of aggregations that has been proposed for lekking species (Höglund & Alatalo 1995) could also occur in other breeding systems.

The effect of male contest on trait expression was probably due to the socially imposed costs of signalling, i.e. risk of fights. When it comes to red coloration, a male may signal at a lower level than the maximum in the absence of competitors as long as this does not significantly reduce his probability of mating, particularly as red coloration may bear contest-independent costs (discussed later in more detail). However, when competitors are present, the male adjusts his red coloration to the dominance status of other males. A dominant male increases his red coloration to show both other males and bypassing females that he is the superior male, whereas a subdominant male that is less able to sustain a fight decreases his red coloration. Flexible signals that change rapidly in response to environmental conditions have previously been proposed to be less reliable signals of male quality than fixed morphological traits (Møller *et al.* 1998). Contest-dependent costs of signalling could, however, prevent males from cheating about their quality.

However, some contest-independent costs are needed to prevent cheaters from invading the system (Johnstone & Norris 1993). The finding that the colour expression of a male during interaction correlates with his colour expression prior to interaction suggests that contest-independent costs of red coloration or inherent properties of the male limit colour expression. Red coloration is due to carotenoids (Brush & Reisman 1965; Matsuno & Katsuyama 1976; Czeczuga 1980; Wedekind *et al.* 1998), which are essential for the immune system to function properly (e.g. Lozano 1994). Carotenoid intake and the parasite resistance of a male may thus determine how much carotenoids he can allocate to red breeding coloration without reducing his probability of survival and successful brood care (Milinski & Bakker 1990). Moreover, if males have to compete for carotenoid-rich food or the food is costly to obtain, red coloration may come to reflect dominance or the general viability of a male. The overall energy intake of a male or his ability to escape predators may also restrict colour expression, as red coloration may be costly both energetically (Frischknecht 1993) and in terms of an increased risk of predation (Moodie 1972*b*; Whoriskey & FitzGerald 1985). However, males may also acquire knowledge of their dominance status before the onset of the breeding season and adjust their red coloration accordingly. Red coloration cannot be immediately adjusted to the appearance of a competitor and any alterations in coloration might be costly. Males may thus be forced to maintain a signal level that largely reflects their dominance and fighting ability although no competitors are in sight.

Courtship activity, on the other hand, requires a socially imposed cost of signalling for honest signalling of dominance to prevail. Courtship is thus a less reliable indicator of dominance than courtship activity in the absence of competitors. However, under competition, courtship may strengthen the dominance signalling function of red coloration and contribute to the facilitation of female choice.

To conclude, this study shows that male–male competition can facilitate female choice by increasing the difference between males in signal expression. This highlights the importance of separating between male–male competition and female choice when trying to determine the mechanisms of sexual selection.

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