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MALE MATING PREFERENCE IN STICKLEBACKS: EFFECTS OF REPEATED TESTING AND OWN ATTRACTIVENESS

by

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(With 3 Figures)
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Summary

In sticklebacks, *Gasterosteus aculeatus*, males have conspicuous nuptial coloration, whereas females are cryptically coloured. Usually females are the choosy sex in mate choice, but under certain conditions males may be choosy too. Females signal their spawning readiness, among others, by displaying a head-up courtship posture while pointing at the preferred male. We tested the male's preference for this posture by offering males a simultaneous choice of two stylized dummies of ripe females, one in head-up posture and one horizontal. The males directed relatively more courtship to the head-up dummy, and tended to do the more so the more intense the blue iris of their own eyes (corrected for differences in male length). Because the blue eye colour is a criterion of female choice in this population, attractive males tended to be choosier. Upon repeated presentation of the dummies to the same males on subsequent days, the males' preference for the head-up dummy disappeared, but there was no change in total courtship activity. When confronted with a different, more realistic pair of dummies, the same males showed again a preference for the head-up posture suggesting that male preference can be influenced by experience.

Introduction

Usually females are the choosy sex in mating as witnessed by the numerous examples of female mate choice that have been collected during the past decade (ANDERSSON, 1994). Males are expected to be less choosy, but the evolution of male mate choice should be favoured if females vary in quality and if males are limited in the maximum number

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of females with which they can mate (SARGENT *et al.*, 1986). Male choosiness could thus pay when for instance his sperm supply is limited or sperm is costly (*e.g.* in the case of spermatophores), when the operational sex-ratio is female biased, when females pose a risk to the male (*e.g.* by transmitting parasites), his resources (*e.g.* by disturbing his nest), or his progeny (*e.g.* by cannibalism), or when females differ in fecundity or parental care ability. In several animal species females signal their receptivity (references in ROWLAND *et al.*, 1991; SIKKEL, 1993) indicating that males may be choosy.

Because male sticklebacks, *Gasterosteus aculeatus*, have a greater potential reproductive rate than females, females should be selective in choosing a mating partner (CLUTTON-BROCK & VINCENT, 1991; CLUTTON-BROCK & PARKER, 1993). Indeed, female sticklebacks prefer more intensely red coloured males (McLENNAN & McPHAIL, 1990; MILINSKI & BAKKER, 1990, 1992; BAKKER & MILINSKI, 1991; BAKKER, 1993; BAKKER & MUNDWILER, 1994; see also BAUBE *et al.*, this volume; and McDONALD *et al.*, this volume), males with blue irises over males with silver irises (ROWLAND, 1994), and larger males (ROWLAND, 1989). A male stickleback should accept every ripe female during the 3-4 days that he is collecting eggs provided that a) the availability of ripe females is limited, b) ripe females pose no danger to the nest or spawn, and c) the number of eggs does not reduce the survival of embryos disproportionately. Choosiness of male sticklebacks might further be promoted by the high paternal investment (care for eggs and young; see WOOTTON *et al.*, this volume). Limitations in sperm supply are not known in sticklebacks, but cannot be excluded because androgens inhibit spermatogenesis in this species (BORG & MAYER, this volume)

Although female sticklebacks usually exercise mate choice, there are situations in which males may also mate selectively. After fertilization of a clutch of eggs the male is unwilling to court additional ripe females for an hour or so (SEVENSTER-BOL, 1962), although this period may be much shorter (TCMB, pers. observ.). Thus, a male should be choosy when the frequency of ripe females entering his territory is greater than say one per hour. In the extreme case of a simultaneous choice of more than one ripe female, male choosiness should be expected. Male sticklebacks direct more courtship in such situation to the more fecund (larger or more distended) female indeed (ROWLAND, 1982, 1989; ROWLAND & SEVENSTER, 1985; SARGENT *et al.*, 1986). Sticklebacks are potential egg predators

(e.g. FITZGERALD, 1991). Eggs may be eaten by single males and females and by raider packs that consist of females and non-reproductive males. In addition, single males may steal eggs in order to bring them into their own nests, thereby increasing their chances in getting spawnings (MORI, this volume). In some stickleback populations egg cannibalism occurs so frequently that males have reduced or even given up courtship display (FOSTER, 1994, this volume). The risk of becoming a victim of egg predation and stealing seems to be especially high during courtship and right after spawning. Thus, a courting male with eggs should weigh the probability of spawning against the risk of predation.

Female sticklebacks provide a number of visual, and possibly olfactory cues that signal their receptivity. One obvious signal is the extended abdomen of ripe females; when given a simultaneous choice between two dummy females that differ in the degree of abdominal distention, males direct more courtship to the more distended one (ROWLAND, 1982, 1989; ROWLAND & SEVENSTER, 1985). Ripe females also develop a mottled or bar-like dark pigmentation pattern that intensifies when they are courted by a male (ROWLAND *et al.*, 1991; TCMB, pers. observ.). When given a simultaneous choice between two dummy females, one with and one without dark bars, males courted the barred dummy more intensively (ROWLAND *et al.*, 1991). Furthermore, ripe females assume a head-up courtship posture while pointing at the courting male, and persist in doing so even when attacked by the male. The duration of the head-up posture correlates positively with the probability of spawning (MCLENNAN & MCPHAIL, 1990). As part of the head-up posture the female may lift her tail, so that her ovulated eggs may become visible.

Male sticklebacks in a previous study, however, counter-intuitively preferred the horizontal over the head-up posture of simultaneously presented, all-silver dummies of ripe females (ROWLAND & SEVENSTER, 1985). The aim of the present study was to further investigate the signal function of the female's head-up posture in combination with the bar pattern.

Material and methods

Subjects.

Adult fish were sampled from marine populations (monomorphic for the completely plated morph, forma *trachura*) on Long Island and Rhode Island, New York, in April and May 1992. The fish were transported to the laboratory in Bloomington, Indiana, and maintained on a 16:8 light:dark cycle in brackish water (12 parts per thousand) at $16.5 \pm 1^\circ\text{C}$.

The males used in the experiments had been maintained individually in tanks of various sizes, and during the summer of 1992 were used in various diet experiments (till about one month prior to the experiments). One week prior to the experiments (end of August 1992), 14 reproductively active males were placed, one each, into aquaria (25 × 50 cm), containing 15 cm brackish water, a sand-filled nesting dish (12.5 × 12.5 × 1.5 cm) and an artificial *Vallisneria* plant placed against the back wall, and some live *Enteromorpha* sp. for nesting material. Each tank was maintained at $19 \pm 1^\circ\text{C}$ and a 25 Watt bulb that hung about 10 cm above the water surface illuminated two tanks. The tanks were separated from each other by opaque partitions. The males were fed once a day with frozen *Artemia salina*.

Pre-treatment.

In the week prior to the experiments, each male was daily stimulated with a ripe female at least twice for 15 min or more at each presentation. The females were confined to a clear plastic chamber suspended outside of the male's tank.

Two days prior to the experiments the males' standard length and mass were measured. The breeding coloration of each male was quantified immediately after stimulation by a ripe female by taking 35 mm slides of his orange-red throat and blue-green eyes while he was enclosed in a glass-walled box (for details, see FRISCHKNECHT, 1993; BAKKER & MUNDWILER, 1994). The box contained brackish water and the male was fixed in position with a soft sponge. Slides were taken of the anterior half of the ventral region of the body and of one randomly chosen lateral side of the male. The slides were analysed with a densitometer (filters: red 700 nm, green 546.1 nm, and blue 435.8 nm). In the red throat region, the intensity of red (one minus the optical density of red relative to the total colour density; optical densities were corrected for differences in film development) was calculated at 10 defined points (diameter 0.5 mm). Likewise, the intensity of blue (similar calculation as for red) was calculated at 3 defined points on the iris of the eye. The highest intensities of red and blue were used in the analyses. The intensity of red measured from the slides correlated well with the intensity of red calculated from reflectance spectra of the same males (BAKKER & MUNDWILER, 1994).

Choice tests.

Each male was given four different choice tests. On Day 1 the males were offered two barred dummies of ripe females, one in horizontal and one in head-up position; on Day 2 a similar choice but with all-silver dummies was given; on Day 3 the choice of Day 1 was repeated, and on Day 8 the choice of Day 2 was repeated with different all-silver dummies. The dummies used on Days 1, 2, and 3 were stylized epoxy castings with a total length of 6.3 cm (see ROWLAND *et al.*, 1991), those used on Day 8 were realistic, soft vinyl castings of ripe females with a standard length of 4.6 cm and a tail fin of about 0.6 cm. The head-up soft vinyl dummy had additionally a concave back and the tail was lifted. All dummies were painted uniformly silver with a black eye-spot, while those used on Day 1 and 3 had an additional dark-olive vertical bar pattern painted on their dorsum, upper flanks and tail stem (see ROWLAND *et al.*, 1991). On days when no choice tests were carried out, the males were stimulated with enclosed ripe females, as during the pretreatment phase.

The dummies were attached to fine green iron wires and hung side by side in the males' tanks, 19.5 cm apart, 5 cm off the bottom (Day 8: 3 cm), and 35 cm from and facing the nest. In each test one dummy was presented in a horizontal posture, the other in a 45° head-up position. Male responses were video-recorded from the end in which the dummies were presented and observed from a monitor placed 1 m from the tanks behind a screen.

Males were stimulated with a live ripe female for about 10 min 1-2 hours before each choice test. Each dummy pair was presented in a 2 + 2-min test, with the dummy positions switched midway through the test (male behaviour was not recorded during 1 min after switching) to control for side bias. A test began when the male responded to a dummy but

not within a minimum acclimatization time of 30 sec after introduction of the dummies. The position of the head-up dummy was alternated between tests, and to half of the males in each test the head-up dummy was presented to the left. On Day 8 (test 4), we presented the dummy pair for only 2 min, thus without switching dummy positions. Statistical tests including courtship in test 4 were therefore based on the first 2 min of presentation. In comparisons not involving test 4, the more reliable data based on a test duration of 4 min were used. However, analyses based on only the first 2 min of each test led to the same conclusions.

The intensity of male courtship was quantified by counting the number of zigzags (zz) directed towards each dummy. Each zigzag consists of a quick, more or less pronounced sideway jump, away from and then towards the dummy. Male preference for the head-up dummy was expressed by a preference index: $(\# \text{ zz to headup} - \# \text{ zz to horizontal}) / (\# \text{ zz to headup} + \# \text{ zz to horizontal})$, with 0 meaning no preference, +1 an absolute preference for head-up, and -1 an absolute preference for horizontal. We also recorded the number of bites against each dummy, which occur at low frequency during courtship. Males did not show dorsal pricking behaviour towards the dummies, and leading movements to the nest were infrequent and could not clearly be distinguished from normal swimming behaviour in the small tanks.

All statistical tests are conservative, nonparametric, two-tailed tests. In the analysis of male choice related to male traits, also the results of parametric tests are given by comparison.

Results

Male choice related to female traits.

The males averaged a standard length of 5.10 cm (SD = 0.22 cm, range = 4.8 - 5.5, N = 14) and a weight of 1.39 g (SD = 0.25 g, range = 0.91 - 1.76). Most males courted (total zz in four choice tests: median 97, range 65-288, N = 10) at a rate comparable to males in previous publications (e.g. ROWLAND *et al.*, 1991). Four of the 14 males tested exhibited little courtship (total zz in four choice tests were ≤ 15) thus making their preference indexes unreliable, and were therefore left out of the analysis. However, analyses based on all 14 males led to the same conclusions. Most males responded within 30 sec to the dummies in the choice tests, the longest latency being 3 min.

Males courted the head-up dummy more than the horizontal dummy when both dummies had bars (Fig. 1; Wilcoxon matched-pairs signed-ranks test, $T = 3$, N = 10, $p < 0.01$). Because this result was the reverse of that found in an earlier study with all-silver dummies (ROWLAND & SEVENSTER, 1985), we repeated the experiment with the same males but with all-silver dummies to determine whether the bar pattern had affected this apparent contrast between studies. In this second presentation, the males no longer preferred the head-up dummy (Fig. 1; Wilcoxon

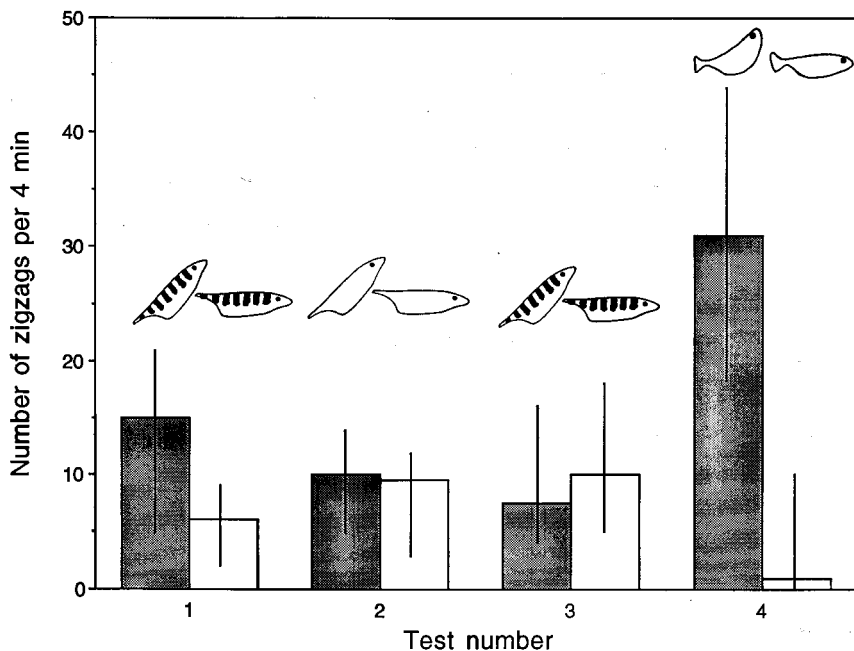


Fig. 1. Male courtship activity (expressed as the medium number of zigzags during 4 min choice tests; error bars give quartiles) shown by 10 males during 4 successive simultaneous choice tests with dummies of ripe females. The stippled bars show the number of zigzags directed at the dummy in head-up posture, the open bars those directed at the horizontal dummy. The dummies in test 1 and 3 were stylized, silver dummies with a bar-pattern, those in test 2 were similar dummies without bars, and those in test 4 were realistic, all silver dummies. Male response in test 4 was counted during 2 min and extrapolated to 4 min. Because courtship activities directed at either dummy were somewhat higher in the first 2 min than in the second 2 min of tests but not significantly so (test 1, 2, and 3, Wilcoxon matched-pairs signed-ranks test, all $p > 0.12$), this extrapolation will tend to overestimate courtship activity in test 4.

matched-pairs signed-ranks test, $T = 20$, $N = 10$, $p > 0.49$). In order to decide whether the second male response was due to the absence of the barring or to the males' experience with the dummies, we repeated the first presentation with the barred dummies. In this test series, too, the males preferred neither dummy over the other although both were barred (Fig. 1; Wilcoxon matched-pairs signed-ranks test, $T = 27$, $N = 10$, $p = 1$) suggesting an influence of experience on male preference. This influence was tested in a fourth choice test by presenting a completely different set of all-silver dummies. In this test series, the males again preferred the

dummy in head-up posture (Fig. 1; Wilcoxon matched-pairs signed-ranks test, $T = 0$, $N = 10$, $p = 0.002$). In the graphical comparison of male responses between tests, the frequencies of males activities in this test were extrapolated to a test duration of 4 min.

The changed response to the dummies from the first to the third choice test was not due to a decreasing overall interest in the dummies: the total number of zigzags directed at one or the other dummy was not significantly different between the first and the third choice test (Wilcoxon matched-pairs signed-ranks test, $T = 19.5$, $N = 9$, $p > 0.70$). The preference index tended to be different between the first and third test (Fig. 2; Wilcoxon matched-pairs signed-ranks test, $T = 7$, $N = 9$, $p < 0.075$), and was marginally significantly so when only the first 2 min of the choice tests were considered (Fig. 2; Wilcoxon matched-pairs signed-ranks test, $T = 6$, $N = 9$, $p = 0.055$) changing from a preference for the head-up dummy to no preference. The change in preference index seemed thus to be due to a combined tendency to habituate to the head-up dummy (Wilcoxon matched-pairs signed-ranks test, $T = 16.5$, $N = 9$, $p > 0.50$;

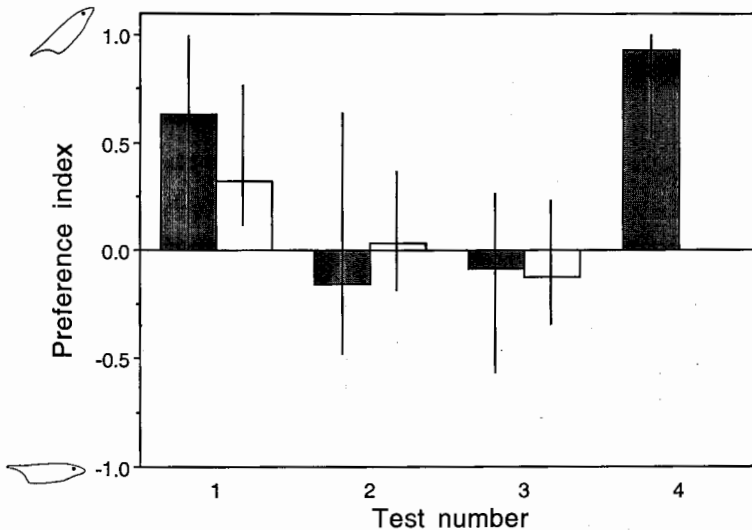


Fig. 2. Median preference index (positive values mean a preference for head-up posture, negative for horizontal) of 10 males in 4 successive simultaneous choice tests with dummies of ripe females, one in head-up position and one horizontal. Stippled bars give preference indexes in the first 2 min, open bars in the total test duration of 4 min. Error bars give quartiles. The dummies were the same as in Fig. 1.

first 2 min, $T = 7$, $N = 8$, $p > 0.14$) and to direct more courtship to the horizontal dummy (Wilcoxon matched-pairs signed-ranks test, $T = 8$, $N = 8$, $p > 0.19$; first 2 min, $T = 3$, $N = 8$, $p < 0.04$). Likewise, the renewed interest in the head-up dummy in test four was reflected in a significant change in the preference index from the third to the fourth test (Wilcoxon matched-pairs signed-ranks test, $T = 5$, $N = 10$, $p < 0.02$) due to an increased tendency to direct courtship activity to the head-up dummy and a non-significant tendency to decrease the number of zigzags to the horizontal dummy (Wilcoxon matched-pairs signed-ranks test, $T = 9$, $N = 10$, $p < 0.07$ and $T = 16.5$, $N = 10$, $p > 0.29$, respectively). The courtship activity levels (directed at the head-up, at the horizontal, and at both dummies) and preferences were not significantly different between the first and fourth choice test (all $p > 0.11$).

Most males failed to attack the dummies during the choice tests (total number of bites and bumps in 4 choice tests: median 4, range 0 - 175, $N = 10$), at a level sufficient to detect any significant trends in this activity.

Male choice related to male traits.

The preference index of the males in the first choice test was not correlated with male traits that are possibly attractive to females in this or other stickleback populations: the intensity of his blue eyes (Kendall rank-order correlation coefficient $T = 0.31$, $N = 10$, $p > 0.20$), standard body length ($T = -0.21$, $N = 10$, $p > 0.20$), the intensity of red throat coloration ($T = 0.04$, $N = 10$, $p > 0.20$), and the total number of zigzags ($T = 0.13$, $N = 10$, $p > 0.20$).

The two attractive male traits of the Long Island population, *i.e.* the intensity of the blue eyes and body length, tended to correlate positively with each other (Fig. 3; $T = 0.42$, $N = 10$, $p = 0.11$; least squares linear regression, $r = 0.68$, $p < 0.03$). The relationship between the preference index and either of these male traits may be influenced by the confounding influence of the other male trait. The influence of the confounding variable was therefore partialled out by calculating Kendall partial rank-order correlation coefficients. Unconfounded by the influence of the other attractive male trait, the preference index tended then to correlate positively with the intensity of the blue eye ($T = 0.44$, $N = 10$, $p = 0.08$; parametric partial correlation, $r = 0.74$, $p < 0.02$) and weakly negatively

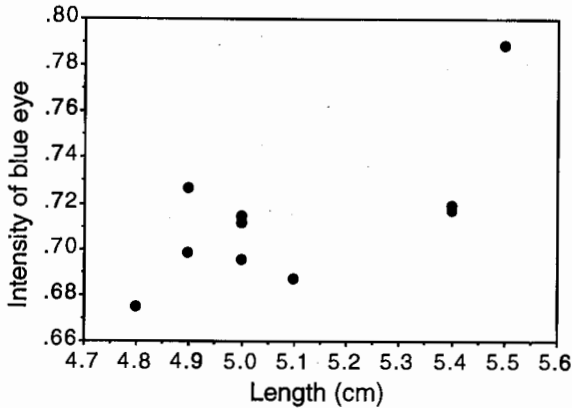


Fig. 3. The relationship between standard male body length in cm and the intensity of the blue eye ($N = 10$).

with male length ($T = -0.38$, $N = 10$, $p = 0.14$; parametric partial correlation, $r = -0.65$, $p < 0.05$).

Discussion

In simultaneous choice tests with novel dummies, male sticklebacks preferred to court dummies of ripe females in head-up courtship posture over ones in horizontal posture. The head-up posture is one of the traits that signals spawning readiness in female sticklebacks. Under laboratory conditions, the readiness to assume a head-up posture increases with time in the second half of the interval between successive spawnings (WOOTTON, 1974a, b). A gravid female can spawn her entire clutch of mature eggs probably at any time within a few days after ovulation, and will do so spontaneously if she has not found a partner within a certain time period. The closer she gets to the point of spawning spontaneously the longer she will maintain the head-up posture in front of a courting male (TCMB, unpubl. data). Thus, by preferentially courting females in head-up posture males appear to maximize courtship success.

Upon repeated presentation of the female dummies, the males' preference for the head-up dummy disappeared. There was a tendency of waning of courtship directed at the formerly preferred head-up dummy suggesting habituation (see PEEKE, this volume) to the pre-potent head-up stimulus, accompanied by a shift in attention to the less potent horizontal

stimulus, especially in the first 2 min of presentation. A ripe female that assumes a head-up posture, when courted, will usually follow the male to his nest (WOOTTON, 1976). Failure of the head-up dummy to do so may make her less attractive: she might represent a female unwilling to spawn (MCLENNAN & MCPHAIL, 1990). Reluctant females may pose a direct danger to the male's nest or spawn and protract courtship, thereby increasing the risk of cannibalism and predation. It would thus make sense when experience interferes with male preference. In field observations of two Dutch freshwater populations, at least one third of the females entering a nest left without having spawned (GOLDSCHMIDT & BAKKER, 1990; GOLDSCHMIDT *et al.*, 1993). A ripe female that does not assume a head-up posture when courted will usually not follow the male to his nest but will flee. Failure of the horizontal dummy to do so may make her more attractive: she might be ready to spawn. There thus seems to be some kind of plastic process that interacts with more fixed components to yield a male mating choice.

Because males initially directed more than twice as many zigzags to the head-up dummy than to the horizontal one, the opportunity to learn was greater with respect to head-up. The opposite changes in the male's response to the horizontal posture may thus have resulted from a re-allocation of zigzags in a no-preference situation.

In a preliminary study by one of us (WJR, unpubl. data), two Dutch male sticklebacks initially showed no preference when offered two all-silver dummies of ripe female sticklebacks one in head-up and one horizontal. Upon repeated presentations of the same dummies (two choice tests a day during five days) the males significantly preferred the horizontal dummy from test 2 and 3, respectively, onwards. The change in preference during repeated presentations with the same dummies in this and the present experiment indicate that experience has indeed an effect on the male's response to female posture. Both the male's response to courting females and the female's response to courting males is less fixed and more plastic than is often realized (*e.g.* TINBERGEN, 1951).

The preference for the head-up dummy in the first choice test and the regained interest in head-up when different dummies were presented suggest that the head-up posture is a more reliable signal for spawning readiness than horizontal posture. Perhaps ripe females can most easily assume and maintain a head-up posture without much movement of the

pectoral fins because the center of gravity has shifted caudally. The ease with which females can assume this posture when they are egg-laden may therefore help insure honesty of signalling ripeness.

The presence of vertical bars (test 1) did not seem to be necessary for the males' preference for head-up since the preference for head-up was also shown when a different, all-silver set of dummies was offered to the males (test 4). Nor did the bar pattern prevent a change in preference upon repeated presentation (test 3), even though males preferred barred dummies over all-silver ones when both were presented in horizontal pose (ROWLAND *et al.*, 1991). It is unknown whether changes in pigmentation pattern are costly and thus honest, but there may well be physiological costs as well as genetical constraints for this trait (ZIMMERER & KALLMAN, 1988).

The presence of multiple signals of spawning readiness in female sticklebacks raises the question of redundancy of information: do the different signals transmit the same information or do they provide additive information to the male (*e.g.* MØLLER & POMIANKOWSKI, 1993)? The presence of multiple signals of spawning readiness suggests that it is hard to get access to a male stickleback's nest. The present study suggests that attractive males are choosier (see below), making access to such males probably even harder for females. Thus, if signals of spawning readiness also contain information about female quality (such as resistance to parasites, physical condition, probability of egg raiding), they may lead high quality males to mate preferentially with high quality females (MØLLER, 1991).

The plasticity in male mating preference may allow a male stickleback to maximize his courtship success when the proportion of ripe females that signal their spawning readiness with a head-up courtship posture varies in the population. Virtually nothing is known about whether the use of head-up posture as a signal for spawning-readiness varies among and within populations. Nor do we know the risk males run when courting ripe females that show head-up *versus* those that do not show it; is the ratio of spawning:cannibalizing eggs different for females that show head-up?

The present study also showed that male preference for head-up posture tended to correlate with his own attractiveness. There were no obvious relationships in our small sample size of male preference for head-up posture with male body length and the intensity of the blue eye,

two male traits that are attractive to ripe females in the Long Island population (ROWLAND, 1989, 1994, respectively), with the intensity of red coloration, a preferred male trait in several other stickleback populations (McLENNAN & MCPHAIL, 1990; MILINSKI & BAKKER, 1990, 1992; BAKKER & MILINSKI, 1991; BAKKER, 1993; BAKKER & MUNDWILER, 1994), or with the intensity of male courtship, which has been suggested to influence female choice (JAMIESON & COLGAN, 1989). The intensity of the blue eye colour tended to correlate positively with male length, as it does in some other populations (FRISCHKNECHT, 1993; TCMB, unpubl. data), suggesting that the blue eye colour reflects long-term physical condition. When the relationship between male preference for head-up posture and each of the attractive male traits in this population was statistically separated from the other traits, there emerged a tendency of a positive correlation with the intensity of the blue eye and a weakly negative one with male body length.

The tendency of a positive relationship between male preference for head-up and the intensity of the blue eye suggests that attractive males are choosier when given a choice of mates. The weak tendency of a negative relationship between male preference and male body length cannot, however, be interpreted simply as smaller males having stronger preferences for head-up. The dummies that we used in our first choice test measured 6.3 cm in length, whereas the standard length of the males ranged from 4.8 to 5.5 cm. Thus in all cases dummies were larger than the male but the discrepancy in length between the sexes varied. Maybe it is not the male's body length per se that determines his choosiness, but the ratio of his attractiveness to female fecundity, as measured by the body lengths of the sexes. This hypothesis suggests that risk of egg cannibalism (rather than the probability of spawning) by females that show head-up may be greater when males are more attractive (*i.e.* larger) and females less attractive (*i.e.* smaller).

Former experiments of male preference for head-up posture gave results opposite to those found in the present study. In similar experiments of ROWLAND & SEVENSTER (1985), males from different populations preferred to court the horizontal dummy over the dummy in head-up posture. There are two obvious differences between ROWLAND & SEVENSTER's (1985) study and the present one. They used stylized, all-silver dummies of ripe females as we did in our test 2 but of a smaller size (50

mm), whereas male body length was on average larger. One difference was thus the relative size difference between male and female. The apparent difference between studies seems thus to support the foregoing hypothesis that male preference for head-up is a function of the attractiveness of both sexes. But body size differences can not be the only reason for the different male preferences between studies because in other choice experiments with the same realistic dummies that we used in test 4, males from the Long Island population significantly preferred the horizontal over the head-up posture (WJR, unpubl. data). A further difference between our choice experiments and the other experiments on male mate choice was the degree to which males were exposed to courting females before the choice tests. Before starting the experiments, we regularly stimulated the males with (in most cases) ripe females, so the males had experienced courting females, although in nature the frequency with which males encounter ripe females will often be higher (*e.g.* GOLDSCHMIDT & BAKKER, 1990). In the other male choice experiments (ROWLAND & SEVENSTER, 1985; WJR, unpubl. data), males had not been stimulated with courting females before the choice tests. The results of the present study suggest an influence of experience on male mate choice. Preliminary experiments in which males were trained with an horizontal or head-up dummy before testing their mating preference also point to the role of experience in shaping preferences (WJR, unpubl. data).

In conclusion, the present experiments showed a male preference for the head-up posture of ripe females, a signal of spawning readiness, over horizontal. Male choosiness tended to correlate with male attractiveness (intensity of blue eyes) as well as weakly with the relative attractiveness of both partners as determined by their body lengths, and male preference could be influenced by experience.

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