

Selective copying in mate choice of female sticklebacks

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Abstract. There is evidence that female three-spined sticklebacks, *Gasterosteus aculeatus* L., prefer to mate with males whose nests contain eggs rather than with males with empty nests. While there is consensus on this point, a dispute exists about whether this preference should be attributed to a direct effect of the eggs on the female's entering the nest or, alternatively, to a positive impact of the eggs on the courtship behaviour and breeding coloration of the male. In the field experiment reported here females strongly preferred nests with eggs over empty nests. Additionally, females were less likely to enter risky nests with eggs: nests that contained fewer eggs than one average clutch or more eggs than the average nest content of parental males in this population. However, in the field possible differences in male attractiveness were not controlled for. In supplementary laboratory experiments the effect on female choice of possible changes in male attractiveness (intensified courtship and coloration) as a result of the presence of eggs in the nest was tested. Other differences in male attractiveness as a result of differences in male quality (body size, breeding coloration before the test, territory quality and size) were controlled for. When females had no access to the nests, they showed no preference for males with eggs in their nests in simultaneous choice tests. These results, together with the earlier published data, make it likely that the preference of females for nests with eggs is partly a direct consequence of the eggs themselves. So female sticklebacks are influenced by the mate choice behaviour of other females, but remain selective as to the actual nest content.

Female mate choice has recently attracted much research (for a recent review see Harvey & Bradbury 1991). In species in which males contribute only genes to the next generation female choice is directed at exaggerated male traits (e.g. Kirkpatrick & Ryan 1991). However, in many species, in addition to genes, the male provides resources. In these cases, females may base their choice on the additional benefits that the male provides (e.g. territory, nuptial gifts, paternal care). Of these benefits paternal care is particularly common among fish (Ridley 1978). In some fish species with exclusive paternal care there is evidence that females prefer males that have already collected eggs (Ridley & Rechten 1981; Constantz 1985; Marconato & Bisazza 1986; Sikkel 1988, 1989; Unger & Sargent

1988; Gronell 1989; Jamieson & Colgan 1989; Knapp & Sargent 1989; Belles-Isles et al. 1990). Sargent (1988) proposed three hypotheses on the evolution of this female preference: a male's ability to obtain eggs may be correlated with his ability to care for them (the phenotypic-quality hypothesis); the risk of predation for an individual egg may be inversely related to egg number by a dilution effect (the selfish-herd hypothesis: Rohwer 1978), or paternal care and thus egg survival may both increase as egg number increases because of the increased value of the brood (the parental-investment hypothesis). To these we can add another hypothesis to explain the evolution of this type of female preference. Males with eggs have apparently been attractive to other females; by copying other females, a female may produce offspring of good genetic quality or 'sexy sons', assuming that those desirable traits are inherited (e.g. Ridley 1978; Losey et al. 1986; Wade & Pruett-Jones 1990).

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In three-spined sticklebacks, *Gasterosteus aculeatus* L., only the male bestows parental care. Reproductive males defend a territory in which they build a nest. As soon as the male creeps through the nest he is ready to collect eggs (Sevenster 1961). If a courted female follows the male and noses into the nest entrance, she may then decide either to flee or to enter the nest. After entering she may spawn or leave the nest gravid. Female choice experiments showed that female sticklebacks prefer to spawn with males whose nests contain eggs (Ridley & Rechten 1981; Jamieson & Colgan 1989; Belles-Isles et al. 1990). Ridley & Rechten (1981) attributed this female preference to a direct effect of eggs on the female's entering the nest; in sequential choice experiments, males with eggs were no more likely to be followed than those without eggs, and there was no difference in the following times. In simultaneous choice experiments, furthermore, Jamieson & Colgan (1989) found that males with eggs achieved more spawnings than those with empty nests. In contrast to Ridley & Rechten (1981), however, they attributed this difference to the greater success of males with eggs at leading females to their nests. According to their hypothesis, the presence of eggs in the nest improved male attractiveness by intensifying male courtship and coloration.

In this paper we report a combined field-laboratory study which investigates (1) whether in the natural environment females prefer to spawn in nests with eggs, and (2) whether a possible female preference depends upon a direct effect on nest entering exerted by the eggs or upon intensified male courtship and/or coloration as a result of recently laid eggs.

METHODS

Field Experiments

Experiments were conducted in a pond (7500 m²) at a trout hatchery 'de Zwaanspreng', Apeldoorn, The Netherlands. The pond was fed with water from a brook. Three-spined sticklebacks (forma *leiura*) nested both inside and outside vegetation (predominantly *Glyceria maxima*). The bottom was sandy. All observations were made from the shoreline and all nests were in water of 1 m depth or less. We observed 58 males. Most observations (approximately 150 h) were made during the

breeding season of 1985. In addition, some data collected in 1978 with similar methods were included.

Courting males were selected, that is, only those males were used that were seen to creep through the nest or display courtship. The observer then waited until a courtship sequence reached the stage at which the female nosed into the nest entrance. At this stage the female decided either to flee or to enter the nest. If the female fled, the nest was removed and checked for the presence of eggs. If, by contrast, the female entered the nest, the observer waited until the courtship sequence was concluded, resulting either in spawning or in the female disappearing without having spawned. Subsequently, the nest was taken away to check whether it had already contained eggs. The number of eggs were counted, their developmental stage was determined, and, if possible, the number of clutches was assessed.

Laboratory Experiments

F1 of wild-caught sticklebacks of the low-plated morph (forma *leiura*) were used. The parents had been sampled from a trout hatchery, 't Smaller', Emst (near Vaasen, The Netherlands). Juvenile fish were kept under summer conditions (16:8 h light:dark, 18–20°C). When they approached sexual maturity they were transferred to winter conditions (8:16 h light:dark, 10°C) and kept in non-reproductive conditions until required. Before the start of the experiments, the fish were transferred to summer conditions; females were kept together in large 150-litre tanks, and males were housed singly in plastic tanks (17 × 34 × 20 cm). The tanks with males were placed in a row separated by opaque partitions. A 36-W fluorescent lamp (14 cm above the tanks) illuminated six tanks. The fish were fed twice a day with live *Tubifex* worms. The tanks of the males were provided with a petri dish filled with sand with a *Vallisneria* plant, and some filamentous algae. All males built their nests in the petri dish.

The males used were similar in length ($\bar{X} \pm SD = 5.5 \pm 0.2$ cm, $N = 32$) and breeding coloration (see below) owing to standardized rearing conditions and exclusion of extreme individuals. Therefore each pair of neighbouring tanks (i.e. random pairing of males) was used in choice experiments. In the 1st or 2nd week after nest building, ripe females were randomly introduced into one tank of each pair. After having spawned, they were removed.

A ripe female in a transparent tube was shown to the neighbouring male during this male's spawning sequence. The sight of an enclosed ripe female is as strong a stimulus for the male as a free-swimming ripe female (Wootton 1976).

We carried out female choice experiments on the following day. Inexperienced females were selected for choice tests by making use of a male that was trained to court well in the storage tanks with females. Only those females that responded with a head-up posture to this male were selected. Females were used once. A cell (12 × 8 × 20 cm, opaque side walls) containing a ripe female was positioned centrally in front of each pair of neighbouring tanks. As soon as both males had approached the female and the female had reacted to both males, the test started. The duration of the female's head-up display while she was pointing towards each of the two males was scored for a 5-min period. This behaviour correlates positively with her probability of spawning with that male (McLennan & McPhail 1990). The average percentage of test time the females directed towards the pairs of males was 67.7 ± 17.5% ($\bar{X} \pm \text{SD}$, $N = 16$), while 95.4 ± 8.9% ($\bar{X} \pm \text{SD}$, $N = 16$) of this time they displayed the head-up posture.

Before and after each choice test the brightness of the males' breeding coloration was classified on a four-point scale. The scale is defined in Bakker & Sevenster (1983), but was reversed for the present classification, i.e. a score of 1 was assigned to the duller males and a score of 4 to the brightest males. The average score was 2.6 ± 0.6 ($\bar{X} \pm \text{SD}$, $N = 30$, no colour data for two of the males) before the tests.

The males of each pair that were used in female choice tests differed consistently only with respect to the presence of eggs in the nest. Other differences in male attractiveness as a result of differences in male quality were kept constant (territory size and territory quality) or minimized and randomized with respect to the presence of eggs (body size, breeding coloration before the test). The difference in standard length between neighbouring males ranged from 0 to 0.5, median = 0.1 cm, $N = 16$; males with eggs were in seven cases smaller and in seven cases bigger than their neighbours without eggs, and in two cases there was no difference. The difference in brightness ranged from 0 to 2, median = 1, $N = 15$; males with eggs were in six cases brighter and in six cases duller than their neighbours without eggs, and in three cases there was no difference.

Table I. Number of females that, after nosing into the nest entrance of nests with eggs or empty nests, either entered the nest, or fled

	With eggs	Without eggs
Female enters	11	1
Female flees	17	29

Yates corrected $\chi^2 = 9.32$, $df = 1$, $P < 0.005$, one-tailed. $N = 58$ nests at de Zwaanspreng.

Table II. Number of females that, after nosing into the nest entrance of nests with eggs or empty nests, either spawned or not

	With eggs	Without eggs
Female spawns	7	1
Female does not spawn	21	29

Yates corrected $\chi^2 = 4.04$, $df = 1$, $P < 0.025$, one-tailed. $N = 58$ nests at de Zwaanspreng.

RESULTS

In the field, females that nosed into the nest entrance were more likely to enter a nest with eggs than an empty nest (Table I). The likelihood of spawning was also significantly greater in nests with eggs (Table II). Four of the 11 females entering a nest with eggs left it without having spawned. These females may not have been ripe enough to spawn. The probability of leaving the nest gravid (4/11 = 0.36) agrees with other data from the same population (6/18 = 0.33; T. Goldschmidt, unpublished data) and data from the population at 't Smaller' (15/35 = 0.43; Goldschmidt & Bakker 1990). The latter data were obtained from spawning events in nests with unknown nest contents.

At 'de Zwaanspreng' the average clutch size, estimated from spawned clutches in the nests, was 56.9 ± 36.4 eggs ($\bar{X} \pm \text{SD}$, $N = 31$, range 10–180). The average number of eggs in the nests of courting males prior to the field experiment was 87.1 ± 52.7 eggs ($\bar{X} \pm \text{SD}$, $N = 26$, range 10–200). The average number of eggs in nests of males that had completed their collection of clutches (i.e. they no longer courted) was 125.4 ± 101.8 eggs ($\bar{X} \pm \text{SD}$, $N = 43$, range 2–365; randomly sampled nests of males caring for eggs, collected at 'de Zwaanspreng' in 1981; T. Goldschmidt, unpublished data).

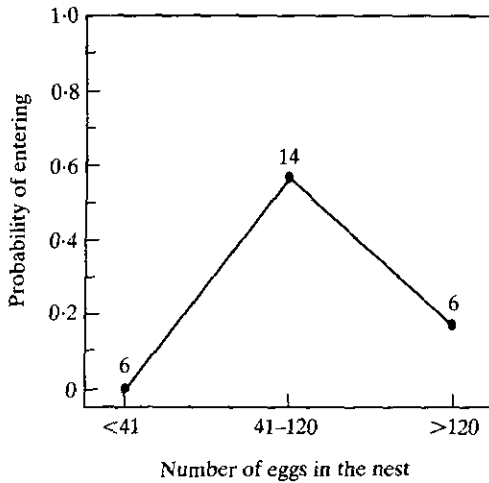


Figure 1. The probability of nest entering by nosing females as a function of the number of eggs in the nest. Numbers of nosing females are indicated.

The probability of nest entering by nosing females in nests with eggs differed between nests containing different numbers of eggs (Fig. 1). Females were less likely to enter risky nests with eggs, that is nests that contained clearly less than one average clutch (less than 41 eggs; eggs probably obtained by raiding, Goldschmidt & Bakker 1990) and nests that contained as many as or more than the average numbers in a full nest (more than 120 eggs, see above); few and many eggs were tested versus an intermediate number of eggs with the Fisher exact probability test, $P=0.012$, one-tailed.

In the laboratory experiments the body size and coloration of males with and without eggs in their nests did not differ (Table III). Males were more brightly coloured after the choice test ($\bar{X} \pm \text{SD} = 3.6 \pm 0.5$, $N=30$) than they were before the test (2.6 ± 0.6 , $N=30$; Wilcoxon matched-pairs signed-ranks test, $N=27$, $P<0.0001$). Females did not show a preference for courting males belonging to either of the two categories, viz. with a clutch of eggs or with an empty nest (Table III). The duration of the head-up posture directed towards the male with eggs and the one without eggs in each pair was not significantly different (Wilcoxon matched-pairs signed-ranks test, $T=59$, $N=16$, $P>0.30$).

DISCUSSION

Evidence was found in the field that female sticklebacks, after having nosed into the nest entrance,

prefer to mate with males whose nests contain eggs rather than with males with empty nests. Female preference for males with eggs in their nests was observed in the laboratory for solitary males (sequential choice experiments) by Ridley & Rechten (1981) as well as for males in rival situations (Jamieson & Colgan 1989; Belles-Isles et al. 1990).

Our field observation of a high fraction of aborted entries especially in empty nests (Table I) suggests that females sample nests and/or males (cf. Kynard 1978; Bakker & Milinski 1991). High fractions of aborted entries are known from other stickleback populations (Goldschmidt & Bakker 1990; S. A. Foster, personal communication), and are not laboratory artefacts, as suggested by Jamieson & Colgan (1989).

We found an effect not only of the presence of eggs on nest entering, but also of number of eggs present; females were more likely to enter nests with an intermediate number of eggs than risky nests that contained either clearly less than one average entire clutch or at least as many eggs as the average number in nests of parental males in this population (Fig. 1).

The presence of relatively few eggs (less than the average number produced by females in this population) in the nest may indicate that the female has encountered a 'sneaky' male that has raided his eggs (Goldschmidt & Bakker 1990), instead of acquiring these eggs by successful courtship. It may be adaptive for a female to discriminate against nests that contain only raided eggs (possibly on average lower quality males, possibly higher chance that her eggs will be eaten or that the male will not complete the brood cycle) in favour of nests with eggs that were at least partially collected by successful courtship. Even when a previous female has spawned in the male's nest, the presence of few eggs may indicate that the male has eaten part of this clutch.

It may also be disadvantageous to spawn as the last female in a row; the last clutch receives paternal care during a shorter period and may be more vulnerable to predation by the nest owner or conspecifics. The last clutch is likely to be most accessible to predators, the eggs are more nutritious than are more developed eggs (Gilbert 1985), and to the guardian male younger eggs have less reproductive value (FitzGerald 1991). Guardian males with limited foraging opportunities benefit by eating some of their own eggs, and when most of the

Table III. Characteristics of males with or without a clutch and the outcome of female choice experiments between them

	With eggs	Without eggs	<i>P</i>
Male characteristics			
Length	5.5 ± 0.2 (16)	5.5 ± 0.2 (16)	>0.20
Colour before	2.7 ± 0.7 (15)	2.6 ± 0.5 (15)	>0.20
Colour after	3.5 ± 0.5 (15)	3.8 ± 0.4 (15)	>0.10
Female behaviour			
Head-up	94.0 ± 42.2 (16)	98.8 ± 36.6 (16)	>0.25
Choice	7	9	>0.25

Numbers of males and females are given in parentheses. Length ($\bar{X} \pm \text{SD}$) is standard length in cm. The coloration of the males ($\bar{X} \pm \text{SD}$) was assessed on a four-point scale before and after each choice experiment. Length and colour differences were tested with a Mann-Whitney *U*-test, two-tailed, duration of head-up posture ($\bar{X} \pm \text{SD}$ in s) with a Mann-Whitney *U*-test, one-tailed, female choice (duration of head-up directed towards one male exceeded that directed towards its neighbour) with a chi-squared test, one-tailed.

eggs have hatched, by eating the remainder as an investment in future brood cycles (Rohwer 1978). Rejection of nests with relatively many eggs was also found in Canadian sticklebacks (Belles-Isles et al. 1990). When given the choice of spawning with a male with one to five clutches of eggs (about 360 eggs per clutch) or with a male without eggs, females preferred to spawn in nests with one or two clutches, but seemed to avoid spawning in nests with four or five clutches (Belles-Isles et al. 1990). Competition for oxygen among crowded eggs, as suggested by Belles-Isles et al. (1990; see also Reebs et al. 1984), seems unlikely in our case where males did not collect more than 300–400 eggs.

Is female preference for nests with eggs a direct consequence of the eggs themselves? The field data suggest that the female's decision to enter a nest or not occurs after she has nosed into the nest entrance. Female choice behaviour seems thus to be influenced by the mate choice of other females. This choice behaviour is known as copying (e.g. Losey et al. 1986; Wade & Pruett-Jones 1990). However, in our field experiments, no control was made for possible differences in male attractiveness as a result of the presence of eggs in the nest. Other studies have suggested an increased attractiveness of male sticklebacks after the acquisition of the first clutch of eggs; the male may become more brightly coloured (Jamieson & Colgan 1989) and its sexual activity may increase for 1–2 days (van Iersel 1953; Sevenster-Bol 1962; Segaar et al. 1983; Segaar & de

Bruin 1985, 't Hart 1985). In simultaneous choice tests in the laboratory, we let females choose between two males that differed in the presence of a clutch of eggs in the nest while differences in male quality per se (territory quality and size, body size, breeding coloration) were controlled for. The female choice experiments did not reveal any preference for either category of male (Table III). This result makes it likely that the female preference for nests with eggs is a direct consequence of the eggs themselves.

Our results support the interpretation of Ridley & Rechten (1981) which was questioned by Jamieson & Colgan (1989). The latter authors argued that males with eggs courted more vigorously and possessed a brighter nuptial coloration than males without eggs. They claimed that the female preference could be explained by these differences in male behaviour and coloration rather than by the presence of eggs. However, their data demonstrate a strong preference for males with eggs ($P < 0.001$), while the differences in courtship intensity and brightness of coloration are less convincing ($P = 0.06$ and 0.03 , respectively) and may be biased by the choice behaviour of the females (see also Goldschmidt & Bakker 1990).

By copying the mate choice of other females but remaining selective as to the actual nest content, a female stickleback maximizes the survival of her offspring. This may be achieved either through direct benefits of the presence of other eggs (selfish-

herd hypothesis, see Introduction), through high quality of paternal care (phenotypic-quality hypothesis and parental-investment hypothesis, see Introduction), or indirectly through high male genetic quality (e.g. parasite resistance: Milinski & Bakker 1990; but see Wedekind 1992).

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