'False orgasm' in female brown trout: trick or treat?

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The mating system of anadromous brown trout, *Salmo trutta* L., resembles that of many other oviparous aquatic vertebrates, and may be characterized by male dominance monogamy and female coyness. In such mating systems males usually court females to obtain them as mates and the courtship can be regarded as a contest between male salesmanship and female sales resistance (Williams 1966). If male courtship is simple and brief it may be easy for a low-quality male to perform as well as one of high quality. If the only indicator a female has of a male's 'quality' is his courtship, there will be strong selection favouring female coyness and/or more elaborate courtship (Halliday 1978). Before spawning takes place in brown trout, a female selects a spawning site and starts to cut a bed for the brood. At the same time, the males begin courting the female by 'quivering' (by vibrating the trunk muscles). One male tries to monopolize the female by fighting and chasing away other males. Subordinate males line up downstream from the pair at a 'safe' distance (Jones & Ball 1954). After the female has excavated the bed she assumes the 'crouch' position, opens her mouth and quivers violently. This is called prespawning quivering, and sometimes the female is joined by a male. He also opens his mouth and quivers violently. On some occasions the pair relinquish the crouch position and the female continues probing and digging and the males continue courting and fighting. At 'false orgasm' the male releases sperm when quivering, but the female does not release eggs; at spawning eggs and sperm are extruded almost simultaneously. After a spawning the female covers the eggs with gravel. A female may spawn up to eight times (each time in a new nest) in order to deposit all her eggs (see Jones & Ball 1954 and Petersson & Järvi 1997 for a more detailed description of mating by brown trout). After a false orgasm the female does not cover the nest. The term 'false orgasm' was first used by Jones & Ball (1954), but the behaviour has also been noted for other fish species, although other terms have been used (see for example Schneider 1971; Roy & Pal 1986; Ridgeway et al. 1989; Satou et al. 1991).

In oviparous reproductive systems, mating is impossible unless the female allows the male to mate. Each sex can choose a persistence time to hold out against the other. During a spawning climax the costs accrue unequally for the two sexes. Mating occurs if the female gives up being unreceptive before the male gives up courting. Such a process is regarded as being the outcome of an evolutionary game called a 'sexual war of attrition' (Hammerstein & Parker 1982) or 'persistence game' (Hammerstein & Parker 1987). In most species females have a limited number of eggs available, but males have the potential to father offspring at a higher rate than females can produce them (e.g. Bateman 1948). The cost for a female of releasing eggs without the male releasing sperm is therefore higher than vice versa. Hence, the persistence game hypothesis suggests that males should release sperm 'by mistake' when females do not release their eggs more than vice versa.

In some mating systems females may benefit by mixing paternity to achieve phenotypic variation among their offspring. This variation may minimize inbreeding depression and track seasonal changes, as has been suggested for poeciliid fish (Constanz 1984). Females can achieve this in two ways, either by spawning with many males on one occasion, or by spawning with different males on successive occasions. Alternatively a female may increase her fertilization success by spawning with more than one male as an insurance against males being infertile.

A third hypothesis explaining false orgasm is that oviparous females have evolved a reproductive tactic by which they can increase their control of mates. Dominance hierarchies provide an opportunity for different kinds of satellite male behaviour. One frequently noted alternative mating tactic for subordinate males in fish is to sneak close to the spawning pair and release sperm at the moment when the dominant male and female are releasing gametes (e.g. Jones & Ball 1954; Keenleyside & Dupuis 1988; Maekawa et al. 1994). From the dominant male's point of view, sneaking males may reduce his reproductive success, because his released

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spermatozoa have to compete with those of the other males. Sneaking may not be favoured by a female either (but see Gross 1996) as she cannot control the paternity of her offspring, which may negatively influence their genetic and phenotypic quality. Some studies on insects, fish and frogs do show that the female's choice of mate influences the quality of her offspring (see Andersson 1994). To reduce the risk that an unwanted male participates in spawning, the female might fool him into releasing sperm by false orgasm. After the male has released his sperm he should act as if he had spawned and move away from the female. The 'mate control' hypothesis suggests that false orgasm allows the female to reduce the risk of having 'unwanted' fathers for her offspring.

A fourth hypothesis is 'male misinterpretation'. Females may not wilfully attempt to trick males, but rather males occasionally misinterpret female cues. The cost of occasional misinterpretation may be less than that of missing a spawning opportunity or being late in arriving at spawning, especially when multiple males are participating.

We tested the predictions derived from the four hypotheses, the persistence game, mate control, mixed paternity and male misinterpretation hypothesis, on brown trout. We present data on the frequency of false orgasm, how it changes as the time for spawning approaches, how the number of males and their quality differ between males involved in false orgasms and males involved in spawnings.

Methods

We used data sets that have been partly published (Petersson & Järvi 1997; Petersson et al. 1999), and we refer to those papers for more detailed information about methods. The first study (the 'high-density' trial) consisted of three replicates, each including 12 males and 12 females, and the females were allowed to spawn several times. The other study (the 'low-density' trial) consisted of 19 replicates which each included one female and two males, and the females were allowed to spawn only once. Because false orgasms were more frequent around the time of spawning, and we could not observe the females at all times, the total number of false orgasms observed probably does not reveal the female's 'propensity' to have false orgasms. Hence, we divided the time before spawning into 30-min periods, log-transformed, and used this as the independent variable and the number of false orgasms for each female in each time period as the dependent variable. The least squared mean for each female was then used as a normalized mean value. In general, females spawn just once in each redd, but two females each spawned four times in one redd without totally covering the eggs between spawnings. However, these 'multiple spawnings' could be distinguished from false orgasm because the deposited eggs could be seen and because female behaviour differed (some covering always occurred after spawning).

We used the following variables: male secondary sexual traits (size of adipose fin, kype, jaw and nose, all adjusted for male body size), male body weight, male dominance index (following Boyd & Silk 1983), male mating success (number of spawnings), number of males in the redd, and number of males near the redd (closer than 3 m, which includes the male(s) in the redd). We also used the average values of the last two variables for both the males in the redd and the males near the redd. The values for male secondary sexual traits differed between years and were therefore standardized (the mean was set to zero). Thereafter canonical scores for the males were calculated on these four variables. The differences between false orgasms and spawning are expressed as the value for each male variable at spawning minus the value for the false orgasms preceding it. We used averages for each female. These variables were independent variables and female false orgasm frequency (see above) was the dependent variable.

We used SAS statistical software. Backward elimination was used to find out which variables explained female false orgasm frequency. All independent variables were initially included in the model, but variables having a level of significance lower than 0.1 were excluded, one by one. At each step, the variable showing the smallest contribution to the model was deleted.

Results

Of 128 cases in which only one sex shed gametes, only males were observed doing so, that is, 128 cases of false orgasm were observed. Out of 117 spawnings that provided good observation sequences leading up to spawning, 69 were preceded by one or more false orgasms prior to genuine spawning. On 50 occasions the female spawned with the same male(s) with whom she had earlier had a false orgasm, on three occasions with another male, and on 16 occasions with both the spawning male and another male. The number of false orgasms in the high-density trials preceding a spawning was correlated with the number of males in the nest at spawning (r_s=0.219, N=98, P=0.031), but not with the number of males in the vicinity of the nest at spawning (r_s= − 0.134, N=98, P=0.188). The number of prespawning quiverings preceding spawning was not correlated with the number of males in the nest at spawning (r_s=0.126, N=98, P=0.186).

The frequency of false orgasm increased when the time for spawning approached. More than 70% of false orgasms were observed within 1 h of spawning (Fig. 1). Average false orgasm frequency (uncorrected) was 2.16 (median 1.15, minimum 0.0, maximum 8.91, N=41). The high-density trials revealed that females did not increase or decrease their frequency of false orgasm between subsequent spawnings (r_s=0.220, NS) if all females were pooled, in total 59 spawnings. In none of the trials did the males in the nest leave the female after a false orgasm. After a short delay (1–5 min) the female continued to prepare the nest and the males resumed fighting and courting. Usually a male stayed with the female for 5–20 min after spawning.

In the high-density trials the mean number of males in the vicinity of the female on each false orgasm occasion ± SE was $1.46 ± 0.84$ (N=111), and in the low-density
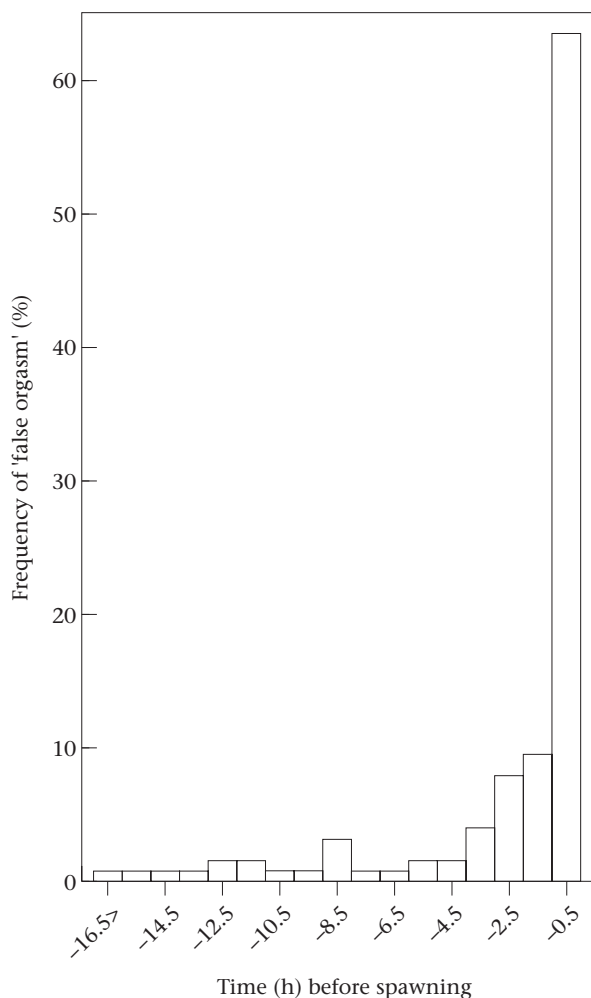
Figure 1. Number of false orgasms prior to spawning in brown trout. The data are based on the high-density trials (see text), in total 24 females and 111 spawnings. Four females did not spawn, and for eight spawning females the data were insufficient (too few observations prior to spawning) or no false orgasm was observed prior to spawning.

trials each female was on average $\pm$ SE surrounded by 1.07 ± 0.24 males ($N=17$; Wilcoxon two-sample test: $Z=2.30$, $P<0.022$). False orgasm frequency differed between the two experiments (high density: mean 2.69, median 2.15, minimum 0.09, maximum 7.46, $N=22$; low density: mean 1.54, median 0, minimum 0, maximum 8.91, $N=19$; Wilcoxon two-sample test: $Z=2.60$, $P<0.01$). Because the females in the low-density trial were allowed to spawn only once, it might be more appropriate to compare their frequency of false orgasms with the frequency of false orgasms at first spawning of the females in the high-density trials. Eight females in the high-density trial had to be excluded because of insufficient observations at their first spawning. The frequency of false orgasms at first spawning in the high-density trials was on average 3.03 (median 2.80, minimum 1.8, maximum 7.8), which differed from the low-density trial (Wilcoxon two-sample test: $Z=1.98$, $P=0.049$). The frequency of false orgasms for the rest of the spawnings in the high-density

trial was on average 2.09 (median 1.39, minimum 0, maximum 5.80) which was lower than the frequency for the first spawning (Wilcoxon matched-pairs signed-ranks test: $T=71$, $P<0.05$).

A backward elimination procedure on the data from the high-density trials revealed that 10 variables, each significant at the 0.1 level, together explained about 72% of the variation in female false orgasm frequency (Table 1). Females having a high frequency of false orgasm also had (1) an increase in the number of males in the redd from the false orgasm to the actual spawning; (2) a greater decrease in male dominance index (that is males involved in false orgasm were on average lower ranked than males involved in spawning); (3) a reduction in the number of males in the vicinity; (4) a reduction in the elaboration of secondary sexual traits of males in the vicinity; (5) an increase in the elaboration of secondary sexual traits of males in the redd; (6) a reduction in weight of males in the vicinity; and (7) an increase in weight of males in the redd.

Discussion

All four hypotheses suggest that if only one sex releases the gametes during courtship, it should be the male. Our results correspond with this prediction. According to the theory of the war of attrition, which is the theory behind the persistence game hypothesis, the probability of making a mistake should increase towards spawning, which agrees with our results. The persistence game hypothesis assumes, furthermore, that a female plays her game towards only one courting male. Hence, it is reasonable to suggest that female coyness should not be affected by the number of males in the vicinity nor by the quality of the males outside the nest, which our results show. It is, therefore, reasonable to assume that the persistence game hypothesis is not a valid explanation for the evolution and maintenance of false orgasm.

The mixed paternity hypothesis assumes that females perform false orgasm to increase the number of males during the spawning act; hence, more males should attend the spawning act than during false orgasm. Because the number of males participating in the spawning increased with increasing frequency of false orgasm, our results do not contradict the prediction made and hence, the mixed paternity hypothesis could not be ruled out.

The mate control hypothesis suggests that the female is coy to control with whom she mates. If this hypothesis is valid, then (1) because of established dominance rank hierarchies, there should be fewer males during spawning than during false orgasm; (2) the 'quality' (e.g. social dominance rank or expression of secondary sexual characters) of the mating males should be higher than that of males involved in false orgasm; and (3) males outside the nest should be of higher quality than males courting the females during false orgasm. Since more mates participated in spawning than in false orgasm, the first prediction is not fulfilled. However, the other two predictions agree with our results, suggesting that the mate control hypothesis may be valid. Female brown trout may

Table 1. The outcome of a backward elimination procedure to find which variables explain female false orgasm frequency in brown trout

Variable	Parameter estimate	SE	F	P
Intercept	0.359	0.076	22.11	0.001
No. males in the vicinity	−0.788	0.314	6.30	0.029
No. males in the redd	2.09	0.611	11.71	0.006
Male dominance index	−0.411	0.186	4.89	0.049
Secondary sex traits of males in the vicinity	0.359	0.097	8.67	0.016
Secondary sex traits of males in the redd	−0.551	0.214	6.65	0.026
Weight of males in the vicinity	−1.38	0.457	9.13	0.012
Weight of males in the redd	0.81	0.317	6.50	0.028

The values for male secondary sexual traits of males are based on four variables (see text). Model $r^2=0.726$, $F_{7,23}=3.82$, $P<0.047$, based on 24 females.

trick males to avoid unwanted males fertilizing their eggs, but the 'mixed paternity' hypothesis may operate simultaneously. It may even be advantageous for the female to spawn with a sneaking male. The males adopting a sneaking strategy in our study were mainly grilse (3-year-old males), that is, males that have grown faster during their first summer in the sea than the dominant males (mostly 4 years old). Thus, mating with grilse may be a more successful strategy in the long term (cf. Gross 1996).

The male misinterpretation hypothesis suggests that more males should be present at false orgasm than at spawning, because males are keener to release sperm when there are several competitors around. In the low-density trials, where fewer males were present, false orgasm was less frequent than in the high-density trials. As noted above, the backward elimination procedure on the high-density data revealed that the number of males in the redd increased between false orgasm and spawning, whereas the number of males in the vicinity decreased. Which factor was most important (i.e. most disturbing) for a courting male is not known and therefore our data do not necessarily support this hypothesis.

The reduction in number of males in the vicinity and the increase in number of males in the redd between false orgasm and spawning probably indicates that the dominant male chased away most of the males adopting a fighting strategy, but that he could not successfully chase away males that had adopted a sneaking strategy. The measures of the secondary sexual traits corroborate the interpretation of the behavioural variables. In brown trout, sneaking males tend to have less elaborate secondary sexual traits, as in many other salmonids (cf. Gross 1985). Fighting males remaining in the vicinity of the spawning pair seemed to be smaller than those that left the area. Alternatively, the remaining males in the vicinity at the time of spawning might have been those that tried, but failed, to sneak fertilizations.

The hypotheses we tested might explain the ultimate factors behind the evolution and maintenance of false orgasm in salmonids; however, they do not explain the proximate mechanism by which females trick males. Studies on chum salmon, *Oncorhynchus keta* (Uematsu & Yammamori 1982), and kokanee salmon, *O. nerka* (Satou et al. 1991), show that it is the male that initiates spawning by trunk muscle vibrations. This indicates that the female knows when the male is ready to release his milt, but the male cannot be sure whether the female is going to release eggs. The female can then interrupt spawning if she does not receive the proper information about the male's readiness to spawn. According to Satou et al. (1991), false orgasms are distinguishable from spawning in having long male–female distances and poor timing of body vibrations of males. This supports the view that false orgasm in salmonids depends on males that misinterpret female signalling and become in proximate terms 'over-excited'. Thus, 'false orgasm' might not be the right term for the behaviour; perhaps 'premature ejaculation' is better. Nevertheless, our results suggest that the female tricks males into joining the spawning to increase either the genetic diversity of her offspring or the quality of the particating males.

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