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Why do males tolerate sneakers? Tests with the European bitterling, *Rhodeus sericeus*

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Abstract In most species, males attack other males that attempt to gain fertilizations through sneak copulations. Here we report on a system where dominant males show a low level of aggression against sneakers at the initial stages of territory establishment. Females of the European bitterling, *Rhodeus sericeus*, lay their eggs in living mussels and males fertilize the eggs by releasing sperm over the mussels both before and after egg laying. When we allowed males to court females to a mussel containing no eggs at different male densities – one, two, four, or six males – the dominant male showed a low level of aggression against other males that released sperm. The dominant male became aggressive toward the other males only after eggs had been laid. This unusual pattern could be due to either some benefit of accepting sneakers or a high cost of aggression. We found support for both possibilities. The presence of several males decreased the time until a female spawned, whereas increased aggression by the dominant male against other males during a second female presentation, when the male was more territorial, interrupted courtship and increased the time until spawning. Females appeared to be attracted by both the presence of several males around a mussel and increased courtship under male competition. The bitterling mating system possibly differs from that of other species due to lack of investment in nest building and parental care, and high costs of defending the spawning site against sneakers.

Keywords Alternative mating behavior · Sperm competition · Mate choice · Reproductive trade-offs · Sexual selection

Introduction

Alternative male mating behaviors can arise during competition for mates if individual males differ in their competitive ability (Gross 1996). A male with a low probability of mating through courtship or the monopolization of resources may maximize his fitness by parasitizing the investment of others (Arak 1984; Taborsky 1994, 1998). This is the case in several territorial species where resident males court females while non-territorial males attempt to gain fertilizations through sneak copulations, e.g., in threespine sticklebacks *Gasterosteus aculeatus* (Goldschmidt et al. 1992), African frogs *Chiromantis xerampelina* (Jennions et al. 1992), ring-necked pheasants *Phasianus colchicus* (Ridley and Hill 1987), and red deer *Cervus elaphus* (Clutton-Brock et al. 1979). Sneakers are then usually attacked by territorial males if detected.

However, in a few species, sneakers are not always driven off by territorial males. In the bluegill sunfish, *Lepomis macrochirus*, some sneakers, called satellites, mimic females and appear to fool the territorial male into believing that they are potential mates (Gross and Charnov 1980; Gross 1982). In other species, males seem to be able to recognize sneakers as competing males and yet do not reject them. For example, in the ruff, *Philomachus pugnax*, satellite males are accepted on the territory of resident males and sometimes obtain copulations (Lank et al. 1995; Widemo 1998). Acceptance of sneakers could be adaptive if (1) aggression against sneakers is costly and reduces mating success by, for example, interrupting courtship, or (2) the presence of sneakers is beneficial for attracting females. Male aggression toward sneakers should then balance the benefits of higher paternity against the costs of fewer mating opportunities.

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In a freshwater fish species, the European bitterling, *Rhodeus sericeus* (Cyprinidae), some males establish territories around living freshwater mussels (Unionidae), which are used as the spawning site, while others remain as sneakers. The adoption of a sneaker tactic is conditional and depends on the availability of mussels and the competitive ability of the male, as most males are able to adopt the territorial, courtship tactic if given a mussel in the absence of dominating males. Territorial males court females by attempting to lead them to the mussels to spawn and by performing a distinct quivering display and releasing sperm over the inhalent siphon of the mussels. Males often have more than one mussel in their territory, and the presence of multiple mussels increases the total number of eggs laid in the territory (Reynolds et al. 1997). Females lay two to four eggs at a time into the gills by rapidly inserting a long ovipositor into the exhalent siphon of the mussel (Wiepkema 1961; Heschl 1989). Males fertilize the eggs by releasing sperm over the inhalent siphon both before and after egg laying. Females spawn repeatedly and several females may spawn in one mussel. Eggs hatch in 1–2 days and the embryos remain inside the mussel for 3–6 weeks (Reynolds et al. 1997). Mussel availability is limited in the field and almost all mussels contain bitterling embryos at the height of the season (Reynolds and Guillaume 1998). Sneakers are common in the field and few spawnings occur during the peak reproductive period in the absence of sneakers. Territorial males are often overwhelmed by groups of sneakers that release sperm over the mussel both before and after egg laying. Studies of a closely related species, the rose bitterling, *R. ocellatus*, showed that fertilization success of the territorial male decreases with the number of sneakers (Kano 1996, 2000).

The current study was prompted by the observation that males of the European bitterling sometimes show a low level of aggression against other males that release sperm over the inhalent siphon of the mussel. This appears to occur at the initial stages of territory establishment, as long as no female has spawned in the mussel; males become more aggressive after they have received some matings. We hypothesized that the acceptance of other males at the initial stages of territory establishment could be due to lower costs of accepting sneakers than chasing them away. This could occur because (1) high levels of aggression decrease the number of spawning females, for example, due to a trade-off between courtship and aggression, and/or (2) the presence of sneakers around a mussel is beneficial in attracting females. The cost of accepting sneakers could be low as long as no females have spawned and there is a low risk of sneaker sperm remaining viable until spawning. From the female's viewpoint, an attraction to sneakers could occur for several reasons, such as greater conspicuousness of a group of males in spawning condition, enhanced fertilization success, or benefits of mixed paternity or paternity by genetically superior males. The proximate cue could be based on the group of males themselves, or the presence of their sperm in mussels, which females may

smell when inspecting the flow of water from the exhalent siphon. Here, we recorded the behavior of dominant males toward other males during courtship at different male densities and we investigated the mechanisms that may lead to a low level of aggression against sneakers at the initial stages of territory establishment. We investigated both the benefit of sneakers and the cost of aggression against sneakers in female attraction. Finally, we discuss why females may prefer to spawn in the presence of several males.

Methods

Bitterling were collected in March 2000 by electrofishing from Reach Lode, a slow-flowing canal that feeds into the River Cam in Cambridgeshire, UK (see Reynolds et al. 1997; Reynolds and Guillaume 1998). Mussels, *Anodonta anatina*, were collected from the same canal at the same time. Fish and mussels were transported to the University of East Anglia and kept separately in large aquaria (120×60 cm, 40 cm high) in the laboratory. The temperature of the water was increased gradually from 12 to 18°C and the light cycle set to match the natural cycle so that the fish would enter reproductive condition. Two to three mussels were put into the aquaria with the bitterling to stimulate the females to develop ovipositors, but the mussels were covered as soon as one female had started to develop an ovipositor to prevent females from spawning before experimentation. The fish were fed a variety of frozen invertebrates (chironomid larvae, *Tubifex* and *Daphnia*) ad libitum. Mussels were fed green algae (*Chlorella vulgaris*).

To determine female and male behaviors at different male densities, a randomized block experimental design was applied with four different male densities as treatments and females as the blocking factor. Four experimental aquaria (120×60 cm, 40 cm high) were established with either one, two, four, or six males. The males ranged in size from 50 to 61 mm standard length and were chosen randomly for each replicate. All aquaria had an undergravel filter system, both artificial and real vegetation, and a mussel that did not contain bitterling embryos or larvae. The day after the males had been placed into the aquaria, a single female with a newly developed ovipositor was sequentially introduced to each of the four male density treatments. The order was alternated between replicates according to a predetermined scheme to eliminate an effect of order on the results. Females with developed ovipositors can spawn up to eight times during 1–2 days (personal observation) and the female was given a 2-h resting period after each period of time in an experimental aquarium. The female was first enclosed in a net bag to acclimatize her to the aquarium, but after 1 min she was released. The fish were video-filmed until 2 min after spawning or until 15 min had elapsed since the female first inspected the mussel in cases where the female did not try to spawn within this time. When the female did not try to spawn within 15 min, the time until spawning was set at 15 min, which is a conservative measure. A time limit of 15 min was chosen because females in the field usually spend less than a minute with a male before deciding whether or not to spawn.

One hour after the female was removed from each aquarium, a second female was introduced and the same procedures with a randomized block design were followed. This was done because males become more aggressive once they have received some eggs. Again, the same female was transferred among all four male density treatments with a 2-h rest interval. Thus, each female was tested four times (four male densities) and each set of males was tested twice (first and second female). We had 15 replicates with different individual fish and mussels.

The following male and female behaviors were recorded from the video tapes of each spawning trial: (1) time until the female first inspected the flow of water from the mussel, (2) time from inspection to first spawning attempt (i.e., when the female dips

down suddenly onto the mussel and strikes the exhalent siphon with her ovipositor), (3) attacks on males by the dominant male and attacks on the female by all males, (4) the percentage of time that the dominant male spent courting the female by attempting to lead her to the mussel and by releasing sperm over the mussel, and (v) rate of ejaculations by the dominant male and by the sneakers. Spawning attempts were recorded instead of successful spawnings because the success of spawning depends in part on the opening of the mussel's siphon. Females may fail to penetrate the siphon with the ovipositor if the opening is small. The dominant male was the male that after spawning chased away the other males. He could be separated from the other males by his behavior, by his bright-red nuptial coloration during courtship, and by usually being the largest male (see Candolin and Reynolds 2001).

Non-parametric tests were used when the assumptions of parametric tests were not met. Courtship activity was arcsine square-root transformed before analyses. All probabilities are two-tailed.

Results

Male aggression, courtship behavior, and ejaculation rate

The rate of attacks by the dominant male against other males was low during the first female presentation before spawning and did not differ significantly among the male densities (Fig. 1a, Table 1). After spawning, the rate of attacks increased (Wilcoxon matched-pairs signed-rank test on the mean rate of attacks of the three male densities, $T_+ = 120$, $n = 15$, $P < 0.001$) and the highest rate occurred at the highest densities (Fig. 1a, Table 1). During the second female presentation, the rate of attacks by the dominant male before spawning was higher than during the first female presentation ($T_+ = 119$, $n = 15$, $P < 0.001$; Fig. 1b) but did not differ significantly among male densities (Table 1). Again, the dominant male increased his rate of attacks greatly after spawning ($T_+ = 120$, $n = 15$, $P = 0.001$) and was most aggressive at higher male densities (Fig. 1b, Table 1).

The rate of attacks by males on the female before spawning was low with both the first female (mean \pm SE rate of attacks of the four male densities = 0.12 ± 0.04 , $n = 15$) and the second female (0.17 ± 0.04) and did not differ among male densities (Table 1). Similar results were obtained if the analyses were carried out separately for the dominant and the other males.

Courtship activity of the dominant male was negatively related to his rate of attacks on other males

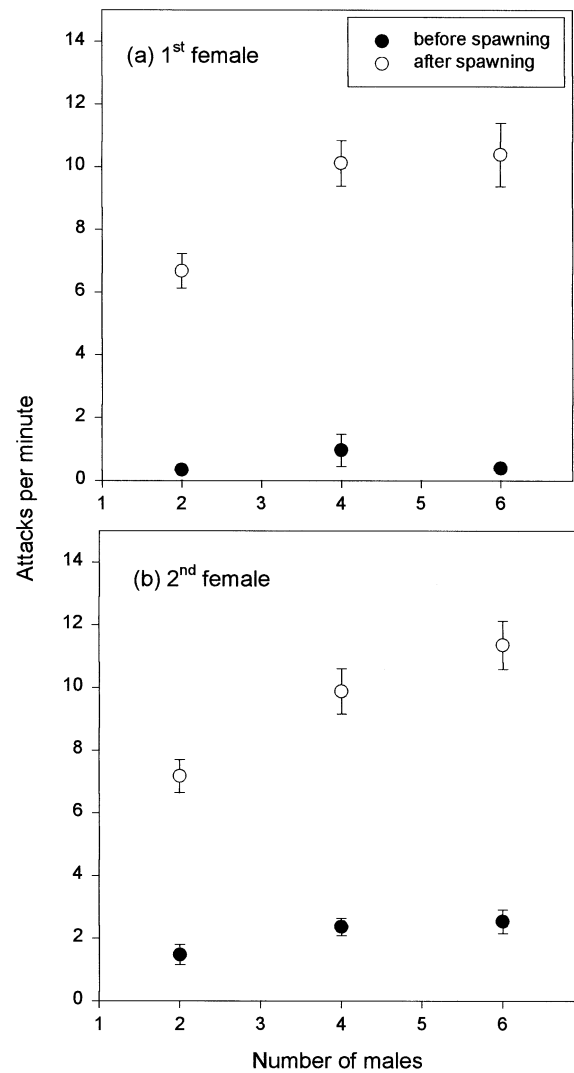


Fig. 1 The rate of attacks (mean \pm SE) by the dominant male against other males before and after spawning with the first female (a) and the second female (b)

(Fig. 2). This was true for both the first and the second female, at each of the three male densities (all $r_s < -0.53$, $P < 0.041$), except at a density of four males with the second female ($r_s = -0.36$, $P = 0.19$). Courtship activity by the

Table 1 Effects of male densities on behavior of the dominant male, and on attacks by all males against females. Friedman's test (χ^2) and mixed-model ANOVA (F) with female as a random factor were used for analyses

		First female			Second female		
		χ^2/F	<i>df</i>	<i>P</i>	χ^2/F	<i>df</i>	<i>P</i>
Attack rate on males	Before spawning	$\chi^2 = 1.23$	2	0.54	$\chi^2 = 4.13$	2	0.13
	After spawning	$\chi^2 = 8.10$	2	0.017	$\chi^2 = 20.8$	2	<0.001
Attack rate on females (by all males)		$\chi^2 = 0.50$	3	0.92	$\chi^2 = 1.58$	3	0.66
Courtship activity (%)		$F = 2.44$	3,42	0.078	$F = 13.41$	3,42	<0.001
Ejaculations (%)	Before spawning	$F = 13.47$	2,28	<0.001	$F = 0.99$	2,28	0.38
	After spawning	$F = 3.48$	2,28	0.045	$F = 2.25$	2,26	0.12

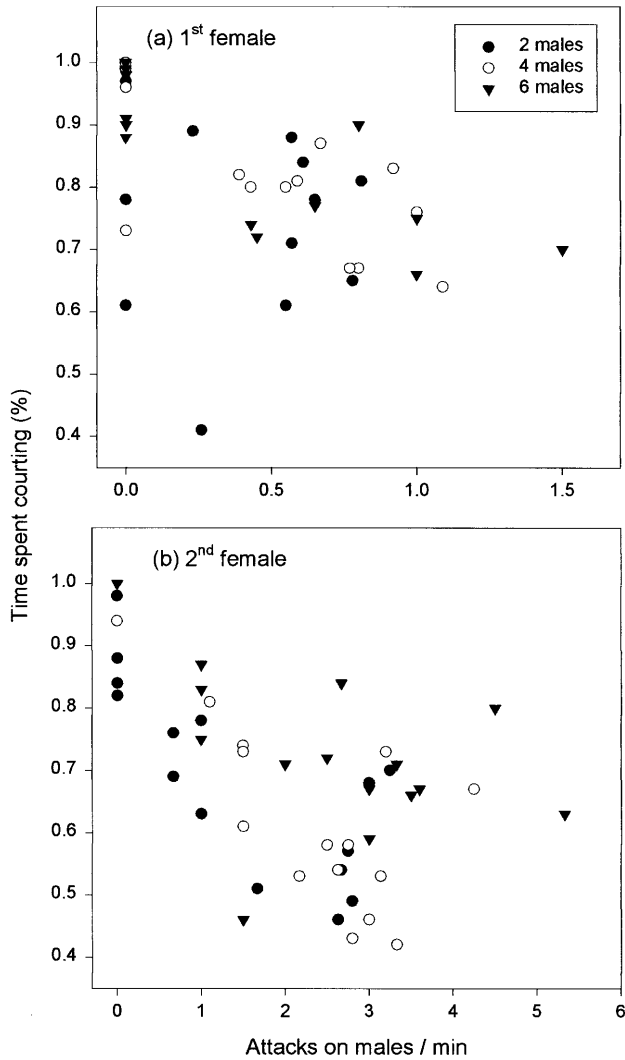


Fig. 2 Relationship between attacks on other males by the dominant male before the female spawned and the proportion of time that he spent courting the female during the first female presentation (a) and the second female presentation (b). Untransformed courtship values are shown

dominant male tended to increase with male density during the first female presentation, whereas single males performed more courtship during the second female presentation (Tukey HSD, $P < 0.004$ for all comparisons between single and multiple males; Fig. 3, Table 1).

The proportion of ejaculations that were performed by the dominant male decreased with male density with the first female, both before and after spawning (Fig. 4a, Table 1), but not with the second female (Fig. 4b, Table 1). However, the proportion of ejaculations that were performed by the dominant male increased after spawning (paired t -test on the mean ejaculation rate of the three male densities combined: first female, $t_{14} = 12.5$, $P < 0.001$; second female, $t_{14} = 6.9$, $P < 0.001$). This was due to the dominant male increasing his ejaculation rate after spawning (first female, $t_{14} = 5.90$, $P < 0.001$; second female, $t_{14} = 3.42$, $P = 0.004$), whereas the other males de-

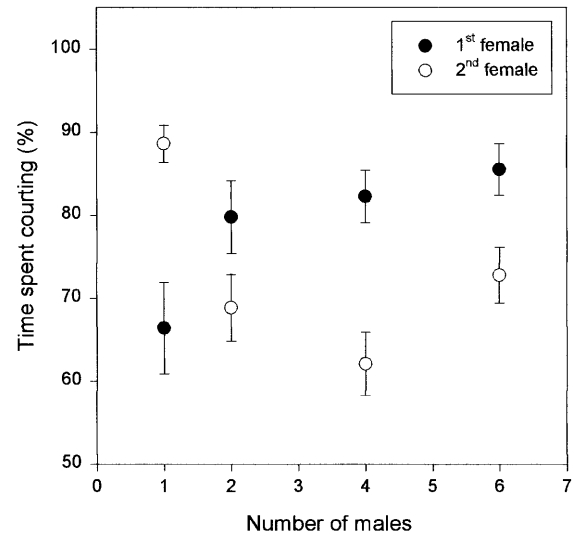


Fig. 3 Mean (\pm SE) time spent by the dominant male courting the first and second female at different male densities. Untransformed courtship values are shown

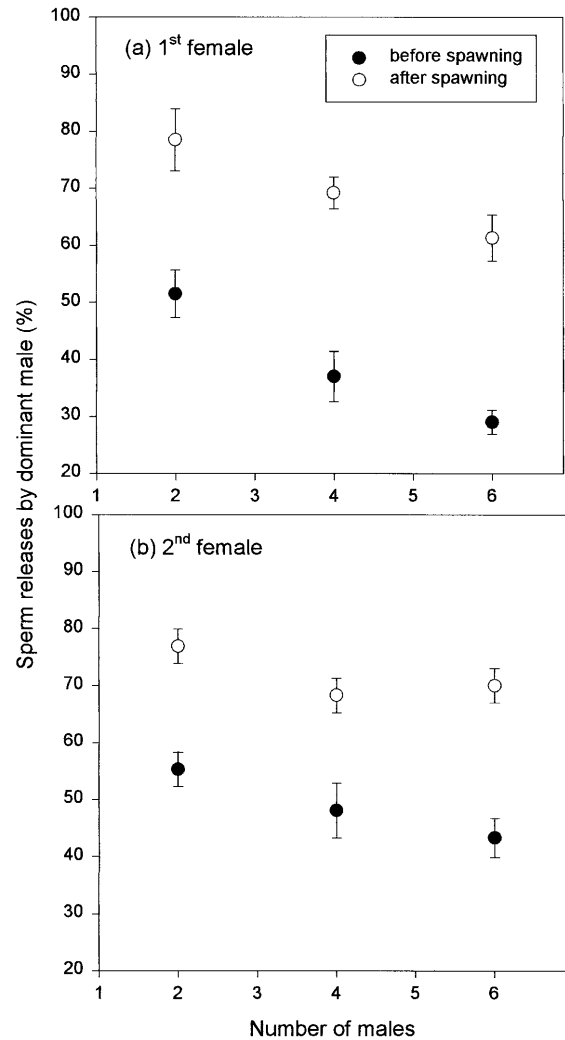


Fig. 4 The proportions of ejaculations (mean \pm SE) performed by the dominant male before and after spawning with the first female (a) and the second female (b)

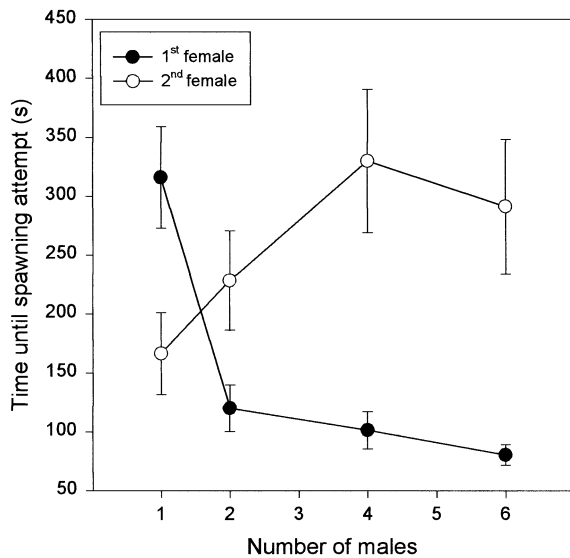


Fig. 5 Time (mean \pm SE) until the first and the second female attempted to spawn at different male densities

creased their ejaculation rate (first female, $t_{14}=3.58$, $P=0.006$; second female, $t_{14}=3.22$, $P=0.003$).

Female behavior

The time until the first female attempted to spawn decreased with the density of males (repeated-measures ANOVA with linear contrast term: $F_{1,14}=24.40$, $P<0.001$; Fig. 5). The decrease remains when controlling for the proportion of time that the dominant male spent courting, although courting activity also influenced the time until spawning attempt (mixed-model ANOVA with courting as covariate: male density, $F_{3,41}=13.48$, $P<0.001$; courting, $F_{1,41}=7.87$, $P=0.008$). The decrease was due both to a decrease in the time until inspection of a mussel (repeated-measures ANOVA with linear contrast term: $F_{1,14}=14.50$, $P=0.002$) and a decrease in the time from inspection to spawning attempt ($F_{1,14}=4.64$, $P=0.049$).

In contrast, the time until the second female attempted to spawn, when males were more aggressive, increased with density (repeated-measures ANOVA with linear contrast term: $F_{1,14}=8.22$, $P=0.012$; Fig. 5). This was not due to the presence of eggs in the mussel, as the time until inspection (before the females had approached the mussel) increased with density (repeated-measures ANOVA with linear contrast term: $F_{1,14}=9.64$, $P<0.008$) whereas the time from inspection to spawning attempt was not significantly affected by male density (repeated-measures ANOVA: $F_{3,42}=0.51$, $P=0.68$). This resulted in the time until a spawning attempt increasing from the first to the second female as the rate of attacks by the dominant male on other males increased (interaction term in repeated-measures ANOVA with rate of attacks

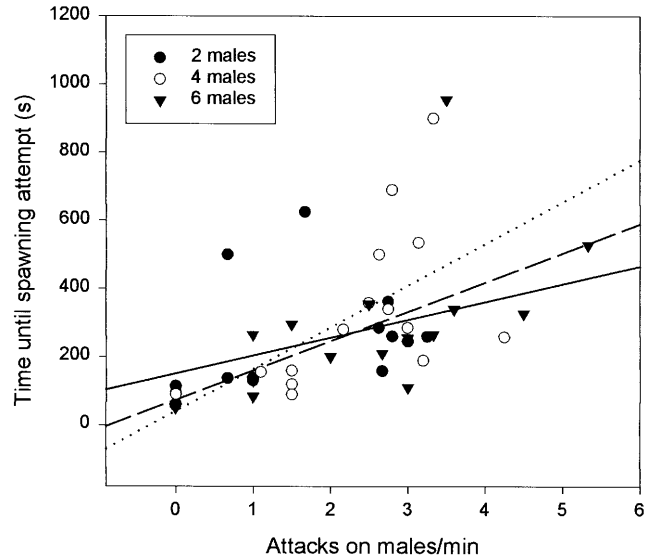


Fig. 6 Relationship between time until females attempted to spawn and rate of attacks by the dominant males on other males at different male densities during the second female presentation (solid line two males, dotted line four males, dashed line six males)

during the second female presentation as covariate: two males, $F_{1,13}=3.31$, $P=0.092$; four males, $F_{1,13}=6.74$, $P=0.022$; six males, $F_{1,13}=5.64$, $P=0.034$).

Male aggression interrupted courtship and the number of times that the second female left the male increased with the rate of attacks by the dominant male on other males (Spearman rank correlation, $n=15$: two males, $r_s=0.81$, $P<0.001$; four males, $r_s=0.49$, $P=0.062$; six males, $r_s=0.65$, $P=0.009$). The time until the second female attempted to spawn increased with male aggression, except when only one other male was present (two males, $r^2=0.18$, $F_{1,13}=2.75$, $P=0.121$; four males, $r^2=0.31$, $F_{1,13}=5.91$, $P=0.030$; six males, $r^2=0.32$, $F_{1,13}=6.17$, $P=0.027$; Fig. 6).

Discussion

Most male bitterling showed a low level of aggression against other males around a mussel as long as a female had not spawned in the mussel. This is in contrast to several other species where sneakers are attacked vigorously from the initial stages of territory establishment. This unusual pattern could be explained by the acceptance of sneakers conferring some benefits or by the cost of aggression being high. We found support for both possibilities. The presence of several males decreased the time until a female spawned during the first female presentation (when the level of aggression was low), whereas increased aggression during the second female presentation interrupted courtship and increased the time until spawning. Time until spawning is an important measure of the willingness of a female to spawn, as females in the field usually spend less than a minute inspecting a mussel before they decide whether to spawn or to leave and

search for another male with a mussel. Thus, females that took a long time before spawning probably would not have spawned with the male under natural conditions. The results therefore suggest that a low level of aggression against sneakers is beneficial in female attraction.

For low aggression against sneakers before spawning to be beneficial to dominant males, the increased spawning success in the presence of sneakers must offset the cost of lost fertilizations. Sneakers may represent little threat if they spawn much before the female because the potential of sperm to fertilize ten eggs has been found to decrease rapidly, from 100 to 10% in 3 min, due to osmotic stress in freshwater (Billard 1986; Kanoh 1996), and because much of the sperm released before female spawning might be ventilated through the mussel or out-competed by sperm released by the dominant male after spawning. Moreover, dominant males appear to minimize the cost of sneakers by becoming highly aggressive against other males after the female has spawned, when there are no more benefits to be gained by accepting sneakers. Most eggs are possibly fertilized by the sperm released after spawning and the dominant male may thus be able to secure a high fertilization success by preventing other males from releasing sperm at this time. Paternity analyses are required to confirm this.

The dominant male was more aggressive against other males during the second female spawning when the mussel already contained some eggs. This could be explained by three different hypotheses. First, a male's assessment of a mussel may change after a female has spawned in it. Females base their final spawning decision on the quality of the mussel (Candolin and Reynolds 2001) and a male may therefore become more aggressive toward competitors when the value of the mussel as an oviposition site has been proven. Second, negative density-dependent survival of eggs in mussels may decrease the value of each new spawning (Smith et al. 2000). Dominant males might therefore have to trade the benefits of sneakers for mate attraction both against reduced fertilization success and an increased mortality rate among offspring already present in the mussel. However, this hypothesis does not explain why single males increase their courtship during the second spawning, and it is contradicted by the unchanged level of aggression against females. A third possibility is that the increase in aggression is a carryover from the first spawning, 1 h earlier, when the male became highly aggressive after the female had spawned.

Why do bitterling females spawn more readily when several males are present? This is in contrast to several other fish species where females avoid spawning with males adopting parasitic strategies (Taborsky 1994). In the Mediterranean wrasse, *Symphodus ocellatus*, female spawning rate has even been found to increase when sneakers are removed (Alonzo and Warner 2000). The proximate cue that attracts bitterling females appears to be both the presence of several males and increased courtship under male competition, as females spawned

sooner when several males were present (at low aggression levels) and this partly correlated with increased courtship activity. Increased harassment by other males cannot explain the reduction in time until spawning, as the rate of attacks on females was low and did not differ between male densities. The ultimate reason for the preference of multiple males is not known. Numerous hypotheses have been suggested for multiple mating in other taxa, invoking either direct or indirect benefits (Reynolds 1996; Jennions and Petrie 2000). The presence of several males could increase fertilization success or the intensity of sperm competition and increase the chances that the best male fertilizes most of the eggs (Eberhard 1998). The presence of several males could also indicate a good spawning site with a high offspring survival rate. Moreover, the cost to the female of spawning with sneakers is possibly lower than in species with male parental care where a male may reduce his investment in the offspring if he is uncertain of his paternity (Wright 1998). Alternatively, the preference could be a non-adaptive social response to the aggregation of males or to increased mating stimuli, but we doubt that selection would end there.

This study also raises the question as to why the response of bitterling males to sneakers differs from that of several other species, such as the threespine stickleback (Goldschmidt et al. 1992) and the common goby, *Pomatoschistus microps* (Magnhagen 1995, 1998), where males attack sneakers even before they have succeeded in gaining any matings. The bitterling system differs from the two other systems in the lack of investment in nest building and in no direct care of the eggs. A bitterling male may therefore have a higher potential reproductive rate and delay investment in defense of a spawning site until it has proved to attract mates. In contrast, a stickleback or a goby male that has invested in nest building will invest in territory defense from the start as he has less energy available for deserting and building a new nest. Moreover, the number of males intruding on a territory might be higher in the bitterling and increase the cost of defending the spawning site against other males.

To conclude, bitterling males showed a low level of aggression against sneakers at the initial stages of territory maintenance as long as the mussel did not contain any eggs. This was beneficial because the presence of sneakers reduced the time until the female spawned and because aggression interrupted courtship and increased the time until spawning. The behavior of the sexes differs, however, from several other species where sneakers are not tolerated and females avoid spawning with them. This could be related to differences in the investment in nest building and parental care, and in costs of defending the spawning site against sneakers.

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