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ARTICLE

Mate availability affects female choice in a fish with paternal care: female counterstrategies against male filial cannibalism

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Abstract Theory predicts that individuals should adopt counterstrategies against intersexual conflict with their mating partners if the counterstrategies are effective and cost-efficient. In fishes, males with parental care often cannibalize their own offspring, which reduces the female's fitness and creates intersexual conflicts. Males of the goby *Rhinogobius flumineus* cannibalize more eggs in the nest when they have access to additional females prior to spawning. Thus, it is predicted that females will strategically avoid spawning with males that have high mate availability. In the present study, we experimentally tested this prediction. When sexual pairs were placed in tanks, most females (control females; 21/22) successfully spawned inside the nest. In contrast, when a gravid female (stimulus female) that was housed in a small transparent cage was shown to the experiment pairs prior to spawning, only about half of the females (experiment females; 16/29) spawned inside the nest; the remaining females released unfertilized eggs outside of the nest. Moreover, experiment females infrequently accepted and followed males into nests, and delayed spawning more often than control females. *R. flumineus* females prefer males that court frequently. Indeed, experiment females that infrequently received courtship tended to spawn outside of the nest. However, infrequent courtship alone could not explain outside-nest spawning, delay in spawning, or the shorter stay of females in nests. These results imply that the presence of a stimulus female dampens female spawning with males. We suggest that *R. flumineus* females may strategically reject or hesitate to spawn with males that have high mate availability, and that this spawning avoidance may be a counterstrategy against male filial cannibalism.

Keywords Female choice · Female counterstrategy · Filial cannibalism · Mate availability · Sexual conflict

Introduction

In many nest brooding fishes, males exclusively care for broods of multiple clutches from different females. In this type of brood care system, males that attend nests occasionally consume their own offspring, a phenomenon known as filial cannibalism (e.g., Trivers 1972; Rohwer 1978; FitzGerald 1992; Sargent 1992; Hoelzer 1995; Manica 2002). Filial cannibalism is widespread among fishes with paternal care and is generally accepted to be an adaptive behavior (e.g., Rohwer 1978; Elgar and Crespi 1992; Sargent 1992; Kondoh and Okuda 2002; Manica 2002). Through the act of filial cannibalism, males use some offspring as an investment in future reproduction, and therefore increase their lifetime reproductive success (e.g., Rohwer 1978; Sargent 1992; Manica 2002). Although filial cannibalism enhances the male's fitness, the female whose eggs are eaten pays a cost because her reproductive fitness depends on the number of successful hatching of the

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current offspring. Therefore, this scenario creates intersexual conflict over the parental investment in the current brood (Lindström 2000; Arnqvist and Rowe 2005). Parental care theory predicts that sexual members often adopt counterstrategies against their mate's egoism with respect to intersexual conflict, if the adoption is advantageous, i.e., has a low cost/benefit ratio (Trivers 1972; Clutton-Brock 1991). Filial cannibalism is one of the major causes of egg mortality in fishes with paternal care (Elgar and Crespi 1992; Manica 2002). Therefore, if females are able to discriminate, they will mate with males that conduct filial cannibalism less frequently (e.g., Lindström 2000; Manica 2002; Okuda et al. 2002; Takahashi and Kohda 2004).

The frequency of filial cannibalism by parental male fish differs significantly among individuals of the same species. For example, caring males that are in poor body condition perform cannibalism more frequently than males in good condition (e.g., Hoelzer 1992, 1995; Marconato et al. 1993; Okuda and Yanagisawa 1996; Kvarnemo et al. 1998; Takahashi and Kohda 2004; but see Gomagano and Kohda 2008). Thus, females will choose males in good condition or those that perform intensive displays because these males are less likely to cannibalize eggs (e.g., Knapp and Sargent 1989; Takahashi and Kohda 2004). This type of female mate choice can be regarded as a counterstrategy against male filial cannibalism (Lindström 2000; Manica 2002).

Another example of strategic female choice among nest-brooding fishes is when females prefer males that have egg-containing nests as opposed to nests without eggs (e.g., Knapp and Sargent 1989; Kraak and Groothuis 1994; Forsgren et al. 1996; Okuda et al. 2002). If a male tends to cannibalize a constant number of eggs, then a new clutch deposited nearby, or mingled with, the previous clutches will be less vulnerable to male filial cannibalism, due mainly to dilution effects. In contrast, a small single clutch will often be cannibalized entirely. Thus, eggs deposited in a nest with previous clutches will have a higher hatching rate than broods deposited alone (e.g., Rohwer 1978; Lindström 2000; Manica 2002; Okuda et al. 2002). This type of female choice is another example of a female counterstrategy against male filial cannibalism.

It has been hypothesized that high mate (female) availability facilitates male filial cannibalism (Okuda and Yanagisawa 1996; Kondoh and Okuda 2002; Okuda et al. 2004). Recently, this hypothesis was experimentally tested in the freshwater goby *Rhinogobius flumineus,* which is a nest brooder (Myint et al., personal observations); when a cage-housed gravid female was shown as a stimulus to males before spawning with another female, the brood that was spawned by the female was cannibalized more often by the male. Thus, it is plausible that *R. flumineus* females will adopt a choice strategy against this type of male filial cannibalism if they can recognize the availability of potential mates for the target male. It may be predicted that when mate availability is high, females may avoid spawning eggs with these males and/or look for other nests to spawn because the eggs will be more likely to be cannibalized than eggs that are spawned at nests with lower mate availability.

The aim of this paper was to experimentally examine whether *R. flumineus* females employ a choice strategy against male filial cannibalism that is facilitated by mate availability. To examine these predictions, female spawning behaviors of sexual pairs were observed in an experimental aquarium in which a gravid female in a small cage (stimulus female) was presented as a visual stimulus. The behaviors of the experimental females were compared to spawning behaviors of control females that were only shown an empty cage. We predicted female reactions as follows. (1) When the experiment females notice the presence of a stimulus female, they will be more likely to refuse to spawn with the males than control females. (2) Alternatively, if experiment females spawn with the males, spawning will be delayed compared to the spawning of control females. (3) Additionally, because if females accept courting males, they will follow the males into the nests frequently and often stay in the nests, experiment females will spend less time inside the male nests before spawning than control females. If these three predictions are confirmed, these results will show that females reject or hesitate to spawn when an additional female is present. Furthermore, positive results would partially support the mate availability hypothesis (Lindström 2000; Kondoh and Okuda 2002; Manica 2002; Myint et al., personal observations). We predict that courtship frequency per female will be lower in the experiment where males will court directly toward two females at a time than in the control where males will exclusively court one female. We also examined whether the females react to courtship infrequencies, because *R. flumineus* females prefer males that perform intensive courtship (Kohda et al. unpublished data).

Materials and methods

Subject fish and maintenance

The lizard goby *Rhinogobius flumineus* inhabits mountain streams in Japan (Mizuno 1960). During the breeding season from late May to early August, adult males construct a nest under a stone in the stream bottom. The goby shows conspicuous sexual dimorphism during the breeding season, with males having longer first dorsal fin than females (Mizuno 1960). Unlike other *Rhinogobius* gobies, this fish spawns small numbers (usually ca. 150 eggs) of larger eggs (ca. 6 mm in long diameter) in a single layer on the ceiling of nest stones (Mizuno 1960). It is suggested that females may spawn eggs twice in a reproductive season, and females spawn almost all of the mature eggs in the ovary during a spawning event (Matsumoto 1996). The mating system in *R. flumineus* is generally monogamous but occasionally polygynous (ca. 10% of breeding nests contain two or three clutches, $n = 214$, Matsumoto 1996). A paternal male attends eggs during the egg care period (16 days at 20°C water temperature) (Seki et al. 2000). During this time, males in the wild close the nest entrance with sand and/or small gravel, if available (Mizuno 1960; Matsumoto and Nagoshi 1996). Thus, males may not have any food other than their eggs and may frequently cannibalize eggs during the care period (Matsumoto 1996; Tsujimoto et al. in preparation).

Subject fish were obtained from the Shigo River (the same site as that in Matsumoto 1996; Matsumoto and Nagoshi 1996), Nara Prefecture, Japan, in late May 2006–2008. About 25 individuals of each sex were kept in 10 stock tanks (30 cm W × 60 cm L × 45 cm H) at about 20°C and under 14L:10D light conditions according to their natural habitat. The fish were fed 4.8 g frozen bloodworms once a day. However, food was not provided for 24 h prior to weighing subject fish (to 0.001 g) to control for the weight of undigested bloodworms. To estimate fish body condition, a condition factor [$\mathrm{CF} = 10^6 \times$ total body weight (g)/standard length^3 (mm)] was used as an index of somatic condition (Bolger and Connolly 1989). Each fish was used only once in an experiment. Fish were not sacrificed in this study, and fish including all the hatched young were released at the river collection site after the experiment.

Procedures

We examined whether *R. flumineus* females will hesitate or refuse to spawn with a male when the availability of potential females to the male is increased in the aquarium. We conducted this experiment over the course of 1 month from early June 2006–2008. We prepared experiment tanks at a size of 17 × 30 × 22 cm (Fig. 1). A nest (a slate tile 10 × 10 × 0.5 cm with 2 cm legs at four corners) was set on the small-gravel bottom (2-cm thick), and fish deposited eggs on the nest ceiling (Seki et al. 2000). We recorded the standard length (SL, to 0.1 mm) and body weight (BW, to 0.001 g) of a male from the stock tank, before introduction into an experiment tank. A gravid female with an enlarged abdomen (experiment female; SL and BW measured) was introduced into each experiment tank on the next day when the male was attending the nest.

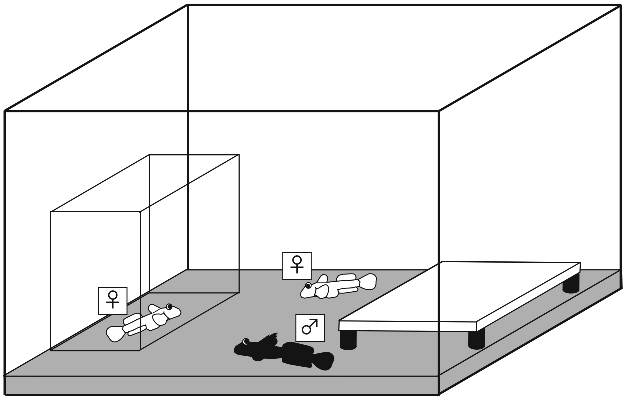

Fig. 1 A sketch of the experimental tank containing a small transparent cage and a nest. A stimulus female is housed in the small cage. A male will court both a spawning female and a stimulus female

To construct a situation of high mate availability, another gravid female with an enlarged abdomen (stimulus female) was housed in a small plastic cage (6.5 × 10 × 10 cm) after being measured for her SL and BW. The stimulus females in the cage were placed on the bottom of the experimental tank immediately after the introduction of the subject female, for a duration of 3 days (Fig. 1). Males and experiment females apparently noticed the stimulus females in the cage because they approached frequently. Stimulus females were shown in 10 trials in 2006, 17 in 2007, and 7 in 2008. If stimulus females spawned eggs inside the cage, they were immediately replaced with another gravid female of similar size. Spawning occurred from the day of introduction to 11 days later. The female's large abdomen shrunk in size after spawning. We checked the female's abdomen and the deposited eggs on the ceiling during the early morning, noon, and evening, and thus, spawning date was precisely determined. Immediately after spawning, females were removed from the tank. Of the 17 experiments with stimulus females in 2007, 5 experiment females entered nests together with males soon after the introduction, and prior to showing the stimulus females, and spawned within 1 day. These cases were omitted from the analyses. As a control treatment, an empty plastic cage was put in the tank (6 trials in 2006 and 16 in 2007).

No food was given during the experiments. Aeration by a water filter system maintained the water quality during the experiments. Water temperature and light conditions were the same as the stock tanks. In this experiment, males closed the nest partially.

Here, we briefly describe the spawning behaviors observed during the experiments. All clutches spawned inside the nests were in a compact egg patch (2–3 cm across) with a single layer on the ceiling of the nest tile.

Some females deposited eggs on the glass wall 10 cm above the bottom of the tank (not as compact as egg patches in the nests). Some females that had spawned outside of the nest remained on the glass wall just before and after spawning. In this outside-nest spawning, females occasionally consumed some of their eggs after spawning. Outside-nest eggs became rotten on the next day and were artificially removed.

To record male courtship activities towards females (including stimulus females in the experiment tanks), fish behaviors in the experiment and control tanks were videotaped (Sony, Video Hi8 CCD-TRV80) for 15 min for the first 3 days (2007 and 2008) after the introduction of the females. Courtship behaviors consisted of (1) approaching females, (2) lateral display and quiver dancing with fin spreading around females, and (3) leading females into nests, directed towards either the spawning female or stimulus female (refer to illustration of similar behavioral patterns in *R.* sp. DA, Takahashi 2000). The mean of the total duration (per 15 min) of these three behaviors towards females (including stimulus females) was used as an indicator for male courtship activities. If spawning occurred on the next day after introduction, the observation on day one was used. Males sometimes performed courtship displays toward both females at the same time. Females sometimes followed the leading males, entered nests, and stayed for 10 s on average (up to about 1 min); however, they often left. Before spawning events, females stayed inside the nest with the male. Thus, we used the duration that the females stayed in the nest as an indicator of female acceptance of males. Some video images were poor and could not be used.

Data and statistical analyses

The sizes of spawning pairs were not different across the 3 years (ANOVA, $F_{2,47} = 2.07$, $P = 0.14$ for females; $F_{2,47} = 0.07$, $P = 0.93$ for males), and thus samples from all 3 years were pooled. Size (TL) and the condition factor (CF) of females did not differ between experiment and control treatments [experiment female ($n = 29$) vs. control female ($n = 21$), mean ± SD = 55.9 ± 3.1 vs. 54.5 ± 3.3 mm, t test, $df = 48$, $t = -1.51$, $P = 0.14$ in size (TL); 22.8 ± 1.5 vs. 22.8 ± 2.0, $df = 48$, $t = -0.13$, $P = 0.89$ in CF). The same results were found for males (experiment tank vs. control tank, 62.4 ± 4.3 vs. 61.3 ± 5.0 mm, $df = 48$, $t = -0.86$, $P = 0.39$ in size; 18.3 ± 1.5 vs. 18.2 ± 1.1, $df = 48$, $t = -0.44$, $P = 0.66$ in CF). All analyses were performed with Statistica software (Stat Soft, UK). Nonparametric statistics were used in most cases where data were not normally distributed. Results are presented as mean ± SD.

Results

Effects of a stimulus female on female spawning

When stimulus females were shown, about one-half (16/29: 6 of 10 in 2006, 6 of 12 in 2007, and 4 of 7 in 2008) of experiment females spawned inside of the nest, while the other 13 females deposited eggs outside of the nest, i.e., on the glass walls of the tanks. Males did not show any aggressions toward these experiment females. The eggs on the glass walls were not cared for by males and all died within 24 h. In contrast, almost all control females (20/21) spawned inside the nest (chi-squared test, Yate's correction, $\chi^2 = 8.27$, $P = 0.004$). These results are consistent with our first prediction.

As secondarily predicted, the number of days that experiment females took to spawn was significantly greater (5.0 ± 2.4 days, range 1–11 days, $n = 29$) than control females (2.8 ± 1.9, 0–9, $n = 21$, Mann–Whitney U test, $z = -3.24$, $P = 0.001$, Fig. 2a). The number of days that experiment females took to spawn did not differ between outside-nest spawning (5.5 ± 2.7 days, $n = 13$) and inside-nest spawning (4.5 ± 2.0, $n = 16$; $U = 87.0$, $P = 0.45$, Fig. 2a). In control treatment, there was one outside-nest spawning, which occurred 8 days after introduction. The number of days that experiment females took to spawn inside nests was significantly greater than the number of days that control females spawned inside nests (2.5 ± 1.9 days, $n = 20$, $U = 90.5$, $P < 0.001$, Fig. 2a).

As was also predicted, experiment females stayed inside the nest significantly less than control females (experiment females 1.18 ± 1.82 min/15 min, $n = 19$; control female 6.42 ± 6.53 min/15 min, $n = 11$; $U = 51.0$, $P = 0.02$, Fig. 2b). Time in the nest before spawning did not differ between experiment females that spawned outside the nest (0.96 ± 1.47 min/15 min, $n = 9$) and experiment females that spawned inside the nest (1.38 ± 2.15 min/15 min, $n = 10$; Mann–Whitney U test, $U = 45.0$; $P = 0.1$, Fig. 2b).

Effect of body size and condition on female behavior

Neither size nor CF differed between the experiment females that spawned inside the nest (56.7 ± 3.5 mm in size, 22.5 ± 1.9 in CF, $n = 15$) and females that spawned outside the nest (55.1 ± 2.3 mm, 23.1 ± 1.4 CF, $n = 14$; Mann–Whitney U test, $U = 70.5$, $P = 0.13$ in size, $U = 73.0$, $P = 0.16$ in CF). Neither male size nor male CF differed between inside-nest spawning and outside-nest spawning ($U = 97.0$, $P = 0.73$ in size; $U = 73.0$, $P = 0.16$ in CF).

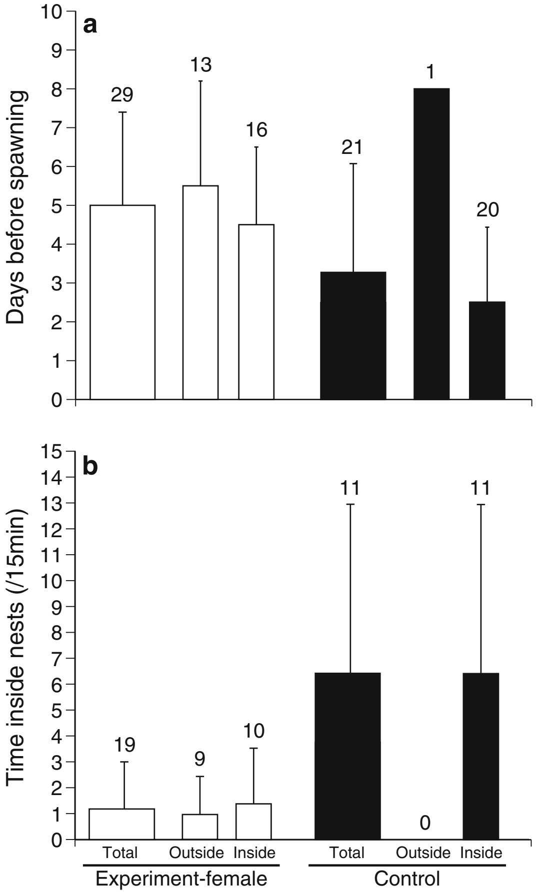

Fig. 2 Days before spawning (**a**) and time spent inside nests (per 15 min) before spawning (**b**) in experiment females and control females. Spawning sites of experiment females (inside or outside nests) are also shown. *Numerals above error bars* are sample sizes

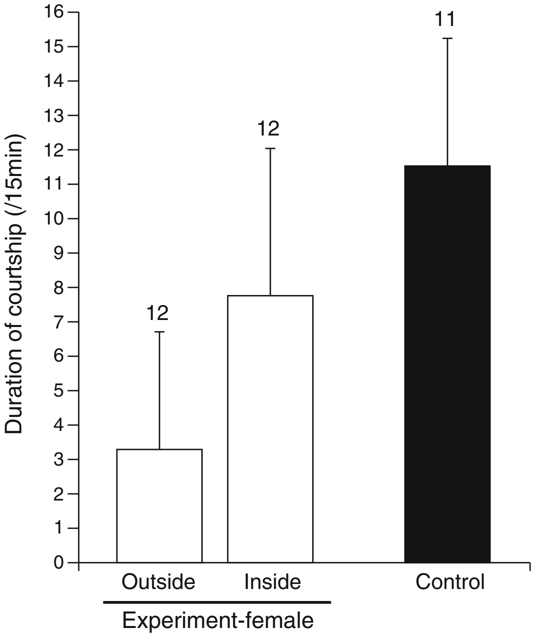

Fig. 3 Courtship duration (per 15 min) toward experiment females who spawned outside the nest and inside the nest, and control females. *Numerals above error bars* are sample sizes

Effect of male courtship on female spawning

We examined courtship intensities, which may affect female spawning behaviors. The duration of courtship (per 15 min) directed towards experiment females that spawned inside the nest (7.76 ± 4.28 min, $n = 12$) was longer than that observed toward outside-nest spawning females (3.29 ± 3.42 min, $n = 12$; Mann–Whitney *U* test, $U = 27.0$, $P = 0.01$), but shorter than control females (11.53 ± 3.71 min, $n = 11$; $U = 31.5$, $P = 0.034$; Fig. 3).

Discussion

Our previous study shows that caring males of *R. flumineus* cannibalize eggs more frequently when their mate availability is higher (Myint et al., personal observations), and we predict the possibility of counterstrategies by spawning females against this type of filial cannibalism (Lindström 2000). Our present experiments provide three major results that are consistent with our predictions: (1) experiment females that noticed the presence of another female spawned less frequently inside nests than control females, (2) experiment females delayed spawning compared to control females, and (3) experiment females rarely stayed inside nests before spawning. Experiment females were courted and never refused or attacked by males, and thus the delay in spawning or outside-nest spawning cannot be ascribed to male rejection. Moreover, female size and body condition did not differ between inside-nest spawning females and outside-nest spawning females. These results may support the hypothesis that *R. flumineus* females avoid and/or hesitate to spawn inside the nests when these males have increased mate availability.

However, an alternative hypothesis should be examined that these females may only respond to the duration of courtship behaviors because *R. flumineus* females prefer mates that court intensively (Kohda et al., unpublished data), similar to many other fishes (e.g., Karino 1995; Knapp and Kovach 1991; Takahashi and Kohda 2004). Indeed, experiment females that spawned inside nests received more courtship time than females that spawned outside nests (Fig. 3). If a female's decision to mate largely depends on courtship duration of males, it is predicted that experiment females that spawned inside nests might spawn more quickly after introduction to tanks and might stay inside nests for longer duration before spawning than experiment females that spawned outside nests, because the females spawning inside nests were courted for significantly longer duration than females spawning outside nests. However, the number of days females spent after introduction and time in nests before spawning were not different between experiment females spawning inside nests and spawning outside nests (Fig. 2). The delay of spawning and shorter duration inside nests of the females that spawned inside nests can not be explained fully by the difference in courtship duration and probably due to the presence of the stimulus female.

In previous studies where females were paired with poor-conditioned males that performed courtship displays less frequently, most females accepted those males and spawned inside the nests (*R. brunneus*, Takahashi and Kohda 2004; *R. flumineus*, Tsujimoto et al., unpublished data). In these studies, stimulus females were not shown. In our present experiments, however, about one-half of experiment females that were shown a stimulus female and were courted less frequently refused to mate with males (although these males were in good condition). The comparison of the previous and the present studies may also suggest that the frequent mating rejections by the experiment females might be not only due to infrequent courtship but also due to the presence of stimulus females.

It has been reported that in sex-role-reversed fish species, or fishes in populations with female-biased operational sex ratios, dominant females may depress spawning behavior of subordinate females (e.g., Kvarnemo and Arnesjo 1996; Shibata and Kohda 2006). Although the sex ratio in the experiment tanks was female-biased, stimulus females housed within the small cage could not attack and prevent the experiment females from staying and spawning inside nests. Thus, an effect of social behaviors of other females on the delay of spawning will not be the case in our study.

It is likely beneficial for experiment females to spawn inside the nest, whereby a portion of eggs will hatch, rather than spawning outside of the nest. Eggs deposited on the glass wall were not fertilized, and spawning outside of the nest is apparently a maladaptive behavior. Females sometimes consumed the eggs on the glass wall, but most were rotten by the next day. In female stock tanks (containing no males), some gravid females released eggs in a loose patch on the glass walls or on the bottom substrates (Myint, personal observations), likely because females with large abdomens were ready to spawn and probably not able to keep mature eggs in their ovaries. The extra-nest spawning behaviors performed by the experiment females resemble the egg releasing of females in the stock tanks. In the wild, many nest sites of *R. fluminus* are in close proximity to rocky streambeds, and females may visit several nests within a short time (Matsumoto 1996; Matsumoto and Nagoshi 1996). Experiment females that released eggs on the glass wall had often stayed on the upper area of the glass wall just prior to spawning (Myint, personal observations), although these females did not receive any aggressive behaviors from males. We regard these females as attempting to look for other nests or other males. That is, the experiment females may have decided not to mate with the male and then tried to locate other nests; however, they were unable to retain the eggs and thus released them on the glass wall. If we had used much larger experiment tanks containing several nests with males, the experiment females may have left nests associated with stimulus females to look for other nests.

The experiment females may have chosen mates based on courtship intensity, and they may also evaluate the presence of the stimulus female. The stimulus female itself may be an immediate (proximate) cue that is used by experiment females to decide whether or not to mate (Neff and Sharman 2002). These female gobies of *R. flumineus* live for 2–3 years, and spawn only once or twice a year (Matsumoto and Nagoshi 1996). *R. flumineus* females leave nests immediately after spawning and do not have a chance to learn the fate of the eggs that they spawn (Myint, personal observation). Thus, the response to the stimulus females will be an innate behavior.

Female spawning rejection of *R. flumineus* in association with high mate availability might be a female counterstrategy against frequent male filial cannibalism. Another type of counterstrategy against male cannibalism, a practice often conducted by poor conditioned males (e.g., Lindström 2000; Manica 2002), has already been identified: female *R. flumineus* discriminate between poor and good condition males based on the frequencies of courtship dances, preferring good condition males who will be less likely to cannibalize eggs. These practices indicate that *R. flumineus* females may adopt at least two female choice strategies to increase the hatching success of eggs. Multiple cues in female preference within a species have been reported in some fishes, but studies have rarely focussed on this issue (e.g., Lindström 2000; Candolin 2003). Future studies should elucidate the costs and benefits of these counterstrategies of *R. fluminus* females, and it will be interesting to evaluate the relative importance of the effects of these mechanisms.

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