Filial cannibalism in the barred-chin blenny *Rhabdoblennius ellipes*: males do not preferentially eat young eggs

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Abstract

Female barred-chin blenny *Rhabdoblennius ellipes* prefer to mate with males tending young eggs, possibly to reduce the risk of male selective filial cannibalism against young eggs in the nests. To test this hypothesis, we conducted aquarium experiments with nests containing eggs at different developmental stages. All egg-tending males consumed both young and old eggs. However, the observed and expected number of consumed young eggs did not differ, indicating that R. ellipes males do not selectively cannibalize young eggs in nests with eggs of mixed developmental stages. Relatively small differences in egg age within a nest may explain this nonselectivity in this species.

Introduction

Parental care improves growth and survival of offspring (Clutton-Brock 1991; Eggert et al. 1998); however, this is achieved at the expense of the parents' condition, such as deterioration of the condition of the body itself (Barbieri et al. 1992; Marconato et al. 1993; Lindström and Hellström 1993; Takahashi and Yanagisawa 1999), reduction in breeding opportunity (Jamieson et al. 1992; Reynolds and Jones 1999; Komdeur et al. 2002; Manica 2002a), and increase in mortality (Dufresne et al. 1990). Therefore, to maximize their future reproductive success, occasionally parents partially or totally consume their offspring as a nutrition source (e.g., Gomagano and Kohda 2008; Mehlis et al. 2009). Filial cannibalism has been documented in a wide range of animal taxa (Polis 1981); it is particularly common in teleost fish with paternal care (Manica 2002b).

Filial cannibalism strongly affects the evolution of the reproductive strategy of the noncannibalistic sex (usually female in fish). Females usually leave the spawning site after egg-laying; therefore, the only strategy for females to avoid or minimize the influence of male filial cannibalism is mate choice (Manica 2002b). In several fish species, females prefer to mate with males defending nests that contain eggs (Marconato and Bisazza 1986; Unger and Sargent 1988; Kraak and Videler 1991; Goldschmidt et al. 1993; Forsgren et al. 1996) because the females reduce the risk of their eggs being cannibalized through the dilution effect (Rohwer 1978; Ridley and Rechten 1981; Unger and Sargent 1988; Forsgren et al. 1996) and benefit from increased male parental investment with an increasing number of eggs (Coleman et al. 1985; Sargent 1988; Petersen 1990; Kraak and Groothuis 1994; Forsgren et al. 1996). Female mate choice is affected not only by the presence of eggs but also by the developmental stage of those eggs. Since the early-stage eggs have higher nutritional value (Rohwer 1978; Petersen and Marchetti 1989) and lower reproductive value because of the lower probability of surviving until hatching and larger requirement of future parental investment (Pressley 1981) compared to the late-stage eggs, male parents are expected to preferentially cannibalize younger eggs if eggs of mixed stages are present in the nests (Rohwer 1978). In such cases, by choosing males caring for young eggs, females can prevent their newly spawned eggs

from being cannibalized by males (Salfert and Moodie 1985; Petersen and Marchetti 1989; Petersen 1990; Sikkel 1989, 1994).

Rhabdoblennius ellipes is a small omnivorous reef fish distributed in the West Pacific Ocean, including the coastal waters of southern Japan; it mainly inhabits intertidal rocky shores (Aizawa 1993). In western Kyushu, Japan, during the breeding season, from late June to early October, males occupy holes made by bivalve mollusks and vacant shells of the vermetid gastropod Serpulorbis imbricatus as spawning nests (Miyano et al. 2006). Spawning occurs in pairs, and the eggs are deposited in a single layer on the inner surface of the nest. Multiple females successively visit a male nest for spawning; therefore, at any single time, males generally care for multiple clutches of eggs at different stages of development. After spawning, males guard and aerate the eggs until they hatch (6–7 days); however, during this period some of the eggs are eaten by egg predators and cannibalized by egg-tending males (Miyano et al. 2006).

Previous study has shown that R. ellipes males caring for young eggs (non-eyed eggs, 0–2 days old) in the nest have approximately ninefold higher mating success than males caring for old eggs (eyed eggs, 3–5 days old) (Matsumoto et al. 2011). The authors conducted egg-switching field experiments between young and old eggs to test the effect of the presence of young or old eggs in the nests on the male mating success; however, contrary to their expectation, the male mating success was neither enhanced by the presence of young eggs in the nests nor inhibited by the presence of old eggs. These results suggested that females choose males with young eggs not by discriminating the developmental stage of eggs in the nests but by using other choice processes (e.g., mate-choice copying; Goulet and Goulet 2006; Alonzo 2008).

It is not clear at this time how R. ellipes females choose males with young eggs and what factors lead to the difference in mating success between males with different ages of eggs, however, examining the adaptive benefits of such a female choice in relation to egg age is indispensable in considering the evolution of the mating processes in this species. There are three possible benefits for females choosing males with young eggs. One obvious benefit is a prolonged dilution effect of egg predation and filial cannibalism on their own eggs. Since the dilution effect increases as the number of eggs in the nest increases, its effect

would be prolonged if females deposited their eggs among young eggs because their eggs would coexist with eggs of other females until those eggs hatch (Sikkel 1989). The second benefit is the avoidance of male egg desertion. R. ellipes males frequently abandon their eggs when they tend a small number of eggs in the nest (Matsumoto et al. 2011), probably because the reproductive value of eggs is lower for the parent than the cost of parental care (Petersen and Marchetti 1989; Forsgren et al. 1996; Lindström and Sargent 1997). If females spawn in nests with young eggs, the number of eggs in the nests should be maintained at a high level for a long period of time. The final possible benefit is avoidance of male selective filial cannibalism of young eggs, as mentioned before. Newly spawned eggs would be selectively cannibalized if females spawn in the nests with old eggs; therefore, they deposit eggs in nests containing young eggs expecting the dilution effect to protect their eggs. To understand the evolution of the reproductive strategy in this species, it is essential to demonstrate the presence of these benefits and to evaluate the relative importance of them. In this study, to test the third hypothesis, we examined male selectivity in filial cannibalism of young eggs by means of egg-manipulating aquarium experiments.

Materials and methods

Fish used in this study were collected in intertidal pools on the Miezaki coast, Nagasaki Prefecture, western Kyushu, Japan (32° 48′ N, 129° 44′ E), from July 28 to September 5, 2007. Males caring for eggs in nests and females with swollen abdomens were captured using a hand net. The sexes were determined by the shape of the genital papillae (Miyano et al. 2006). Five males and 10 females were kept in the experimental tank (140 × 65 × 27 cm) supplied with aerated artificial sea water (35‰; Marine Art Hi, Tomita Pharmaceutical) that contained water to a level of 15 cm and a base covered with sand (5 cm depth). Five concrete blocks (9.5 × 6 × 9.5 cm) with holes (diameter 1.1 cm; length 6.5 cm) were set in the tank as nest sites. Each nest was set to prevent nesting males from facing each other to avoid an influence of the presence of other

individuals on the behavior of the nesting males. A detachable translucent plastic sheet (3.5 × 6.5 cm) was set on the inner surface of the nest side wall to allow it to be withdrawn and repositioned so the number of eggs in the nest could be monitored (Matsumoto et al. 2008). Fish were offered frozen artemia twice a day to satiation; however, no food was provided after spawning.

After spawning, the nest and the egg-tending male were isolated by covering them with a meshed cage (30 × 30 × 30 cm) to avoid egg predation by the other individuals in the tank. Subsequently, the plastic sheet with newly attached eggs (i.e., young eggs <1 day old) was taken from the nest and was carefully cut using scissors into a small rectangular sheet (2.5 × 1.7 cm) almost full of eggs. Old eggs (3–5 days old) used in this experiment were non-kin eggs to the focal males used in these experiments. These old eggs had been collected earlier from artificial nests set in the field near Miezaki coast and kept in a sub-tank with sufficient aeration. R. ellipes males would be unable to discriminate between kin and non-kin eggs in the nests because 96% of males (n = 49) tended experimentally introduced non-kin eggs until the eggs hatched (Matsumoto et al. 2011). A small sheet of old eggs was similarly cut from the egg sheet. The small cut sheet with young eggs and old eggs was attached side-by-side onto another sheet with double-stick tape (Fig. 1). To avoid influence of egg position (depth) within the nest on male egg-eating behavior (Matsumoto et al. 2008; Sikkel 1994), each egg sheet was placed on the main sheet 20 mm from the nest entrance; the side position did not affect the number of consumed eggs (chi-squared test, $\chi 2 = 0.58$, P = 0.45, n = 15). The total initial number of eggs attached on the main sheet (mean ± SD = 712 ± 105 eggs, range 572–971 eggs, n = 15) was adjusted to be under the daily mean number of eggs tended in nests (approximately 1,100 eggs for same-sized artificial nests; Matsumoto et al., unpublished data). The made-up main sheet with eggs of mixed developmental stages was photographed using a digital camera with a macro lighting system (EOS-Kiss Digital N, EF 50 mm Macro Lens and Macro Twin Lite MT-24EX; Canon) to count the initial number of eggs and was then reset into the nests. When the egg sheets were reset into the nests, males readily returned to their nests and began to care for the eggs.

The experiments were stopped when the young or old eggs had been

completely consumed by the males, when the young eggs had been developed to eyed eggs (<2 days), or when the old eggs had been hatched out (2–4 days); all experiments ended within 2 days. Egg sheets were taken from the nests three times per day (1000, 1300, and 1800 h) starting from the day after spawning and were photographed. The digital images of the plastic sheets with eggs were uploaded onto a personal computer, and the young and old eggs on the sheet were counted using counting software (Kachikachi-counter 2.6; GT). No unfertilized or dead eggs were observed in this study. Egg-tending males were not fed after spawning. Neither males nor females that had spawned in the experiments were reused, and both were returned to their respective collection sites after the experiment. For each subsequent experiment, new fish were added to the experimental tank.

The experiment was replicated 18 times, and 15 replications (male SL: mean ± SD = 50.6 ± 5.3 mm, range 42.4–57.4 mm) were used for analysis. The remaining three cases were omitted from the analysis because all eggs were consumed before the first observation; even in such cases, the difference in the initial egg number between young and old eggs causes a slight difference between expected and observed number of cannibalized young eggs (see below). To determine the developmental stage of eggs at which they are preferentially consumed by males, the observed number of young eggs consumed by the males was compared with the expected number of consumed young eggs if males randomly consumed eggs in the nests: expected value = total number of consumed eggs/2. Moreover, to examine the possibility of within-nest site-dependent cannibalism, the number of consumed eggs was compared between those near the entrance and those at a site deep within the nest. R. ellipes males may begin to cannibalize eggs near the entrance using a within-nest positional cue because younger eggs within the nests are usually near the entrance due to the female preference for sites deeper within the nest (Matsumoto et al. 2008). To examine the cannibalism process, both comparisons were tested at the end of the first and second days of the experiment using the Wilcoxon signed-ranks test (Statview version 5.0, SAS).

Results and discussion

Males consumed 121–759 eggs (mean number of consumed eggs $\pm$ SD = 362.7 $\pm$ 226.7 eggs; mean percentage of consumed eggs $\pm$ SD = 52.4 $\pm$ 33.3%, range 12.5–99.3%, n = 15) until the end of the experiments. All males consumed both young and old eggs, and there was no significant difference in the number of consumed young eggs between the observed and expected values at the end of first day (Wilcoxon signed-ranks test, T = 61.0, P > 0.05, n = 15; Fig. 2a) and second day of the experiments (T = 65.0, P > 0.05, n = 15; Fig. 2b). The result indicates that R. ellipes males do not selectively cannibalize young eggs in the nest with eggs of mixed developmental stages. Moreover, the number of consumed eggs did not differ between those near the entrance and those deep within the nest on the first day (Wilcoxon signed-ranks test, T = 61.0, P > 0.05, n = 15) or the second day (T = 34.5, P > 0.05, n = 15), suggesting that there is no possibility of within-nest site-dependent cannibalism in this species.

Manica (2003) reported that there was no selective filial cannibalism against young eggs in male damselfish Abudefduf sexfasciatus, and suggested that it is not likely to evolve if the difference in egg age within a nest is small because of the small differences in egg nutritional and reproductive values between young and old eggs. These differences are thought to depend on the relative difference in egg age in comparison to the incubation period, that is, the effect of a 1-day difference in egg age on the differences in egg nutritional and reproductive values is smaller in species with a long incubation period than in those with a short incubation period. In few studies on the selective filial cannibalism in fish, the relative difference in egg age within a nest is relatively larger in species showing a preference for young eggs than in species showing no preference (Table 1). Thus, the relatively small difference in egg nutritional and reproductive values among clutches within a nest may prevent the evolution of selective filial cannibalism of young eggs in male R. ellipes.

For males, the reproductive value of eggs tended in the nest can be influenced not only by expected future parental investment but also by their effect as an attractive signal for females. In some fishes, the presence of eggs in the nest, particularly eggs at early developmental stages, promotes additional

female spawning to the nest (Unger and Sargent 1988; Sikkel 1989; Petersen and Marchetti 1989; Petersen 1990). In the garibaldi damselfish Hypsypops rubicundus, males cannibalized young eggs in their nest during the parental phase; in contrast, during the mating (courtship) phase, old eggs were selectively cannibalized because females prefer to lay eggs close to young eggs within the nests (Sikkel 1994)—the reproductive value of young eggs for males changes according to the male reproductive phase. Although R. ellipes males with young eggs have higher mating success than those with old eggs, females choose males with young eggs not by discriminating the developmental stage of eggs in the nests but by using other choice processes (e.g., female mate-choice copying; Matsumoto et al. 2011). Thus, in this species, young eggs themselves do not enhance the attraction for females, and therefore young eggs do not enhance the reproductive value of the clutch.

The nonselectivity in filial cannibalism against young eggs in R. ellipes males might be attributed to the difficulty in discriminating egg developmental stage in the nest, as suggested in the female choice of males with young eggs in the garibaldi damselfish (Sikkel 1989). The main nest material of R. ellipes is the vacant shell of Serpulorbis imbricatus. In addition to the closed spiral-tubular structure of the shells, males prefer to use an extremely tight nest (Takegaki et al. 2008), and moreover, females avoid laying eggs near the nest entrance due to the high mortality of these eggs (Matsumoto et al. 2008). These nest structures and nest uses may make it more difficult for R. ellipes males to discriminate visually the developmental stage of eggs in the nests compared with other species in which selective filial cannibalism of young eggs has been detected (Salfert and Moodie 1985; Petersen and Marchetti 1989; Petersen 1990; Sikkel 1989, 1994). In this case, chemical discrimination could be quite effective. For example, parents of convict cichlids identify their eggs at night using chemical cues (Reebs and Colgan 1991). However, to our knowledge, there is no study showing differential stimuli with egg-developmental stage.

To conclude, this study demonstrated that R. ellipes males did not preferentially cannibalize young eggs in the nests, and thus showed that female preference for males tending young eggs is not based on an attempt to avoid selective filial cannibalism against young eggs. The nonselectivity might be due

to the relatively small difference in egg nutritional and reproductive values among clutches in the nests and male difficulty in discriminating egg age. Although the reason why, in the mating process, females choose males with young eggs is not clear at present, it is highly possible that female adaptive benefits associated with egg age reflect two of the three hypotheses proposed in "Introduction": the dilution effect and avoidance of male egg desertion.

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Table.1. Effect of relative difference in egg age within a nest on the presence of selectivity in filial cannibalism to young eggs in paternal brooding fishes

| Species	Difference in egg age within a nest (days)	Incubation period (days)	Range of relative difference	Selectivity to young eggs	Reference
Stegastes rectifaenum	0-3<	4–5	0 – 0.75<	Yes	Petersen & Marchetti (1989)
S. dorsopunicans	0-3	4–5	0 – 0.75	Yes	Petersen (1990)
Microspathodon chrysurus	0-3	4–5	0 – 0.75	Yes	Petersen (1990)
Hypsypops rubucundus	0-9<	12–23	0 – 0.75<	Yes	Sikkel (1994)
Abudefduf sexfascitus	0-2	4–5	0 – 0.50	No	Manica (2003)
Rhabdoblennius ellipes	0-2<	6–7	0 – 0.33<	No	Matsumoto et al. (2011); this study
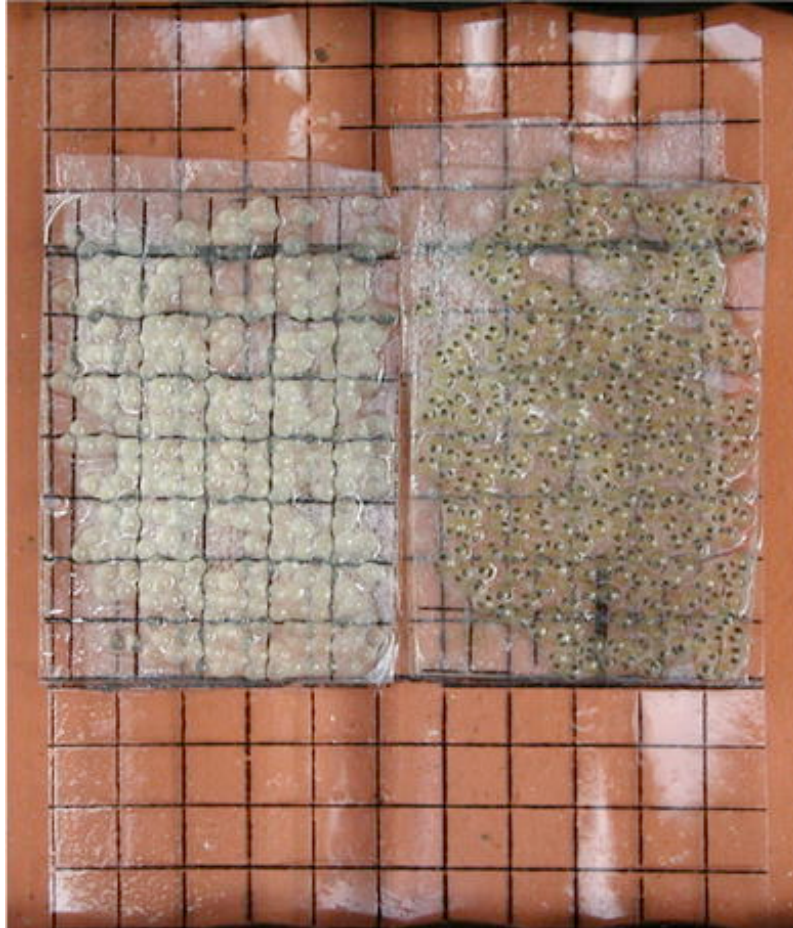
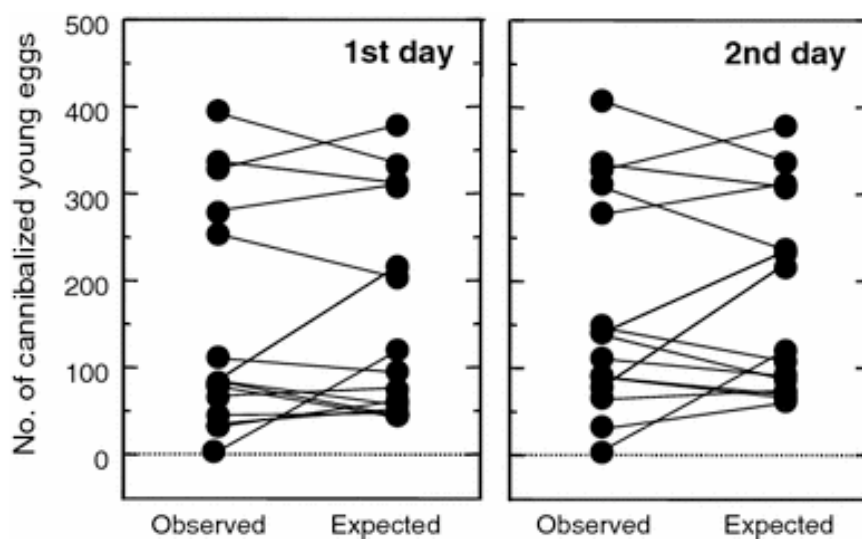**Fig. 1** A manipulated egg sheet with young (*left*) and old (*right*) eggs attached

Fig. 2 Comparison of observed and expected number of cannibalized young eggs at the end of the first day (*left*) and second day (*right*) of the experiments