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ORIGINAL PAPER

Filial cannibalism as a conditional strategy in males of a paternal mouthbrooding fish

Tomohiro Takeyama · Noboru Okuda ·
Yasunobu Yanagisawa

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Abstract Filial cannibalism is widespread in a variety of animal species and has been generally accepted as an adaptive behavior. Within a population, some individuals adopt filial cannibalism and others do not, in spite of its adaptiveness. There is little knowledge of how such a polymorphic trait is maintained in nature. To understand the underlying mechanism of cannibalistic polymorphism, we conducted a long-term field study that involved monitoring of the reproductive experience of marked individuals in the paternal mouthbrooding cardinalfish, *Apogon doederleini*, in which parental males sometimes cannibalize their entire broods. We assumed that filial cannibalism can be described as one of three possible strategies: alternative, mixed or conditional. Individual cannibalistic tendencies, represented by the number of entire brood cannibalism performed by each individual in one breeding season, showed a random distribution within the study population. Moreover, the individual cannibalistic tendencies were not consistent between two successive seasons. These results suggest that filial cannibalism is phenotypically plastic, thus eliminating the alternative strategy as a possible mechanism. Comparison of variance in reproductive success between cannibals and non-cannibals showed that observations were not in accordance with those expected in the case that males adopt filial cannibalism stochastically, that is, as a mixed strategy. Our previous studies have indicated that filial cannibalism is affected

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T. Takeyama
Department of Biology and Geosciences, Graduate School of Science, Osaka City University,
Osaka 558-8585, Japan

N. Okuda
Center for Ecological Research, Kyoto University, Otsu 520-2113, Japan

Yasunobu Yanagisawa
Department of Biology and Earth Sciences, Faculty of Science, Ehime University, Matsuyama
790-8577, Japan

Present Address:
T. Takeyama (✉)
Center for Ecological Research, Kyoto University, 2-509-3, Hirano, Otsu 520-2113, Japan
e-mail: takeyama@ecology.kyoto-u.ac.jp

by male status, such as age, somatic condition and mate availability. In conclusion, filial cannibalism by male *A. doederleini* is carried out as a conditional strategy.

Keywords Alternative tactics · Apogonidae · Paternal cannibalism · Mouthbrooder · Phenotypic polymorphism

Introduction

Within a population, a member of the same sex does not always have only one reproductive style. There often exist alternative ways of reproduction in terms of behavioral, physiological and morphological aspects (Perrill et al. 1982; Austad 1984; Cook 1990; Gross 1991; Taborsky 1994). Game theoretical models have been used to examine the evolutionary conditions for such multiple phenotypes to coexist in a population (Maynard-Smith 1979, 1982). The phenotypic polymorphism is categorized into three different strategies on the basis of genetics, fitness pattern and how natural selection operates in them: alternative, mixed and conditional strategies, respectively. Although the use of these terms has brought confusion among empirical workers, Gross (1996) defined them as follows. The three strategies are primarily divided into two based on genetics: the alternative strategy is genetically polymorphic, whereas the mixed and conditional strategies are genetically monomorphic. In the alternative strategy, multiple genetically different strategies are maintained by the frequency-dependent selection within a population and each individual of the population adopts only a single strategy. In the mixed strategy and the conditional strategy, all individuals adopt the genetically same strategy but each of them expresses different phenotypes alternatively, that is, “alternative tactics.” In either strategy, the alternative tactics is evolutionarily stable at a given proportion in a population (i.e., ESS) but its selection regime is different between them: the alternative tactics of the mixed strategy are maintained by the frequency-dependent selection and those of the conditional strategy by the status-dependent selection. In the mixed strategy, each individual adopt a probabilistic mixture of the tactics, whereas each tactics of the conditional strategy is altered according to its individual ‘status’ which varies ontogenetically or with changing environments.

We can also classify the three strategies into two groups in terms of relative fitness. In cases of the alternative and mixed strategies, fitness is equal among alternative phenotypes, whereas the conditional strategy consists of phenotypes with unequal fitness (Gross 1996). Empirical studies on the phenotypic polymorphism have attempted to examine the frequency of each phenotype and its relative fitness (reviewed by Gross 1996; Shuster and Wade 2003), but they were often unsuccessful in elucidating the genetic background of alternative phenotypes and their underlying mechanisms, except some excellent studies (Zimmerer and Kallman 1989; Shuster and Wade 1991; Ryan et al. 1992; Lank et al. 1995; Shuster and Sassaman 1997; Sinervo and Zamundio 2001).

Filial cannibalism, the eating of offspring by the parent, is prevalent in many animals (Hausfater and Hrdy 1984; Elgar and Crespi 1992). Unlike hetero cannibalism, the eating of non-relatives, filial cannibalism has the direct cost of decreased current reproductive success. Many theoreticians have made considerable effort to determine why this behavior evolved (Rohwer 1978; Sargent 1992; Sargent et al. 1995; Lindström 2000; Kondoh and Okuda 2002; Payne et al. 2004). For filial cannibalism to evolve, it is necessary that an increase in future reproduction outweigh the loss of current reproduction. Such a trade-off between the current and future reproductions is easier for parental males than for parental females because the energetic benefit of eating zygotes is usually higher than the energetic cost of gamete production for the males. Actually, this phenomenon has arisen independently in a variety of fish species with paternal care, supporting the hypothesis that paternal cannibalism is adaptive (FitzGerald 1992; FitzGerald and Whoriskey 1992; Sargent 1992). However, another theoretical problem remains unsolved. As the population frequency of cannibalistic males increases through their improved fitness, they will have difficulty in getting additional mates to offset the current reproductive loss entailed by filial cannibalism. This is because males remain reproductively receptive after filial cannibalism, while females whose eggs were exploited enter the refractory phase, resulting in low mate availability for the males (Kvarnemo 1998). The situation will, in turn, lead to a decrease in the cannibal's fitness. Thus, it is unlikely that all males adopt filial cannibalism. Using a game theoretical model, Kondoh and Okuda (2002) demonstrated that the number of clutches cannibalized by males converges to an evolutionary equilibrium, assuming that male cannibalistic phenotype is genetically determined and that its population frequency affects the mate availability for males at a given time and consequently, their fitness.

Many empirical studies have reported the approximate factors causing filial cannibalism in paternal fishes, often linking them with the energetic costs of parental care (Belles-Isles and FitzGerald 1991; Okuda and Yanagisawa 1996b; Kvarnemo et al. 1998; Lindström 1998). However, most of them were conducted during a few breeding cycles or at most one breeding season, and none of them showed the long-term fitness effects of filial cannibalism explicitly. It is also unclear to what extent laboratory studies can explain the nature of this phenomenon found in the field.

The cardinalfish (Apogonidae), *Apogon doederleini*, is a paternal mouthbrooder in which males can brood only an egg mass during one breeding cycle. For this fish, it has been reported that mouthbrooding males sometimes eat their own broods (Okuda and Yanagisawa 1996a, b). The objective of the present study is to understand what strategy represents filial cannibalism in a field population of *A. doederleini*, by monitoring marked individuals over a total of four entire breeding seasons. If individual tendencies toward filial cannibalism show a polymodal distribution within the breeding population and such cannibalistic tendencies are consistent through successive seasons, it is suggested that filial cannibalism is phenotypically unaltered polymorphism, that is, an alternative strategy. In contrast, if the individual cannibalistic tendencies show phenotypic plasticity, it is a mixed or conditional strategy. In the case of a mixed strategy, we expect that males will adopt filial cannibalism stochastically irrespective of their status or environmental conditions and cannibals will enjoy reproductive success equal to that of non-cannibals. In the case of a conditional strategy, the males will adopt filial cannibalism depending on their status, and their reproductive success will be unequal to that of non-cannibals.

Methods

Study species

Apogon doederleini inhabits the shallow waters of the West Pacific. It is solitary and sedentary throughout its lifetime, except for the breeding season during which pairs are formed (Okuda and Yanagisawa 1996a). The fish always reach maturity at the age of one and reproduce perennially, surviving up to 8 years (Okuda et al. 1998; Takeyama et al. 2002). During the breeding season (May–August), both males and females experience multiple matings sequentially (Okuda and Yanagisawa 1996a). Prior to spawning, males often receive courtships from multiple females, due to female-biased operational sex ratio that is characteristic of sex-role reversal (Okuda and Yanagisawa 1996a). After spawning, pairs are usually divorced and mates frequently change between successive spawning events, resulting in a highly polygamous mating system (Okuda and Yanagisawa 1996a; Takeyama et al. 2002).

In this fish, the mouthbrooding males perform two types of filial cannibalism: the eating of a partial or entire brood (Okuda and Yanagisawa 1996b). The partial brood cannibalism is considered to serve as male adjustment of the brood size to its buccal capacity rather than as a means of energy acquisition (Okuda et al. 1998). The occurrence of the entire brood cannibalism is frequent and unique: in almost all cases, it occurs within one day of spawning and its agent usually remates soon after cannibalism (Okuda and Yanagisawa 1996a, b; Takeyama et al. 2002). The ability to remate so quickly is possible due to the female-biased operational sex ratio of this fish (Okuda and Yanagisawa 1996a; Takeyama et al. 2002). In the present study, we focus on the entire brood cannibalism and regard it as a cannibalistic phenotype.

Field observations

We conducted field observations at Morode Beach, Shikoku Island, Japan, from 1993 to 1997, except 1994 by the aid of SCUBA. Prior to each breeding season, we captured all *A. doederleini* inhabiting a 10 × 20 m quadrant of the boulder area at a depth of 5.8–9.0 m and marked them underwater by pulling out two or three dorsal and/or anal fin rays. We measured their standard length (SL) to the nearest 0.5 mm, removed several scales from the lateral side of their body to determine the age of the fish, and then released them at the same capture site. Throughout the entire breeding season, we conducted the daily observations for individual males to record their mating experience. We also noted the incidence of entire brood disappearance from their mouths before the expected day of hatching and, if it occurred, confirmed whether or not it was due to filial cannibalism by checking stomach contents of such a male with a needle-less syringe of 1 ml plunged through the esophagus under anesthesia (Okuda and Yanagisawa 1996a, Takeyama et al. 2002). Using data on recapture of the marked fish in the successive seasons, we calculated the annual growth rate ($G = 10{,}000\ (\ln L_{t2} – \ln L_{t1})/(t_2 – t_1)$; where L_{t1} and L_{t2} are the SL on the first capture date t_1 and the recapture date t_2 in the next season, respectively). The age was determined according to the procedure of Okuda et al. (1998). The age determination was failed for some males. Details of the field study have been also presented elsewhere (Okuda and Yanagisawa 1996a, b; Takeyama et al. 2002).

Data analysis

We statistically analyzed whether individual tendencies toward filial cannibalism show a polymodal distribution within the study population. The individual cannibalistic tendency was defined as the number of entire brood cannibalism performed by each individual in a breeding season. We used the χ^2 test for goodness of fit to determine whether the frequency distribution of the individual cannibalistic tendencies was fitted to the Poisson distribution, in which cannibalistic individuals are expected to appear at random, assuming that there is no bias in the cannibalistic tendencies among individuals. In order to examine the influence of male age, body size and the number of matings on the individual cannibalistic tendencies, we performed the stepwise multiple regression analysis. Because of a high correlation between age and body size ($r^2 = 0.61$, $P < 0.0001$, $n = 111$), the residual of the SL against the age substituted as the independent variable. The individual cannibalistic tendencies were square root transformed to fit the normal distribution. In addition, we compared three fitness components, the annual growth rate, the survival rate and the number of successful breeding cycles, between cannibals, defined as males that adopted filial cannibalism at least once in a season, and non-cannibals.

To examine the annual consistency of the individual cannibalistic tendencies, we compared the cannibalistic tendency of each male between two successive seasons using the correlation analysis. Even if the individual cannibalistic tendencies were annually consistent, we cannot conclude that filial cannibalism is a genetically polymorphic alternative strategy. For instance, environmental factors such as higher quality territory may make some males more attractive and thus more cannibalistic every year. Such a case is also possible in a conditional strategy. Thus we checked the annual consistency of male mating attractiveness, defined as the number of broods received from females in a season, between the two successive seasons. As another approach, we classified males into three phenotypes: males adopting filial cannibalism in both of two successive seasons (Both), in either of the two seasons (Either) and in neither of the two seasons (Neither). We calculated the expected population frequency of cannibals (p) and non-cannibals ($q = 1-p$) in a given season by taking the average of the field data for a total of four seasons. If males become cannibals at random in each season, the expected frequencies of the three male phenotypes, Both, Either and Neither, are p^2, $2pq$ and q^2, respectively. If the individual cannibalistic tendencies are annually consistent, their expected frequencies are p, 0 and q, respectively. We performed the Kolmogorov-Smirnov test to examine the deviation of the observations from these expectations. To clarify whether the phenotypic expression of filial cannibalism was ontogenetically determined, we examined the effects of the age and the SL on the decision-making for cannibals and non-cannibals in the following season, using the logistic regression analysis. Among these three phenotypes (Both, Either and Neither), we also compared growth rate and reproductive success as fitness components. We used MANOVA to compare the overall fitness consequence in two successive seasons instead of comparing their fitness components in each season separately with ANOVA. All data from respective seasons were pooled for the comparison of the fitness components.

Results

Males received one to ten egg masses (mean ± SD; 4.95 ± 1.72, $n = 120$) from females and performed filial cannibalism up to four times in one season. Individual variation in cannibalistic tendencies did not significantly deviate from the Poisson distribution in any of the seasons (Fig. 1; 1993: df = 1, $\chi^2 = 1.11$, $P = 0.29$; 1995: df = 1, $\chi^2 = 1.72$, $P = 0.19$; 1996: df = 1, $\chi^2 = 0.18$, $P = 0.67$; 1997: df = 1, $\chi^2 = 0.34$, $P = 0.56$). The correlation analysis showed that the individual cannibalistic tendencies were not consistent between two successive seasons ($r^2 = 0.025$, $P = 0.44$,

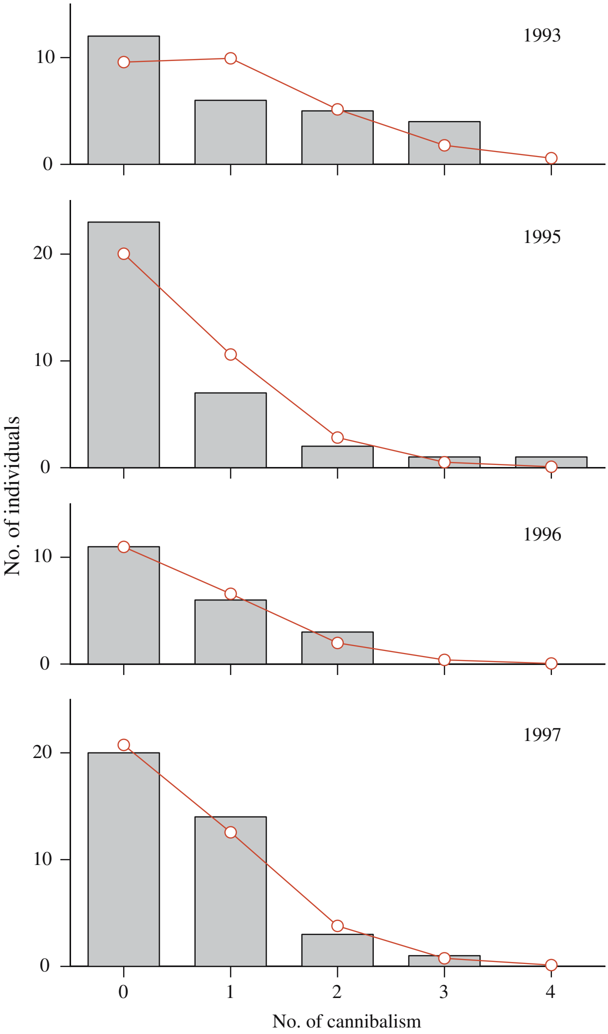

Fig. 1 The number of male *Apogon doederleini* that performed filial cannibalism with a different frequency in each of four breeding seasons. The values observed (bars), and the values expected (lines) based on the Poisson distribution

$n = 26$). Their mate attractiveness did not also show the annual consistency ($r^2 = 0.34$, $P = 0.11$, $n = 23$). The cannibalistic tendencies were affected by the number of matings (Stepwise multiple regression analysis, $r^2 = 0.28$, $P < 0.0001$, $n = 111$), but not by age or body size corrected for the age. Males that were more cannibalistic did not have increased reproductive success, measured as the number of successful breeding cycles in the current season ($r^2 = 0.021$, $P = 0.82$, $n = 120$). Reproductive success did not differ between cannibals (mean ± SD; 4.15 ± 1.39 breeding cycles, $n = 54$) and non-cannibals (4.27 ± 1.49, $n = 66$; Unpaired *t*-test, df $= 126$, $t = -0.15$, $P = 0.88$). The coefficients of variance (CVs) in reproductive success were nearly equal (cannibal: 38.1, non-cannibal: 38.8). Furthermore, there were neither differences in the growth rate (cannibals: 2.30 ± 2.28 per day, $n = 22$;

non-cannibals: 2.83 ± 2.54 per day, $n = 32$; Unpaired t-test, df = 52, $t = -0.78$, $P = 0.44$) nor differences in the survival rate (cannibals: 61.0%, $n = 41$, non-cannibals: 80.0%, $n = 45$; Chi-square test, df = 1, $\chi^2 = 2.90$, $P = 0.089$).

The population frequency of cannibals did not vary among seasons (1993: 58.8%, $n = 34$; 1995: 30.8%, $n = 39$; 1996: 47.8%, $n = 23$; 1997: 48.4%, $n = 31$; Chi-square test, df = 3, $\chi^2 = 5.04$, $P = 0.57$). From these data, the expected frequencies for cannibals (p) and non-cannibals ($q = 1-p$) were estimated to be 0.46 and 0.54, respectively. A total of 26 marked males were monitored for two successive seasons. Of the 26 males, eight adopted filial cannibalism in both seasons (Both), 11 did in either of the two seasons (Either) and 7 did in neither season (Neither) (Fig. 2a). Their observed frequencies significantly deviated from those expected in the case that males showed annual consistency of their cannibalistic tendencies (Both: $26 \times 0.46 = 12.0$, Either: $26 \times 0 = 0.0$, Neither: $26 \times 0.54 = 14.0$; One-sample Kolmogorov-Smirnov test, $P < 0.05$; Fig. 2b). In contrast, there was no difference between the observations and the expected results in the case that males become cannibals at random (Both: $26 \times 0.46^2 = 5.5$, Either: $26 \times 0.46 \times 0.54 \times 2 = 13.0$, Neither: $26 \times 0.54^2 = 7.6$; One-sample Kolmogorov-Smirnov test, $P > 0.2$; Fig. 2c). The age and size had no effects on the decision-making on whether to cannibalize or not in the following season in the cannibals (Logistic regression analysis, age: coefficient = 0.49, $P = 0.53$, size: coefficient = −0.038, $P = 0.68$, $n = 13$) or in the

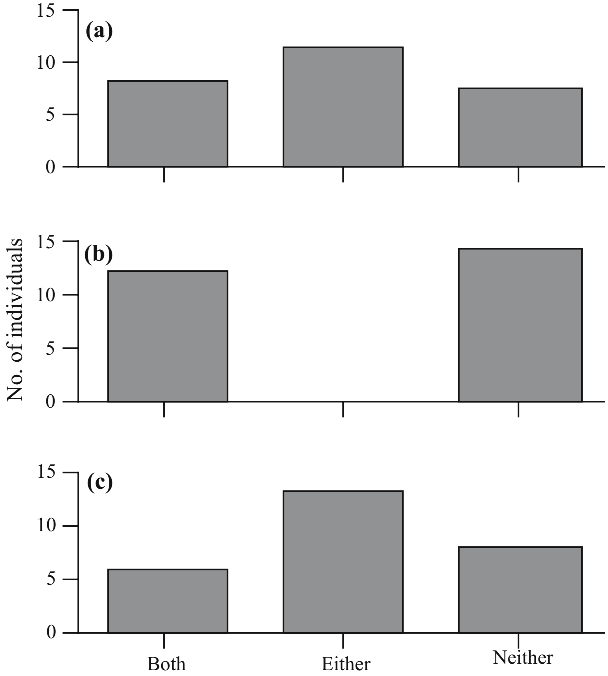

Fig. 2 The population frequency of three male phenotypes in relation to filial cannibalism. Males adopted filial cannibalism in both of two successive seasons (Both), in either of the seasons (Eiher) and in neither of the seasons (Neither). The frequency observed in nature (**a**), frequency expected if males will show annual consistency of their cannibalistic tendencies (**b**) and if males will become cannibals at random in each season (**c**)

non-cannibals (age: coefficient = 0.42, $P = 0.58$, size: coefficient = –0.35, $P = 0.27$, $n = 12$). Neither the growth rate nor the reproductive success differed among these three phenotypes (Table 1; ANOVA, growth rate: df = 2, $F = 0.22$, $P = 0.80$; MANOVA, reproductive success, df = 2, $F = 0.56$, Roy's greatest root = 0.049, $P = 0.58$).

Discussion

The long-term follow-up study of marked male *A. doederleini* revealed that individual cannibalistic tendencies and their annual consistency were subject to random distribution. This means that filial cannibalism is phenotypically plastic polymorphism within the study population, eliminating the alternative strategy as a possible mechanism. In a viviparous fish (genus *Poeciliopsis*) and a flour beetle (*Tribolium confusum*), cannibalistic and non-cannibalistic strains were established by artificial breeding (Thibault 1974; Lima and Vrijenhoek 1996; Stevens and Mertz 1985). Although these studies suggest the genetic basis of cannibalistic behavior, it is unclear how the frequencies of the two strains and their hybrids are maintained in natural populations (Thibault 1974). In theory, the evolutionary conditions for the coexistence of multiple genotypes are limited (Maynard-Smith 1982; Gross 1996; Sinervo and Zamudio 2001). In fact, there is little evidence that the phenotypic polymorphism would represent alternative strategies (Gross 1996; Shuster and Wade 2003).

In male *A. doederleini*, although the individual cannibalistic tendencies were not age-specific, the seasonal occurrence pattern of filial cannibalism varied with age: young males frequently cannibalize their broods early in the breeding season whereas old males, late in the season (Okuda et al. 1997, Takeyama et al. 2002). Okuda et al. (1997) and Takeyama et al. (2002) suggested that filial cannibalism by young males would serve as a delay of current reproduction, by which they can increase their growth and consequently their buccal capacity in future reproduction. In contrast, for the old males that are depleted of energy late in the season due to frequent breeding attempts, filial cannibalism has the function of improving their somatic condition (Okuda and Yanagisawa 1996b). Therefore, we argue that filial cannibalism would show a status-dependent expression, judging from these previous knowledge.

The present result that males acquiring more mates in a season were more cannibalistic supports Okuda and Yanagisawa's (1996a) hypothesis that current mating opportunities (i.e., mate availability) will influence filial cannibalism by males. In

Table 1 Age and body size (standard length, mm) of first season, daily specific growth rate (*G*), and reproductive success (=number of hatching broods) of first (RS_1) and second (RS_2) season in two successive breeding seasons, among three categorized males that based on experiences of filial cannibalism: males adopting filial cannibalism in both of two successive seasons (Both), in either of the two seasons (Either) and in neither of the two seasons (Neither)

Cannibalism	Age	Body size	*G*	RS_1	RS_2
Both	2.13 ± 1.25 (8)	78.71 ± 8.41 (7)	2.16 ± 1.40 (7)	3.50 ± 141 (8)	4.75 ± 0.46 (8)
Either	3.82 ± 2.56 (11)	81.68 ± 12.25 (11)	2.08 ± 2.30 (11)	3.82 ± 1.72 (11)	4.55 ± 0.69 (11)
Neither	1.85 ± 1.46 (7)	76.71 ± 10.01 (7)	2.72 ± 2.13 (7)	3.57 ± 1.27 (7)	4.86 ± 0.90 (7)

Mean ± SD and sample size in parenthesis

A. doederleini, cannibalistic males usually remate with a new female soon after they cannibalize eggs from another female (Okuda and Yanagisawa 1996a). Thus, they can offset the current reproductive loss effectively by quickly remating, thereby energetically profiting from the egg consumption. Although the idea that filial cannibalism is affected by mate availability has been hitherto neglected to date, Kondoh and Okuda (2002) stressed the importance of mate availability in the occurrence of filial cannibalism in paternal species using a game theoretic model. Recently, Okuda et al. (2004) demonstrated that in a substrate brooding fish, parental males became more cannibalistic with increasing mate availability under laboratory conditions by experimentally manipulating sex ratio and nest space (i.e., brooding capacity). The female-biased sex ratio and limited nest space are expected to have the positive effects on the male mate availability, resulting in the increased egg cannibalism (Kondoh and Okuda 2002). Also in *A. doederleini*, males may adopt filial cannibalism according to their social status as well as their intrinsic status, as in the case of conditional strategy.

Here let us consider the case of mixed strategy where each male adopts filial cannibalism stochastically. In *A. doederleini*, males, on average, enjoy high mate availability because of the female-biased operational sex ratio (Okuda and Yanagisawa 1996a). One may, therefore, predict that cannibalistic males can always compensate for the current reproductive loss by quickly remating since they have the potential to pair with additional mates after cannibalism. However, when broods were experimentally removed from the non-cannibals on the day following their spawning to simulate the occurrence of filial cannibalism, the non-cannibals took longer to remate than the cannibals did (Okuda and Yanagisawa 1996a). This suggests that not all males enjoy the high mate availability; in other words, their mate availability varies individually and temporally. If the occurrence of filial cannibalism is stochastic, the cannibals unsuccessful in remating quickly will decrease their mating frequency and thus reproductive success. In such a situation, it is expected that the variation in reproductive success is greater for the cannibals than for the non-cannibals. However, this expectation was not in accordance with the observation, as shown by the nearly equal CVs of the reproductive success for the cannibals and the non-cannibals. The equal variation in the reproductive success will be realized only when males with high mate availability adopt filial cannibalism, i.e. the strategy is conditional. Thus we suggest that mixed strategy, where cannibalistic phenotypes are determined stochastically, is unlikely to evolve, owing to the high risk of protracted inter-spawning intervals.

In the case of *A. doederleini*, the cannibals did not raise more broods in one season than the non-cannibals. In some paternal fishes, it has been considered that parental males perform filial cannibalism to extend their breeding period by gaining energy through the egg consumption, resulting in an increased number of eggs received in one season (Rohwer 1978; Marconato and Bisazza 1988; Petersen and Marchetti 1989; Belles-Isles and FitzGerald 1991). In contrast, in mouthbrooders, the number of broods received by males is restricted by the temperature-dependent embryonic development and the short breeding period (Okuda et al. 1998). Such a reproductive constraint explains why the cannibals did not exceed the reproductive success of the non-cannibals.

If filial cannibalism by male *A. doederleini* evolves as a conditional strategy, then the average fitness would be expected to differ between the two phenotypes, cannibal and non-cannibal (Gross 1996). Contrary to expectation, no differences in fitness components were found. However, this does not mean that the possibility of the conditional strategy is eliminated. Omori et al. (unpublished data) found that in *A. doederleini*, the cannibals just after their cannibalistic events were in poorer condition than the non-cannibals during the mouthbrooding period. The males in poor condition may be able to increase their lifetime reproductive success through cannibalism, by which they effectively improve their somatic condition and thus survival, compared to the case in which they did not adopt cannibalism. To confirm the existence of the conditional strategy, it is more important to measure how the fitness is changed when an individual switches tactics or when individuals of the same status adopt different tactics, and not to compare the fitness between individuals of different status that adopt different tactics. Further study needs to conduct experimental manipulation for males in the same status as well as the field observations.

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