ARTICLE

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Interspecific differences in male cannibalistic behavior between two sympatric cardinalfishes (Pisces: Apogonidae)

Abstract Cannibalistic behavior of a paternal mouth-brooding cardinalfish, *Apogon notatus*, was examined and compared with that of a sympatric congener, *Apogon doederleini*. In both species, males sometimes cannibalized their own entire broods, but their postcannibalistic behavior was markedly different. Males of *A. doederleini* respawned within a few days of cannibalism, usually changing mates, whereas males of *A. notatus* took several weeks to respawn, less frequently changing mates. This difference was attributed to mate availability for males. The operational sex ratio was female biased in *A. doederleini* but male biased in *A. notatus*, suggesting that the former males have higher mate availability and thus opportunities for remating soon after cannibalism. For male apogonids that accept only one clutch at a time, an effective way to compensate for reproductive loss entailed by filial cannibalism is to remate as soon as possible after cannibalism. The higher rate of filial cannibalism by *A. doederleini* than by *A. notatus* suggests that this cannibalism is facilitated by high mate availability. In contrast to filial cannibalism, heterocannibalism was more frequent in *A. notatus*. High population density and gregariousness may be important factors contributing to the frequent occurrence of heterocannibalism.

Key words Filial cannibalism · Heterocannibalism · Mate availability · Operational sex ratio · Paternal mouthbrooder

Introduction

Cannibalism (i.e., intraspecific predation) is a widespread phenomenon among animals (Hausfater and Hrdy 1984; Elgar and Crespi 1992). If there is no genetic relation between a cannibal and its victim (i.e., heterocannibalism), the cannibal can profit simply by consuming conspecifics as

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food, or by reducông intraspecific competition for resources if the victim is a potential competitor. A special case of hemerocannibalism is the killing and consumption of offspring cared for by a potential mate (it is defined as infanticide when not accompanied by eating of the offspring; see Hrdy 1979). This cannibalism is facilitated by intense mating competition in one sex. Such cannibals not only decrease the reproductive success of same-sex competitors but also increase their own mating opportunities by inciting the victim's parent to remate sooner with themselves (Hrdy 1979).

The occurrence of cannibalism between genetically related individuals is less common. The particular case in which a parent eats its own offspring is called filial cannibalism. This behavior is viewed as a parental strategy in which the parent increases its fitness through offsetting the current reproductive loss by the future gain from cannibalism (Rohwer 1978). Filial cannibalism is more often reported for species with paternal care than for those with maternal care. This biased pattern of filial cannibalism is associated with sexual asymmetry of parental investment: males make a smaller gametic investment than do females, so that the net benefit from eating their zygotes is potentially greater for males.

Both hetero- and filial cannibalism are prevalent in fishes (Dominey and Blumer 1984; Smith and Reay 1991; FitzGerald and Whoriskey 1992). There are some reasons why cannibalism is so common in fishes. Because the victims, usually eggs or larvae, are defenseless and very small relative to adults, they are easily handled as prey by the cannibals (Dominey and Blumer 1984). The predominance of paternal care among fishes is also an important factor accounting for filial cannibalism (FitzGerald 1992). In such species, males usually reduce their feeding opportunities during the care period (Smith and Wootton 1995).

The occurrence and frequency of cannibalism, whether filial or hetero-, are highly variable among paternal fishes. If competition for food or mates is intense, then heterocannibalism will increase. On the other hand, if the future potential benefit for a parent to eat its own offspring is great, then filial cannibalism will increase. Therefore, cannibalistic

behavior may differ among closely related species, among populations, or even among individuals within a population, depending on their ecological and life historical conditions (Whoriskey and FitzGerald 1985; Hyatt and Ringler 1989; Petersen 1990; Belles-Isles and FitzGerald 1991; Okuda et al. 1997).

Cardinalfishes (Pisces: Apogonidae) are marine paternal mouthbrooders. The mouthbrooding behavior forces male parents to fast during the care period, and consequently their somatic condition deteriorates as the breeding season progresses (Okuda and Yanagisawa 1996a). This is a critical situation for male apogonids that practice filial cannibalism (Okuda and Yanagisawa 1996a), as in many other fishes (DeMartini 1987; Belles-Isles and FitzGerald 1991; Sargent 1992; Marconato et al. 1993). On the other hand, hetero-cannibalism is very rare in apogonids because mouthbrooding is effective in protecting broods against egg predators (Okuda and Yanagisawa 1996a; but see Okuda 1999a). Cannibalism in apogonids has been compared between two species, the boulder-dwelling *Apogon doederleini* and the sand-dwelling *Apogon niger*: the incidence of filial cannibalism and postcannibalistic behavior are markedly different between them (Okuda 1999b). Okuda (1999b) suggests that these differences are primarily the result of their habitat differences. In this study, I focused on the differences in cannibalistic behavior between two sympatric species. The subject species, *A. notatus*, breeds in boulder areas together with its congener *A. doederleini*, which has already been described in detail (Okuda and Yanagisawa 1996a,b). Because these species live under similar ecological and physical conditions, any interspecific differences should be ascribed to other factors. I here describe the patterns of hetero- and filial cannibalism in *A. notatus* and compare them with those in *A. doederleini*.

Materials and methods

Study species

Apogon notatus is a common species inhabiting shallow waters of the West Pacific (Nakabo 1993). In the non-breeding season, large shoals of this fish are formed in the water column of the boulder area (Kuwamura 1983, 1985), and its population density is among the highest in apogonids (Okuda 1997). Before the breeding season, females exclusively establish and maintain breeding territories on the boulder substratum to form pairs. Within pairs, females are more active than males in courtship and in attacks against conspecific intruders. Pairs show a strong mate fidelity during the courtship period but usually separate after spawning (Kuwamura 1985; Okuda 1999a). After separation, males alone mouthbrood eggs until hatching. The males often remain unpaired during the mouthbrooding period, while their mates quickly resume pairing with other males in their breeding territories. Because of male excess (male:female = 2:1–3:1 in this study site; Okuda 1999a), the operational sex ratio is male biased and

many unpaired males form loose aggregations in midwater. Females leave their breeding territories after the last spawning in the season, and all fish become gregarious again.

Field observations

The fieldwork was carried out at Murote Beach, Shikoku Island, Japan, in 1995 and 1996. General methods have been described elsewhere (Okuda 1999a). I made observations under water with the aid of SCUBA in a $10 \times 20\,m$ quadrat that had been set on the boulder area for the study of *A. doederleini* (Okuda and Yanagisawa 1996a,b; Okuda et al. 1997). Before the breeding season, I captured 314 adult *A. notatus* in and around the quadrat, using a seine and hand net. After anesthetizing the fish with quinaldine, I measured their standard length (SL) to the nearest 0.5 mm and marked them individually by subcutaneously injecting colored liquid latex and uprooting a few dorsal and/or anal fin rays. I released the fish at their capture sites after they recovered from the anesthesia. Of these marked fish, 153 were found in the quadrat during the breeding season. The fish were sexed on the basis of behavioral differences between sexes: mouthbrooding for males and territorial behavior for females (Okuda 1999a).

During the entire breeding season (June–September) of 1995, I made daily censuses to obtain information on reproductive experiences of each marked male. In these censuses, I also noted mates of the marked males. When marked males mated with unmarked females, I sketched lines and spots on the head, which showed enough individual variations to identify these females.

I sometimes found the entire brood had disappeared from a male's mouth before the expected day of hatching. Previous work had revealed that some of the brood disappearances were the result of filial cannibalism, by means of checking stomach contents of such males (Okuda 1999a). For males that practiced filial cannibalism, I noted the time (days) until next mating, if they mated again, and identified their mates.

In October, soon after the breeding season, I recaptured the marked fish and measured their SL. The growth rate for each male was calculated as follows:

$$G = 100 \times (\ln L_{t_2} - \ln L_{t_1})/(t_2 - t_1)$$

where G represents the daily specific growth rate (% day^{-1}), and L_{t_1} and L_{t_2} the SL (mm) on the first measurement (t_1) and the last measurement (t_2), respectively (Wootton 1990). The times t_1 and t_2 are transformed from the measurement date into a continuous sequence of days.

At the beginning of the next breeding season, I conducted a follow-up survey of marked fish to estimate annual mortality. As *A. notatus* shows site fidelity, the mortality was approximated by disappearance rate (%), which was calculated from the proportion of marked fish that disappeared to all marked fish observed in the quadrat at the beginning of the breeding season in the previous year (Okuda 1999a).

Three fitness parameters – growth rate, reproductive success, and mortality – were compared between cannibal males, defined as males that practiced filial cannibalism at least once in a season, and noncannibal males.

Statistical analysis

For data analysis, I used parametric tests when requirements were fulfilled; otherwise I used nonparametric tests. All statistical probabilities are two-tailed.

Results

Males of *A. notatus* raised on average 2.5 broods (± 1.0 SD; $n = 39$) during an entire breeding season. They took 23.4 days (± 7.9 SD; $n = 95$) to complete one breeding cycle (i.e., interspawning interval). The proportion of the mouthbrooding period in the interspawning interval was 52.5% (± 16.3 SD; $n = 83$).

Of 214 broods observed, 31 disappeared from the male's mouth before the expected day of hatching. All brood disappearances occurred within a few days of spawning. In the previous work (Okuda 1999a), I reported how these 31 broods disappeared: 13 were due to filial cannibalism, 8 due to egg predation (heterocannibalism or interspecific predation), and 10 due to unknown causes. The rate of brood disappearances was significantly different among months of the breeding season ($\chi^2 = 12.3$; df = 3, $P < 0.007$), whereas the filial cannibalism rate showed no seasonal pattern (extended Fisher's exact probability test, $P = 0.87$; Table 1).

Of the 13 males that practiced filial cannibalism, 8 remated within the current breeding season but 5 did not. In the former case, half the males changed mates in the next spawning. The rate of mate change for them (50.0%, $n = 8$) was not significantly different from that for males that did not practice filial cannibalism (47.1%, $n = 85$; Fisher's exact probability test, $P = 0.99$). The former males took on average 24.5 days (± 14.6 SD, $n = 8$) to remate after filial cannibalism, whereas the latter males took 13.0 days (± 7.7 SD, $n = 85$) to remate after hatching of their eggs. This difference was significant (Mann–Whitney U-test; $z = -2.66$, $P < 0.008$).

Brood disappearance other than by filial cannibalism occurred within an hour of spawning. In these cases, males that had lost their broods were usually mobbed by a group of unpaired conspecifics. For the males that lost their broods, the remating time was 19.5 days (± 2.08 SD, $n = 4$), which was longer than that for males who hatched eggs ($\bar{x} \pm$ SD = 13.0 ± 7.7 days, $n = 85$; Mann–Whitney U-test, $z = -2.40$, $P < 0.02$). Females took longer to respawn when their broods disappeared ($\bar{x} \pm$ SD = 18.1 ± 10.8 days, $n = 15$) than when their broods were mouthbrooded until hatching ($\bar{x} \pm$ SD = 13.4 ± 3.6 days, $n = 164$; Mann–Whitney U-test, $z = -2.07$, $P < 0.04$).

Cannibals were not different in size from noncannibals (Table 2). The occurrence of filial cannibalism was independent of the size difference in pairs (male SL − female SL) (cannibalism, $\bar{x} \pm$ SD = 2.0 ± 3.1 mm, $n = 6$; no cannibalism, 2.0 ± 3.9 mm, $n = 75$; $t = -0.01$, df = 79, $P = 0.99$). The cannibals did not gain an advantage over the noncannibals in terms of growth rate, reproductive success, or disappearance rate (Table 2).

Discussion

Male cannibalistic behavior of *Apogon notatus* was compared with that of a sympatric congener, *A. doederleini* (Table 3). In *A. doederleini*, filial cannibalism more frequently occurred late in the breeding season, whereas

Table 1. Monthly changes in the rate of brood disappearance and filial cannibalism in *Apogon notatus*

Month	June	July	August	September	Total
No. of spawnings	62	88	51	13	214
Brood disappearance rate (%)[a]	16.1	11.4	9.8	46.2	14.5
Filial cannibalism rate (%)	6.5	6.8	3.9	7.7	6.1

[a] All cases in which a brood disappeared from the male's mouth are included

Table 2. Comparison of fitness parameters between cannibal and noncannibal males of *A. notatus*

	Cannibals	Noncannibals	P value
SL (mm)	84.8 ± 7.2 SD (9)	86.8 ± 6.7 SD (25)	0.20*
Specific growth rate (% day^{-1}) ($\times 10^{-2}$)	1.01 ± 2.74 SD (9)	0.76 ± 2.2 SD (19)[a]	0.77*
No. of broods raised	2.4 ± 1.2 SD (9)	2.6 ± 0.9 SD (25)	0.62**
Annual disappearance rate (%)	77.8 (9)	56.0 (25)	0.43***

SL, standard length; SD, standard deviation
[a] Some fish could not be measured soon after the breeding season
* Mann–Whitney U-test
** t-test
*** Fisher's exact probability test
Individuals that did not survive to the end of the breeding season and whose broods disappeared due to unknown causes are excluded; sample sizes in parentheses

Table 3. Comparison of population characters and male cannibalistic behavior between *A. notatus* and *A. doederleini*

Species	A. notatus	A. doederleini	P
Habitat	Boulder area[a]	Boulder area[b]	
Population density (fish/m²)	1.51–3.28[a]	0.55[b]	
Breeding season	June–September[a]	May–August[b]	
Social behaviors	Gregarious and territorial[a]	Solitary and nonterritorial[c]	
Operational sex ratio	Male-biased[a]	Female-biased[c]	
Seasonal pattern of filial cannibalism	No seasonality[d]	Frequent in the late season[b]	
Remating time (days) after filial cannibalism	24.5[d]	3.1[c]	0.0001*
Mate change rate (%) after filial cannibalism	50.0[d]	97.9[e]	0.0009**
Mate preference in filial cannibalism	Absent[d]	Present[c]	
Filial cannibalism rate (%)	6.1–10.7[a]	15.9[e]	0.0005–0.09***
Brood loss rate (%) other than by filial cannibalism	3.7–8.4[a]	1.0[b]	0.06–0.0003***

[a] Okuda (1999a)
[b] Okuda and Yanagisawa (1996a)
[c] Okuda and Yanagisawa (1996b)
[d] Present study
[e] Okuda et al. (1997)
* Mann-Whitney *U*-test
** Fisher's exact probability test
*** χ^2 test; the range indicates *P* values when comparing under- and overestimated values for *A. notatus*

that of *A. notatus* showed no seasonality. Okuda and Yanagisawa (1996a) reported that the seasonal pattern in *A. doederleini* was caused by the deterioration of somatic condition in males, which spent about 80% of the interspawning interval in mouthbrooding. On the other hand, the proportion of time that male *A. notatus* spent mouthbrooding was no more than 53%. Late in the breeding season, the somatic condition of male *A. notatus* may not have been as critical as that of male *A. doederleini* (N. Okuda, unpublished data).

In both species, filial cannibalism usually occurred within a day of spawning. However, postcannibalistic behavior was markedly different between them: male *A. doederleini* remated within a few days of filial cannibalism, while male *A. notatus* took several weeks to remate or never remated within the season (Table 3). This difference may be related to mate availability for cannibals. The operational sex ratio was female biased in *A. doederleini* but male biased in *A. notatus*, suggesting that mate availability for males is higher in the former species. This high mate availability provides opportunities for males to remate with other females quickly after filial cannibalism (Okuda and Yanagisawa 1996b).

Female behavior may also be a factor affecting differences in male cannibalistic behavior between the two species. Females of *A. notatus* become territorial in the breeding season; pairing females keep conspecific invaders away from their mates until spawning is completed. On the other hand, female *A. doederleini* temporarily and promiscuously court multiple males without guarding mates at their home sites (Kuwamura 1985; Okuda and Yanagisawa 1996b). Consequently, males of *A. doederleini* have easy access to neighboring females, allowing them to assess the maturity of potential mates. Thus, they can estimate the possibility of remating with other mates after filial cannibalism. In *A. notatus*, in contrast, territorial behavior by paired females would prevent males from estimating their mate availability.

In *A. doederleini*, males preferentially cannibalize broods given by females that are small relative to themselves or are unfamiliar to themselves (Okuda and Yanagisawa 1996b). Mating with small females will incite males to commit filial cannibalism because the reproductive return from fewer eggs produced by such females may not exceed the cost of parental care (Petersen and Marchetti 1989; Petersen 1990; Lindström and Sargent 1997). In *A. notatus*, however, filial cannibalism was unaffected by the size difference in pairs. Because of the male-biased operational sex ratio, males may have little chance of cannibalizing broods from small females and subsequently remating with more favorable females. This interspecific difference can be explained in terms of sexual selection theory, predicting that the limiting sex should be more choosy (Trivers 1972; Williams 1975).

Fitness advantage of filial cannibalism, measured as growth, reproduction, or survival, was not found in *A. notatus*, as well as in some other apogonids (Okuda et al. 1997; Okuda 1999b). In species in which males care for multiple clutches, such as sticklebacks, males have the potential for a great increase in future reproductive success, so that it is possible for cannibal males to offset the current reproductive loss by future gain (Rohwer 1978). However, for male apogonids that accept only one clutch at a time, such an increase in future reproduction cannot be expected (Okuda et al. 1998). They need another way to compensate for the reproductive loss entailed by filial cannibalism. Okuda and Yanagisawa (1996b) suggested that cannibals can minimize the reproductive loss by replacing the cannibalized brood with another brood as soon as possible. It is therefore predicted that filial cannibalism in apogonids is more likely to occur in species in which mate availability is high for males. This prediction is supported by the higher incidence of filial cannibalism in *A. doederleini* than in *A. notatus* (Table 3).

Between the two species, there was a marked difference in the proportion of brood loss by means other than filial

cannibalism (see Table 3). Frequent brood losses in *A. notatus* are attributable to heterocannibalism by unpaired males (Okuda 1999a). In apogonids, eggs are most vulnerable when they are transferred from the female to the male. In *A. notatus*, a group of unpaired males was often observed to chase males just before and after spawning. Hrdy (1979) hypothesized that heterocannibalism would function as the intrasexual competition through which cannibals could gain increased opportunities for mating with a victim's parent. However, this is not applicable to the case of *A. notatus* in which females did not shorten their remating time when their broods were cannibalized. Heterocannibals are less likely to increase the mating opportunities with these females.

In *A. notatus*, heterocannibals can benefit simply by exploiting the eggs. Such cannibalism usually increases with population density (Polis 1981; Dong and Polis 1992). This fish has an extremely high population density in this study site and shows gregariousness with intense interference interactions between conspecifics (Kuwamura 1983, 1985; Okuda 1999a). Brood disappearances of this fish occurred most frequently in September, the last month of the breeding season (Table 1). In this month, most individuals become unpaired and gregarious (Okuda 1999a). In sticklebacks in which nest-raiding by conspecific shoals and subsequent heterocannibalism is often observed, males cannot effectively guard their eggs from the raiding shoal as the shoal size increases, resulting in increased incidence of heterocannibalism (Ridgway and McPhail 1988; FitzGerald et al. 1992). High population density and gregariousness may account for the frequent occurrence of heterocannibalism in *A. notatus*.

In this study, although the interspecific differences in cannibalistic behavior were undoubtedly clear, the problem involved in comparative methods remains unsolved. The comparison between sympatric related species allows us to disregard the physical and ecological effects on interspecific difference. However, we still have difficulty in exactly determining a causal factor of the difference because comparable species are usually different from each other in some aspects. To elucidate what determines the behavioral difference, further studies are needed to experimentally manipulate the predicted factors.

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