



Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish

NOBORU OKUDA

Department of Biology and Earth Sciences, Ehime University

(Received 13 July 1998; initial acceptance 7 October 1998;
final acceptance 2 April 1999; MS. number: 5942R)

I investigated male and female sexual strategies of a cardinalfish, *Apogon niger*, which breeds in sandy areas at sporadic coral colonies. Males mouthbrood an egg mass received from one female at a time. Because of the lengthy mouthbrooding period, the interspawning interval was shorter for females than for males. Females moved between coral colonies to find mates more extensively than did males, and more frequently deserted mates after spawning. The females shortened their interspawning intervals by changing mates, especially in the late breeding season, when their mobility was highest. Their mobility was positively correlated with their disappearance rate, suggesting that mate search increases mortality. This may reduce competition between females for males, resulting in an unbiased rather than female-biased operational sex ratio. Males, on the other hand, practised filial cannibalism of entire broods, which might allow them partially to compensate for the lack of food during the mouthbrooding period. The reproductive loss entailed by filial cannibalism could be effectively offset if males remate soon afterwards. However, cannibal males took a long time to remate because few females were available. Filial cannibalism was less frequent than in a boulder-dwelling congener in which males have easy access to mates. Low mate availability may inhibit male *A. niger* from committing filial cannibalism.

© 1999 The Association for the Study of Animal Behaviour

Sexual conflict is due primarily to sexual asymmetry of investment in offspring (Parker 1979). Although the quality and quantity of parental investment may differ between the sexes, their genetic contribution to offspring is always equal. Thus, the sex that invests least in current reproduction can enhance its fitness by increasing its future opportunity for reproduction (Trivers 1972). Such conflict has led to the coevolution of male and female sexual strategies where each sex increases its reproductive success at the expense of the other (Stockley 1997).

In fish, parental investment reflects a great diversity of reproductive patterns (Breder & Rosen 1966; Balon 1975), and because of this diversity, the type and degree of sexual conflict also differ between species (Halliday 1988; Leonard 1993; Magurran & Seghers 1994; Warner et al. 1995). These sexual conflicts need to be taken into account if we are to understand the evolution of the unique reproductive behaviours and variable mating patterns found in fish (Henson & Warner 1997).

In cardinalfish (Pisces: Apogonidae), males alone mouthbrood an egg mass received from one female (Blumer 1982). The mouthbrooding period lasts for a few

weeks, depending on water temperature (Okuda 1997). Since males do not eat while mouthbrooding, their body condition declines greatly and their mortality increases late in the breeding season (Okuda & Yanagisawa 1996a). Males thus incur a large cost by mouthbrooding. In many species with paternal care, males are reported to eat their own brood (i.e. filial cannibalism) to compensate for the cost of parental care (Dominey & Blumer 1984; FitzGerald & Whoriskey 1992). This is also the case in apogonids, in which males eat the entire brood (Okuda & Yanagisawa 1996a; Okuda 1997). This behaviour may increase male fitness by enhancing future reproduction or survival, but is clearly detrimental to females.

Female apogonids are freed from parental care, and thus can increase their investment in future reproduction. They have a high potential for future reproduction because of their high egg production rate relative to the rate of egg rearing by males per unit time (Okuda & Yanagisawa 1996b; Okuda 1997). In species where the potential reproductive rate is higher in females than in males, the females can enjoy greater reproductive success by changing mates than by remaining in pair bonds, just as in males of species with conventional sex roles (Jenni 1974; Emlen & Oring 1977). In apogonids, therefore, females are more likely than males to be unfaithful to their mates.

Correspondence: N. Okuda, Department of Biology and Earth Sciences, Ehime University, 2-5 Bunkyo-cho, Matsuyama, P.O. Box 790-8577, Japan (email: nokuda@sci.ehime-u.ac.jp).

In this paper, I report female mating behaviour and male filial cannibalism in a sand-dwelling cardinalfish, *Apogon niger*, in the light of their sexual strategies. I also discuss factors affecting the two sexual strategies.

METHODS

General Ecology

Apogon niger is a small fish inhabiting sandy reefs in the shallow waters of the west Pacific. They use many types of structures on the sand floor, such as rock, corals and dumped fishing gear, as shelter against sand-dwelling piscivorous fish (Okuda 1997). They also use these sites for courtship and spawning, showing no territoriality (Kuwamura 1983), leaving them to feed on small benthic invertebrates at dusk and returning at dawn (personal observation). While foraging, they are always solitary and reproductively inactive.

Individuals attain maturity at 1 year of age and breed for several years (Okuda 1997). Over the breeding season (May–October), both males and females spawn several times.

Field Observations

I studied the reproductive ecology of *A. niger* from 1992 to 1994 at Murote Beach (33°00'N, 132°30'E), Shikoku Island, Japan. I set a quadrat measuring 20 × 60 m, with a 5-m grid, on the sand floor and made field observations with the aid of scuba equipment. In the quadrat, there were live poritid and acroporid coral colonies, sea anemones and artefacts such as an anchor and rope; I noted their size and locations on the quadrat map.

At the beginning of the breeding season in 1992, I captured all individuals of *A. niger* in the quadrat, using a seine and hand net, and marked them by uprooting a few dorsal and/or anal fin rays under a quinaldine anaesthetic. Whenever unmarked *A. niger* immigrated into the quadrat, I captured and marked them. In 1992 and 1993, I marked a total of 53 and 62 fish, of which 42 and 60, respectively, were continually found within the quadrat. In each month from June 1992 to October 1993, I checked the presence of marked fish in the daytime on 6–30 consecutive days and recorded their locations on the map. For each individual, the distance of daily movements between shelters was measured and averaged for each month: this value was used as an index of mobility because fish were so immobile that short-term mobility was less measurable. I also calculated the monthly disappearance rate as the proportion of marked fish observed in the previous month that disappeared: individuals were considered to have disappeared if they were never found in later censuses.

Throughout the breeding season of 1993, I made daily censuses to monitor reproductive events for each marked fish, mainly between 1200 and 1600 hours: a preliminary observation in 1992 showed almost no reproductive behaviours in the morning and evening (also see Kuwamura 1985). In each census, I noted courtship and

spawning behaviours of marked fish and identified their mates: postspawning behaviour, which lasts for more than 1 h (Kuwamura 1985), enabled me to identify spawning pairs accurately. I also recorded the brooding status of each male (mouthbrooding or nonbrooding) and the maturity of each female by five stages according to Okuda & Yanagisawa's (1996b) classification based on the degree of belly expansion. From these censuses, I estimated the operational sex ratio, defined as the ratio of reproductively receptive males to mature females.

I sometimes found that an entire brood disappeared from a male's mouth before the expected day of hatching. To confirm the occurrence of filial cannibalism, I extracted a small portion of the stomach contents from some of these males, using a small needleless syringe after anaesthetizing the fish: the brood disappearance was attributed to filial cannibalism if the stomach contents included eggs of the same developmental stage as those mouthbrooded by the male (Okuda & Yanagisawa 1996a).

To examine individual growth, I measured the standard length (SL) of marked fish to the nearest 0.5 mm with a pair of callipers prior to the breeding season. Since few fish survived to the end of the breeding season, I recaptured and measured them up to four times. After the last measurement for each individual, I calculated the growth rate (%/day) as:

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

where G is the daily specific growth rate, 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.

Prior to the breeding season of 1994, I conducted a follow-up survey of marked fish. I calculated the annual disappearance rate (%) in the same way as the monthly disappearance rate. To find out whether the disappearances were probably due to death and not emigration, I censused *A. niger* individuals outside the quadrat, throughout this small beach (about 300 × 400 m), soon after the breeding season. Of 32 marked fish that disappeared during the breeding season in 1992, two were found within several metres of the quadrat and the others were not found elsewhere. Considering their low mobility (see below), it is unlikely that the latter fish emigrated from the beach. Accordingly, I thereafter assumed that marked fish that disappeared had died, provided they were never found within 10 m of the quadrat.

Ethical Note

The marking technique used in this study was proposed by Goto (1985), who reported that it did not adversely affect fish behaviour. This method also enabled me to observe marked fish over more than 1 year. The small wound caused by uprooting the fin rays healed within a few weeks of marking and the broken fin regenerated completely without becoming diseased. In a congener, *A. doederleini*, some marked fish have been observed for

Table 1. The distance (m) of daily movements between shelters by marked individuals of *A. niger*

Period	Total*	Male	Female	Sexual difference†	
				<i>t</i>	<i>P</i>
June–October 1992 (breeding season)	1.65±0.95 (32)	1.43±0.72 (17)	2.16±0.97 (12)	2.33	0.03
November 1992–April 1993 (nonbreeding season)	0.67±0.33 (16)	0.58±0.32 (10)	0.79±0.34 (5)	1.18	0.26
May–October 1993 (breeding season)	1.70±0.91 (36)	1.34±0.51 (13)	2.38±0.98 (13)	3.39	0.003

Sample sizes are given in parentheses.

*Marked fish include individuals that disappeared before being sexed.

†Student's *t* test.

more than 5 years, indicating that long-term survival is unlikely to be impaired by the technique (the maximum life span is 7 years; see Okuda et al. 1998).

The method of confirming filial cannibalism has also been used in other apogonids (Okuda & Yanagisawa 1996a; Okuda, in press). This method does not involve dissecting fish to check the stomach contents, so that information on the mating experiences of cannibal fish can still be obtained. Since I extracted only a small portion of the stomach contents, the energy gain from eating eggs would not be reduced by much.

Apogon niger is a common species and not a commercial one. No licences are required to capture and experiment on it in Japan.

Statistical Analysis

For data analysis, I used parametric tests when data fitted a normal distribution. When this requirement was not fulfilled or the data distribution was different between two groups, I used nonparametric Mann-Whitney *U* tests. Means are given ± SD, for descriptive purposes, and all *P* values are two tailed.

RESULTS

Mobility and Disappearance

The population density of *A. niger* was very low (0.016 and 0.033 fish/m² in May 1992 and 1993, respectively). Adults mainly used poritid coral colonies as their sheltering and spawning sites. Poritid colonies large enough to be used as shelters (more than 50 cm in diameter) were sporadically distributed (0.09 colonies/m²). During the nonbreeding season, adult fish lived solitarily in their shelters showing a strong site fidelity, whereas those in the breeding season moved between shelters extensively to form pairs (Student's *t* test: breeding season of 1992 versus nonbreeding season: $t_{46}=3.96$, $P<0.001$; nonbreeding season versus breeding season of 1993: $t_{50}=4.35$, $P<0.001$; breeding season of 1992 versus breeding season of 1993: $t_{66}=0.21$, $P=0.83$; Table 1). During the breeding season, females moved between shelters more extensively than did males (Table 1). Female mobility was higher late in the season (August–October) than early in the season (May–July; two-way repeated measures ANOVA:

sex: $F_{1,14}=8.29$, $P<0.02$; season: $F_{1,14}=10.7$, $P<0.006$; interaction: $F_{1,14}=0.34$, $P=0.57$).

During the breeding season, adult fish frequently disappeared from the quadrat (Fig. 1). The monthly disappearance rate was positively correlated with the monthly mean of daily movements by marked individuals ($r=0.55$, $F=6.01$, $N=16$, $P<0.03$; Fig. 1). Fish that disappeared during the breeding season tended to move more extensively early in the season (1.64 ± 0.89 m, $N=24$) than those that did not disappear (1.08 ± 0.53 m, $N=11$; $t_{33}=1.93$, $P=0.06$).

The annual disappearance rate was 88.1% in 1992 ($N=42$) and 88.3% in 1993 ($N=60$). This rate did not differ significantly between the sexes (Fisher's exact probability test: $P=0.63$ in 1992, male 80.0%, female 92.3%; $P=0.69$ in 1993, male 87.5%, female 81.8%).

Growth and Reproduction

The onset of the first spawning varied greatly between individuals, from 18 May to 26 September. Smaller males started the first spawning later ($r = -0.79$, $F=30.6$, $N=21$, $P<0.001$), whereas the onset of the first spawning by females was not dependent on their body size ($r = -0.23$, $F=1.06$, $N=22$, $P=0.31$). For individuals measured several times during the breeding season, the growth rate was significantly higher early than late in the season,

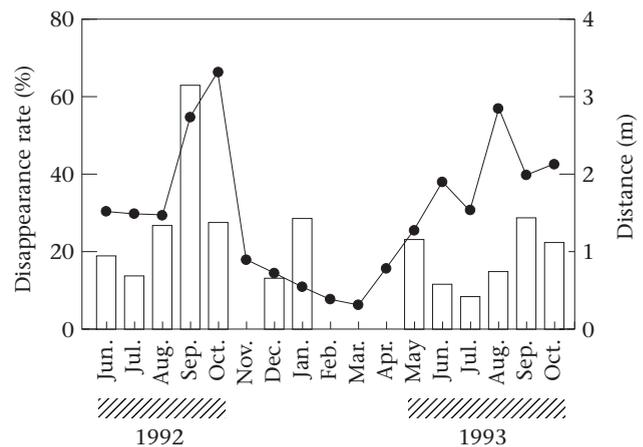


Figure 1. Monthly changes in the disappearance rate (□) and the mean distance of daily movements (●) for marked individuals. Hatching indicates the duration of the breeding season.

and marginally higher in females than in males (two-way repeated measures ANOVA: season: $F_{1,9}=49.6$, $P<0.0001$; sex: $F_{1,9}=3.71$, $P<0.09$; interaction: $F_{1,9}=0.48$, $P=0.51$).

Courtship displays took place between individuals that lived in the same or adjacent shelters. Courtship of a pair was repeated intermittently over 4.1 ± 3.6 days ($N=82$). Prior to spawning, males shared the shelter with 1.28 ± 0.58 females ($N=89$) and females with 1.27 ± 0.52 males ($N=90$). Sharing with multiple potential mates occurred not simultaneously but in sequence, so that agonistic intrasexual encounters were rarely observed.

Spawning usually occurred between 1200 and 1600 hours (88.9% of the cases in which spawning time was known). Spawning pairs were not size assortative early in the breeding season ($r=0.21$, $F=0.69$, $N=17$, $P=0.42$), but weakly size assortative late in the breeding season ($r=0.36$, $F=8.63$, $N=60$, $P<0.005$). Within pairs early in the season, males were significantly larger than females, by 6.1 mm (paired t test: $t_{16}=2.39$, $P<0.03$), whereas the size differences were not significant late in the season (paired t test, $t_{59}=0.67$, $P=0.51$). Throughout the breeding season, only two pairs showed mate fidelity until the next spawning, and the majority of pairs ($N=64$) separated within a few days of spawning. Where separation occurred, 39 females and four males left their mates in the spawning sites. The rate of mate desertion was significantly higher for females than for males ($\chi^2_1=17.2$, $P<0.001$). In the remaining 21 cases, it was unknown which sex deserted because both sexes left their spawning sites on the same day. Some pairs that separated were re-established in the next spawning. As a result, the rate of mate change between two successive spawnings was 38.5 and 60.3% for males and females, respectively, and was significantly higher for females ($\chi^2_1=7.18$, $P<0.008$).

Males mouthbrooded eggs for 7–13 days and remated 1–44 days after their eggs hatched (Fig. 2). The mouthbrooding period was negatively correlated with ambient water temperature (18.9–25.0°C; $r=-0.93$, $F=537.3$, $N=86$, $P<0.001$, water temperature log-transformed), while the time taken to remate after the eggs hatched was independent of water temperature ($r=-0.10$, $F=0.82$, $N=64$, $P=0.42$). Males spent on average 58.0% of interspawning intervals in mouthbrooding. The interspawning intervals were significantly shorter for females than for males (Mann–Whitney U test: $Z=-2.81$, $N_1=66$, $N_2=64$, $P<0.005$; Fig. 2). The interspawning intervals were shorter late in the season, when the water temperature was higher, than early in the season (Mann–Whitney U test: males: $Z=-3.80$, $N_1=14$, $N_2=52$, $P<0.001$); females: $Z=-4.13$, $N_1=14$, $N_2=50$, $P<0.001$). Late in the season, the females shortened their interspawning intervals more when they changed mates (Table 2). For males, mate change never affected their interspawning interval.

During the breeding season, each male spawned on average 5.6 ± 2.0 times ($N=10$) and each female spawned 5.4 ± 17.3 times ($N=7$). The number of spawnings did not differ significantly between the sexes ($t_{15}=-0.12$, $P=0.90$).

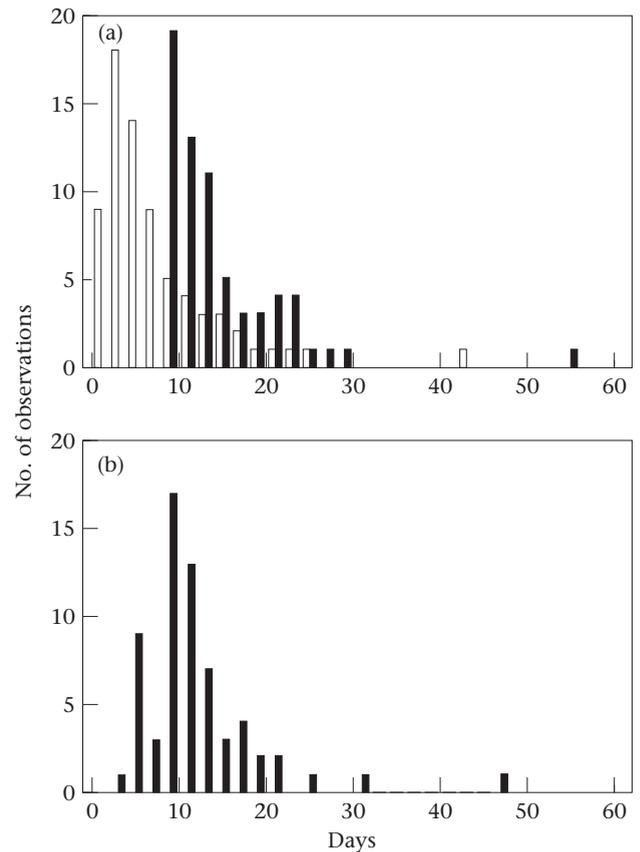


Figure 2. Frequency distribution of the interspawning intervals (■) for (a) males and (b) females. □: Time taken for males to remate after their eggs hatched.

Filial Cannibalism

Of 113 clutches mouthbrooded, 10 disappeared from the male's mouth before the expected day of hatching, eight of these within a day of spawning. For all six males whose stomach contents were checked, eggs at the same developmental stage as those mouthbrooded were found. These six males were abnormally potbellied because of the eggs in their stomachs (Okuda & Yanagisawa 1996a). Of the other four males, three were also potbellied, suggesting that they had eaten their own broods. The remaining male, which was not potbellied when his brood disappeared 7 days after spawning, was considered not to have practised filial cannibalism. The filial cannibalism rate was estimated to be 8.0% (9/113).

After filial cannibalism, five of six males changed mates. Their rate of mate change (83.3%) was higher than that of males that did not eat their broods (34.7%, $N=72$; Fisher's exact probability test: $P<0.03$). The time to remate after cannibalism (21.4 days, $N=5$) was significantly longer than the time to remate after hatching for males that did not eat their broods (7.9 days, $N=72$; Mann–Whitney U test: $Z=-2.47$, $P<0.02$).

Cannibal males, defined as males that practised filial cannibalism at least once in a season, were as large as noncannibal males (Table 3). The size difference (male SL minus female SL) in spawning pairs also did not differ

Table 2. The interspawning interval (days) for males and females that did or did not change mates early (May–July) and late (August–October) in the breeding season

Breeding season	Mean water temperature (°C)	Change	No change	U^*	P
Females					
Early	19.9	20.7 (10)	16.8 (4)	18.5	0.83
Late	23.6	9.2 (26)	11.0 (23)	-2.14†	0.03
Males					
Early	19.9	26.1 (7)	16.7 (6)	11.5	0.17
Late	23.6	12.9 (14)	12.9 (36)	-0.04†	0.97

Sample sizes are given in parentheses.

*Mann–Whitney U test.

†Standardized Z values.

Table 3. Comparison of fitness parameters between cannibal and noncannibal males

	Cannibals	Noncannibals	U	P
SL (mm)	70.1 (7)	68.4 (17)	52	0.63†
Growth rate (%/day) ($\times 10^{-2}$)	3.52 (5)	6.85 (5)	9	0.46†
Reproductive success*	5.6 (5)	5.6 (5)	10.5	0.68†
Annual disappearance rate (%)	85.7 (7)	88.2 (17)		0.99‡

Sample sizes are given in parentheses.

*The number of broods reared in a season.

†Mann–Whitney U test.

‡Fisher's exact probability test.

between pairs in which filial cannibalism occurred and those in which it did not (Mann–Whitney U test: $Z = 0.44$, $N_1 = 8$, $N_2 = 80$, $P = 0.66$). Cannibals and noncannibals did not differ significantly in growth, reproductive success or disappearance rate (Table 3).

Sex Ratio

The adult sex ratio (males:females) did not deviate significantly from equality at the beginning of the breeding season (14:15; $\chi^2_1 = 0.03$, $P = 0.85$). This ratio ranged from near equality to a slight male bias as the breeding season progressed (Fig. 3). To estimate the operational sex ratio (receptive males:mature females), I regarded non-brooding males as receptive, because males could remate soon after their eggs hatched (Fig. 2; also see Okuda & Yanagisawa 1996b), and females as mature at the second or more of five maturing stages based on their belly expansion, because those at the second stage often spawned by the next day (17 cases). Since the onset of reproduction varied between individuals, neither males nor females were regarded as receptive until they showed courtship behaviours.

From June to August, the operational sex ratio skewed towards males relative to the adult sex ratio (paired t test: June: $t_{18} = -5.03$, $P < 0.001$; July: $t_{27} = -3.60$, $P < 0.002$; August: $t_{24} = -2.64$, $P < 0.02$; Fig. 3). Late in the breeding season, it did not differ significantly from the adult sex ratio (September: $t_{24} = 1.21$, $P = 0.24$; October: $t_{14} = -1.79$, $P = 0.09$).

DISCUSSION

Adult *A. niger* moved extensively between shelters during the breeding season, whereas they were sedentary during the nonbreeding season. These fish are preyed upon by flounders and lizardfish, which are abundant on the sandy reef (Okuda 1997), especially when they are away from shelter. Since coral shelters and their inhabitants were sporadically distributed in the study area,

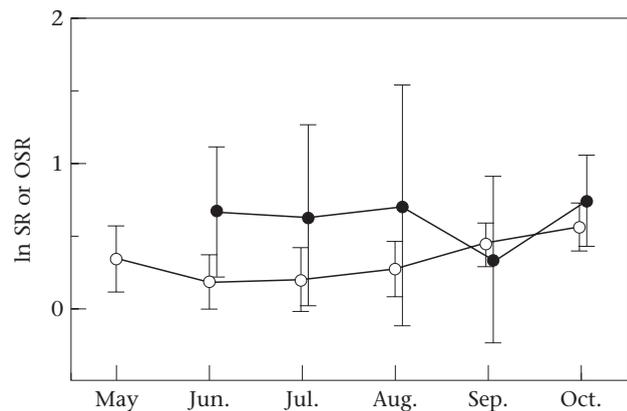


Figure 3. The adult sex ratio (SR; ○) and the operational sex ratio (OSR; ●) in the breeding season of 1993. Each plot is the monthly mean \pm SD of logarithmically transformed values. Positive and negative numbers indicate male-biased and female-biased ratios, respectively. The OSR in May was omitted because few individuals started reproduction (two males and two females).

movement between shelters may increase the fish's chance of encountering mates but also increase predation risk. The monthly disappearance rates were high when the fish became more mobile, and the fish that disappeared probably died. An increase in mortality may be caused by poor body condition, as males fast while mouthbrooding and females expend energy producing eggs. In *A. doederleini*, male mortality is high late in the breeding season because they spend a lot of time (78.1% of the interspawning interval) mouthbrooding and consequently their body condition is greatly reduced (Okuda & Yanagisawa 1996a). In contrast, male *A. niger* spent less time (58.0%) mouthbrooding, and their disappearance rate did not increase as the breeding season progressed. In *A. niger*, disappearances of individuals depended on their mobility but not on their reproductive histories. These results suggest that mate search increases mortality for *A. niger* in this habitat.

The growth rate was higher early in the breeding season, when few fish were ready to reproduce. A negative relationship between their initial body size and the onset of reproduction could be found only for males. As is often the case (Stearns 1992), there may be a trade-off between delayed reproduction and increased growth in male *A. niger*, which incur the greater cost in terms of their reduced feeding opportunities during the mouthbrooding period and consequently their decreased growth. At the onset of reproduction, paired males of *A. niger* were usually larger than their mates. In apogonids, the brood size is limited by the male's buccal capacity but not by female fecundity (Okuda et al. 1998). Since male body size is a function of their brooding capacity, small males can increase their future reproductive success effectively by increasing their growth while delaying reproduction (Okuda et al. 1997). For females, on the other hand, reproductive success will largely depend on the body size of mates available to them. In some boulder-dwelling cardinalfish which have easy access to mates, large females usually mate with large males, resulting in a highly size-assortative mating (Okuda et al. 1998; Okuda, in press). In contrast, pairs of *A. niger* were less size assortative, especially early in the breeding season. The lack of assortative mating suggests that intersexual encounters occur by chance, probably because of sporadic mate distribution and their restricted mobility. In such a situation, where mating is random, the sex with higher fertility does not have the size-dependent fecundity advantage (Warner 1975). Therefore, the body size at the onset of reproduction may be less important to females, which benefit instead from getting receptive mates as soon as possible.

After spawning, females of *A. niger* deserted mates more frequently than did males. Since Trivers (1972), the theory of mate desertion has been refined and developed by many theoretical and empirical studies (Dawkins & Carlisle 1976; Beissinger 1987; Beissinger & Snyder 1987; Lazarus 1990; Choudhury 1995). The main focus of study has been on which sex should desert. The basic assumption is that this decision should be determined by the cost:benefit ratio to the deserter independent of its past investment (Dawkins & Carlisle 1976). Keenleyside

(1983), by experimentally manipulating mate availability for each sex of a biparental cichlid fish, showed that the sex that was ready to remate more quickly was most likely to desert its mate. In *A. niger*, the interspawning interval was potentially shorter for females, because of the lengthy mouthbrooding period of males. Although females gave almost no assistance in parental care, males seldom failed in mouthbrooding, unless they ate the eggs. Thus, the females can enjoy higher reproductive success by deserting than by cooperating with a mate. Desertion by females often occurs in other apogonids (Okuda & Yanagisawa 1996b; Okuda, in press). However, female *A. niger* that deserted mates did not always remate quickly early in the breeding season, when they were not very mobile. Low mate density and low mobility might decrease the opportunities for females to encounter a new receptive male soon after mate desertion.

The higher mobility and higher mate desertion rate of females than males suggest that they are more active in getting mates. The same result was obtained in a congener, *A. doederleini*, in which sex roles are reversed (Okuda & Yanagisawa 1996b). *Apogon niger* also seems to be sex-role reversed. Current theory predicts sex role reversal where the operational sex ratio is female biased (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996). In *A. niger*, however, the operational sex ratio was unbiased, or slightly male biased. As Vincent (1994b) pointed out females, because of anatomical constraints, cannot remain reproductively receptive longer than males. For species in which intersexual encounters are limited by low mate density and low mobility, receptive males may predominate over mature females even when the potential reproductive rate is higher in females (e.g. seahorses: Vincent 1994a). In such species, agonistic intrasexual encounters will also be infrequent. In *A. niger*, sexual selection may act on either sex very weakly rather than on females more strongly.

While females often deserted their mates, some of these mates ate their entire broods soon after being deserted. Entire brood cannibalism by parental males has also been reported in some other apogonids (Okuda & Yanagisawa 1996a; Okuda, in press). This cannibalism can partially compensate for the energetic cost of parental care (K. Omori, R. Manabe, N. Okuda & Y. Yanagisawa, unpublished data). In *A. niger*, however, a fitness advantage of filial cannibalism was unclear in terms of growth, reproduction or survival. Cannibal males have to offset another gain against the current reproductive loss entailed by filial cannibalism. They can do this by remating soon afterwards, so that the brood is substantially replaced by the next one. In a boulder-dwelling congener *A. doederleini*, in which the operational sex ratio is female biased and thus males have easy access to mates, the males remate within a few days of entire brood cannibalism, almost always changing mates (Okuda & Yanagisawa 1996b; Okuda et al. 1997). In *A. niger*, in contrast, males took about 3 weeks to remate after entire brood cannibalism. The males, as well as females, might have difficulty in getting a new receptive mate because of the low mate density and low mobility. The incidence of filial cannibalism is significantly lower in *A. niger* (8.0%) than in

A. doederleini (15.9%, Okuda et al. 1997; $\chi_1^2=4.47$, $P<0.04$), perhaps because low mate availability inhibits male *A. niger* from eating their brood.

Acknowledgments

I am grateful to M. H. A. Keenleyside, T. Kuwamura, M. Taborsky, Y. Yanagisawa, two anonymous referees and the editor, A. Berglund, for constructive comments on the manuscript. I also thank K. Omori for generously providing me with the unpublished data. This study was financially supported by Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists.

References

- Balon, E. K. 1975. Reproductive guilds of fishes: a proposal and definition. *Journal of the Fisheries Research Board of Canada*, **32**, 821–864.
- Beissinger, S. R. 1987. Mate desertion and reproductive effort in the snail kite. *Animal Behaviour*, **35**, 1504–1519.
- Beissinger, S. R. & Snyder, N. F. R. 1987. Mate desertion in the snail kite. *Animal Behaviour*, **35**, 477–487.
- Blumer, L. S. 1982. A bibliography and categorization of bony fishes exhibiting parental care. *Zoological Journal of the Linnean Society*, **76**, 1–22.
- Breder, C. M., Jr & Rosen, D. E. 1966. *Modes of Reproduction in Fishes*. New York: The Natural History Press.
- Choudhury, S. 1995. Divorce in birds: a review of the hypotheses. *Animal Behaviour*, **50**, 413–429.
- Dawkins, R. & Carlisle, T. R. 1976. Parental investment, mate desertion and a fallacy. *Nature*, **262**, 131–133.
- Dominey, W. J. & Blumer, L. S. 1984. Cannibalism of early life stages in fishes. In: *Infanticide: Comparative and Evolutionary Perspectives* (Ed. by G. Hausfater & S. B. Hrdy), pp. 43–64. New York: Aldine Press.
- Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.
- FitzGerald, G. J. & Whoriskey, F. G. 1992. Empirical studies of cannibalism in fish. In: *Cannibalism: Ecology and Evolution among Diverse Taxa* (Ed. by M. A. Elgar & B. J. Crespi), pp. 238–255. Oxford: Oxford University Press.
- Goto, A. 1985. Individual identification by spine and ray clipping for freshwater sculpins. *Japanese Journal of Ichthyology*, **32**, 359–362.
- Halliday, T. 1988. Sexual conflict and female choice in fishes. *Trends in Ecology and Evolution*, **3**, 124–125.
- Henson, S. A. & Warner, R. R. 1997. Male and female alternative reproductive behaviors in fishes: a new approach using intersexual dynamics. *Annual Review of Ecology and Systematics*, **28**, 571–592.
- Jenni, D. A. 1974. Evolution of polyandry in birds. *American Zoologist*, **14**, 129–144.
- Keenleyside, M. H. A. 1983. Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. *Animal Behaviour*, **31**, 683–688.
- Kuwamura, T. 1983. Change of habitat and spacing pattern in the life histories of the cardinalfishes *Apogon* spp. at Shirahama, Japan. *Nankiseibutsu*, **25**, 13–18 (in Japanese).
- Kuwamura, T. 1985. Social and reproductive behavior of three mouthbrooding cardinalfishes, *Apogon doederleini*, *A. niger* and *A. notatus*. *Environmental Biology of Fishes*, **13**, 17–24.
- Kvarnemo, C. & Ahnesjö, I. 1996. The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution*, **11**, 404–408.
- Lazarus, J. 1990. The logic of mate desertion. *Animal Behaviour*, **39**, 672–684.
- Leonard, J. L. 1993. Sexual conflict in simultaneous hermaphrodites: evidence from serranid fishes. *Environmental Biology of Fishes*, **36**, 135–148.
- Magurran, A. E. & Seghers, B. H. 1994. Sexual conflict as a consequence of ecology: evidence from guppy, *Poecilia reticulata*, populations in Trinidad. *Proceedings of the Royal Society of London, Series B*, **255**, 31–36.
- Okuda, N. 1997. Life history and sexual strategies of the cardinal fish (Pisces: Apogonidae) in the temperate sea. Doctoral thesis, Kyoto University.
- Okuda, N. In press. Sex roles are not always reversed when the potential reproductive rate is higher in females. *American Naturalist*.
- Okuda, N. & Yanagisawa, Y. 1996a. Filial cannibalism by mouthbrooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. *Environmental Biology of Fishes*, **45**, 397–404.
- Okuda, N. & Yanagisawa, Y. 1996b. Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. *Animal Behaviour*, **52**, 307–314.
- Okuda, N., Takeyama, T. & Yanagisawa, Y. 1997. Age-specific filial cannibalism in a paternal mouthbrooding fish. *Behavioral Ecology and Sociobiology*, **41**, 363–369.
- Okuda, N., Tayasu, I. & Yanagisawa, Y. 1998. Determinate growth in a paternal mouthbrooding fish whose reproductive success is limited by buccal capacity. *Evolutionary Ecology*, **12**, 681–699.
- Parker, G. A. 1979. Sexual selection and sexual conflict. In: *Sexual Selection and Reproductive Competition in Insects* (Ed. by M. S. Blum & N. A. Blum), pp. 123–166. New York: Academic Press.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stockley, P. 1997. Sexual conflict resulting from adaptations to sperm competition. *Trends in Ecology and Evolution*, **12**, 154–159.
- Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136–179. Chicago: Aldine Press.
- Vincent, A. C. J. 1994a. Seahorses exhibit conventional sex roles in mating competition, despite male pregnancy. *Behaviour*, **128**, 135–151.
- Vincent, A. C. J. 1994b. Operational sex ratios in seahorses. *Behaviour*, **128**, 153–167.
- Warner, R. R. 1975. The adaptive significance of sequential hermaphroditism in animals. *American Naturalist*, **109**, 61–82.
- Warner, R. R., Shapiro, D. Y., Marconato, A. & Petersen, C. W. 1995. Sexual conflict: males with highest mating success convey the lowest fertilization benefits to females. *Proceedings of the Royal Society of London, Series B*, **262**, 135–139.
- Wootton, R. J. 1990. *Ecology of Teleost Fishes*. London: Chapman & Hall.