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Sex Roles Are Not Always Reversed When the Potential Reproductive Rate Is Higher in Females

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ABSTRACT: Sex roles were examined in a cardinalfish, *Apogon notatus*, in which males alone mouthbrood the eggs received from a single female. Before spawning, a male and female formed a pair, within which the female is more active in courtship and attacks against conspecifics. Females had a higher potential for reproduction and on average produced more than twice as many clutches as those mouthbrooded by a male in a season by changing mates after spawning. Animals in which mating competition is more intense among females and, ultimately, sexual selection is more strongly acting on females are defined as sex-role reversed. Sex-role reversal is expected where the operational sex ratio (OSR) is female biased. In *A. notatus*, however, the OSR was male biased throughout the breeding season. This was due primarily to a higher mortality in females. The theory predicts that sexual selection operates more strongly on the sex toward which the OSR is biased. The facts that the variance in reproductive success was greater in males and the males developed a sexual trait suggest that sexual selection is acting more strongly on males than on females. Accordingly, this fish is not sex-role reversed.

Keywords: Apogonidae, operational sex ratio, parental investment, paternal mouthbrooding, sex-role reversal.

Since Darwin (1871) proposed the concept of sexual selection to explain the evolution of sex differences, there have been theoretical and empirical advances in this field (Andersson 1994). In many animals, males develop secondary sexual characters such as conspicuous body colors, exaggerated ornaments, or menacing weapons. The males also directly compete for access to mates. In general, female reproductive success is limited by gamete production, whereas male success is limited by mate availability (Bateman 1948). Hence, males are under stronger selection to acquire mates. In some animals, nevertheless, it has been reported that females are the predominant competitors for mates. Such species are typically described as sex-role reversed (Trivers 1972; Williams 1975) and offer the best opportunity to test our theoretical understanding of sexual selection.

Parental investment (PI) was the first epochal idea to predict which sex would compete more intensely for mates (Trivers 1972). PI is defined as any investment in an offspring resulting in reduced parental ability to invest in other offspring. The sex that invests less in offspring should compete more for mates, because that sex reproduces more often, leading to scarcity of sexually active members of the opposite sex. The relative number of sexually active males and females was called operational sex ratio (OSR) by Emlen and Oring (1977), and they argued that the more abundant sex should be the more competitive one. However, field workers often have difficulty obtaining accurate measurements of PI and OSR in nature (Knapton 1984; Kvarnemo and Ahnesjö 1996). As a more measurable predictor of mating competition, potential reproductive rate (PRR), the maximum number of offspring that each parent can produce per unit time, was advocated by Clutton-Brock and Vincent (1991). They predicted that the mating competition would be more intense among the sex with higher PRR. Recently, a theoretical framework incorporating PI, OSR, and PRR has been constructed by Clutton-Brock and Parker (1992) and modified by Parker and Simmons (1996), who recognize that PRR is an inverse function of "time out" from mating activities, and time out is determined by the relative amount of PI. Either PRR or time out is a direct predictor of OSR, provided that the adult sex ratio is unbiased (Clutton-Brock and Parker 1992; Parker and Simmons 1996). This means that the adult sex ratio can also be a primary factor determining the OSR if it deviates from equality. In animals there may exist biases in the adult sex ratio owing to sexual differences in birth and mortality rates and distribution in space and time. Therefore, we must take into account the population structure when predicting the pattern of mating

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competition and, thus, sexual selection (Lawrence 1986; Kodric-Brown 1988; Madsen and Shine 1993; Kvarnemo et al. 1995).

The cardinalfish *Apogon notatus* (Apogonidae), the subject animal of this study, is a marine mouthbrooder (Kuwamura 1983). Males alone mouthbrood an egg mass received from one female, while females provide no parental care. Reproductive rate of males is restricted by the lengthy mouthbrooding period and is usually lower than that of females (Kuwamura 1985). In terms of PRR or time out, this fish is expected to be a sex-role reversed species, as categorized by Clutton-Brock and Vincent (1991). However, Kuwamura (1983) reported that males predominate in number in a population of *A. notatus.* Thus, further information is needed to predict the pattern of mating competition.

The main purpose of this study is to determine the direction and intensity of mating competition in a natural population of *A. notatus.* I compared sex roles between males and females and estimated some parameters to predict the pattern of sexual selection.

Material and Methods

General Reproductive Ecology

Apogon notatus inhabits shallow waters of the west Pacific. This fish is found in large shoals in the water column from autumn to spring. Before the breeding season (May–October in southern Japan; Kuwamura 1983; Ueno et al. 1987), paired fish begin to settle on the boulder substratum. At the peak of the breeding season, most individuals form pairs, while some remain unpaired, forming loose aggregations in midwater. Paired fish are highly site attached (Usuki 1977) and show aggressive behavior against fish approaching the pair (Kuwamura 1983). Spawning and transfering an egg mass to a male take place within a few seconds, and then the male takes several minutes to completely pack the egg mass into his mouth (Kuwamura 1983). Males alone mouthbrood eggs until hatching. Both males and females experience several spawning cycles in a breeding season. After the last spawning in the season, paired fish abandon the breeding sites and become gregarious again.

Field Observations

The study was carried out at Murote Beach (33°00′N, 132°30′E), Shikoku Island, Japan, in 1995 and 1996. Field observations were made with the aid of SCUBA. A 10 × 20-m quadrat was set on the boulder slope. In and around the quadrat, 314 adult *A. notatus* were captured with a seine and hand net and were anesthetized underwater with quinaldine. The fish were measured to the nearest 0.5 mm in standard length (SL) and were individually marked by hypodermically injecting colored liquid latex (Riley 1966) and extracting a few dorsal and/or anal fin rays (Okuda and Yanagisawa 1996*a*). After recovering from the anesthesia, the fish were released at the capture site. This marking technique enabled me to follow the marked fish throughout a long-term study (Okuda et al. 1997, 1998). Reproductive experiences of each marked fish found in the quadrat ($N = 153$) were recorded every day over the entire breeding season (June–September) in 1995. Pre- and postspawning behaviors, which continued for several hours on the day of spawning (Kuwamura 1983), enabled me to predict the spawning event and to identify spawning pairs accurately. For unmarked fish with whom the marked fish mated, lines and spots on the head were sketched, which showed enough intraspecific variation to be discriminated. Since the size distribution of marked fish showed a clear bimodal pattern (fig. 1), the unmarked fish were categorized into two size classes measured by eye: small size class is for fish whose SL is 77 mm and less, and large size class for those more than 77 mm.

Courtship and attack behaviors shown by marked fish in pairs ($N = 132$ in various combinations of 52 males and 44 females) were observed. Courtship displays were classified into four categories (see Kuwamura 1983 for details): warping or circling, displaying a lateral side of the body toward a mate while wriggling or circling round the mate; parallel circling, circling in a parallel position following the mate's response to circling; nuzzling, poking the mate's chin and abdomen with the snout; and extrapair courtship, displaying the above behaviors toward another member of the opposite sex. Attack was defined as the

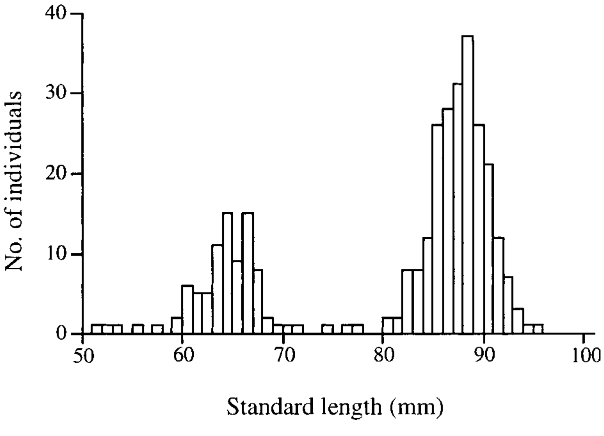

Figure 1: The size distribution of marked fish. Small size class corresponds to 1 yr of age, and large size class to two or more years of age (see Okuda 1997).

repelling of a conspecific or heterospecific fish that approached within 30 cm of the pair. The numbers of these behaviors were scored for 20 min and compared between the sexes in pairs. The pairing period was divided into three phases: the courting phase and the pre- and postspawning phases. The courting phase was defined as the period from pair formation to the day before spawning, the pre- and postspawning phases were the periods before and after releasing spawns on the day of spawning. Unpaired marked fish ($N = 36$) were also observed for 20 min.

The entire brood sometimes disappeared from a male's mouth before the expected day of hatching. I captured some of these males and checked their stomach contents by gently inserting a small syringe through the esophagus after the anesthesia. The brood disappearance was considered to be caused by filial cannibalism if the stomach contents extracted included eggs of the same developmental stage as those the males had been mouthbrooding (Okuda and Yanagisawa 1996*a*).

At the beginning of the next breeding season, a follow-up survey of marked fish was conducted. Since *A. notatus* shows high site fidelity (Usuki 1977), marked fish that had disappeared from the quadrat and were not subsequently found nearby (within about 10 m of the quadrat) were regarded as having died. On the basis of this assumption, the annual mortality (%) 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.

Parameter Estimation in Relation to Sexual Selection

The OSR, the ratio of reproductively receptive males to females, was estimated from monthly censuses in the quadrat in 1995. In each census, all adult fish, whether they were marked or not, were counted and categorized into two size classes. The adult fish were all considered to be participants in breeding since both sexes attain maturity at age 1 (Okuda 1997). For each fish, the mating status (paired or unpaired) and the brooding status (mouthbrooding or nonbrooding) were noted. Receptive males were defined as males that were not mouthbrooding. The number of receptive females was approximated by the total number of adult females multiplied by the monthly mean of the proportion of mature marked females to total marked females in daily censuses. Their maturity was judged from the degree of belly expansion, which was classified into five categories by eye (see Okuda and Yanagisawa 1996*b* for classification).

As an alternative predictor of mating competition, Parker and Simmons's (1996) model was examined as follows:

$$S_m/S_f = (MT - G_m)/(T - G_f),$$

where S_m/S_f is the population ratio of "time in" for males to females. The time in represents the time spent searching and waiting for mates, and this ratio is equivalent to the OSR (Clutton-Brock and Parker 1992). The variables G_m and G_f are time out for males and females, respectively, M is the adult sex ratio (male : female), and T the time taken for one sex to complete an entire reproductive event. This equation applies in the case of species such as *A. notatus*, in which a female gives an entire clutch to one male and a male cares for only one clutch at a time. If the ratio is greater than one, intense male competition is expected and vice versa. In measuring time out, Parker and Simmons (1996) recommended the use of mean value for all breeders but not the maximum possible value for the most successful individual because the OSR is a population character. Thus, time out was considered the mean spawning interval observed for males and females when not constrained by mate availability.

To estimate the overall potential for sexual selection, the variance in reproductive success was calculated as the coefficient of variation (standard deviation per mean) in mating success (Wade 1979) and compared between the sexes. Mating success was defined as the total number of matings for each individual in a season.

Statistical Analysis

For data analysis, parametric tests were used when their requirements were fulfilled. The data of behavioral scores were analyzed by nonparametric tests since they were not subject to the normal distribution. All statistical probabilities are two tailed.

Results

Sex Roles

During the pairing period, females showed courtship displays more frequently than did their mates (table 1). The pair bond was usually stable during the courting phase, but occasionally females showed extrapair courtship exclusively (table 1). Pairs were approached by conspecific fish and a total of 56 other species. A male or female of the pair frequently attacked conspecific intruders (79.4%, $N = 1{,}213$), but they seldom attacked heterospecific intruders (3.5%, $N = 1{,}982$). The attacks against conspecifics were more frequently exerted by females, while the heterospecific attacks were not significantly different be-

Table 1: Sexual differences in courtship and attacking frequency of pairing *Apogon notatus*

Behavior	Male	Female	z^{a}
Courtship:			
Warping or circling	.1 ± .9	23.6 ± 28.2	-9.05^{**}
Parallel circling	3.14 ± 11.55[b]		…
Nuzzling	.6 ± 2.8	5.7 ± 16.8	-2.63^{*}
Extrapair courtship	.0 ± .0	.4 ± 1.8	-2.93^{*}
Attack:			
Intraspecific	2.0 ± 3.6	5.3 ± 7.2	-6.47^{**}
Interspecific	.1 ± .3	.1 ± .2	−.56

Note: Numerals are the mean number of each behavior per 20-min observation and the standard deviation.

[a] Wilcoxon signed rank test.

[b] This behavior is shown by the sexes in pairs.

* $P < .01$.

** $P < .001$.

tween the sexes (table 1). The attacks by females were more frequent during the postspawning phase ($\bar{X} \pm \mathrm{SD} = 9.9 \pm 11.3$ per 20 min, $N = 22$) than during the courting phase (4.2 ± 5.7, $N = 93$) and the prespawning phase (5.4 ± 5.4, $N = 17$; Kruskal-Wallis test, $\mathrm{df} = 2$, $H = 7.31$, $P < .03$). Females whose broods disappeared from their mates' mouths after spawning had exerted attacks less frequently ($\bar{X} \pm \mathrm{SD} = 2.3 \pm 5.1$, $N = 25$) than females whose broods were successfully raised by mates (5.0 ± 5.6, $N = 85$; Mann-Whitney *U*-test, $U = 588$, $P < .001$).

Of 220 pairs, 164 separated after spawning and the others kept the pair bond until the next spawning. Most of the separations occurred during the postspawning phase (95.8%). As soon as a pair separated, the female formed a new pair with another male at her spawning site. All marked females that were observed over the entire breeding season maintained the paired status until their last spawning, and they became unpaired on average 22.0 d after the last spawning (on September 8 to October 13, $N = 16$). In contrast, mouthbrooding males that separated from their mates loosely aggregated together with other unpaired fish. They remained unpaired until forming a pair with another female at her breeding site or with the previous partner again. Unpaired males sometimes approached a pair to court a female ($\bar{X} \pm \mathrm{SD} = 1.0 \pm 1.8$ per 20 min, $N = 36$), but they were driven away by the male or female of the pair. In 15 of 36 observations, unpaired males chased a prespawning or postspawning male in collusion with other unpaired fish. When unpaired fish were close to each other, they less often showed agonistic behaviors (2.3 ± 3.9) than no displays (5.2 ± 5.4; Wilcoxon signed rank test, $z = -2.64$, $P < .009$).

Brood Disappearance

In 31 of 214 cases, broods disappeared from the male's mouth within a few days of spawning. For 15 of such males, stomach contents were checked and eggs were found in 12 stomachs, all of which were judged to be the result of filial cannibalism. Of the other 16 males, one was observed to swallow the egg mass, five lost their broods just after spawning, and 10 lost their broods to unknown causes. Therefore, the incidence of filial cannibalism was estimated to range between 6.1% and 10.7% ($N = 214$), and the incidence of brood loss that cannot be attributed to filial cannibalism between 3.7% and 8.4% ($N = 214$).

Mating Pattern

All females in the large size class ($N = 176$) mated with males in the large size class, and most females in the small size class (55 of 71) mated with males in the small size class. Spawning pairs in which the body size of both sexes were known were highly size assortative (Spearman's rank correlation, $r_s = 0.83$, $P < .001$, $N = 28$).

Males took 8–14 d to mouthbrood eggs until hatching, and this period was strongly affected by ambient water temperature, irrespective of the body size of males and their mates (Stepwise multiple regression analysis, $R^2 = 0.84$, $F = 305.3$, $P < .0001$, $N = 59$). The spawning intervals for males were significantly longer than for females throughout the breeding season (table 2). Female spawning intervals did not differ between size classes (two-factorial ANOVA, month: $F = 5.69$, $\mathrm{df} = 2$, $P < .005$; size: $F = 1.52$, $\mathrm{df} = 1$, $P = .22$; interaction: $F = 1.26$, $\mathrm{df} = 2$, $P = .29$, excluding data in September because of the small sample size).

Females showed a higher rate of mate change (86.7%, $N = 180$) than did males (48.2%, $N = 114$, $\chi^2 = 50.9$, $\mathrm{df} = 1$, $P < .0001$). The females more quickly respawned when they changed mates than when they did not do so, whereas male spawning interval was independent of mate change (table 3).

Mating Success and Mortality

During the entire breeding season, each male spawned 3.0 times on average (± 1.1 SD, $N = 39$), while each female

Table 2: Spawning intervals for males and females

Month	Spawning interval ($\bar{X} \pm$ SD d) Male[a]	Female	t	P
June	24.5 ± 7.5 (31)	15.5 ± 3.9 (44)	−6.73	<.0001
July	22.4 ± 8.1 (48)	13.0 ± 5.6 (77)	−7.68	<.0001
August	24.3 ± 8.2 (16)	13.5 ± 4.0 (58)	−7.33	<.0001
September	…	15.8 ± 5.5 (4)	…	…

Note: Sample sizes are in parentheses.

[a] Cases in which broods disappeared are excluded.

Table 3: The spawning intervals ($\overline{X} \pm$ SD d) for males and females that did or did not change mates

	Male				Female[a]			
Month	Change	No change	t	P	Change	No change	t	P
June	26.1 ± 9.1 (16)	22.7 ± 5.1 (15)	−1.27	.22	14.5 ± 2.9 (33)	18.7 ± 4.7 (11)	3.56	.0009
July	22.0 ± 9.4 (23)	22.7 ± 6.8 (25)	.27	.79	12.1 ± 2.9 (69)	20.5 ± 13.5 (8)	4.50	<.0001
August	28.3 ± 17.2 (3)	23.3 ± 5.4 (13)	N.A.	N.A.	12.8 ± 3.4 (49)	19.0 ± 4.2 (5)	3.78	.0004
September	…	…	…	…	15.8 ± 5.5 (4)	…		…

Note: Sample sizes are in parentheses. N.A. indicates not applicable.

[a] Difference in sample size between tables 2 and 3 is caused by excluding cases in which their next mates could not be identified.

spawned 6.5 times (± 1.7 SD, $N = 16$). The mating success was significantly greater in females ($t = 9.27$, df = 53, $P < .0001$), while the coefficient of variation in mating success was greater in males (0.37) than in females (0.26). The mating success was not correlated with body size in either males (Spearman's rank correlation, $r_s = -0.01$, $P = .97$, $N = 39$) or females ($r_s = -0.00$, $P = .99$, $N = 16$).

The annual mortality rate was much higher in females (89.8%, $N = 49$) than in males (57.3%, $N = 75$, $\chi^2 = 14.9$, df = 1, $P < .0001$). There was no difference in the mortality between the size classes either in males (large: 58.5%, small: 54.5%; $\chi^2 = 0.10$, df = 1, $P = .75$) or in females (large: 91.4%, small: 85.7%; Fisher's exact probability test, $P = .62$).

Operational Sex Ratio

At the peak of the breeding season, the majority of unpaired fish were mouthbrooding (73.6% in July and 76.2% in August; table 4). Judging from the observations that marked females never showed unpaired status until their last spawning and that most unpaired fish were mouthbrooding, the unpaired fish are considered to be males (this presumption is also supported by the sampling work; N. Okuda, unpublished data). On the basis of these data, the adult sex ratio was estimated (table 4). The sex ratio in the small size class was slightly male biased but did not significantly deviate from equality (June: $\chi^2 = 1.21$, df = 1, $P = .27$; July: $\chi^2 = 3.34$, df = 1, $P = .07$; August: $\chi^2 = 2.10$, df = 1, $P = .15$). In contrast, the sex ratio of large adults was significantly male biased (June: $\chi^2 = 11.1$, df = 1, $P < .001$; July: $\chi^2 = 16.5$, df = 1, $P < .0001$; August: $\chi^2 = 21.0$, df = 1, $P < .0001$). Late in the breeding season, the number of pairs decreased, while the number of gregarious fish increased with females abandoning their breeding sites (table 4). Therefore, the sex ratio in September and October could not be estimated from censuses.

The proportion of mature marked females to all marked females was on average 0.17, 0.23, and 0.17 in June, July, and August, respectively. Incorporating them into the estimation of receptive females, the OSRs (males : females) were calculated separately in the two size classes as there was a highly size-assortative mating (fig. 2). The OSRs were male biased both in small and large adult populations throughout the breeding season.

From Parker and Simmons's (1996) model, S_m/S_f was calculated. Here, male spawning cycle was substituted for T and the mean spawning interval of males and females that changed mates for G_m and G_f, respectively. The S_m/S_f of large adults was consistently male biased, while that of small adults was unbiased or slightly female biased (fig. 2).

Discussion

Sex-Role Reversal

Females of *Apogon notatus* played a more active role than males in courtship and attacks against conspecifics. Animals with this feature are generally regarded as sex-role reversed (Trivers 1972; Williams 1975; Gwynne 1991). In this fish, females frequently left their mates soon after spawning, and the subsequent mate changes resulted in their shortened reproductive cycle. This is because the female spawning interval was potentially shorter than that of males. The same result was obtained in a related species, *Apogon doederleini*, in which sex roles are reversed (Okuda and Yanagisawa 1996*b*). Females who are ready to quickly remate can enjoy greater mating success through polyandry. The polyandrous mating pattern is characteristic of sex-role reversed animals (Jenni 1974; Emlen and Oring 1977).

Sex-role reversal is often the case in paternal egg bearers (e.g., pipefishes: Vincent et al. 1992; Rosenqvist 1993; and water bugs: Smith 1979; Ichikawa 1989; but see seahorses: Vincent 1994; Masonjones and Lewis 1996). This is primarily because of the restricted brooding space of males and their long brooding period relative to the female refractory period in these species; in other words, females have the higher PRR (Clutton-Brock and Vincent 1991) or the shorter time out (Parker and Simmons 1996). If the adult sex ratio is unbiased, females with the higher PRR or the shorter time out would compete more intensely for mates because the females remating at a higher rate run short of receptive males; that is, the OSR becomes female biased (Clutton-Brock and Parker 1992; Parker and Simmons 1996). Also, in apogonids with paternal mouthbrooding, the limited male buccal capacity and their lengthy mouthbrooding period decrease the number of males available for female spawning (Okuda and Yanagisawa 1996*b*; Okuda et al. 1998). Therefore, apogonids are a likely candidate for sex-role reversed animals (Okuda 1997).

However, this study revealed that the OSR in *A. notatus* was male biased throughout the breeding season. By contrast, the examination of S_m/S_f showed lower values than the estimated OSR. In the natural population of this fish, male spawning intervals may always be constrained by their low mate availability even when they change mates, suggesting that male time out was overestimated, and thus the actual ratios would be shifted toward males. In either case, the ratios did not tend to skew greatly toward females. These results do not seem to agree with sexual selection theory predicting sex-role reversal under a female-biased OSR.

Operation of Sexual Selection

As shown in *A. notatus*, vigorous courtship by females is common in apogonids (Thresher 1984; Kuwamura 1985; T. Takeyama, unpublished data). In some phonotactically communicating insects, the direction of courtship roles flexibly changes depending on the OSR, with male call being frequent under female scarcity (Gwynne and Simmons 1990; Gwynne 1993). In such species, the calling is signaled to neighboring members of the opposite sex to court or those of the same sex to compete with, rather than to a certain individual. In *A. notatus*, in contrast, courtship displays, except for extrapair courtship, are directed only to a partner in pairs and are somewhat ritualized. The courtship roles performed by paired apogonids may be mainly involved in maintenance of social contact between members of a pair and synchronization of their reproductive timing (Kuwamura 1985; also see Gronell 1984 for pair-spawning pipefishes). Mating competition is defined as any intra- or intersexual interactions to get more mates than do rivals (Kvarnemo and Ahnesjö 1996). In *A. notatus*, therefore, the active courtship role taken by paired females does not necessarily reflect their intense mating competition.

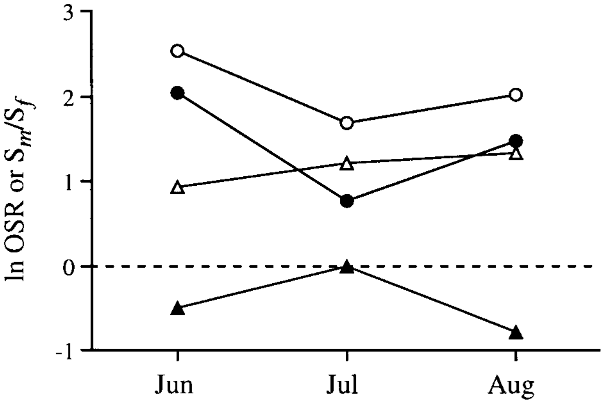

Figure 2: The operational sex ration (*circles*) and S_m/S_f (*triangles*) of large (*white*) and small (*black*) adults. The values were logarithmically transformed. Positive and negative numbers indicate a male bias and female bias in the ratios, respectively.

In this fish, broods often disappeared from males' mouths. Okuda and Yanagisawa (1996*a*, 1996*b*) reported the frequent occurrence of brood disappearance in a related species *A. doederleini*. They demonstrated that most disappearances were caused by filial cannibalism by males. In *A. notatus*, however, the proportion of brood disappearance that cannot be attributed to filial cannibalism was 3.7%–8.4%, which was significantly higher than the

Table 4: The sex ratio (males : females) of large and small adults in the quadrat

	June	July	August	September	October
Large adult:[a]					
Number of pairs	54 (0)	48 (5)	40 (8)	32 (2)	13 (0)
Number of unpaired fish	60 (0)	73 (57)	79 (60)	16 (1)	1 (0)
Sex ratio	2.11	2.52	2.98	...	...
Small adult:					
Number of pairs	58 (0)	85 (56)	68 (23)	14 (0)	4 (0)
Number of unpaired fish	18 (0)	37 (24)	26 (20)	10 (0)	4 (0)
Sex ratio	1.31	1.44	1.38	...	...
Number of gregarious fish	0	0	0	537 (17)	Thousands
Total	302	376	321	655	Uncountable

Note: Numerals in parentheses represent the number of mouthbrooding males.

[a] Pairs of a large and small adult are included.

1.0% in *A. doederleini* (Okuda 1997). This type of brood loss in *A. notatus* may be due mainly to hetero cannibalism, that is, egg consumption by nonrelated conspecifics, because the pre- and postspawning males were often observed to be chased by a group of unpaired conspecifics. The incidence of brood disappearance increased as female partners were less active in the attacks against intruders. The eggs are most likely exposed to predation just after spawning since it takes a parental male several minutes to completely pack an egg mass into his mouth (Kuwamura 1983). Therefore, the frequent attacks exerted by paired females, especially during the postspawning phase, may be effective in protecting eggs against conspecifics, most of which are unpaired males. This result suggests that a possible function of female attacks is to guard their own eggs rather than to compete for mates.

This fish is a gregarious species with a high population density, unlike other sex-role reversed apogonids, which are usually solitary. Kuwamura (1983) reported that females of *A. notatus* established and maintained the breeding sites as early as 2 mo before the breeding season, and he suggested that the function of such behavior would be to secure the better spawning sites, away from conspecific aggregations, by which they might reduce intraspecific interference. For females, however, maintaining the breeding sites for a long time would be energetically costly, as supported by data showing that their somatic condition deteriorates more than that of males during that period (N. Okuda, unpublished data). The maintenance of breeding sites including attacks against conspecific intruders may represent female parental investment, because these activities would, at least partially, improve their offspring survival but decrease the female's ability to produce future offspring, because of increased mortality caused by deterioration of somatic condition.

Female parental expenditure was also greater than that of males in relation to gamete production: on average they produced more than twice as many clutches as a male mouthbrooded in a season. Female mating success is no longer limited by access to mates because of the male-biased sex ratio, whose origin might be an increase in female mortality resulting from the high parental investment in offspring survival. The mortality of females reproducing at a higher rate will be accelerated, further skewing the population sex ratio toward males with age. Simmons (1995) demonstrated in annual katydids that relative parental investment determined the sexual difference in time out, a primary element of OSR. In *A. notatus*, which is a perennial species, parental investment appears to affect future parental survival and thus the population sex ratio. As Clutton-Brock and Parker (1992) and Parker and Simmons (1996) pointed out, the effect of the adult sex ratio on the OSR is more significant as it deviates from equality. In *A. notatus*, therefore, the high parental investment by females may be a causal factor in the male-biased OSR, which would lead to conventional sex roles.

Is sexual selection actually acting on males in *A. notatus*? This study showed that variation in mating success of *A. notatus* was greater among males than among females. The variance in reproductive success per se does not necessarily determine the intensity of sexual selection but provides a measure of the maximum opportunity for selection (Wade 1979; Arnold and Wade 1984). The sexual difference in reproductive variance is more likely produced by a skew of OSR than expected by random mating (Colwell and Oring 1988). In *A. notatus*, the male bias in OSR may have permitted the larger variance in male reproductive success, and thus a greater opportunity for sexual selection on males.

The theory also predicts that the more competitive sex will develop distinctive sexual traits, while the opposite sex should be more choosy (Trivers 1972; Williams 1975; but see Owens and Thompson 1994). In *A. notatus*, females sometimes showed extrapair courtship, through which they can assess future potential mates before they complete the current reproductive cycle. Males, however were just waiting for a female's invitation to her breeding site, less frequently showing combative competition among themselves. Sexual selection may operate on males intersexually through female mate choice. In this fish, body size was not an important measure of male mating success, since there is no sexual size difference (Okuda 1997). Recently, the author found a sexual dimorphism in *A. notatus*: the male's lower lip markedly protrudes in the breeding season (N. Okuda, unpublished data). This male trait is not shared by males of many other apogonids that are expected to be role reversed (M. Miyazaki, N. Okuda, and Y. Yanagisawa, unpublished data). Although the effect of this ornament on mate attractiveness has not been yet investigated, the finding suggests a possibility of sexual selection acting more strongly on males.

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