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Noboru Okuda · Kayoko Fukumori · Yasunobu Yanagisawa

Male ornamentation and its condition-dependence in a paternal mouthbrooding cardinalfish with extraordinary sex roles

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Abstract Cardinalfishes, in which males alone provide mouthbrooding, are likely candidates for sex-role reversal because of a higher potential reproductive rate for females than for males. In the gregarious cardinalfish, *Apogon notatus*, females establish breeding territories to form pairs prior to the breeding season. Within breeding pairs, females are more active in courtship and in attacks against conspecific intruders. Sex roles thus seem to be behaviorally reversed. The operational sex ratio is, however, male-biased because females suffer higher mortality than males and consequently males predominate in number in the adult population, leading to the prediction that males would be sexually selected. In the present study, morphological measurements showed that males had a protrudent lower lip that was expressed markedly during the breeding season. Field observation revealed that males with a longer and wider lip were preferentially accepted as a mating partner by territorial females. The male lip size positively correlated with their somatic condition, suggesting that the ornamental lip has evolved through indicator mechanisms of sexual selection. By contrast, females had longer fins than males, but these sexual dimorphisms were less pronounced and most of them were seasonally constant. These results support the prediction that sexual selection acts on males in this fish.

Key words Apogonidae · Indicator mechanism · Mate choice · Mouthbrooding · Sexual ornament · Sexual selection

Introduction

Sexual ornaments, defined as morphological, behavioral or physiological modifications that are sexually attractive to the opposite sex, are generally expressed more by males than by females. This is because sexual selection acts more strongly on males, whose potential reproductive rate is higher than that of females and, hence, the operational sex ratios distort toward males, leading to more intense competition among them for access to mates (Emlen and Oring 1977; Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjö 1996; Parker and Simmons 1996; also see Kokko and Monaghan 2001). Males with more exaggerated sexual ornaments gain a mating advantage over those with less showy ornaments through female mate choice, while females can benefit from mating with more ornate males because they derive direct phenotypic benefits from ornament holders (Heywood 1989; Hoelzer 1989; Price 1993; Kokko 1998) and/or indirect genetic benefits, such as heritable sexual attractiveness (Lande 1981; Kirkpatrick 1982; Pomiankowski et al. 1991) and heritable viability (Andersson 1986; Iwasa et al. 1991). For male ornaments and female preferences to co-evolve, it is often, but not always, necessary that the ornaments honestly signal the male quality to females (i.e., indicator mechanisms; Andersson 1994).

There are some exceptions in which females are the ornate sex and males the choosy sex, i.e., sex-role reversal (Williams 1975). Although the sex-role reversal is taxonomically sporadic (Gwynne 1991), some reproductive features are shared among role-reversed species. In these species, males make a higher parental investment than do females in terms of energetically expensive testicular production, such as spermatophore in copulatory insects (Simmons 1992, 1995), or of elaborated paternal care that restricts the number of mates received by males at once, as in external bearers (Ichikawa 1989; Vincent et al. 1992; Balshine-Earn and McAndrew 1995) and some birds (Ligon 1999). Such features result in a decrease in reproductive rate of males relative to females and consequently produce female-biased

N. Okuda (✉)
Center for Marine Environmental Studies, Ehime University,
3 Bunkyo-cho, Matsuyama 790-8577, Japan
Tel. +81-89-9279622; Fax +81-89-9279630
e-mail: nokuda@sci.ehime-u.ac.jp

K. Fukumori · Y. Yanagisawa
Department of Biology and Earth Sciences, Ehime University,
Matsuyama, Japan

operational sex ratios (Clutton-Brock and Parker 1992; Parker and Simmons 1996). In a situation where female reproduction is limited by access to mates but not by fecundity, females compete for mates more intensely than do males, and sometimes even develop sexual ornaments for which males show preferences (Rosenqvist 1990; Berglund and Rosenqvist 2001).

Most cardinalfishes (Apogonidae), in which males alone provide mouthbrooding, also show characteristics of sex-role reversal. In this group, the potential reproductive rate is lower in males because their reproduction is restricted by the buccal space and the developmental time of embryos (Okuda et al. 1998). As a result of female-biased operational sex ratios, mating competition is more intense among females (Okuda and Yanagisawa 1996b). Courtship behaviors are also performed by females more vigorously (Thresher 1984; Kuwamura 1985, 1987).

The subject species, *Apogon notatus*, is a gregarious cardinalfish, which inhabits shallow waters of the northwest Pacific (Hayashi 2002). In this fish, sex roles are extraordinary. A few months before the breeding season, females exclusively establish breeding territories on the boulder substrata, where they simultaneously invite a prospective partner from conspecific shoals (Kuwamura 1983). Within pairs, the females play a leading role in courtship and in attacks against conspecific intruders (Okuda 1999b). While maintaining the breeding territories to spawn repeatedly throughout the breeding season (June–September), females usually change mates in each spawning (Okuda 1999b). This is because females can enhance their reproductive rate by remating quickly with another male ready to mouthbrood, as in some other cardinalfishes (Okuda and Yanagisawa 1996b; Okuda 1999a). In terms of such reproductive features, Clutton-Brock and Vincent (1991) regarded *A. notatus* as sex-role reversed. However, Okuda (1999b) suggested that the sex roles of *A. notatus* would not be reversed because its courtship-role reversal and female territoriality were less likely to confer an advantage on females in competing for mates. Furthermore, Okuda (1999b) showed that the operational sex ratios of this fish are male-biased and not female-biased. The male-biased sex ratios in this species likely result from higher mortality for females that incur a large energetic cost of territory maintenance as well as egg production (Okuda 2001). In theory, it is predicted that sexual selection should act on males in this fish.

Okuda (1999b) also found male *A. notatus* has a protrudent lower lip, which is not shared by other cardinalfishes. According to the current theory predicting that sexual ornaments should be expressed by the more abundant sex, this trait is expected to serve as a sexual ornament. In the present study, the main aim was to explore the function of the protrudent lip in male *A. notatus*, posing the following questions: Does the lower lip influence sexual attractiveness, and if so, does this trait honestly signal male quality?

Methods

Morphological measurements

To take morphological measurements, we used specimens of *Apogon notatus* collected monthly at Murote Beach, Shikoku Island, Japan, from February 2000 to January 2001. A sampling design is shown in Table 1. This sample size was less likely to affect the population of this fish because its abundance was very high. In addition, since the sampling areas were several hundred meters away from a quadrat for subsequent field observations, the sampling did not have substantial effects on results of selection gradient analysis (see below).

For each fresh specimen, we took magnified photographs of the lips in lateral and dorsal views, using a digital camera (COOLPIX950, Nikon, Japan) under a dissecting microscope. The digital images were then scanned by image analysis software (NIH image, National Institutes of Health, USA). We measured the length (LLL) and width (LLW) of the lower lip in a dorsal view (Fig. 1) and the thickness of the upper lip (ULT) in a lateral view to the nearest 1 μm . Digital images of the yellow spot on the lower lip (Fig. 1) were processed by an image editing software (Adobe Photoshop, Adobe System, USA) and those yellow spot areas (YSA) with a brightness over 80 (black = 0, white = 100) were measured.

We also measured nine morphological characteristics with a pair of calipers to the nearest 0.1 mm: standard length (SL), body height (BH), first dorsal fin length (1DFL), second dorsal fin length (2DFL), average length of the right and left pectoral fins (PFL), average length of the right and left ventral fins (VFL), anal fin length (AFL), upper caudal fin lobe length (UCFL) and lower caudal fin lobe length (LCFL).

These morphological measurements were compared between the sexes with a two-factor ANCOVA incorporating sex and month as factors. Since SL is significantly larger in males than in females (two-factor ANOVA, sex: $df = 1$,

Table 1. The number of male and female specimens of *Apogon notatus* and their standard length

Year	Month	Male length		Female length	
		<i>n</i>	Mean \pm SD	<i>n</i>	Mean \pm SD
2000	Feb	19	83.48 \pm 3.62	21	80.48 \pm 3.86
	Mar	20	79.25 \pm 3.84	20	79.50 \pm 4.93
	Apr	20	84.27 \pm 3.48	18	82.88 \pm 3.26
	May	20	83.32 \pm 3.47	20	81.07 \pm 4.00
	Jun	20	83.93 \pm 3.04	20	79.98 \pm 3.18
	Jul	20	82.31 \pm 2.67	20	81.51 \pm 3.20
	Aug	20	84.09 \pm 2.60	20	81.23 \pm 2.48
	Sep	20	83.22 \pm 2.38	18	80.77 \pm 2.62
	Oct	21	84.12 \pm 3.79	18	79.76 \pm 2.46
	Nov	19	82.54 \pm 2.51	21	80.02 \pm 3.08
	Dec	20	81.50 \pm 4.49	20	78.77 \pm 3.67
	2001	Jan	21	83.53 \pm 3.07	19

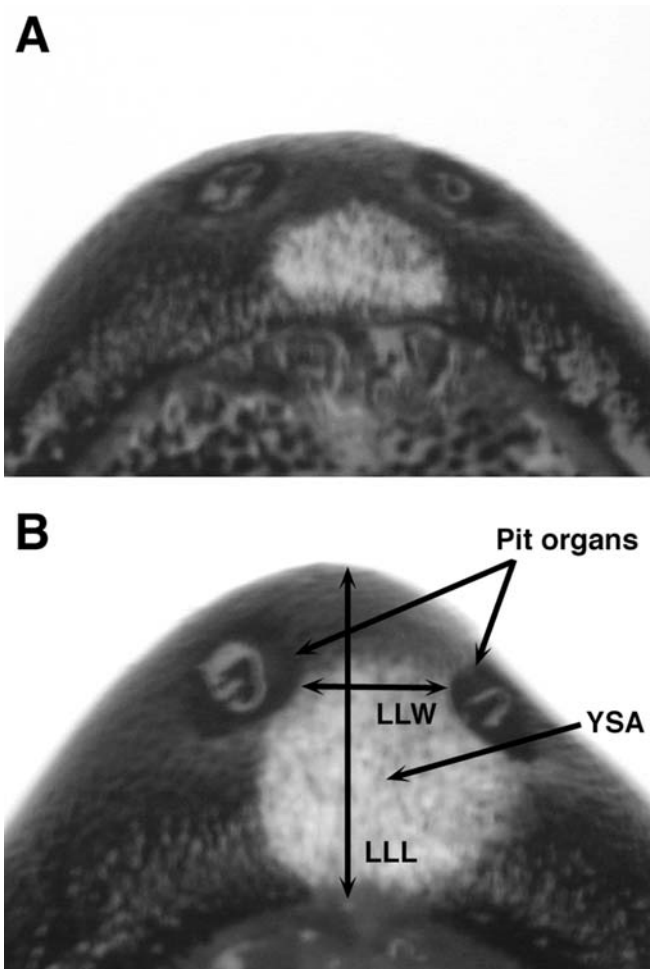


Fig. 1. Photographs of lower lip of female (A) and male (B) of *Apogon notatus* in a dorsal view. *LLL* is the lower lip length (from the tip to posterior margin), *LLW* the lower lip width (between two pit organs opened into the mandibular canal) and *YSA* the area of yellow spot on the lower lip (*whitish area*)

$F = 60.95$, $P < 0.001$, month: $df = 11$, $F = 4.23$, $P < 0.001$; Table 1), these morphological variables were compared after adjusting for the covariate, *SL*, provided that there was no significant interaction between sex and *SL*. We further examined the seasonal pattern of sexual dimorphism (sex \times month interaction) only if these two factors did not interact with *SL*.

Field observations and selection gradient analysis

We made field observations in relation to female mate choice. A small proportion of males were captured from large shoals of *A. notatus* in a 10×20 -m quadrat on the boulder slope of Murote Beach in late March 2000, the beginning of female territory settlement. We selected adult fish from the largest size class of a bimodal distribution because small adults, 1-year-old fish, have a reproductive schedule different from that of large adults, delaying reproduction about 1 month (Okuda 1999b; N. Okuda,

unpublished data). We marked these males underwater by hypodermically injecting the VIE (Visible Impact Fluorescent Elastomer; Northwest Marine Technology, USA) in three colors laterally before releasing them at the capture sites. This marking technique has least effect on their behavior and reproductive schedule (Okuda 1999b).

We censused the quadrat every 2 or 3 days, during the period from 3 April to 27 May, when the earliest spawnings were observed in this population. In each census, we recorded the location of marked males and the dates they were solicited by territorial females and became paired. During the period 29–31 May, we captured 28 marked males inhabiting the quadrat. In the laboratory, we took photographs of their lips and measured their morphological characteristics, according to the above methods. Six marked males could not be observed consecutively in the quadrat, so that we have no reliable data on when they became paired. These data were thus excluded from the subsequent analysis.

For the remaining 22 males, we performed a selection gradient analysis to measure the direct forces of phenotypic sexual selection on their morphological characteristics (Lande and Arnold 1983; Arnold and Wade 1984). We used a survival regression analysis with a proportional hazard model for multivariates (statistical package: StatView 5.0), which detects factors affecting the time of occurrence of any event, i.e., pairing in this case. In this model, we incorporated days from the onset of observations to pairing as the time variable and morphological measurements as covariates. Cases in which marked males remained unpaired until the end of the observations were treated as censored data. We also incorporated wet body weight, but not dry body weight, as a covariate because males may retain water in their soma to pretend robustness. Prior to the analysis, the body weight and the yellow spot area were transformed into a linear dimension by taking the cube root and square root, respectively. Since there were strong correlations among the body weight (BW), BH and SL (BW vs SL: $r = 0.90$, BH vs SL: $r = 0.76$, BW vs BH: $r = 0.86$), we substituted residuals of the BW and BH against the SL for covariates to reduce the effect of collinearity on the multiple regression analysis (Reist 1985). The results were obtained using a full model and a reduced model with a stepwise method.

To examine the condition-dependence of sexual ornaments, we measured somatic condition for each marked male. We dissected fish to part the liver, gonad and fat body (i.e., a fatty tissue enveloping the viscera). These three parts and the eviscerated carcass from which gut contents were removed were dried at 60°C for 24 h and weighed to the nearest 0.1 mg. After the measurements, we calculated four indices: hepatosomatic index ($\text{HSI} = 100 \times \text{liver weight} / \text{total body weight}$), fat body-somatic index ($\text{FSI} = 100 \times \text{fat body weight} / \text{total body weight}$), condition factor ($\text{K} = 10^3 \times \text{total body weight} / \text{TL}^3$) and gonadosomatic index ($\text{GSI} = 100 \times \text{gonad weight} / \text{total body weight}$) (Okuda 2001). These indices were incorporated as explanatory variates into a model of stepwise multiple regression against the ornament size.

Results

Sexual dimorphism

From comparison of 12 morphological characteristics between sexes, we found that BH was significantly higher in females than in males and that all fins were longer in females (Table 2). Males, in contrast, had a greater ULT than females (Table 2). The regression slopes of the LLL and the YSA against SL were significantly different between the sexes (ANCOVA, sex \times SL interaction, LLL: $df = 1$, $F = 4.38$, $P < 0.04$; YSA: $df = 1$, $F = 4.13$, $P < 0.04$). All but pectoral fins were consistently longer in females throughout the year, while the upper lip was consistently thicker in males (Table 2). The female PFL proportional to SL showed a tendency to increase during the winter season and subsequent territory settlement, in contrast to the less seasonally

variable male PFL (Fig. 2A). Among males, the lower lip characters, LLL, LLW and YSA, were developed markedly during the breeding season (Fig. 2B–D).

Sexual ornament and condition-dependence

For 22 marked males, we observed the earliest pairing on 12 April. Of them, three remained unpaired until 27 May, the end of the observation. The selection gradient analysis with a full model showed that an increase in the LLL and the AFL shortened the time to pairing (Table 3). With a reduced model, however, it was concluded that males with a longer and wider lower lip became paired earlier (Table 3).

LLW positively correlated with HSI ($F = 9.41$) and K ($F = 4.94$; Stepwise multiple regression analysis, $R = 0.54$, $F_{2,25} = 5.14$, $P < 0.02$), but LLL did not correlate with any

Table 2. Sexual dimorphism and its seasonal pattern (sex \times month interaction)

Character	Sexual dimorphism				Seasonal pattern	
	Male	Female	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
	Mean \pm SD	Mean \pm SD				
BH (mm)	28.87 \pm 1.07	29.24 \pm 1.07	13.56	0.001	1.22	0.27
1DFL (mm)	11.94 \pm 0.78	12.29 \pm 0.78	22.23	0.001	0.60	0.83
2DFL (mm)	17.69 \pm 0.85	18.05 \pm 0.85	19.81	0.001	0.68	0.76
PFL (mm)	21.70 \pm 0.87	22.38 \pm 0.87	67.73	0.001	2.82	.001
VFL (mm)	17.88 \pm 1.01	18.22 \pm 0.84	19.72	0.001	1.66	0.08
AFL (mm)	15.65 \pm 0.79	16.02 \pm 0.79	24.29	0.001	1.28	0.23
UCFL (mm)	21.75 \pm 1.17	22.01 \pm 1.17	5.40	0.02	0.63	0.80
LCFL (mm)	21.21 \pm 1.27	21.49 \pm 1.24	5.59	0.02	0.92	0.52
ULT (μ m)	888.8 \pm 121.5	863.7 \pm 121.6	4.79	0.03	1.23	0.27
LLL (μ m)	NA ^a				15.03	0.001
LLW (μ m)	872.2 \pm 169.3	856.8 \pm 169.6	0.93	0.34	2.13	0.02
YSA (μ m ²)	NA ^a				9.82	0.001

^a Not applicable to ANCOVA because there exists significant sex \times SL interaction (see text)

Table 3. The selection analysis of male characters affecting the time to pairing

Character	Full			Reduced		
	Coefficient	χ^2	<i>P</i>	Coefficient	χ^2	<i>P</i>
SL	-0.40	1.40	0.24			
BW	10.48	0.39	0.53			
BH	-0.34	0.21	0.65			
1DFL	-0.39	0.85	0.36			
2DFL	-1.22	1.70	0.19			
PFL	-0.55	0.41	0.52			
VFL	-0.07	0.01	0.93			
AFL	3.01	5.57	0.02			
UCFL	-0.30	2.45	0.12			
LCFL	0.59	2.88	0.09			
ULT	-0.18	0.00	0.98			
LLL	11.69	6.76	0.01	3.47	5.77	0.02
LLW	0.04	0.00	0.99	3.29	6.23	0.01
YSA	-0.13	0.00	0.97			
Likelihood ratio test	$\chi^2 = 27.07$, $df = 14$, $P = 0.02$			$\chi^2 = 10.11$, $df = 2$, $P = 0.006$		

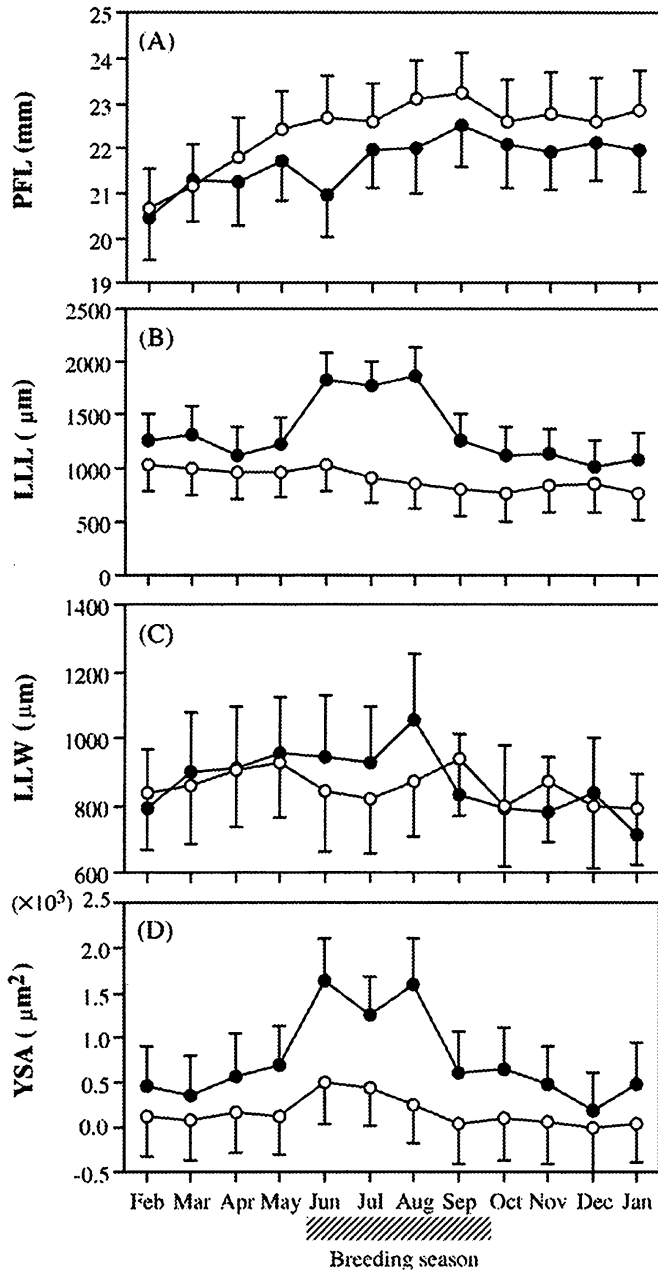


Fig. 2. Seasonal changes in sexual dimorphisms. *PFL* is the pectoral fin length (A), *LLL* the lower lip length (B), *LLW* the lower lip width (C), and *YSA* the yellow spot area (D) for males (closed circles) and females (open circles). With the two-factor ANCOVA, the adjusted mean and SD are given

condition indices. When the product of *LLL* multiplied by *LLW*, which reflects a surface area of lower lip in a dorsal view (Fig. 1), was incorporated as a dependent variable, the stepwise multiple regression model showed a significantly positive correlation between the lower lip size and HSI ($R = 0.45$, $F_{1,26} = 6.54$, $P < 0.02$; Fig. 3). This correlation was unchanged after considering the effect of body size on the lower lip size.

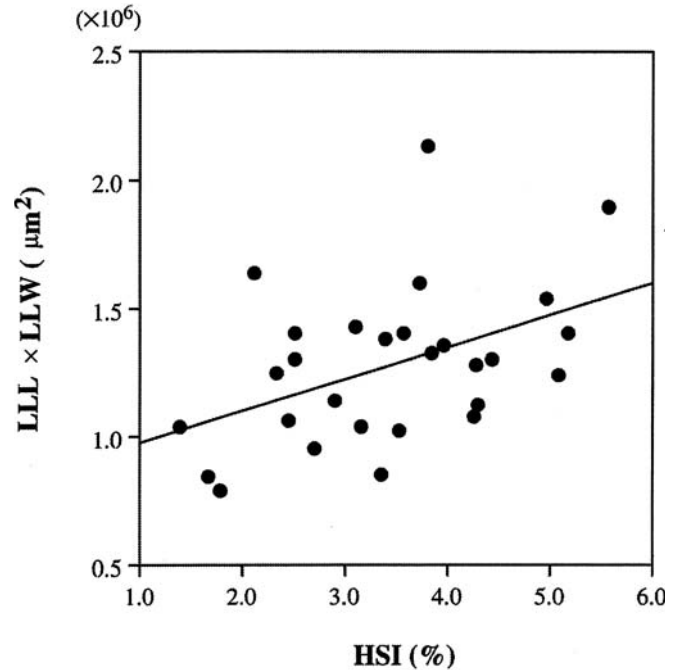


Fig. 3. Condition-dependence of lower lip size (the product of *LLL* multiplied by *LLW*) on the hepatosomatic index (HSI) of marked males

Discussion

In *Apogon notatus*, males had a protrudent lower lip that was expressed markedly during the breeding season. In paternal mouthbrooding cardinalfishes, males often have an enlarged buccal morphology (Lachner 1953; Omori and Takahashi 1980). In a congener *A. doederleini*, it was found that sexual differences in buccal morphology are due to a flexible morphological change caused by mouthbrooding actions (Okuda et al. 2002). Such a flexible morphological change is associated with sexual dimorphism in the jaw osteology, which involves extension of the buccal space. However, the seasonally protrusible lip found in male *A. notatus* is not shared by other cardinalfishes so far reported, suggesting that it is not a functional trait for mouthbrooding.

Our field study revealed that male *A. notatus* with a longer and wider lower lip became paired earlier prior to the breeding season. When studying mate choice with an observational approach, field workers often have difficulty in separating intersexual selection from intrasexual selection (but see Moore 1990; Warner and Schultz 1992). The selection analysis can determine the direct forces of overall selection of characteristics, but not the relative importance of different sources of selection. One may expect that the lower lip of male *A. notatus* is an intrasexually selected trait that functions to signal dominant status among males competing for mates, as seen in some birds (Jones 1990; Jones and Hunter 1999). However, there are some reasons to believe that the lower lip is not intrasexually selected. In this fish, males never supplant already paired males: they

are driven away by a territorial female as soon as they approach a pair (Okuda 1999b). To be paired, the males form aggregations in mid water, where they wait for a female's invitation to her territory, rarely displaying aggressions among them, in spite of their close proximity and frequent encounters (Okuda 1999b). These pieces of evidence suggest that intrasexual competition for mates is of less importance in male *A. notatus*. Moreover, our selection analysis showed that variance in first pairing dates among males cannot be explained by variance in their body length and weight. Therefore we conclude that male pairing success greatly depends on female preference for a larger ornamental lip.

In the following discussion, we concern ourselves with two questions in relation to the evolution of male ornamental lip in this fish. First, what is the mechanism by which the lower lip signals its holder's quality? Among males, the lower lip size reflected their HSI, a proportional weight of liver to total body. In this fish, the liver is the main lipid reservoir and shows great temporal variation in weight, peaking in May (Okuda 2001). Since the lip protrusion resulted from accumulation of labial subcutaneous fat (N. Okuda, personal observation), it is probable that males allocated a portion of their lipid reserves to lip protrusion to advertise their quality. Although such a condition-dependent expression of male ornament is common in species with conventional sex roles (Andersson 1994), male ornamentation in *A. notatus* was not as exaggerated as found in typical role-conventional species. A modest and honest advertisement is theoretically predicted to evolve in species where parental care is provided by males and their opportunities for multiple matings are limited (Kokko 1998), the very case for this fish.

Second, what do females gain by choosing males with a larger lower lip? One possible answer is that such males may be good parents who can mouthbrood eggs effectively. In cardinalfishes, mouthbrooding males sometimes cannibalize their own brood entirely (Okuda and Yanagisawa 1996b; Okuda 1999a, 2000) and the incidence of this cannibalism is high when they are in poor somatic condition (Okuda and Yanagisawa 1996a). Females can reduce the risk of filial cannibalism by choosing males in better condition. However, it is less likely in *A. notatus* because male somatic condition is, on average, good in May (Okuda 2001), the pre-breeding month when females exert mate choice. In fact, brood loss to filial cannibalism is negligible early in the breeding season of this species (Okuda 2000).

Another possible benefit deriving from such female preference for larger lipped males is the avoidance of parasitically burdened mates, as reported in studies of parasite-mediated sexual selection in animals with conventional sex roles (reviewed by Clayton 1991). In *A. notatus*, both males and females are frequently infected by gonad-parasitic nematode (N. Okuda, unpublished data). This parasite burdens the sexes differently: the more nematodes in a female, the fewer the number of eggs in its ovary, while heavily parasitized males have a lowered somatic condition. Thus, the male lower lip may serve as an indicator of parasite infection that cannot be inspected directly by females.

Although our results support the prediction that sexual selection will act on males in *A. notatus*, we cannot make conclusion as to which sex is more sexually selected. Morphological measurements revealed that females had longer fins than males. These dimorphisms, although measurable, were too small to be detected by the naked eye, and most of them were seasonally constant, suggesting a weak selection in female morphological characteristics. The exception to this was the elongation of female pectoral fins during the competitive period of territory settlement. An analysis of the phenotypic selection on female fins will be helpful in understanding overall sexual selection in this fish with extraordinary sex roles in that its operational sex ratio is male-biased but breeding territoriality is exclusively female.

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