

Female territoriality in a paternal mouthbrooding cardinalfish to avoid predation against spawned eggs

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Abstract: Generally, paternal mouthbrooding cardinalfishes are characteristic of sex-role-reversed animals: females have a higher potential reproductive rate and are more active in mating competition than males, and the operational sex ratio (OSR) is female-biased. However, one species of cardinalfish, *Apogon notatus* (Houttuyn, 1782), shows unusual sex roles: females alone defend their breeding territories to form pairs, even though the OSR is male-biased. This is inconsistent with the general rule that breeding territoriality is shown by the more abundant sex. We examined the function of female breeding territory in this fish using field observations. Prior to the breeding season, large females established their territories earlier than small females. Earlier settlers occupied deeper areas with larger boulders where conspecifics were less likely to aggregate. As the level of conspecific aggregation increased, spawning females suffered from frequent intraspecific interference and subsequent egg predation, leading to increased time or energy spent on territorial defense. For the females, territories that have more boulders and fewer conspecifics might be of higher quality because such places are safe from egg predation and less costly to defend. We conclude that females defend their breeding territories to avoid predation of spawned eggs rather than to guard high-quality mates or to increase mating opportunities.

Résumé : Les poissons-cardinaux qui élèvent leur portée dans la bouche du mâle possèdent les caractéristiques des animaux dont le rôle sexuel est inversé; les femelles ont un taux reproductif potentiel supérieur et sont plus actives dans la compétition que les mâles; de plus, la proportion opérationnelle relative des sexes (OSR) favorise les femelles. Cependant, une espèce de poisson-cardinal, *Apogon notatus* (Houttuyn, 1782), possède des rôles sexuels inusités : seules les femelles défendent les territoires de reproduction pour la formation des couples, même si OSR favorise les mâles. Cette situation est incompatible avec la règle générale qui veut que ce soit le sexe plus abondant qui possède une territorialité reproductive. Nous examinons le rôle de la territorialité reproductive chez ce poisson par des observations de terrain. Avant la saison de reproduction, les femelles de grande taille établissent leur territoire avant les femelles de petite taille. Les premières occupantes choisissent des zones plus profondes avec des rochers plus gros, où les individus de même espèce sont moins susceptibles de se rassembler. À mesure que les individus conspécifiques se rassemblent, les femelles en fraie connaissent de fréquentes interférences intraspécifiques et une prédation subséquente des œufs, ce qui représente un accroissement du temps et de l'énergie dépensés pour la défense du territoire. Les territoires qui contiennent plus de rochers et moins de poissons de même espèce peuvent constituer pour les femelles des sites de meilleure qualité, car ils sont protégés de la prédation des œufs et moins coûteux à défendre. Nous concluons que les femelles défendent leur territoire de reproduction pour éviter la prédation des œufs pondus plutôt que pour conserver des partenaires de haute qualité ou pour augmenter leurs occasions d'accouplement.

[Traduit par la Rédaction]

Introduction

The defense of a breeding territory by males is a conspicuous component of many animal mating systems (Clutton-Brock 1989; Davies 1991; Ligon 1999). Males defend an area to exclude intrasexual competitors to gain access to multiple mates, thereby increasing their mating success (Emlen and Oring 1977; Clutton-Brock 1988). Males of

some species guard mates that are within the territory (Langmore 1996; Reavis and Barlow 1998; Tobias and Seddon 2000), whereas in others males defend a high-quality territory that then attracts mates (Alatalo et al. 1986; Bisazza et al. 1989). In an exceedingly small number of species, females alone establish a breeding territory and attract mates (Jenni 1974). This behavioral pattern is mainly observed in sex-role-reversed species (Trivers 1972).

In cardinalfishes (Pisces: Apogonidae), males alone mouthbrood an egg mass given by a female (Blumer 1982). In most species of this fish group, the operational sex ratio (OSR), a principal determinant of the direction and intensity of sexual selection, is female-biased because of the higher potential reproductive rate of females (Okuda and Yanagisawa 1996; Okuda 1999a). In these species, females play the leading role in courtship and mate search, which is characteristic of sex-role-reversed animals (Thresher 1984; Okuda and Yanagisawa 1996; Okuda 1999a). Although they

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usually show high site fidelity, they do not defend a certain fixed area as the breeding territory.

One exceptional case is seen in the cardinalfish *Apogon notatus* (Houttuyn, 1782) (Okuda 1999b), one of the most common fish species in the coastal waters of the Northwest Pacific. This fish forms large shoals in the water column near boulder substrata from autumn to spring. A few months prior to the breeding season (June–September), females start to establish small territories on the substrata into which they invite a male partner from a shoal (Kuwamura 1983; Okuda 1999b, 2001). In a mating pair, the female is more active in courtship and more aggressively attacks intruders (Kuwamura 1985). Both males and females leave the territories every evening to forage in the water column during the night, but return to the same site in the early morning (Usuki 1977). The mating pair remains together for several weeks until spawning, at which time the male leaves the territory to mouthbrood in a shoal. (Kuwamura 1985; Okuda 1999b). Soon after separation, females resume pairing with other males in their territories. Both males and females undergo several spawning cycles in one breeding season (Okuda 1999b). After their final spawning in the season, females become gregarious again. In winter, this fish migrates offshore, returning to the coastal breeding ground to settle a new territory the following spring (Fukumori et al. 2008).

In this species, the potential reproductive rate is higher for females, but the OSR is male-biased, which is unlike other cardinalfishes and is contradictory to the theory (Okuda 1999b). This arises because adult mortality is higher for females, which incur a large energetic cost for territory maintenance (Okuda 2001), and consequently, the adult sex ratio skews extremely toward males (Okuda 1999b). Males develop a sexual ornament in their lower lip, and females mate preferentially with more ornamented males (Okuda et al. 2003). This conforms to the current theory that sexual selection operates more strongly in the sex in excess.

Although female *A. notatus* hold breeding territories over a long period of time, the functions of their territories remain unclear. There are three hypotheses that could account for female territoriality. One possibility is that females have territories to increase offspring survival, i.e., to avoid predation against eggs at the moment of spawning. This hypothesis predicts that female territorial behavior will be directed toward potential egg predators rather than toward mating competitors (same sex). The second hypothesis is that females show breeding territoriality to guard a high-quality mate. We predict that female territorial behavior will be directed towards rival females rather than toward conspecific males and other species. We also predict that the females will form a pair bond with a previous mate and will not mate with a new mate after spawning. The third hypothesis is that female territoriality serves to acquire more mates. However, the latter hypothesis is less likely, because potential mates are always available for females owing to a constantly male-biased OSR (Okuda 1999b). Furthermore, we discuss whether territory quality varies in relation to offspring survival but not to mating opportunities. We also discuss whether females will compete among themselves to occupy a high-quality territory that increases offspring survival. Here, we conducted field observations to verify these hypotheses.

Materials and methods

Censuses of paired and unpaired fish

To determine the population sex ratio, we conducted 15 weekly censuses of *A. notatus* with the aid of SCUBA at Morode Beach, Shikoku Island, Japan, during the breeding season of 1999 (May–October in southern Japan; Kuwamura 1983; Ueno et al. 1987). We set a quadrat (10 m × 20 m) with 2 m grids on the boulder slope. At the beginning of the breeding season, we caught 350 adults (mostly females) in and around the quadrat using seine and hand nets, and marked them by subcutaneous injections of VIE (visible impact fluorescent elastomer; Northwest Marine Technology, Inc., Shaw Island, Washington; for details and ethical notes see Okuda 1999b). After measuring standard length to the nearest 1 mm, we released them at their capture sites.

In each census, we recorded the number of paired fish (fish in the territories) and unpaired fish (fish in shoals) found in each grid. We determined the sex of captured fish by checking for the presence or absence of the male sexual ornament of the lower lip (Okuda et al. 2003).

Territorial behaviour

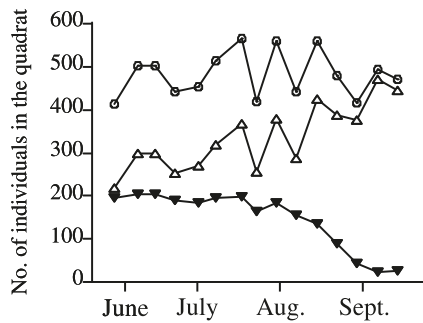
To examine competitive interactions between territorial fish and aggressive behavior against intruders, we made behavioral observations for a total of 247 pairs (93 pairs on the day of spawning and 154 pairs on other days). We selected one focal pair in the quadrat and observed it for 30 min, recording the frequency of intrusions upon the territory and subsequent attacks by the territorial fish on the intruders. Territory intruders were defined as fish, either conspecific or heterospecific, approaching within ~30 cm (equivalent to the territory area) of the focal pair with territorial attacks defined as a rush by a member of the focal pair to the intruder. For 66 of 93 pairs observed on the day of spawning, spawning occurred during the observation time. For these pairs, we made an additional 30 min observation of postspawning events. Using the data of postspawning events, we examined in which type of territories egg predation is more likely to occur and whether frequent territory intrusions are more likely to result in egg predation.

The period from the day following pair formation to the day before spawning was defined as the courtship phase, and the day of spawning as the spawning phase (sensu Okuda 1999b). Behavioral data were averaged for each phase of each month. For pairs observed two or more times in a single month, we used monthly averages of the data to avoid pooling fallacy associated with repeated samplings of the same subject (Machlis et al. 1985). This procedure reduced the sample size to 220 (127 in the courtship phase and 93 in the spawning phase).

Territory quality

As an index of territory quality, we used three physical and two biological features of each 2 m grid in the breeding season of 1999. On each grid, we measured water depth and the length along the major axis and vertical height of all boulders larger than 10 cm in diameter. We approximated the size of each boulder as a product of the major axis length and vertical height and calculated the mean boulder size. As an index of microhabitat complexity, we used the

Fig. 1. Seasonal changes in the number of paired (▼) and unpaired (△) cardinalfish *Apogon notatus* and the total number of fish (○) during the breeding season.



coefficient of variation in the boulder size. We counted the number of territorial females in the grid as potential mating competitors and the number of unpaired fish in a shoal within the grid as potential egg predators.

Establishment of territories during the next year

During the year following field observations, we conducted a follow-up survey of marked females to examine whether they preferentially established territories of high quality during the previous season. We censused the marked fish returning to the quadrat every 1–3 days, from 3 April to 27 May 2000, when the earliest spawning was observed. We examined which territory characteristics were preferred by these earlier settlers.

Data analysis

We used parametric tests if the data were normally distributed. Behavioral data were normalized by logarithmic or square-root transformations when appropriate. We used two-way factorial ANOVAs to compare the frequencies of intrusion between months and phases, because we observed different pairs during different months or phases. We used the contrast method or Tukey's test as post hoc comparisons. We used multiple regression analysis to examine (i) the effects of territorial characteristics on the potential risk of egg predation as indicated by the frequency of intrusions upon female territories, (ii) the strength of territory defense as indicated by the proportion of female territorial attacks relative to territory intrusions, and (iii) to examine which territory characteristics were preferred by these earlier settlers, incorporating the date of territorial settlement as a dependent variable and territory characteristics as the independent variables. We used the stepwise forward selection procedure with a criterion of $\alpha = 0.05$. We also performed logistic regression analysis to examine which territory characteristics increased the incidence of egg predation and to examine if frequent territory intrusions increased the incidence of egg predation.

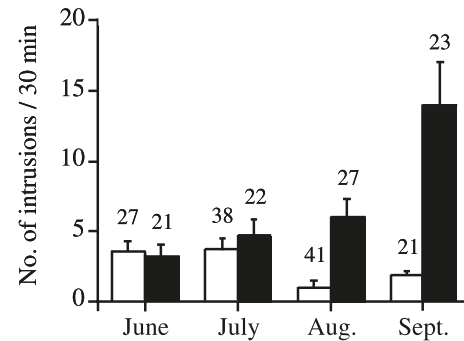
All statistical probabilities were two-tailed. For descriptive purposes, values are means \pm SE.

Results

Maintenance of territories

The number of pairs in the quadrat was nearly constant in June and July, but gradually decreased in August and Sep-

Fig. 2. Seasonal changes in mean (\pm SE) frequency of intrusions upon female territories in the courtship (open bars) and spawning (solid bars) phases of the cardinalfish *Apogon notatus*. Numbers above bars denote sample sizes (number of observed pairs).



tember (Fig. 1). Correspondingly, unpaired fish increased in August and September. In June and July, all females had territories and unpaired males were abundant in the population. The population sex ratio (male:female) at this time was estimated to be 2.56 ± 0.37 .

The frequencies of intrusions upon territories were relatively low in both the courtship and spawning phases in June and July (Fig. 2), but intrusions increased drastically in the spawning phase as the season progressed (two-way factorial ANOVA — month: $F_{[3,212]} = 4.94$, $P = 0.002$; phase: $F_{[1,212]} = 28.29$, $P = 0.001$; month \times phase: $F_{[3,212]} = 3.84$, $P = 0.01$). The majority of intruders in the courtship phase were neighboring paired females (one-way factorial ANOVA — $F_{[3,504]} = 17.02$, $P = 0.001$; Fig. 3), whereas major intruders in the spawning phase were unpaired conspecifics and other species (one-way factorial ANOVA — $F_{[3,368]} = 7.97$, $P = 0.001$). Of all heterospecific intrusions observed ($N = 71$), 82.9% were done by wrasses (family Labridae) such as *Labroides dimidiatus* (Valenciennes in Cuvier and Valenciennes, 1839), *Pseudolabrus eoethinus* (Richardson, 1846), and *Halichoeres tenuispinis* (Günther, 1862). The frequency of intrusions by paired females did not differ between the phases (unpaired t test — $t_{[218]} = -0.44$, $P = 0.66$), but intrusions by unpaired conspecifics and other species were more frequent in the spawning phase than in the courtship phase (t test — unpaired conspecifics: $t_{[218]} = -3.84$, $P = 0.002$; other species: $t_{[218]} = -6.20$, $P = 0.001$). There was no intrusion of paired males into a territory.

Corresponding with the seasonal changes in intrusion rate, the frequency of female attacks increased late in the breeding season (two-way factorial ANOVA — month: $F_{[3,212]} = 10.73$, $P = 0.001$; Fig. 4). The proportion of attacks relative to territory intrusions was higher in the spawning phase (phase: $F_{[1,212]} = 46.94$, $P = 0.001$; month \times phase: $F_{[3,212]} = 7.76$, $P = 0.001$) and late in the breeding season (month: $F_{[3,212]} = 5.57$, $P = 0.001$). Females attacked unpaired conspecifics selectively in either phase (one-way factorial ANOVA — courtship phase: $F_{[3,133]} = 27.86$, $P < 0.001$, with Tukey's test between unpaired conspecifics and paired female, paired male, and other species (all $P < 0.05$); spawning phase: $F_{[3,135]} = 12.78$, $P < 0.001$, with Tukey's test between unpaired conspecifics and paired female, paired male, and other species (all $P < 0.05$); Fig. 5). Attacks

Fig. 3. Frequency of intrusions upon female territory by conspecific and heterospecific fish in the courtship (a) and spawning (b) phases of the cardinalfish *Apogon notatus*.

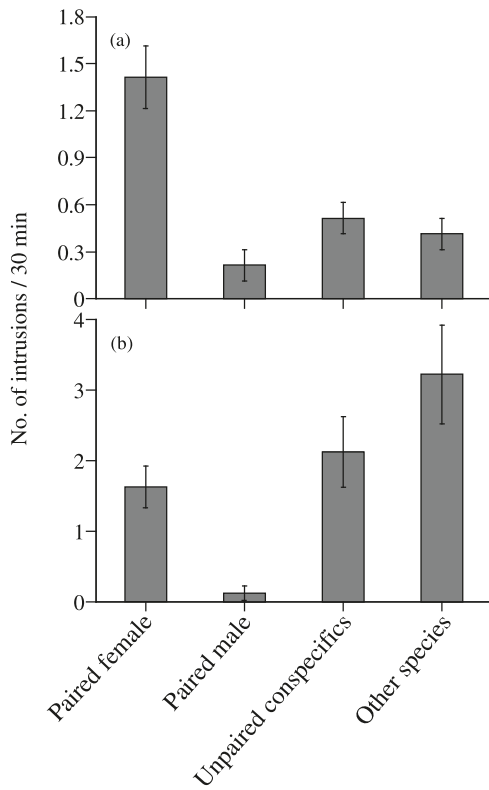
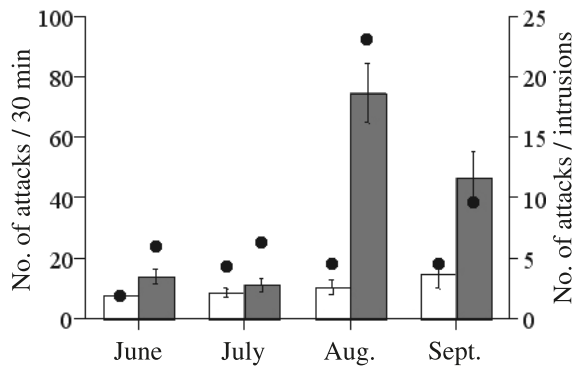


Fig. 4. Seasonal changes in the mean (\pm SE) frequency of female attacks and their relative frequency to territory intrusions (●) in the courtship (open bars) and spawning (shaded bars) phases of the cardinalfish *Apogon notatus*. Numbers above bars denote sample sizes (number of observed pairs).

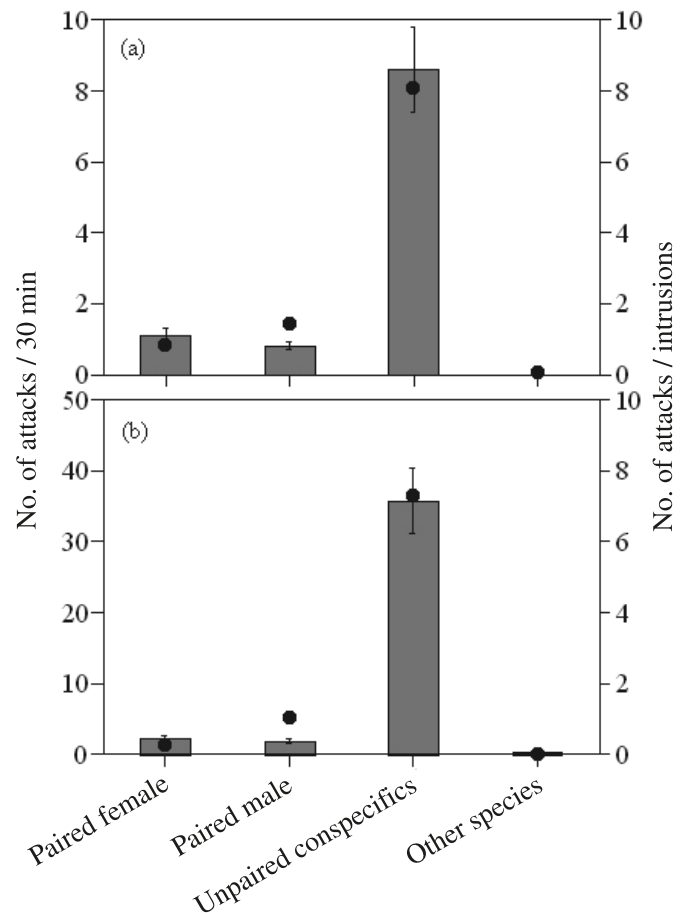


against wrasses accounted for 82.1% of the total heterospecific attacks.

Territory quality and egg predation

In the spawning phase, frequent intrusions occurred as the season progressed in territories where unpaired conspecifics were abundant (Table 1). In the courtship phase, the relative frequency of female attacks to intrusions was lower in territories where water depth was greater and coefficient of variation in boulder size was higher (Table 2). Neither the frequency of intrusions in the courtship phase nor the fre-

Fig. 5. Frequency of attacks (shaded bars) by females against conspecifics and heterospecific fish and their relative frequency to territory intrusions (●) in the courtship (a) and spawning (b) phases of the cardinalfish *Apogon notatus*.



quency of female attacks in the spawning phase were related to any territorial characteristics (Tables 1, 2). Additional analysis showed that the intrusion frequency and the number of attacks/intrusion were not affected by female body size ($P > 0.05$).

Egg predation occurred in 19.7% of spawnings observed (13 of 66). In all cases, eggs were eaten at the moment the egg mass was transferred from the female to the male, or immediately after the completion of egg transfer. The incidence of egg predation tended to increase late in the season ($\chi^2_{[3]} = 7.29, P = 0.06$; June: 9.1% and $N = 11$; July: 11.8% and $N = 17$; August: 13.0% and $N = 23$; September: 46.7% and $N = 15$). Of the 13 egg losses observed, 4 were caused by unpaired conspecifics, 7 by heterospecific predators, and 2 by both of them. Heterospecific predators involved were nine wrasses and three damselfishes. The incidence of egg predation was higher in territories where intrusions were more frequent (logistic regression analysis — Wald = 36.92, odds ratio = 0.16, $P = 0.001$). None the territory characteristics were related to the incidence of egg predation (all $P > 0.05$). For 66 of 93 pairs observed on the day of spawning, 49 females found a new, nonbrooding male soon after spawning.

Table 1. Multiple regression analysis of effects of female territory characteristics on the intrusion frequency upon its territory in the courtship and spawning phases of the cardinalfish *Apogon notatus*.

	Courtship phase (<i>n</i> = 127)		Spawning phase (<i>n</i> = 93)	
	Full	Reduced	Full	Reduced
Seasonal				
Month	-0.15		0.30*	0.37***
Physical				
Water depth	-0.01		0.15	
Average boulder size	-0.06		0.02	
Coefficient of variation in the boulder size	-0.08		-0.07	
Biological				
Number of pairs	-0.13		-0.07	
Number of unpaired conspecifics	0.14		0.28**	0.28**
Adjusted r^2	0.04		0.25	0.21
<i>P</i>	0.64		<0.001	<0.001

Note: Standardized regression coefficients are shown for full and reduced (stepwise forward selection) models. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 2. Multiple regression analysis of effects of female territory characteristics on the proportion of female territorial attacks relative to territory intrusions in the courtship and spawning phases of the cardinalfish *Apogon notatus*.

	Courtship phase (<i>n</i> = 127)		Spawning phase (<i>n</i> = 93)	
	Full	Reduced	Full	Reduced
Seasonal				
Month	0.25		0.13	
Physical				
Water depth	-0.20	-0.24*	-0.14	
Average boulder size	0.10		-0.19	
Coefficient of variation in the boulder size	-0.19	-0.23*	-0.15	
Biological				
Number of pairs	0.08		0.15	
Number of unpaired conspecifics	-0.10		-0.11	
Adjusted r^2	0.15	0.10	0.95	
<i>P</i>	0.05	0.01	0.46	

Note: Standardized regression coefficients are shown for full and reduced (stepwise forward selection) models. *, $P < 0.05$.

Establishment of territories before the breeding season

In the season following the quantitative assessment of territory quality in 1999, we monitored how females establish their territories in the quadrat. More than 2 months before the onset of the breeding season, some females started to establish their territories. Since the size distribution of adult fish showed a clear bimodal pattern (Okuda 1999b), the females were categorized into two size classes. The mean size of small (age 1) and large (age ≥ 2) females were 65.6 and 87.5 cm, respectively. Large females settled in their territories earlier than did small females (Kolmogorov–Smirnov two-sample test — $\chi^2_{[194]} = 103.9$, $P = 0.001$). They also settled in deeper areas than small females ($t_{[194]} = 2.7$, $P = 0.01$). The deeper areas were also places where unpaired conspecifics were less likely to aggregate (Pearson's correlation coefficient = 0.76, $P < 0.001$). Multiple regression analysis showed a significant negative correlation between the date of territorial settlement and boulder size (reduced model: $R^2 = 0.05$, $F_{[1,194]} = 5.00$, $N = 94$, $P = 0.03$), suggest-

ing that early settlers preferentially occupied areas with larger boulders.

Discussion

In *A. notatus*, egg predation sometimes occurred at the moment of egg transfer from the female to the male, or immediately after the completion of egg transfer. Mouthbrooding is one of the most effective means to guard eggs as reported for two sympatric cardinalfishes (*Apogon doederleini* Jordan and Snyder, 1901 and *Apogon niger* Döderlein in Steindachner and Döderlein, 1883) in which the incidence of egg predation is low except for filial cannibalism (Okuda and Yanagisawa 1996; Okuda 1999a). Such an interspecific difference in egg predation may be associated with their social behavior, i.e., *A. notatus* is gregarious, while the latter two are solitary. Female *A. notatus* suffered from frequent conspecific intrusions upon their territories during the spawning phase, especially late in the breeding season when many conspecific fish were shoaling nearby. Correspond-

ingly, the incidence of egg predation increased as the breeding season progressed. The fact that territorial females attacked unpaired conspecifics much more frequently than paired females supports our hypothesis that female territorial behavior is directed toward potential egg predators rather than toward mating competitors.

In our observations, female *A. notatus* attacked wrasses far less frequently than unpaired conspecifics, although wrasses were also major egg predators. Wrasses usually rove through the wide home range and participate opportunistically in egg raiding. In the present observations, wrasses rush to the scene where eggs of *A. notatus* were being raided by conspecifics. In addition, wrasses are often considerably larger than *A. notatus*. Thus, females will not be able to defend their territories from this type of egg predator.

One may expect that the female *A. notatus* defends the breeding territory to guard a high-quality mate. In the mate-guarding fish, both sexes attacked intruders of the same sex more intensely than those of the opposite sex (Yamamoto et al. 1999). However, in this study, females attacked unpaired conspecifics more frequently than rival females. In addition, females could find a new, nonbrooding mate soon after spawning as shown in a previous study (Okuda 1999b). Under the condition of male-biased OSR, females are thought to have sufficient opportunities to choose a high-quality mate among males. The present results do not support our hypothesis that female territoriality serves to guard high-quality mates.

In role-reversed birds, females often show breeding territoriality, while males play the greatest part in parental care. In those species, females defend a large territory that encompasses multiple males and allocate their clutches to these males (Emlen and Oring 1977; Oring et al. 1994; Butchart et al. 1999). Such a territory serves to increase their mating opportunities. In contrast, female *A. notatus* cannot allocate their clutches to multiple males, because the clutch corresponds to a form of cohesive egg mass that cannot be divided anatomically. This anatomical constraint prevents female *A. notatus* from increasing the number of mates through territorial defense. Also under the male-biased OSR, females may have enough opportunities to mate with unpaired males. Thus, these facts do not support our hypothesis that females defend their breeding territories to enhance mating opportunities.

Our field observations suggested that greater variation in territory quality in relation to the risk of egg predation. Areas where conspecifics aggregate were of poor-quality territories, because such areas were highly vulnerable to conspecific intrusions and subsequent egg predation. In the threespine stickleback (*Gasterosteus aculeatus* L., 1758) complex in which territorial males provide nest brooding, it has been reported that nonterritorial conspecifics often raid male nests in a shoal to eat eggs (Whoriskey and FitzGerald 1985). In the stickleback, egg predation becomes more frequent as shoal size increases (Ridgway and McPhail 1988). Similarly, territorial female *A. notatus* are not able to guard their newly spawned eggs effectively when intraspecific interference is intensified.

Areas with high structural complexity reduced the relative frequency of territorial attacks to intrusions. In some fishes, energetic costs of territorial behavior are quantitatively

measured on the basis of somatic liver glycogen reserves (Chellappa and Huntingford 1989). Okuda (2001) also reported that female *A. notatus* show decreased body-fat reserves during territorial settlement with almost total depletion at the end of the breeding season (Okuda 2001), suggesting that territorial defense results in considerable energy loss for females. Therefore, female territory quality will show spatial variation in terms of reduced time or energetic cost entailed by territorial defense.

Large females established territories in deeper areas and at an earlier time than small females. Conspecifics were less likely to form large shoals in deeper areas and thus territorial defense might be less costly for large females. In addition, early settlers preferentially occupied areas with larger boulders, which might conceal effectively their spawning from the view of egg predators. In this fish, territorial settlement started more than 2 months before the breeding season and territorial replacement was infrequent during the breeding season. This suggests that female competition for occupation of a high-quality territory was subject to the rule of "first come, first served" as reported for many migratory birds (Møller 1994; Aebischer et al. 1996; Lozano et al. 1996; Hasselquist 1998). In game theory, such competition may evolve under conditions where that the resource defense inflicts high energetic costs on competitors, and so only individuals with high energy reserves can win the endurance game (Kokko 1999). This may be the case for *A. notatus*, in which large females had a large fat reserve sufficient to maintain their territories for a long period (Okuda 2001).

In conclusion, females defend their breeding territories to avoid predation against eggs at the moment of spawning. In other words, females defend their breeding territories to increase offspring survival rather than to guard high-quality mates or to increase mating opportunities. This unusual phenomenon of males being more abundant and competitive and females showing breeding territoriality is consistent with the current sexual selection theory where one sex is more competitive in mating, while the other sex invests more in parental care. Reports of unusual sex roles in which the territorial sex is not identical to the competitive sex are scattered in the literature (Clutton-Brock 1991), but they have been usually neglected in discussing sexual selection. In directing our attention more to this phenomenon, we need to elucidate the functions and consequences of breeding territoriality in such cases, which will lead to a more thorough understanding of sexual selection.

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