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Plasticity in the Mating System of the Longnose Filefish, *Oxymonacanthus longirostris*, in Relation to Mate Availability

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Abstract – The mating system of the longnose filefish, *Oxymonacanthus longirostris*, was examined on coral reefs of Okinawa, Japan. This species has been shown previously to be monogamous. Fish were usually found swimming together in heterosexual pairs with the male and female sharing the same feeding territory. However, both monogamous and polygynous (bigamous) males were found in the present study. Polygynous males, which were larger than monogamous males, visited and stayed several minutes in turn with each female within the territories. Although most males were monogamous in the early breeding season, over 20% of males mated polygynously in the late breeding season. The adult sex ratio in the former was unbiased, but became slightly female-biased toward the end of the breeding season because of the higher disappearance rate of males. The higher disappearance rate may be due mainly to a higher mortality rate of males resulting from a greater deterioration of physical condition during the breeding season. Thus, the mating system varied with the change of the adult sex ratio. Plasticity in the mating system of this species may be the outcome of male mating tactic depending on local mate availability.

Introduction

Animal mating systems are influenced by the distribution patterns of mates and ecological resources (Emlen & Oring, 1977; Davies, 1991; Reynolds, 1996), and may vary depending on the ecological and social factors because they are the outcome of the reproductive strategies of individuals rather than as characteristics of species (Clutton-Brock & Harvey, 1978; Clutton-Brock, 1989). Intraspecific variation in mating systems is well known in birds and mammals (Clutton-Brock, 1989; Davies, 1991; Lott, 1991). Among fishes, for example, facultative monogamy of the predominantly polygynous species occurs in a low population density or where a suitable microhabitat is limited (Donaldson, 1989; Petersen, 1990; Kawase & Nakazono, 1994), and polygyny occurs in predominantly monogamous species when more potential mates are available to males (Keenleyside, 1985; Keenleyside et al., 1990; Kuwamura, 1996).

Some species of coral reef fishes, such as butterflyfishes, usually swim together in heterosexual pairs, and the male and female share the same feeding territory. To our knowledge, such species are monogamous (Neudecker & Lobel, 1982; Fricke, 1986; Yabuta, 1997). According to the classical theory, monogamy is expected to occur when (i) there is no "environmental potential for polygamy (EPP)", which depends upon the degree to which multiple mates or resources critical to gaining multiple mates are economically defendable, or (ii) there is no opportunity to take advantage of the EPP, for example, the need for biparental care (Emlen & Oring, 1977). If there is EPP for males, monogamy may not be the only option also for these coral reef fishes, because males should mate with as many females as possible to gain higher reproductive success. For example, the possibility of polygynous harem formation in the socially-monogamous surgeonfish, *Acanthurus leucosternon*, has been suggested (Robertson et al., 1979).

The longnose filefish, *Oxymonacanthus longirostris* (Monacanthidae) has been shown to be monogamous without parental egg care: a male and female move about as closely coordinated pairs and share the same feeding territory (Barlow, 1987, 1988). However, Oda (1992) reported that some polygynous males occurred in a natural population, although the detailed pattern of occurrence was not shown. This indicates that the male longnose filefish has the environmental potential for mating with multiple females.

The purpose of the present study is to clarify the mating system of *O. longirostris* in detail. Here, we relate our findings and discuss how ecological and social factors affect the mating system of this species.

Materials and methods

The study species

O. longirostris inhabits shallow coral reefs of the Indo-West Pacific, including the Ryukyu Islands (Matsuura, 1984). The sexes are easily distinguished because of their sexual dimorphism; only males have a gaudy orange pelvic flap (Barlow, 1987). The species feeds mainly upon scleractinian coral polyps, mostly *Acropora* spp. (Sano et al., 1984) during the daytime, and sleeps by lying on a branch of coral at night. During the breeding season, females spawn as frequently as every day (Barlow, 1987). Demersal and adhesive eggs are spawned into a tuft of filamentous algae, and hatch shortly after sunset two days later. Neither males nor females provide egg care.

Field observations

We conducted field research using snorkel and SCUBA at Bise, Okinawa, southern Japan (26°42′N, 127°42′E), from March 1997 to February 1998. The moat of the reef had abundant scleractinian corals, especially branching and table-top *Acropora* spp. A 30×40 m quadrat, divided with strings into 5×5 m grids, was established as a study area within the moat at depths of 2–3 m mean sea level. Before the 1997 breeding season (24 March–1 April), all individuals of *O. longirostris* in the study area were captured with a barrier net and tagged with color glass beads. In order to be identified individually, one or two sets of beads were sewed just anterior to the first dorsal spine, or the dorsal or ventral surface of the caudal peduncle. After tagging, we measured the standard length (SL) to the nearest 0.5 mm and body weight (BW) to the nearest 0.1 g, and released the fish at the original sites. We checked the presence and location of each tagged individual at the study area on more than four successive days in the first and latter half of each month. We regarded all tagged individuals as mature adults because even the smallest tagged individuals (a 58 mm SL male and a 57.5 mm SL female) were observed mating after tagging. Although we found many new recruits in the study area in the late breeding season, most of them were immature and formed small groups rather than pairs.

Most tagged individuals were recaptured and measured SL under water in early May (just before the onset of the breeding season), from late July to early August, and in early October 1997 (just after the breeding season). Some recaptured individuals were taken to shore to be weighed. For each individual, the condition factor ($CF_1 = BW/SL^3 \times 10^5$) was calculated.

Behavioral observations were conducted throughout the breeding season (May–October) almost daily except for 11 days, when heavy waves from typhoons did not permit diving. Water temperatures near the bottom ranged from 24.2 to 31.0℃ during the breeding season. Because the spawning time of the fish changed seasonally according to ambient water temperature (Kokita, unpubl. data), observation periods were altered seasonally between 9:00 and 19:30 h to observe courtship and spawning behavior of each pair. In order to confirm the territory and spacing pattern of each pair, we conducted 30-min observations during the daytime except when courtship and spawning occurred so as to exclude the influence of spawning activity. During these observations, we recorded swimming routes and feeding sites. The 30-min observations were carried out only for individuals inhabiting the central area (20×30 m) of the quadrat in late May and early August. We regarded the minimum convex polygon covering all feeding sites and swimming routes of each fish as its territory.

To examine monthly changes in physical and feeding conditions of individuals, we captured monthly about 10 individuals in areas about 1 km distant from the study area. The fish were preserved in 10% formalin-seawater solution. Body length (SL: mm), wet body weight (BW: g), gonad weight (GW: g) and stomach content weight (SCW: g) of each specimen were measured in the laboratory. The condition factor [$CF_2=(BW\text{-}GW)/SL^3 \times 10^5$] and the stomach content index ($SCI=SCW/BW \times 100$) were calculated, respectively.

Results

Seasonal pattern of reproduction

Throughout the breeding season, 212 spawnings by tagged and other individuals were observed between 10:04 to 19:10 h. The first and the last spawnings were observed on 20 May and 7 October, respectively. While spawnings occurred on only 4–5 days around the full and new moon from late May to early June, almost all females spawned every day from mid-June to early September. Spawnings were made in pairs except in one instance when a neighboring male engaged in sneaking during a paired courtship bout. Male courtship displays, including "flutter dive" (i.e., lowering its head, then diving while fluttering with its fin spread) and "nuzzle" (i.e., nuzzling of the female's face), and spawning sequence observed were similar to those described by Barlow (1987). Mating of pairs occurred not only within their territories but also outside of them. About one hour before spawning, females thrust their snout repeatedly into tufts of various species of filamentous algae to select the spawning substrates. Females spawned in the various filamentous algae, such as red algae growing inside the territories of herbivorous damselfish, *Stegastes nigricans*, other red algae, green algae, brown algae and blue-green algae.

In early May, there existed 42 paired males (mean±SD=74.1±5.3 mm SL, n=40) and females (67.0±5.7 mm SL, n=39) and three non-territorial unpaired females (59.8±2.5 mm SL, n=3). Among pairs, male body length was positively correlated with female body length (Spearman's rank correlation coefficient: $r_s=0.34$, $P<0.05$, $n=38$), and were significantly larger than the latter (Wilcoxon signed rank test, $T=22.5$, $P<0.0001$). Unpaired females were smaller than paired females (Mann-Whitney U test, $U=12.5$, $P<0.05$). Unpaired females often approached particular pairs and formed a threesome, but were usually driven away by the paired females.

The numbers of both males and females within the study area decreased gradually as the breeding season progressed (Fig. 1). The disappearance rate of tagged males (43%: 18/42) was significantly higher than that of tagged females (22%: 10/45) during the breeding season ($\chi^2=4.24$, $df=1$, $P<0.05$). Two males that disappeared from the study area were later found outside it and had paired with non-tagged females. One of these males had lost his partner female prior to leaving the study area. The other left the study area even though his previous partner female had remained. As a result of the higher male disappearance rate, the adult sex ratio (ASR: the number of males/the number of males and females) in the study area was slightly biased to females, ranging from 0.42 to 0.49, during the breeding season (Fig. 1), but did not significantly deviate from equality every

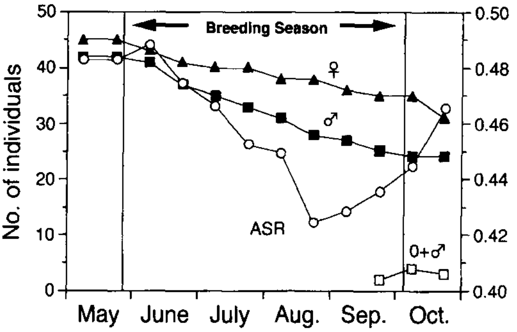

Fig. 1. Seasonal changes of the numbers of males (solid squares) and females (solid triangles), and the adult sex ratio (ASR: the number of males/the number of males and females, open circles) in the study area. Open squares indicate the number of non-tagged paired males, probably aged 0+, that occurred in the study area.

month (binomial test, two-tailed, $p > 0.2$ every month). The ASR skewed gradually to late August, and thereafter equalized in September to October because non-tagged males (mean±SD $= 57.4 \pm 1.3$ mm SL, $n = 4$) judged probably 0+ year age owing to their relatively small body length, immigrated into the study area and paired with the remaining single females.

Occurrence of polygynous males

Heterosexual pairs defended territories against conspecific intruders, and foraged within their territories (Fig. 2). Some males defended territories containing two females which were mutually exclusive. Polygynous (bigamous) males visited and swam together with each female in turns during the daytime, and mated with both females every day. The proportion of polygynous males was 4.7% in May, 7.7% in June, 17.6% in July, 28.8% in August and 20.3% in September, respectively. The seasonal pattern of this proportion was negatively correlated with that of the ASR (Spearman's rank correlation coefficient, $r_s = -1.00$, $P < 0.05$, $n = 5$). Throughout the breeding season, 31% of males (13/42) and 25% of females (11/44) mated with multiple partners although most individuals mated with only a single partner (Table 1).

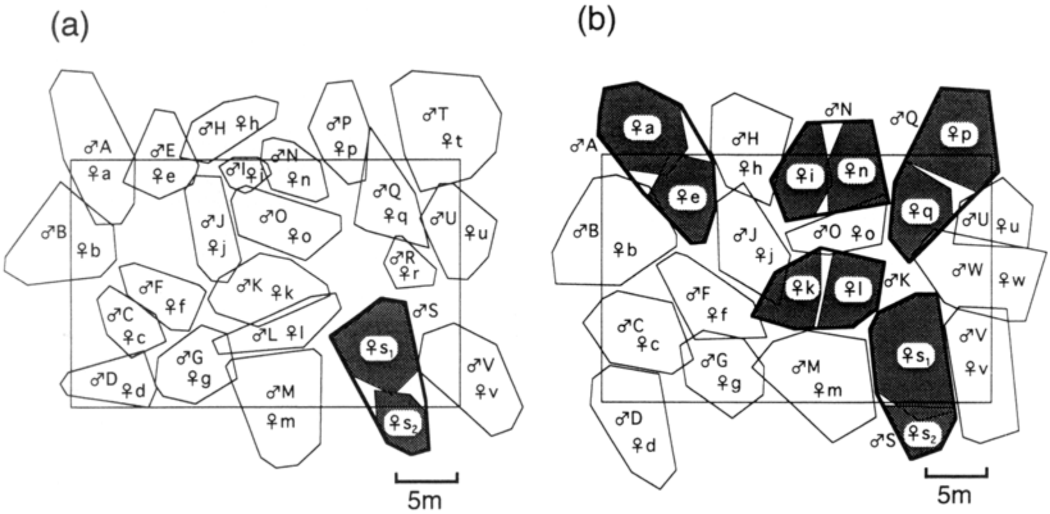

Fig. 2. Location of pair territories (open areas) and territories of polygynous males (bold line) in a portion (20×30 m) of the study area in late May (a) and early August (b). For the polygynous males, the territories were subdivided by each female of the harem (shaded areas).

Table 1. The number of mates for males and females during the breeding season.

	Total number of pairings	Number of sequential partners during the breeding season			P*
		One	Two	Three	
Male	55	29	13**	0	0.02
Female	56***	33	10**	1	0.001

*Numbers of individuals mating with a single partner and multiple partners were tested by binomial test (two-tailed).

**Two individuals which paired with new partners after losing their previous partners are included, respectively.

***One pairing between a tagged female and a non-tagged male is included.

We observed two patterns in the occurrence of polygynous males. One pattern was that unpaired non-territorial females visited a monogamous pair and were received as secondary females of a harem at the onset of the breeding season (e.g., Fig. 2a: male S). In the second pattern, monogamous males expanded their territories and encompassed the territories of adjacent single females whose partner males had disappeared (e.g., Fig. 2b: male A, N, K, Q). The former and latter patterns were observed in two and nine cases, respectively. The functional harems were observed only during the breeding season, and their duration was 74±34 day (mean±SD; range=14-131, n=11).

Polygynous males visited primary females 2.6±0.9 times per 15 min (mean±SD; range=1-4, n=9) and secondary females 2.3±0.5 times (2-3, n=9), and paired with primary females for 441.2±115.2 sec (216-577, n=9) and with secondary females for 411.4±115.8 sec (268-635, n=9). The number of visiting bouts and pair duration did not differ significantly between primary and secondary females, respectively (Wilcoxon signed rank test, T=7, P>0.4 in visiting bouts; T=18, P>0.5 in pair duration). Whenever polygynous males visited females of their harems, both males and females displayed "flutter diving" during a few seconds. The males visited the two females in turns also during the courtship and spawning period. As soon as the males mated with one female, they left her to mate with the other. Spawning interval of the two females ranged from 7 to 88 min (mean±SD=34.2±24.2, n=35). Primary females were the first spawners at a proportion of 57% (20/35), and this proportion was not significantly higher than that for secondary females (binomial test, two-tailed, P>0.4).

SL, BW and territory size of polygynous males were larger than those of monogamous males (Table 2), although the CF_1 did not significantly differ between them. In six out of seven cases in which body sizes of all males adjacent to disappearing males were measured, the largest males among adjacent males became polygynous. When monogamous males became polygynous, their territory size increased from 31.5±13.4 m^2 (mean±SD, n=4) to 61.8±11.5 m^2 (n=4). The primary females were significantly larger (mean±SD=72.0±4.3 mm SL, n=11) than the secondary females (66.3±3.8 mm SL, n=11) in each harem (Wilcoxon signed rank test, T=8, P<0.05).

Sexual difference in physical condition

In monogamous fish throughout the breeding season, the SL of males increased, but their BW decreased during the breeding season (Table 3). Male CF_1 decreased by about 16%. On the other hand, both SL and BW of females increased during the breeding season. Female CF_1 did not differ significantly between May and October (Table 3). In May, there was no significant difference in the CF_1 between sexes (Mann-Whitney U test, U=84, P>0.5), but the

Table 2. Comparison of characteristics between monogamous and polygynous males. The data from late July to early August were used.

	Monogamous male		Polygynous male		Difference*	
	n	Mean±SD (Range)	n	Mean±SD (Range)	Z	P
Body length (mm SL)	22	74.5±4.7 (64.0-81.0)	8	81.6±4.3 (76.5-87.0)	−3.15	0.002
Body weight (g)	15	8.1±1.9 (4.6-11.3)	7	11.1±2.4 (8.6-14.0)	−2.64	0.008
Condition factor	15	1.97±0.14 (1.56-2.13)	7	2.07±0.16 (1.88-2.30)	−0.95	0.34
Territory size (m^2)	12	40.9±12.0 (22.6-61.8)	5	62.4±10.0 (49.0-71.7)	−2.64	0.008

*Mann-Whitney U test

Table 3. Changes in body length (mm SL), body weight (g) and the condition factor of monogamous males and females measured just before and after the breeding seasons. Numerals indicate mean ± SD (range).

	n	Before the breeding season (May)	After the breeding season (October)	Difference*	
				Z	P
Male					
Body length	16	74.2±4.3 (67.5–82.0)	77.3±3.4 (70.0–82.0)	−3.31	0.0009
Body weight	14	9.0±1.4 (6.8–11.9)	8.6±1.2 (6.6–11.0)	−2.28	0.02
Condition factor	14	2.18±0.18 (1.84–2.57)	1.84±0.09 (1.71–2.00)	−3.18	0.002
Female					
Body length	19	66.7±5.0 (57.5–78.0)	69.7±4.3 (60.5–79.0)	−3.63	0.0003
Body weight	14	7.0±1.6 (4.0–10.2)	7.6±1.1 (6.1–9.8)	−2.32	0.03
Condition factor	14	2.22±0.13 (2.00–2.47)	2.12±0.12 (1.82–2.29)	−1.48	0.14

*Wilcoxon signed rank test

CF_1 of females was significantly higher than that of males in October ($U=8$, $P<0.0001$). Moreover, 9 out of 15 monogamous males, in which CF_1 were measured from late July to early August, survived at the end of the breeding season, and their CF_1 (mean ± SD $=2.02\pm0.08$, $n=9$) were significantly higher than the CF_1 of disappearing males (mean ± SD $=1.88\pm0.18$, $n=6$; Mann-Whitney U test, $U=8$, $P<0.05$).

Data obtained from monthly collections of fish specimens were consistent with these data (Fig. 3a). Although there was no significant difference in the CF_2 between sexes during the non-breeding season (two-way ANOVA, $F=1.1$, $df=1$, $P>0.2$), males had worse physical condition than females during the breeding season ($F=44.6$, $df=1$, $P<0.0001$). Both sexes, especially males, recovered their physical condition rapidly after the breeding season ended. The SCI of males was significantly lower than that of females during the breeding season (two-way ANOVA, $F=36.2$, $df=1$, $P<0.0001$), especially in July when female SCI was more than three times higher than that of males (Fig. 3b). However, there was no significant difference in the SCI during the non-breeding season ($F=3.1$, $df=1$, $P>0.05$).

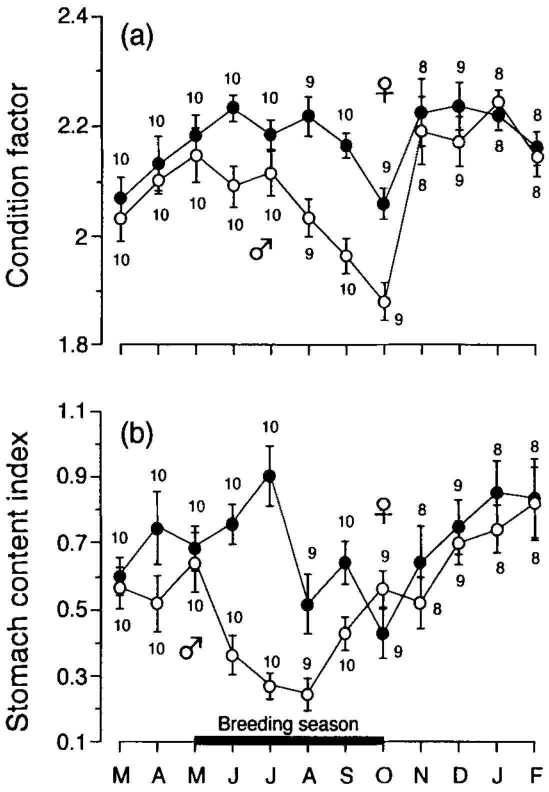

Fig. 3. Monthly changes (mean ± SE) in the condition factor (a) and stomach content index (b) for males (open circles) and females (closed circles). Attached numerals near circles denote the sample size.

Discussion

The present study revealed that the mating system of the longnose filefish was predominantly monogamous but, depending on the ASR, also became polygynous. As the ASR of the studied population became slightly female-biased, some males had opportunities to take advantage of multiple-mate availability. It is well known that some males become polygynous in predominantly monogamous birds (Alatalo et al., 1981; Hannon, 1984; Møller, 1986; Petit, 1991; Veiga, 1992) and fishes (Keenleyside, 1985; Keenleyside et al., 1990; Kuwamura, 1996). Polygyny in these species could be induced experimentally by skewing the sex ratio (Hannon, 1984; Keenleyside, 1985; Petit, 1991). Moreover, a haremic social organization similar to that described here for the longnose filefish has been reported in the socially-monogamous surgeonfish *Acanthurus leucosternon*, usually living in heterosexual pairs, although mating was not confirmed in this species (Robertson et al., 1979). The ASR of this surgeonfish tended to be slightly biased toward females. Male polygynous behavior of both fishes is characterized by alternative pairing with each female. Thus, monogamy should not be the only option for these fishes although they were observed in pairs.

In some cases, polygyny is associated with differential survival between the sexes (Promislow, 1992). Intense male-male competition and their subsequent high mortality may result in the monopolization of mates by surviving males. In the study population of the longnose filefish, males had a higher disappearance rate than females. As we found two tagged males outside of the study area, some males may leave the area and search for new females. However, the most important reason for the higher disappearance rate in males can be explained as follows. Males may have a higher mortality rate as a result of deterioration in physical condition during the breeding season. Actually, the CF of disappearing males was lower than that of surviving males. The body weight of the male clearly decreased and the male CF deteriorated greatly during the breeding season. The somatic weight loss of territorial males during the breeding season has been observed in other animals (Deutsch et al., 1990; van den Berghe, 1992; Maekawa et al., 1996). On the other hand, the female physical condition did not deteriorate greatly although the female reproductive investment was usually greater than that of males in terms of gamete production. This could be accounted for by sexual differences in the feeding condition during the breeding season. The SCI of males was much lower than that of females only during the breeding season. Moreover, males fed at a lower frequency than females during the breeding season (Kokita & Nakazono, in prep.). Pair territoriality in this species functioned to defend food resources (Barlow, 1987; Kokita & Nakazono, in prep.). Lower feeding activity of males would be because males contribute most to the defense of the pair territory (Kokita & Nakazono, in prep.), as has been shown in monogamous butterflyfishes (Fricke, 1986; Hourigan, 1989).

Polygynous males of the longnose filefish were larger than monogamous males and defended larger territories. As pairs were formed size-assortively, harem formation by relatively larger males resulted in the difference in body size between the primary and secondary females. Thus, male-male competition may affect monopolization of multiple females. Larger males could obtain higher reproductive success although maintaining larger territories and monopolizing more than one female may be more costly. Emlen & Oring (1977) predicted that polygyny may evolve if the EPP existed. Obviously, at least relatively larger males of the species are economically defendable to gain multiple mates. A restricted opportunity to take advantage of the EPP for males would be one of the factors causing the prevalence of monogamy in this species. Thus, plasticity in the mating system of this species may be the outcome of male mating tactic depending on local mate availability.

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