Sex-role reversal of a monogamous pipefish without higher potential reproductive rate in females

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In monogamous animals, males are usually the predominant competitors for mates. However, a strictly monogamous pipefish *Corythoichthys haematopterus* exceptionally exhibits a reversed sex role. To understand why its sex role is reversed, we measured the adult sex ratio and the potential reproductive rate (PRR), two principal factors influencing the operational sex ratio (OSR), in a natural population of southern Japan. The adult sex ratio was biased towards females throughout the breeding season, but the PRR, which increased with water temperature, did not show sexual difference. We found that an alternative index of the OSR (S_f/S_m : sex ratio of 'time in') calculated from the monthly data was consistently biased towards females. The female-biased OSR associated with sex-role reversal has been reported in some polyandrous or promiscuous pipefish, but factors biasing the OSR differed between these pipefish and *C. haematopterus*. We concluded that the similar PRR between the sexes in *C. haematopterus* does not confer reproductive benefit of polygamous mating on either sex, resulting in strict monogamous mating, and its female-biased adult sex ratio promotes female–female competition for a mate, resulting in sex-role reversal.

Keywords: potential reproductive rate; operational sex ratio; sex-role reversal; Syngnathidae; *Corythoichthys haematopterus*; monogamy

1. INTRODUCTION

Sexual selection arises from differential reproductive success based on intrasexual competition and mate choice (Andersson 1994). The direction and intensity of sexual selection are principally determined by the operational sex ratio (OSR), defined as the ratio of males to females ready to mate in a population at a given moment (Emlen & Oring 1977), although other factors such as variance in mate quality and cost of breeding also have some effect on them (Clutton-Brock & Parker 1992; Owens & Thompson 1994; Johnstone *et al.* 1996; Kvarnemo & Ahnesjö 1996, 2002; Kokko & Monaghan 2001). The OSR is strongly influenced by sexual difference in the potential reproductive rate (PRR), the population mean value of the maximum rate of reproduction each individual achieves when not constrained by mate availability, while other natural limitations remain in operation (Berglund *et al.* 1989; Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992; Kvarnemo & Ahnesjö 1996, 2002; Parker & Simmons 1996). In most animals, the PRR of females is lower than that of males owing to their higher energy and time expenditure in gamete production and parental care (Trivers 1972), and therefore the OSR becomes male-biased and intense male–male competition for mates is expected (i.e. conventional sex role). In some animals, however, it has been reported that females have a higher PRR than males and consequently females are predominant competitors for mates (i.e. sex-role reversal, Oring & Lank (1986) and Berglund *et al.* (1989)). Together with

sex differences in PRR, the adult sex ratio (more exactly the qualified sex ratio, Ahnesjö *et al.* (2001)) is considered a major determinant of OSR (Berglund *et al.* 1989; Kraus 1989; Clutton-Brock & Parker 1992; Madsen & Shine 1993; Parker & Simmons 1996).

There is a strong association between mating patterns and sexual selection (Andersson 1994). Because the opportunity for sexual selection increases with variance in the reproductive success between individuals, the intensity of sexual selection is generally stronger in polygamous than monogamous species. As a result, sexual dimorphism in size, weaponry or ornamentation and sexual dichromatism increase with the degree of polygamy (Andersson 1994). In pipefish and seahorses (Pisces: Syngnathidae) which are characterized by paternal care in the brood pouch or on the ventral surface (Herald 1959), a clear association between mating patterns and sex roles has been reported: polyandrous or promiscuous species exhibit sex-role reversal, whereas the sex role of monogamous species is conventional (Vincent *et al.* 1992; Wilson *et al.* 2003). In polygamous species (e.g. *Syngnathus floridae*, *Syngnathus scovelli*, *Syngnathus typhle* and *Nerophis ophidion*), females are predominant competitors for mates and possess secondary sexual traits such as larger body size, skin fold and coloration to attract males (Jones & Avise 2001; Berglund & Rosenqvist 2003). In monogamous species, on the contrary, aggressive behaviour is observed only in males and sexual traits are expressed only in males (Dawson 1977; Vincent 1994a). As predicted by theory, the OSR of polygamous species is biased towards females, whereas that of monogamous species is only slightly male-biased (Berglund & Rosenqvist 1993;

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Vincent 1994b; Vincent *et al.* 1994). An exception is the pipefish species *Corythoichthys haematopterus*, which reproduces monogamously but its sex role is reversed (Matsumoto & Yanagisawa 2001).

Corythoichthys haematopterus is a tail-brooding pipefish (subfamily: Urophori, less than 15 cm total length (TL)) inhabiting shallow waters of the Indo-Pacific (Dawson 1977). Long-term field observation revealed that male and female *C. haematopterus* form a lifelong pair bond and repeat mating exclusively (Matsumoto & Yanagisawa 2001). There are many unpaired females searching for mates in a population due to the female-biased adult sex ratio and the strict monogamous mating pattern. Matsumoto & Yanagisawa (2001) suggested that the OSR of *C. haematopterus* is constantly biased towards females, but they never made a practical examination of the OSR.

In this study, we estimated seasonal fluctuations in the OSR of *C. haematopterus* from the PRR of each sex and the adult sex ratio in a natural population of southern Japan. We explained the reason for a combination of sex-role reversal and monogamous mating pattern, taking into account factors biasing the OSR.

2. MATERIAL AND METHODS

(a) Field observations

This study was carried out using SCUBA at Morode Beach (33°00' N, 132°30' E) on the west coast of Shikoku Island, Japan, from April to August 2004. We set up a 125 × 20 m quadrat on the boulder area (depth 2–8 m). Prior to the beginning of the study, we collected all adult *C. haematopterus* (more than 90 mm TL) found in the quadrat using a hand net, and then measured TL and marked individually giving a hypodermic injection of red VIFE (Visible Implant Fluorescent Elastomer; Northwest Marine Technology, USA) at up to three out of ten fixed dorsal sites. Marked individuals were caged for a day to recover from the handling stress, and were released at the site of capture. Throughout the study period, every unmarked adult *C. haematopterus* found in the quadrat was captured, measured and marked individually. Among 135 adult fish (56 males and 79 females) marked in total, 8 individuals (5.9%, 3 males and 5 females) were never observed in the quadrat after releasing. This marking technique did not seem to affect the behaviour of fish and conspicuousness to predators. No license was required for catching, tagging and experimental use of this fish in Japan.

We censused the quadrat daily for approximately 3 hours between 05.00 to 19.00 hours during the period from 30 April to 25 August in 2004. We marked the location of each marked fish on the map, and checked the presence or the absence of embryos in the male's brood pouch and their developmental stage. We identified pair members by observing their 'greeting' behaviour and/or copulation.

(b) Calculation of PRR

The PRR is expressed as the inverse of 'time out' (G) defined as the time when an individual is incapable of mating (Clutton-Brock & Parker 1992; Parker & Simmons 1996). Activities during time out include gamete production, courtship, parental care and so on (Clutton-Brock & Parker 1992; Parker & Simmons 1996). In the present study, the $PRR = 1/G$ because the unit of one clutch (or brood) was used. Because male *C. haematopterus* receive only one clutch from a female and females give all matured eggs in their ovary

to a male in one spawning event, it is justified to use a clutch, instead of the exact number of eggs, as the unit of PRR.

To calculate the male PRR, we defined male time out (G_m) as the period of brooding, i.e. days from spawning to hatching of the brood because males were capable of mating in the first morning after hatching of his previous brood at night (Matsumoto & Yanagisawa 2001; Sogabe *et al.* 2007). We calculated the brooding period for 30 males from the census data (30 April–24 August), and then converted it into the male PRR. We defined female time out (G_f) as the period required to prepare mature eggs. Because it is impossible to discern the completion of egg maturation under the natural condition, we used an experimental approach to estimate female time out as follows.

We carried out the experiment in 18 females from 21 May to 25 August. Every early morning, paired *C. haematopterus* engaged in ritualized intra-pair interactions called greetings (Sogabe & Yanagisawa 2007). Their behavioural repertoire in the greeting changed on the day of spawning, and therefore we were able to identify a pair likely to spawn. After finding a focal pair, we observed their greeting and courtship until the pair members mutually exhibited the tail-end courtship behaviour called *Position* (Gronell 1984). At this stage of courtship, we captured the female, which had already completed egg hydration (A. Sogabe 2003, personal observation), and isolated her in a plastic cage (16 × 27 × 20 cm) for a day. On the next morning, we checked that the female had released hydrated eggs in the cage, and then released her at the greeting site. In all cases, the female resumed greetings with her mate. Subsequently, we monitored the pair once a day and recorded the day of first spawning after the manipulation. In the preliminary observation of ovaries of three females after releasing hydrated eggs, we confirmed that their ovaries contained only eggs of early immature stages. We expected the experimental female to provide a new clutch as fast as possible for the male whose brood pouch was empty. We regarded the interval from releasing hydrated eggs to spawning as G_f . In all cases, the female produced a clutch of normal size.

To detect the influence of water temperature on PRR, we used the mean of daily water temperatures during time out. Body size was not significantly different between males and females used for the estimation of PRR (mean ± s.d.: male: 126.9 ± 10.3 mm, $n = 30$; female: 127.0 ± 12.0 mm, $n = 18$; unpaired t -test: $t = 0.03$, $p = 0.97$). For the analysis, we used each male and female only once to avoid pseudoreplication.

(c) Calculation of OSR

To estimate the monthly OSR, we adopted an approach begun by Clutton-Brock & Parker (1992) and further developed by Parker & Simmons (1996). The OSR is equivalent to the population mean ratio of the time spent searching and waiting for mating (i.e. time in) in females (S_f) and males (S_m ; Clutton-Brock & Parker 1992). If $S_f > S_m$, females are expected to have more time available for mating (i.e. the OSR is biased towards females) and therefore expected to be predominant competitors for mates, and vice versa (Parker & Simmons 1996). We followed the Parker & Simmons's (1996) model to estimate the monthly OSR (see also Okuda 1999):

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

where F is the monthly adult sex ratio (female/male) and T the time taken for males to complete an entire reproductive

Table 1. The sex ratio of adult *C. haematopterus* in the quadrat. (χ^2 -test for deviation from equality was used.)

month	sex ratio (female/male)	χ^2	<i>p</i>
May	1.33 (40 : 30)	1.42	> 0.05
June	1.76 (44 : 25)	5.23	< 0.05
July	2.26 (43 : 19)	9.29	< 0.005
August	1.84 (35 : 19)	4.74	< 0.05

cycle. In the present study, we used the monthly mean of male interspawning interval as *T*. In *C. haematopterus*, a given reproductive event involves only one male and female, because a female gives an entire clutch to one male and a male cares for only one brood at a time. Therefore, the collateral investment (*sensu* Parker & Simmons 1996) need not be considered (see also Ahnesjö *et al.* 2001).

3. RESULTS

The monthly adult sex ratio was significantly biased towards females throughout the study period, except in May (table 1). All adult males brooded the eggs during the study period, whereas there were many nomadic unpaired females searching for mates. The disappearance rate of fish (the proportion of marked fish which had disappeared from the quadrat during the study period to all marked fish) did not differ between the sexes (48.9% for males and 57.7% for females, χ^2 -test: $\chi^2_1 = 0.84$, $p = 0.36$).

Time out (*G*) of both sexes fluctuated during the study period, ranging from 9 to 22 days in males and from 10 to 19 days in females, resulting in a broad range of PRR (male: 0.045–0.111 clutches per day, $n = 30$; female: 0.053–0.100 clutches per day, $n = 18$). Simple linear regression analyses revealed that water temperature during time out affected PRR ($R^2 = 0.92$, $n = 48$, $p < 0.0001$), whereas the body size of fish had no effect on PRR ($R^2 = 0.02$, $n = 48$, $p = 0.31$). The slopes of the regressions of PRR on temperature during time out did not differ among the sexes (male: $y = 0.008x - 0.123$; female: $y = 0.008x - 0.109$; ANCOVA: sex $\times$ temperature, $F_{1,44} = 0.67$, $p = 0.42$; figure 1). This interaction term was then removed from the ANCOVA, revealing a significant effect of temperature, but not of sex (temperature: $F_{1,45} = 534.60$, $p < 0.0001$; sex: $F_{1,45} = 2.01$, $p = 0.16$).

We calculated the monthly S_f/S_m using the monthly adult sex ratio (table 1) and the monthly mean *G* of each sex (male: May 18.38, $n = 8$; June 13.25, $n = 8$; July 11.00, $n = 9$; August 9.80, $n = 5$; female: May 18.50, $n = 4$; June 13.13, $n = 8$; July 11.00, $n = 3$; August 10.33, $n = 3$) and *T* (May 18.88, $n = 8$; June 13.50, $n = 8$; July 11.22, $n = 9$; August 10.00, $n = 5$). The S_f/S_m was consistently female-biased (figure 2).

4. DISCUSSION

This study showed that the OSR of *C. haematopterus* is biased towards females throughout the breeding season. The OSR is a principal factor influencing the direction and intensity of competition for mates and hence of sexual selection (Emlen & Oring 1977; Clutton-Brock & Parker 1992; Reynolds 1996; Kvarnemo & Ahnesjö 2002). Our results were consistent with the previous report that female *C. haematopterus* are more active in searching for

Figure 1. PRR of female and male *C. haematopterus* in relation to water temperature during 'time out'. Filled circles, females; open triangles, males. Lines (solid, female; dashed, male) denote linear regressions fitted to data.

Figure 2. Population mean ratio of 'time in' for females to males (S_f/S_m) in *C. haematopterus*. Values were logarithmically transformed. A positive number indicates a female bias in the ratio.

mates and in courtship displays than males (Matsumoto & Yanagisawa 2001).

Sex-role reversal associated with the female-biased OSR shown in *C. haematopterus* has also been reported in two other pipefish, *N. ophidion* and *S. typhle* (Berglund & Rosenqvist 1993, 2003; Vincent *et al.* 1994). In *C. haematopterus*, the female-biased OSR was not due to the sexual difference in PRR but due to a bias in the adult sex ratio (Berglund *et al.* 1989; Ahnesjö 1995; Vincent *et al.* 1995). Females of *N. ophidion* and *S. typhle*, which mature their eggs continuously in their ovaries, can produce more eggs than those received by males during a certain time period (Berglund *et al.* 1989; Vincent *et al.* 1994). Accordingly, females of these species can obtain higher reproductive success by searching for a new mate rather than by waiting for the completion of brooding by the current mate and remating with him (Berglund *et al.* 1988, 1989; Rosenqvist 1990). Such a situation will naturally lead to polygamous mating.

Although both these polygamous pipefish and *C. haematopterus* exhibit reversed sex roles, female members participating in mating competition differ between them. In the polygamous pipefish, all adult females are potential competitors for acquiring multiple mates. In *C. haematopterus*, in contrast, paired females

do not participate in mating competition; only unpaired females are active in acquiring a mate, although they succeed in securing a paired status only after the disappearance of a paired female (Matsumoto & Yanagisawa 2001). Indeed, in our population, only unpaired females participated in courtship and aggressive behaviours (details in the electronic supplementary material, table S1). In addition, unpaired females had larger home ranges and moved longer distances per unit time than paired males and females, whereas no substantial differences were detected in these activities between paired males and females (details in the electronic supplementary material, figure S1). These facts suggest that sex-role reversal in *C. haematopterus* is caused by mating competition among nomadic unpaired females.

Sex-role reversal associated with strict monogamy was found first in *C. haematopterus* (Matsumoto & Yanagisawa 2001) and recently reported in two seahorses, *Hippocampus abdominalis* and *Hippocampus subelongatus* (Kvarnemo *et al.* 2007; Wilson & Martin-Smith 2007). Why do these syngnathid fish reproduce monogamously despite the reversed sex role? In *C. haematopterus* which shows no sexual differences in PRR, females will gain little reproductive benefit by changing mates. Moreover, the female-biased adult sex ratio will give females few opportunities to find a new mate. Therefore, females are expected to have a better reproductive success by securing one mate and mating repeatedly with him (Matsumoto & Yanagisawa 2001). Male *C. haematopterus* also seem to gain little reproductive benefit by changing mates. In a field study where female *C. haematopterus* were removed from mating pairs, reproductive efficiency of their partners decreased due to the time required for a new mate to prepare mature eggs (Sogabe *et al.* 2007). A decrease in male reproductive efficiency following the mate switching is also reported in *H. subelongatus* (Kvarnemo *et al.* 2000).

A puzzling problem pertaining to *C. haematopterus* is that the adult sex ratio is always female-biased (Matsumoto & Yanagisawa 2001; Sogabe *et al.* 2007). In general, such a biased ratio can arise from a differential mortality between the sexes and/or a bias in the primary sex ratio (Clutton-Brock & Parker 1992). It is unlikely that the female-biased adult sex ratio in our population is caused by a higher mortality rate of adult males because the disappearance rate of adults did not differ between the sexes (see also Matsumoto & Yanagisawa 2001). It will be worthwhile to examine whether the sex ratio of *C. haematopterus* is female-biased at birth and, if not, at which developmental stages the sex ratio becomes biased. It is of interest that the adult sex ratio of other sex-role reversed monogamous syngnathids, *H. abdominalis* and *H. subelongatus*, is also biased towards females (Kvarnemo *et al.* 2007; Wilson & Martin-Smith 2007).

The sexual difference in PRR is an important factor determining the strength of sexual selection and hence the mating patterns (Kirby *et al.* 2006; Mobley & Jones 2007; Wilson & Martin-Smith 2007). The dependence of male PRR on ambient temperature has been reported in many ectotherms with paternal care (Kraus 1989; Kvarnemo 1994; Ahnesjö 1995). In syngnathids in which males care for embryos in their brood pouch, the developmental speed of embryos is under the control of temperature, and therefore the male PRR depends heavily on it. In contrast, the speed of egg production and maturation by females usually depends more on food intake than on ambient

temperature (Wootton 1979; Kvarnemo 1997). Social factors such as the presence of dominant neighbouring females may also affect the speed of egg production and maturation (Ahnesjö 1995).

In *C. haematopterus*, the PRR increased with temperature but exhibited no sexual difference at any temperature (figure 1). The unbiased PRR between the sexes, which provides a low potential for multiple mating in either sex, can be a major causal factor for the evolution of monogamy. However, one may argue that the sexually similar PRR observed in *C. haematopterus* is not a cause of monogamy but a secondary adaptation to monogamy. Although it is premature to derive a conclusion, we infer that the sexual difference in PRR provides a basic framework for the evolution of polygamy or monogamy. Once monogamy has evolved, however, females may fine-tune their speed of egg production and maturation to the developmental speed of embryos cared by their mates to promote reproductive efficiencies of the monogamous pair. If this is true, the monogamous mating system of *C. haematopterus* may be more resistant to environmental fluctuations than we expect.

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