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SEX-ROLE REVERSAL IN THE BLACK-CHINNED TILAPIA, SAROTHERODON MELANOTHERON (RÜPPEL) (CICHLIDAE)

by

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> (With 6 Figures) (Acc. 13-VI-1995)

Summary

In the animal kingdom most species follow standard sex roles: males compete more intensely for mates and females exert greater mate choice. Recent theory suggests that the direction of sexual selection is the outcome of sexual differences in potential reproductive rates (PRRs): the sex with the higher PRR will compete for mates and the sex with the lower PRR will be most selective. This study tests the theory experimentally by examining competition for mates and mate choice in the black-chinned tilapia, *Sarotherodon melanotheron*, a paternal mouth brooding cichlid. In this species, the PRR of males is lower than that of females. In laboratory competition trials, females were more aggressive: they bit, chased and initiated mouth fights more often than males. Dominant females were also much better at monopolising potential mates compared to dominant males. A second experiment confirmed that males were choosy for size, preferring large partners over small ones, while females did not discriminate for size. Therefore, the prediction of sex role reversal (competitive females and discriminating males) is confirmed.

Introduction

Differences between the sexes in competition and choosiness are believed to be a consequence of the operational sex ratio (OSR), the ratio of males that are ready to mate to females that are ready to mate (EMLEN & ORING,

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1977). Commonly, male-biased OSRs are found because males have higher reproductive rates than females and consequently males compete for access to a limited number of ready females (CLUTTON-BROCK & VINCENT, 1991). Female care tends to exaggerate this sexual difference in reproductive rates, while male care can reverse it. However, paternal care does not in itself result in sex-role reversal; role reversal will occur only when females have higher rates of reproduction, *i.e.* when females produce more eggs than males can care for.

The black-chinned tilapia, Sarotherodon melanotheron, a small West African mouth-brooding fish, is the only known cichlid species in which males exclusively care for offspring and have lower PRRs than females (ARON-SON, 1949). Males take longer to brood eggs than females take to lay another clutch (KEENLEYSIDE, 1991). Three studies have shown that females are more active in courtship and nest building (ARONSON, 1948; HEINRICH, 1967; ELLIS, 1971). Thus several authors have suggested that the black-chinned tilapia may be sex-role reversed (WILLIAMS, 1975; RIDLEY, 1978; KEENLEYSIDE, 1991).

Evidence for sex-role reversal is rare in fishes; there are only three fish species in which it is known to occur: Nerophis ophidion, Syngnathus typhle (BERGLUND et al., 1986a, 1989) and Apogon notatus (KUWAMURA, 1985). All three role reversed fish are brooders; males brood eggs and young in or on their body. Males of the two syngnathid species carry, osmoregulate and nourish the developing young by gluing fertilised eggs on their ventral surfaces. Male A. notatus mouth brood their eggs. Males that guard eggs in open nests can care for several clutches at once while brooding males have a physical limitation of space in the brooding cavities. Because male egg bearers' reproductive rates are limited by the number of eggs they can fit into the brooding cavity and the time it takes the eggs to develop they might be expected to be choosy and to prefer high quality females. Sometimes the reproductive rates are so restricted in these male brooding species that they are lower than female rates of reproduction. So male brooders are the most likely candidates for role reversal (VINCENT, 1992).

To quantify selectivity in the present study, mate size was singled out as an important preference trait as it has important fitness consequences for both sexes. Male fish have been shown to prefer large females (SARGENT *et al.*, 1986) and this may be because 1) large females are more fecund; 2) large females are better parents with more resources with which to provision and protect offspring or 3) large females may have better genes. Females too, prefer large males in several fish species (DOWNHOWER & BROWN, 1980; BISAZZA & MARCONATO, 1988; COTE & HUNTE, 1989) probably because large size confers either superior protective capabilities (direct benefits) and/or genetic qualities (indirect benefits).

The study described in this paper aimed to test the prediction of sex role reversal *i.e.* that: 1) female black- chinned tilapia are most competitive for mates and 2) males are most choosy about their prospective mating partners.

Materials and methods

General methods.

The fish used in the following experiments were first and second generation laboratory stock from the *Tilapia* Reference Collection at the Institute of Aquaculture, University of Stirling. The fish in the competition experiments were four years old and the fish in the mate choice experiments were three years old. The fish dealer who obtained the parents did not know their geographical source. The two sexes were kept in different aquaria for two weeks until experimentation began.

Competition experiment (Experiments 1-4).

Sixty-four male and 64 female black-chinned tilapia were randomly chosen from the stock tank and placed in two separate-sex glass habituation tanks.

These experiments were conducted in two aquaria, each measuring 122 (length) \times 44 (width) \times 44 cm (height) and equipped with one water heater, an Eheim water filter and an air stone. The tanks were lined with a 3 cm deep layer of 5 mm granite gravel. Throughout the experiment a $27\pm2^{\circ}$ C water temperature regime was maintained, the pH varied from 7-7.5, and a 12.5:11.5 h light:dark regime maintained. The test aquarium was divided into three compartments: two long thin compartments and a small rectangular compartment at one end. The two long compartments were separated from each other by a removable opaque barrier and each contained a black hollow plastic tube of diameter 5 cm, which served as refugia. The small end compartment wars separated from the other two with both a removable opaque barrier and a fixed transparent barrier. The barriers formed a T shape inside each aquaria (see Fig. 1).

To test for sexual differences in competition abilities, two fish of the same sex were matched for weight, total and standard length (Table 1) and then placed in the aquarium, one in each of the long compartments. A fish of the opposite sex (a potential mate) was placed in the end compartment. The fish were given four hours to habituate before all opaque barriers were removed, allowing the two males or two females to see the end fish and interact with each other but not with the end fish of the opposite sex. Ripe males and females were used for all tests; ripeness was assessed by external swellings of the genitalia.

In all tests, the time each fish of the pair spent by the end fish was recorded, the courtship display rate (rate of shakes, quivers and scrunches) towards the end fish, and the number of intrasexual aggressive interactions between the pair were recorded. Aggressive behaviours included chases, bites, mouth fights, and retreats. Each test was videotaped with a camcorder and the data were collected manually with a Psion Organiser.

A total of 16 female tests and 16 male tests were conducted. To test whether males or females were more aggressive in non-mating situations an additional 16 control tests for



Fig. 1. Schematic diagram of the competition tank set up. The trial would begin when the middle and the end opaque barriers were removed allowing the competitors access to one another and a view of the end fish.

each sex were conducted using similar sized male and female Oreochromis niloticus as end fish instead of the black-chinned tilapia, Sarotherodon melanotheron.

Mate choice experiment (Experiments 5-7).

As in the previous experiment the two sexes were kept in different aquaria for two weeks until the experiments began.

The mate choice experiments were conducted in an aquarium measuring 92 (length) \times 39 (width) \times 36 cm (height) and equipped with one water heater and an air stone. Water temperature was maintained at 27 ± 2°C and the light regime was 12:12 h light:dark for all three experiments. The test aquarium was divided into three compartments – two small end compartments and a larger middle compartment. Each end compartment was separated from the middle by a fixed transparent barrier and a removable opaque barrier. In addition, two 60%-width opaque barriers were placed in the middle compartment such that there was no direct line of sight between the end compartments (see Fig. 2).

Female mate size preference was investigated in Experiment 5 by placing one large male and one small male in opposite end compartments of the test aquarium. The males were prevented from entering the middle compartment by the fixed transparent barrier. The males were given 48 hours to habituate to the test aquarium. In each trial, a single blackchinned tilapia female was placed in the centre compartment of the test aquarium. After four hours of habituation, the full opaque barriers were removed. The 15 minute choice trial began once the test female had swum into each end compartment and viewed each

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	Males	SE	Females	SE	
Mean body weight (g)	54.0	1.6	48.3	1.9	
Mean difference in body weight (g) between competing fish	0.70	0.60	0.12	0.60	
Mean body length (cm)	15.2	0.16	14.6	0.20	
Mean difference in total body length (cm) between competing fish	0.10	0.07	0.05	0.07	

TABLE 1.	The	mean	difference	in	body	size	between	32	pairs	of	males	and
				f	femal	es						



Fig. 2. Schematic diagram of the mate choice tank set up. The middle chamber was divided by two partial barriers restricting the vision between the two end chambers but allowing the test fish to swim freely to either end of the middle chamber.

male once. In total 14 females were tested with the pair of males being replaced after seven females. The first pair of males differed in weight by 42.8 g and the second pair differed by 47.8 g. To control for end preferences the large male was in the right end compartment in the first seven tests and in the left end compartment in the second seven tests.

In each test, the time the female spent with each male and the display rates of each fish was recorded. The tests were videotaped with a camcorder and the data were collected with the aid of a Psion Organiser.

Experiment 6 was identical in design to Experiment 5 but males were tested and females

used as end fish. Fourteen males were tested for mate size preference with two sets of female pairs varying in size by 32.8 and 40.8 g, respectively.

A seventh experiment was conducted to investigate whether the apparent mate preferences recorded in experiments 5 and 6 really did indicate mate choice. Five males and then five females were tested as in Experiments 5 and 6 but after the 15 minute focal watch, the transparent barriers were removed as well. When the barriers were removed two hollow plastic tubes were placed in the aquarium to serve as refugia. A second focal watch was conducted 24 hours later to establish whether the test fish had paired up with its preferred mate from the choice tests.

Results

Competition experiment.

Females were more aggressive than males. Females displayed aggressive behaviour (bites, chases and mouth fights) more often than males (Fig. 3, Mann-Whitney U-test, z = -2.62, p = 0.009). Females were more aggressive than males in the control tests as well (Mann-Whitney U-test, z = -2.18, p = 0.03). Aggression levels did not differ between the control trials and the main experiment (Mann-Whitney U-tests; females: z = -0.416, p = 0.68; males: z = -0.153, p = 0.88).

In Aronson's (1949) study females courted more than males. In the present study males and females performed courtship displays towards the end fish at a similar frequency (Mann-Whitney U-tests; experimental: z = -0.735, p = 0.46; control: z = -0.419, p = 0.68). In the controls, when the end fish was of a different species and therefore not a potential mate, courtship behaviour dropped significantly in frequency and intensity in both sexes [Table 2, Mann-Whitney U-tests: males (experimental *versus* control): z = -2.616, p = 0.03, females (experimental *versus* control): z = -2.66, p = 0.008].

Fish were closely matched for size in each test, but after removing the barriers only one fish of the pair became coloured (its dorsal and caudal fins turning red, the margins of all fins turning black and black spots appearing on the head area, especially on the chin), the other fish of the pair always remained paler. The more colourful of the pair, regardless of sex, was dominant and initiated the majority of the aggressive behaviour. Fish would colour up after the first aggressive interaction.

If dominants did not care at all about where subordinates placed themselves, we would expect to find subordinates in each half of the tank with equal probability. Both dominant males and females attempted to keep the subordinate away from the end fish. The sexes did not differ



Fig. 3. The average number of aggressive behaviours (chases, bites and mouth fights) per focal watch. Bars show standard errors.

significantly in keeping subordinates away from potential mates temporally in either the experimental tests or the control tests (Table 2, Mann-Whitney U-test; experimental: z = -1.376, p = 0.17; control: z = -0.603, p = 0.55). However, by categorising each test into whether subordinate spent more or less than half the time in the half of the aquarium with the end fish a clear pattern emerged; in the experimental tests females were much better than males at spatially keeping subordinates away from the end fish but they did bother to do this in the control situation (Fig. 4 and Table 3).

Mate choice experiment.

Females did not select their mating partners on the basis of size. Preference was measured by the amount of time spent near each male and the number of courtship displays directed at each male. In Experiment 5 females spent equal amounts of time with small *versus* large males (Fig. 5a, Wilcoxon signed ranks, z = -1.3, p = 0.20) and performed a similar rate of courtship display to large and small males (Fig. 5b, Wilcoxon signed ranks test, z = -0.36, p = 0.72).

In contrast to females, males showed a strong preference for large females by spending more time near larger females (Fig. 6a, Wilcoxon signed ranks, z = -2.5, p = 0.01). Males tended to perform courtship displays at a higher rate to large females (Fig. 6b, Wilcoxon signed ranks test, z = -1.804, p = 0.07).

	$\bar{x} \pm SE$ number of court- ship displays/15 minutes		$\bar{x} \pm SE$ Number of minutes the subordinate spent near end fish/15 minutes	
Experimental males	10 ± 2.1	16	5.9 ± 1.1	14
Experimental females	14 ± 3.0	16	3.9 ± 0.8	14
Control males	4 ± 0.8	16	6.4 ± 1.3	16
Control females	4 ± 0.7	16	7.0 ± 3.1	16

TABLE 2. The mean number of courtship displays (± standard errors) andthe amount of time subordinate fish spent near (less than one body lengthapart) the end fish per focal watch

 TABLE 3. The number of tests where the subordinate spent more than half
 of the test near the end fish

	Observed Expected		G statistic	p value	
Males experimental N = 14	6	7	0.07	p < 0.80	
Females experimental $N = 14$	1	7	9.87	p < 0.01	
Males control $N = 16$	5	8	1.59	p < 0.20	
Females control $N = 16$	6	8	0.57	p < 0.40	



Fig. 4. The number of cases where the dominant did not monopolize the area around the end fish's compartment in experimental *versus* control tests. Black bars are males and white bars are females.



Fig. 5. a: The average amount of time females spent with large versus small males. Bars show standard errors. b: The mean rate of display females performed to large versus small males. Bars show standard errors.

The rates of display of end fish did not differ in either experiment (Expt 5: $\bar{x} \pm SE$ large male = 3.6 ± 0.6 , small male = 2.4 ± 0.6 , Mann-Whitney U-tests, U = 51, p = 0.23, Expt 6. large female = 3.0 ± 0.5 , small female = 3.0 ± 0.6 , U = 68, p = 0.82). Consequently, differences in display rates could not have caused the preferences observed.

Nine of the ten tests in Experiment 7, resulted in pair-bonding (*i.e.* courting and swimming in close proximity: less than one fish length apart) with the partner preferred in the choice test 24 hours earlier (G = 5.41, df = 1, p = 0.02). The test fish courted the preferred fish and never courted



Fig. 6. a: The mean time males spent with large versus small females. Bars show standard errors. b: The mean rate of display (displays/minute) males performed to large versus small females. Bars show standard errors.

the other fish. One of the ten test fish, a female, did not pair at all. Another test fish spawned with its preferred partner in the 24 hour interval between focal watches. In nine out of the ten tests the preferred partner was the larger of the two fish.

Discussion

Females were more aggressive than males both in the presence and absence of potential mates. However, females were clearly competing for mates as they monopolised the area near the end fish only when potential mates were available. In the mate choice trials, preference was defined in two ways: (1) time spent near and (2) display rates to potential mates. Females did not show a preference for large partners. In contrast, males showed a preference by spending more time near large females but their rate of display did not vary significantly between the females they visited. Although females have been reported to be the most active sex in courtship (ARONSON, 1949; HEINRICH, 1967; ELLIS, 1971) in the present study there were neither qualitative nor quantitative sexual differences in courtship behaviour.

Female black-chinned tilapia can spawn several times per year and the interval between successive spawns is on average 15 days (range eight days to a year). Males incubate the eggs and young for a mean of 14 days (range 7-20 days) but need additional 'time out' to recover condition lost during mouth brooding before they will care again (ARONSON, 1949, 1951). Despite the relatively small difference between the sexes in PRR the results of this study support the idea that the black-chinned tilapia is a sex-role reversed species. The present experiments suggest that males are usually more choosy than females but it remains likely that both sexes benefit from some level of competition and mate choice in the wild.

There are several inherent limitations in the design and analysis of the experiment that may have influenced the results. First, as only the number of displays was considered, we cannot unequivocally rule out the possibility that females may have been showing a preference for large males by their intensity and duration of display. Intensity and duration of displays were ignored because they appeared to vary little and were more difficult to quantify accurately.

Second, it remains possible that both sexes prefer partners who display frequently as this may be a measure of mate quality. Since, there was no difference in display rates between the end fish, this possibility could not be assessed. For males, size appears to be a more important criterion than display rate since males preferred large females who were displaying at a similar rate to small females. Nevertheless, it is possible that a single display from a large individual is a stronger signal than the same display from a small individual. How display rates affect mate choice per se was not investigated.

Third, use of several stimulus end fish in the mate choice experiment, to control for preferences for particular individuals would have strengthened the result that males preferred large females. It is possible that males were not attracted by size but by some other unknown trait. In addition, females in this study did not show a choice for large partners but it remains possible that females based mate choice on some other trait correlated with parental quality but not with body size (*e.g.* display rate, operculum colour, general brightness, or body condition). This would be expected if male size does not correlate well with brood capacity, as in some other brooding fish species (BERGLUND *et al.*, 1986b; RANA, 1986).

In general, animal species can be divided into two groups, those with large and those with small sexual differences in reproductive rates. When the magnitude of sexual differences in PRR is great, then the OSR will always be biased in the same direction and the sex with the lower PRR will always be choosy and the other sex will always be competitive. However, when the differences are small, like in the black-chinned tilapia, the OSR may be variable in time and location and sexual selection patterns will fluctuate accordingly. Such flexibility in sexual selection patterns can be caused by changes in temperature and/or food availability, as these affect PRRs and hence the OSR. In nutrient-poor habitats, females will probably take longer to produce eggs and parents may take longer to recover from parental investment (GWYNNE, 1990, 1991; SIM-MONS, 1992). Temperature also affects the reproductive rates by influencing oogensis and/or development (incubation duration) (KVARNEMO, 1994, Sarah BUSH, personal communication).

When sexual differences in PRR are small, the extent of variation in mate quality will have a substantial impact on patterns of sexual selection. Indeed the sex with the lower reproductive rate may not always be choosy (OWENS *et al.*, 1994), if the variation in mate quality is low then it may not pay to be choosy.

In fish, females vary substantially in quality as fecundity increases dramatically with body size. However, in contrast to the abundance of examples of female choice in fish, the evidence for male mate choice is scarce. Only seven non-role reversed species have been shown to exhibit male mate choice for size (*Cottus bairdi*, DOWNHOWER & BROWN, 1981, *Cyprinodon macularius californiensis*, Loiselle, 1982; *Gasterosteus aculeatus*, ROWLAND, 1982; *Micrometrus minimus*, WARNER & HARLAN, 1982; *Oncorhynchus kitsutch*, SARGENT et al., 1986, *Thalassoma bifasciatum*, VAN DEN BERGHE & WARNER, 1989; *Ophioblennius atlanticus*, COTE & HUNTE, 1989). SEX-ROLE REVERSAL

The rarity of male mate choice is probably a result of the high costs of being choosy when the number of reproductively capable females is limited. In role-reversed species, males limit the reproductive rate of females. To date, in all cases of role reversal in fish, male mate choice has been observed. For example, male N. ophidion prefer partners with more blue body coloration and male S. typhle prefer large females (BERGLUND et al., 1986b).

The absence of female preference for large males and the presence of highly competitive females support the hypothesis that the black-chinned tilapia is a sex role reversed species. However, the possibility remains that as in other species where males provide all the parental care (BERGLUND et al., 1986b), either sex may compete for mates or be most choosy depending on time, place and environmental conditions. Further studies, especially field studies, are needed to address this intriguing possibility.

References

- ARONSON, L.R. (1948). Problems in the behavior and physiology of a species of African mouthbreeding fish. - Trans. New York Acad. Sci. 2, p. 33-42.
- ----- (1949). An analysis of reproductive behavior in the mouthbreeding cichlid fish, *Tilapia* macrocephala (Bleeker). — Zoologica 34, p. 133-158.
- -- (1951). Factors influencing the spawning frequency in the female cichlid fish *Tilapia* macrocephala. — Amer. Mus. Novitates 1484, p. 1-26.
- VAN DEN BERGHE, E.P. & WARNER, R.R. (1989). The effects of mating system on male mate choice in a coral reef fish. - Behav. Ecol. & Sociobiol. 24, p. 409-415.
- BERGLUND, A., ROSENQVIST, G. & SVENSSON, I. (1986a). Reversed sex roles and parental energy investment in zygotes of two pipefish (Syngnathidae) species. - Marine Ecol. Progr. Series 29, p. 209-215.
- ----, ---- & ---- (1986b). Mate choice, fecundity and sexual dimorphism in two pipefish species (Syngnathidae). -Behav. Ecol. Sociobiol. 19, p. 301-307.
- -, --- & --- (1989). Reproductive success of females limited by males in two pipefish species. - Am. Nat. 133, p. 506-516.
- BISAZZA, A. & MARCONATO, A. (1988). Female mate choice, male-male competition and parental care in the river bullhead, Cottus gobio L. (Pisces, Cottidae). - Anim. Behav. 36, p. 1352-1360.
- CLUTTON-BROCK, T.H. & VINCENT, A.J.C. (1991). Sexual selection and the potential reproductive rates of males and females. - Nature 351, p. 58-59.
- COTE, I.M. & HUNTE, W. (1989). Male and female mate choice in the redlip blenny: why bigger is better. - Anim. Behav. 38, p. 78-88.
- DOWNHOWER, J.F. & BROWN, L. (1980). Mate preferences of female mottled sculpins, Cottus
- *bairdi.* Anim. Behav. 28, p. 728-734. & (1981). The timing of reproduction and its behavioral consequences for mottled sculpins, Cottus bairdi. - In: Natural selection and social behaviour: Recent research and new theory (R.D. ALEXANDER & D.W. TINKLE, eds). Chiron Press, New York, p. 78-95.
- ELLIS, K.R. (1971). An ethological study of tilapia T. macrocephala in small groups. Diss. Abstracts 31, 5018B.

- EMLEN, S.T. & ORING, L.W. (1977). Ecology, sexual selection, and evolution of mating systems. — Science 197, p. 215-223.
- GWYNNE, D.T. (1990). Testing parental investment and the control of sexual selection in katydids: The operational sex ratio. Am. Nat. 136 p. 474-484.
- HEINRICH, W. (1967). Untersuchungen zum sexualverhalten in der gattung Tilapia (Cichlidae, Telostei) und bei artbastarden. — Z. Tierpsychol. 24, p. 684-754.
- KEENLEYSIDE, M.H.A. (1991). Cichlid fishes: Behaviour, ecology and evolution. Fish and Fisheries Series 2, Chapman and Hall, London.
- KUWAMURA, T. (1985). Social and reproductive behavior of three mouthbrooding cardinal fishes, Apogon doederleini, A. niger and A. notatus. — Environm. Biol. Fishes 13, p. 17-24.
- KVARNEMO, C. (1994). Temperature differentially affects male and female reproductive rates in the sand goby: consequences for operational sex ratio. — Proc. Royal Soc. London (B) 256, p. 151-156.
- LOISELLE, P.V. (1982). Male spawning-partner preferences in an arena breeding teleost, *Cyprinodon macularius californiensis* Girard (Atherinomorpha: Cyprinodontidae) — Am. Nat. 120, p. 721-732.
- OWENS, I.P.F., BURKE, T. & THOMPSON, D.B.A. (1994). Extraordinary sex roles in the Eurasian dotterel: Female mating arenas, female-female competition, and female mate choice. — Am. Nat. 144, p. 76-100.
- RANA, K. (1986). Parental influences on egg quality, fry production and fry performance in Oreochromis niloticus (Linnaeus) and O. mossambicus (Peters). — PhD thesis, Institute of Aquaculture, University of Stirling, Scotland.
- RIDLEY, M. (1978). Paternal care. Anim. Behav. 26, p. 904-932.
- RowLAND, W.J. (1982). Mate choice by male sticklebacks Gasterosteus aculeatus. -Anim. Behav. 30, p. 1093-1098.
- SARGENT, R.C., GROSS, M.R. & VAN DEN BERGHE, E.P. (1986). Male mate choice in fishes. — Anim. Behav. 34, p. 545-550.
- SIMMONS, L.W. (1992). Quantification of role reversal in relative parental investment in a bush cricket. Nature 358, p. 61-63.
- VINCENT, A.C.J. (1992). Prospects for sex role reversal in teleost fishes. Neth. J. Zool. 42, p. 392-399.
- WARNER, R.R. & HARLAN, R.K. (1982). Sperm competition and sperm storage as determinants of sexual dimorphism in the dwarf surfperch, *Micrometrus minimus*. — Evolution 36, p. 44-55.
- WILLIAMS, G.C. (1975). Sex and evolution. Vol. 8. Monographs in Population Biology (R.M. MAY, ed.). Princeton University Press, Princeton, N.J.