



Sexual dichromatism in convict cichlids: the ethological significance of female ventral coloration

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(Received 2 October 1997; initial acceptance 24 December 1997;
final acceptance 2 April 1998; MS. number: A8032)

ABSTRACT

Female convict cichlids, *Cichlasoma nigrofasciatum*, typically develop orange ventral coloration which males do not. We investigated the behavioural significance of this sexual dichromatism using both live and dummy stimulus fish. In our experiments, males were insensitive to variation in ventral coloration. Females, however, appeared to use this colour pattern as a visual cue. Females directed significantly more behaviour, including aggressive behaviour, towards more brightly coloured stimulus fish, as well as towards dummies with orange ventral coloration compared with those without. Bright females displayed the least aggression towards an intruding female of intermediate coloration. Thus, sexual dichromatism in the convict cichlid is shown to affect intrasexual aggression among females.

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Many teleost fish display a diversity of dermal chromatophore types under complex neuroendocrine control. This system permits the expression of multiple species-typical colour patterns, including sexually dimorphic coloration (Fujii 1993). The evolution of sex differences in coloration (sexual dichromatism) was explained by Darwin (1889) as the result of sexual selection. Darwin predicted that both competition among members of a sex, and mate choice by members of the opposite sex, can drive the evolution of extravagant coloration among members of the competitive or chosen sex.

As Trivers (1972) demonstrated, anisogamy and differential parental investment predispose the male more often to be the extravagantly coloured sex. Recent empirical evidence strongly supports the role of sexual selection in the evolution and maintenance of conspicuous male coloration among sexually dichromatic fish. Male colour patterns can both attract females, as in the guppy *Poecilia reticulata* (Brooks & Caithness 1995) and intimidate rivals, as in the firemouth cichlid *Cichlasoma meeki* (Evans & Norris 1996).

Less commonly, females may exhibit conspicuous coloration not found in males, and such 'reversed' sexual dimorphism is often associated with female territoriality and female–female aggression (Krebs & Davies 1993). For example, McLennan (1994) found that female brook sticklebacks, *Culaea inconstans*, display dynamic nuptial colour patterns, and that the expression of these patterns

is correlated with aggression directed towards conspecifics, as well as with sexual receptivity towards males.

The convict cichlid, *Cichlasoma nigrofasciatum*, is a monogamous, substrate-spawning Neotropical cichlid that shows several forms of sexual dimorphism, including differences in body size (McKaye 1986), fin morphology (Paysan 1975), behaviour (Mackereth & Keenleyside 1993) and colour pattern (Noonan 1983). Both sexes aggressively defend breeding territories in the laboratory (Mackereth & Keenleyside 1993) and field (McKaye 1977). Female convict cichlids typically develop a conspicuous orange ventral coloration not observed in males. In the present study, we tested the behavioural significance of this colour pattern to explore the role of sexual selection in the evolution of sexual dichromatism in convict cichlids. By presenting live and dummy conspecifics to both male and female *C. nigrofasciatum*, we identify an intraspecific colour pattern signal in the convict cichlid and provide evidence of its role as an intrasexual signal.

METHODS

Subjects

We obtained mixed-sex stocks of *C. nigrofasciatum* from a local distributor and maintained them in single-sex groups of 10–30 individuals in large (250 litre), filtered holding aquaria prior to experimentation. We randomly selected subjects from these stocks and placed them individually into 80-litre test aquaria. Each subject's aquarium (61.5 × 32 × 42.5 cm) included 2–3 cm of gravel

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substrate, a corner box filter and a clay flowerpot to serve as a shelter. All fish were maintained at 27°C on a 14:10 h light:dark cycle and fed commercial cichlid pellets (Hikari Cichlid Gold, Kamihata Fish Ind. Lmt., Japan) once daily. Test aquaria were positioned to provide each subject with visual access to at least one other same-sex subject during the period of acclimation to the laboratory. Under these conditions, the fish rapidly entered reproductive condition, as evidenced by their excavation of spawning sites in the substratum. Subjects were allowed visual contact with fish in adjacent aquaria until 48 h before experimentation began. At that time, opaque screens were installed between aquaria to isolate the subjects visually.

Live-female Presentation Experiments

We visually isolated the subjects 2 days prior to testing on three sides of their aquaria, and positioned a video camera in front of the aquarium. The next day, we confined two 'stimulus females' in 1200-ml glass cylinders (6 cm diameter × 44 cm height) and placed them simultaneously within the subject's aquarium. The stimulus females were chosen from the holding aquaria, and matched for size and activity level as much as possible. The only apparent difference between stimulus females was the intensity of their orange ventral coloration. One female possessed a bright coloration ('bright female') and the other possessed a dull or nearly absent coloration ('dull female'). We presented stimulus females side-by-side in the subject's aquarium, 3–4 cm from the front of the tank and 15 cm apart and determined the relative position of the cylinders (i.e. bright female left or right) randomly. We reversed the cylinders after 5 min to control for possible side bias, and continued the presentation for an additional 5 min, yielding a total observation period of 10 min.

We videotaped presentations and scored them later by recording the frequency of occurrence of the following activities (after Baerends & Baerends-van Roon 1950): (1) approach: subject swims within one body length of a cylinder; (2) lateral display: subject orients laterally to a treatment fish and erects unpaired fins; (3) frontal display: subject orients head first and flares opercula while erecting fins; (4) bites: subject makes contact with cylinder with mouth open. We tested a total of 13 female and 10 male subjects. We analysed the data with a two-tailed Wilcoxon signed-ranks test to compare subject responses towards dull versus bright stimulus fish.

Dummy-presentation Experiments

We constructed two solid epoxy dummies of 40 mm total length using the method of Rowland (1979). We made unpaired fins by photocopying fin rays onto acetate sheets. We then cut the fins from the acetate and affixed them with epoxy resin to the dummy bodies. We painted 'orange' and 'plain' colour patterns onto the dummies using enamel paints, and these patterns mimicked as closely as possible the actual colour patterns observed in *C. nigrofasciatum*. We applied background body colour

with spray paint (Krylon pearl grey No. 1617), and added eight vertical bars with black paint (Krylon semiflat black No. 1613). We also added an orange (Krylon safety orange No. 2410) ventral patch to one dummy. The testing procedure and data analysis were identical to those for live female presentations (above) except that (1) dummies were suspended in the tank 4 cm above the substrate instead of being placed in cylinders, and (2) we conducted presentations for 15 min, then reversed dummy positions and continued the presentation for an additional 15 min. We tested a total of 18 female and 16 male subjects.

Three-way Choice Experiment

We constructed a three-way choice testing apparatus using three 38-litre 'stimulus aquaria' juxtaposed with a 110-litre 'test aquarium' (Fig. 1). Each aquarium was aerated and visually isolated by opaque screens. We placed a single male subject in the test aquarium, and a single female in each of the stimulus aquaria. We selected 'bright', 'medium' or 'dull' ventrum females from the holding aquaria, matched them for size, and randomly assigned them a stimulus aquarium.

After 24 h of acclimation, we removed the partition between the test and stimulus aquaria, allowing each male visual access to three females, but each female visual access only to the male. A video camera with a time-lapse feature recorded activity in the apparatus for 1 s each minute from the position shown in Fig. 1a.

We replaced the partition after 6 h and shuffled the females so that each was randomly assigned a different stimulus aquarium. The next day, we again removed the partition and repeated the observation. No two males were presented with the same three stimulus females. We later scored the videotapes by recording male position with respect to the three stimulus aquaria once each minute for 6 h/day. We performed a repeated measures analysis of variance (ANOVA) on the within-subject rank-transformed data to test for female colour and position effects on male visiting behaviour.

Female Aggression Test

To examine the relationship between a female's colour and behaviour, we first asked four independent judges to rank the brightness of 11 female subjects on a scale from 0 (no orange) to 5 (brightest orange) after showing them a typical male (score=0) and an extremely bright female (score=5) selected from the holding aquaria. We tested agreement among the judges using Kendall's coefficient of concordance (Siegel 1956), and assigned each subject its average brightness score. We then placed a stimulus fish of intermediate brightness, confined in a glass cylinder, in each subject's aquarium, and videotaped the presentation for 15 min. Videotapes were scored later using the same criteria as in the paired presentations described above. We computed Spearman's coefficient of rank correlation to examine the relationship between subject colour (average of judge's scores) and subject

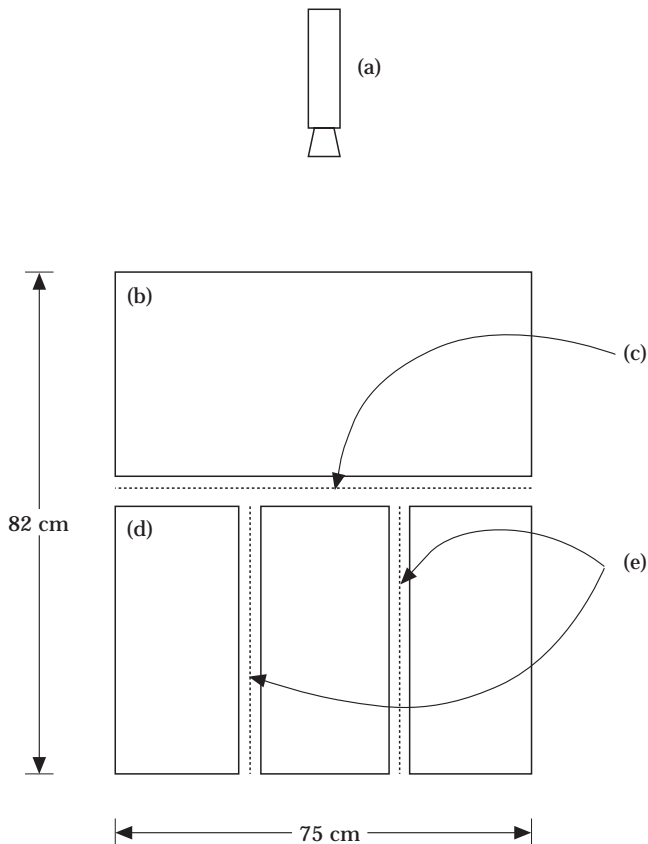


Figure 1. Three-way choice apparatus: (a) video camera, (b) test aquarium, (c) removable opaque screen, (d) stimulus aquarium and (e) permanent opaque screens.

behaviour (frequency of approach, lateral display, frontal display and bite).

RESULTS

Live-female Presentation Experiments

Twelve of 13 female subjects approached at least one stimulus female, and eight approached the bright female more frequently ($T_s=10.5$, $P<0.05$). Bright stimulus females elicited significantly more lateral displays ($T_s=4$, $P<0.01$), frontal displays ($T_s=2$, $P<0.01$), and bites ($T_s=0$, $P<0.01$) from subject females than did dull females (Fig. 2).

All male subjects ($N=10$) approached stimulus females during presentations. However, the frequency of approaches, lateral displays, frontal displays and bites elicited by bright and dull stimulus females did not differ significantly for male subjects (Fig. 3).

Dummy-presentation Experiments

Results for the dummy presentation experiments paralleled those for live female presentations. All females ($N=18$) approached at least one dummy during the observation period. Orange dummies elicited significantly more approaches ($T_s=4$, $P<0.01$) and lateral displays

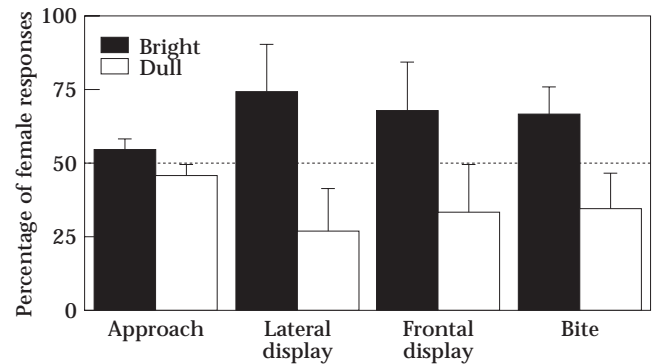


Figure 2. Mean \pm SD percentage of approach, lateral display, frontal display and bite towards bright and dull stimulus females by 13 female convict cichlid subjects.

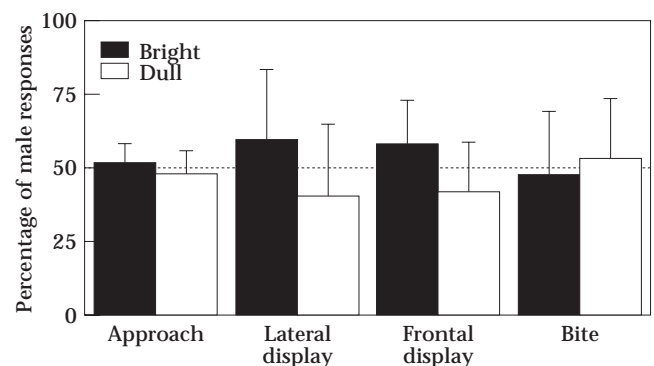


Figure 3. Mean \pm SD percentage of approach, lateral display, frontal display and bite towards bright and dull stimulus females by 10 male convict cichlid subjects.

($T_s=18$, $P<0.05$) than did dull dummies, but differences in frontal displays and bites were not significant. All males ($N=16$) approached dummies, but no differences in response towards the two dummies were detected.

Three-way Choice Experiment

Males in the three-way choice apparatus engaged almost continuously in 'mutual swimming' (Keenleyside et al. 1985) with one of the stimulus females. Females were usually observed near the aquarium wall separating them from the male's test aquarium, regardless of the male's position in the test aquarium. All males in this experiment ($N=10$) visited each of the females repeatedly during the 2-day trial (Table 1). Overall, female colour ($F_{2,8}=0.69$, $P=0.53$), female position ($F_{1,9}=0.03$, $P=0.87$), and the colour \times position interaction ($F_{2,8}=0.31$, $P=0.74$) did not significantly affect the frequency of male visits.

Female Aggression Test

Judges were found to be in agreement as to subject female colour intensity (Kendall's coefficient of concordance: $W=0.86$, $P<0.001$). Average colour score was found to be negatively correlated with frontal display and bite (Table 2).

Table 1. Frequency (%) of visits to dull, medium and bright stimulus females by 10 male convict cichlids

Male no.	Female colour			Total
	Dull	Medium	Bright	
1	142 (20)	318 (44)	260 (36)	720 (100)
2	290 (40)	265 (37)	165 (23)	720 (100)
3	209 (29)	331 (46)	180 (25)	720 (100)
4	181 (25)	292 (41)	247 (34)	720 (100)
5	379 (53)	193 (27)	148 (21)	720 (100)
6	267 (37)	274 (38)	179 (25)	720 (100)
7	281 (39)	229 (32)	210 (29)	720 (100)
8	233 (32)	252 (35)	235 (32)	720 (100)
9	368 (51)	187 (26)	165 (23)	720 (100)
10	138 (19)	139 (19)	443 (61)	720 (100)
Total	2488 (35)	2480 (34)	2232 (31)	7200 (100)

DISCUSSION

Sexual dichromatism in fish generally follows a pattern in which brilliantly coloured males compete for access to less conspicuously coloured females. 'Competition' in this context may involve direct, male-male combat over females or resources, such as breeding territories (Rowland 1989), or indirect contests of advertisement, which exploit female mating preferences (Endler & Houde 1995). Darwin explained how either form of competition could drive the evolution of bright or conspicuous colour in males, while noting its rarely fulfilled potential to similarly produce conspicuous coloration

among females (Darwin 1889, page 366). Where reversed sexual dichromatism occurs (i.e. extravagant female coloration), sexual selection theory predicts a concurrent reversal of ethological traits, namely, female-female competition for mates or resources, male mate choice, or both (Krebs & Davies 1993). The conspicuous orange ventral coloration of female convict cichlids suggests that sexual selection in the form of female-female competition or male mate choice may be operating in the convict cichlid mating system.

In our paired-presentation experiments, female convict cichlids discriminated between bright and dull female intruders, and between orange and nonorange coloured dummies. Among female subjects, colourful intruders elicited more behavioural interaction than dull intruders, and more intensely orange intruders were attacked more vigorously. Males under identical experimental conditions did not discriminate on the basis of ventral coloration. Bright intruders elicited no more or less activity than dull intruders among male subjects. These experiments support the role of female ventral coloration as a signal that functions in female-female aggression. The data do not, however, indicate that female coloration is a visual cue important in male mate choice.

Compared with paired-presentation experiments, our three-way choice experiment was designed to permit males to choose among more females of variable ventral colour intensity, over a longer period of time. Although males consorted almost continuously with females during 12 h of testing, they did not consistently choose to associate with the brightest available female (Table 1). Male mate choice in fish has been demonstrated using both live (Downhower & Brown 1981) and dummy (Rowland 1982) stimuli. Indeed, male convict cichlids have been shown to prefer gravid over nongravid females, and to prefer the larger of two gravid females (Nuttall & Keenleyside 1993). However, the present study found no evidence that male convict cichlids discriminate among females on the basis of this sexually dichromatic colour pattern.

Table 2. Colour scores, mean colour score and frequency of four activities for female subjects in the aggression test, and Spearman rank-order correlation coefficients and associated *P* values for each activity and mean colour score

Subject	Judge				Mean score	Activity			
	1	2	3	4		Approach	Lateral display	Frontal display	Bite
1	5	5	5	5	5	3	9	7	7
2	4	4	3	2	3.25	6	5	0	4
3	4	3	3	3	3.25	6	15	10	8
4	3	3	4	2	3	11	10	3	36
5	4	2	4	2	3	12	7	4	17
6	2	3	3	3	2.75	17	9	6	65
7	3	3	2	2	2.5	13	82	19	37
8	2	1	1	1	1.25	13	54	17	41
9	2	0	2	1	1.25	12	7	54	42
10	1	0	2	1	1	20	28	26	11
11	1	1	1	0	0.75	16	16	80	44
					$r_s =$ $P <$	-0.65 (NS)	-0.51 (NS)	-0.77 0.005	-0.69 0.02

Colour pattern is often a good predictor of motivational state in cichlid fish (references in Beeching 1995). Because bright females elicited greater response from conspecific females, we used the aggression test to determine whether bright female coloration predicts aggressive motivation. When presented a live female intruder of moderate ventral coloration intensity, brighter females displayed significantly less agonistic activities than did duller females. Thus, while female ventral coloration appears to predict female aggression, bright females were less, not more aggressive than dull ones in our aggression test.

In fish, the functions of colour-pattern signals often depend upon the behavioural context in which they are expressed (Bolyard & Rowland 1996), and the inverse relationship between aggression and colour intensity found in our study may not exist in every social context. Indeed, several aspects of convict cichlid behaviour appear to be sensitive to experimental conditions (Mackereth & Keenleyside 1993). For example, the use of stimuli that prohibit normal behavioural interactions between subject and intruder, such as dummies or glass cylinders, can affect the expression of aggressive behaviour (Barlow & Siri 1994). Nevertheless, the finding that brighter females are less aggressive is unexpected, in light of the aggression-eliciting property of ventral coloration.

Because nonbreeding territoriality and aggression have only been transiently observed in *C. nigrofasciatum* (McKaye 1977), female–female aggression is probably a result of competition for mates and breeding sites. Among convict cichlids, brighter females may be less stimulated by intruders than dull females, or females in different colour states may use different territorial strategies accordingly. Female ventral coloration is probably correlated with some behavioural or ecological factor not yet identified, and future studies should explore colour changes in females across the ovulatory cycle, through the onset of sexual maturity, and within dominance hierarchies (e.g. Weber & Weber 1976).

Reversed sexual dichromatism is rare among fish, although it occurs in at least one other cichlid (Stewart & Roberts 1984). Among birds, reversed sexual dichromatism occurs in several shorebird species characterized by relatively large, aggressive females in competition for males giving parental care (Krebs & Davies 1993). Thus, avian sex-role reversal is associated with a derived mating system in which male parental care limits reproductive success, and females are capable of multiple broods per year. The occurrence of colourful, aggressive females in convict cichlids predicts that male parental care should be an important, limited resource (Petrie 1983), and females should be particularly vigilant against female intruders. A conspecific female intruder may represent a potential loss of male parental investment in the form of cuckoldry, as well as a potential brood predator or nest-site competitor (Wisenden 1994).

Evidence from several studies suggests both of these predictions are correct. In the laboratory, intrasexual aggression is the predominant form of agonistic activity among convict cichlids (Mackereth & Keenleyside 1993), and males spend significantly more time away from the

brood during the parental phase than do females (Lavery & Keenleyside 1990), providing them with the opportunity for brood desertion and extrapair fertilization. Deserted or bigamously mated females often incur higher parental costs, in the form of increased attacks against intruders and decreased foraging opportunities, compared with monogamous females (Keenleyside et al. 1990).

Keenleyside (1983) found that males of the Central American cichlid *Herotilapia multispinosa* often deserted broods to form new pair bonds when unpaired females were available, but were less likely to do so when sex ratios were even or when males were in surplus. Thus, female–female aggression in convict cichlids might be expected to reduce a male's probability of desertion or bigamy by reducing his opportunities for extrapair courtships. Male convict cichlids in experimental ponds with a surplus of females will pair bigamously (i.e. simultaneously with two females), and attempts by wild males to pair bigamously have been observed (Keenleyside et al. 1990). Although Wisenden (1994) found that almost 8% of free-ranging Costa Rican male convict cichlids deserted their mates, he was unable to determine whether the availability of females (i.e. remating opportunities) affects the probability of male desertion. The prolonged periods of favourable breeding available to convict cichlids in the wild (Wisenden 1994; McKaye 1977) indicates that females may be able to rear multiple broods if they are able to maintain their pair bond and territory. Thus, the mating system of biparental cichlids may favour the evolution of aggressive female–female competition and reversed secondary sexual characteristics in response to sexual selection.

Acknowledgments

G. W. Barlow and C. Annett helped to improve an earlier version of this manuscript, and their efforts are greatly appreciated. This research was supported by the College of Arts and Sciences and the Department of Biology, Slippery Rock University. The research presented here was described in Animal Research Protocol No. R94003 approved on 6 October 1994 by the Institutional Animal Care and Use Committee of Slippery Rock University.

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