Sex-reversed dominance and aggression in the cichlid fish *Julidochromis marlieri*

George W. Barlow[1] & Jonathan S. F. Lee[2]

[1] *Department of Integrative Biology & Museum of Vertebrate Zoology, University of California, Berkeley, California 94720-3140, U.S.A. (e-mail: webber@berkeley.edu)*

[2] *Department of Neurobiology & Behavior, Cornell University, Ithaca, NY 14853-2702, U.S.A. (e-mail: JL275@cornell.edu)*

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The plesiomorphic breeding system of the large fish family Cichlidae is a monogamous, biparental pair that cares for eggs and extends care to shepherding and protecting tiny fry. Typically, the male is larger than his mate and dominates her. *Julidochromis marlieri*, an African cichlid from Lake Tanganyika, follows this pattern but with an important difference: the female is larger than her mate; one female was reported mated to two males simultaneously (Yamagishi & Kohda 1996). We asked whether the female also dominates her mate, as in polyandrous, sex-role reversed birds. Additionally, documenting an inherent difference in aggressiveness would clarify the behavioral mechanisms that support pair-bonding in monogamous species. We staged contests between males and females of various relative sizes. When equal in size, females regularly won contests. Females were also more likely to initiate advancement to more aggressive stages of the fight. Thus dominance and aggression are sex-reversed in *Julidochromis marlieri*.

Introduction

In polygynous breeding systems, most obvious in lekking species (Johnsgard 1994), mating is usually characterized by a temporary liaison between male and female. Intersexual aggression is reduced or absent (Andersson 1994, Widemo & Saether 1999). Intrasexually, males compete aggressively for access to mates but females usually do not (Williams 1975).

In contrast, the male and female of a monogamous pair often have the same reproductive success (Clutton-Brock 1988). This is obvious in biparental monogamous cichlid fishes because reproductive success requires substantial parental investment by both parents (Barlow 1998). In such species, both sexes ought to be selective when mating, though the bases of choice can be different and indirect. For example, in the monogamous Midas cichlid, *Amphilophus citrinellus*, restrained females selected the larger male and, independently, the more aggressive male (Rogers & Barlow 1991). However, half the females that selected the most aggressive male were rejected by the male when a barrier was removed (Barlow 1992). Thus pair formation was to some degree indirect and depended on compatibility (*see* Jennions & Petrie 1997).

In general, strongly pair-bonded species tend to be monomorphic in appearance, though nota-

ble exceptions exist, as in birds (Clutton-Brock 1988). Cichlids follow the general principle, with some interesting exceptions, in that the male and female of most monogamous species look much the same (reviewed in Barlow 2000).

Although the sexes in tightly monogamous cichlids look alike, the male is regularly distinctly larger than his mate (McKaye 1986, Erlandsson & Ribbink 1997) and dominates her. Unlike birds and mammals, reproductively mature fishes, including cichlids (e.g. Barlow 1976), vary so greatly in size that small males could potentially pair with females much larger than themselves, but they do not. To varying degrees, males characteristically are more involved in territorial defense and females in nurturing the brood, though both participate in each activity (McKaye & Barlow 1976, Keenleyside & Bietz 1981, Barlow 1991, Annett *et al*. 1999). Males of a territorial pair repel other males, and females other females.

In monogamous cichlids, pair formation is characterized by prolonged and complex behavioral exchanges between the male and female. Their interactions resemble a prelude to a fight. Combative behavior during pair formation is thought to be a means of testing one another's suitability as a mate (Baerends & Baerends-van Roon 1950, Barlow 1998). It also establishes the dominance relationship between the male and female. Domination is expressed as priority in access to resources, and can be determined by observing which fish withdraws from the other. Aggression and the consequent establishment of dominance relationships is thus the central feature of pair bonding. If the two fish succeed in pairing, they then direct their aggression outward against conspecifics and other fishes, a change in behavior that Lorenz (1963) took as the moment of pair bonding. When pairing fails in aquaria, the female tries to flee; the male attacks her so viciously that she must be rescued (Baerends & Baerends-van Roon 1950, Barlow & Ballin 1976, Barlow 2000).

With this background of nearly universal male dominance over the female in pairs of cichlids, we were drawn to the African cichlid *Julidochromis marlieri* because they appear to reverse this relationship. Like most monogamous cichlids, male and female *J. marlieri* are otherwise so alike in appearance that the sexes are indistinguishable without a microscope. Additionally, both the male and female parents participate in the care and defense of eggs, larvae and newly emerged fry (GWB pers. obs.). However, a recent paper by Yamagishi and Kohda (1996) disclosed that the female of a bonded pair of *J. marlieri* in Lake Tanganyika is normally larger than her mate and appears to be the dominant partner. Although the size distributions of males and females overlap widely, paired males were consistently only about 75% the length of their partners (Yamagishi & Kohda 1996); we estimate from a length/weight regression of captive fish that the male is thus on average 56% of the mass of his mate, an appreciable difference.

Females defended territories containing a single male but in one instance two (Yamagishi & Kohda 1996). In this respect, they are similar to some polyandrous, sex-role-reversed birds in which smaller males nest in the territory of a large, dominant female (Jenni & Collier 1972, Butchart 1999). In *J. marlieri*, the reversed size relationship between the male and female was at that time unknown among pair-bonding cichlid fishes and is another characteristic shared with polyandrous, sex-role-reversed birds.

Females larger than their male mates, however, do occur among some species of polygynous mouth-brooding cichlids that feed on non-defensible resources (Erlandsson & Ribbink 1997). In their review of sexual size dimorphism in cichlids, Erlandsson and Ribbink (1997) commented on the paucity of comparative studies, leaving us with a poor understanding of the adaptive significance of such dimorphism.

The inherent behavioral differences in aggressiveness between males and females in general in pair-bonding cichlids are virtually unknown. How is this dominance achieved? Does it result solely from the male's larger size, or are males also inherently more aggressive? By aggressiveness we mean only that combination of behavioral mechanisms that normally leads one of two individual contestants to win a fight, when matched for other factors that influence outcome, such as size and prior residence.

Because *J. marlieri* is facultatively polyandrous with paired females much larger than their mates, fight outcomes might well be reversed,

with the female dominating her partner. Do *J. marlieri* females dominate their partners? If so, is this dominance due to the size difference alone, or is the female also inherently more aggressive than the male? Size is the single most reliable forecaster of winning among fishes (Barlow 1983, Rowland 1989, Huntingford *et al.* 1990, Oliveira & Almada 1996, Kroon *et al.* 2000), so the size difference alone could lead to female dominance over her male mate.

We placed individual males and females together in a situation where we knew from experience that they would immediately fight (they were unresponsive to a mirror image). We varied the relative sizes of male and female contestants to determine the relationship between relative size and the probability of winning a fight. We predicted the female would win even when the two sexes were equal in size. Beyond that we wanted to know the relative size at which the male and the female would have equal chances of winning. We predicted that would be with the female smaller than the male but we could not quantitatively predict the exact relationship. Knowing that relationship would give us insight into the species-typical dominance relationship in mated pairs.

To interpret the mechanisms that may allow females to dominate males, we needed to develop a more complete picture of the process. Two relevant events were readily measured. First, which subject initiated the fight, that is, which showed the higher readiness? In another cichlid fish, initiation proved important in determining the outcome of fights tested in the same way as done here (Barlow *et al.* 1986). Second, once a fight has begun, which subject escalates the fastest? Quicker escalation should imply the more aggressive combatant. We expected that females would initiate more and escalate faster, compared with males.

Methods

Subjects and housing

An importer provided the subjects, which had been collected from Burundi along the shore of Lake Tanganyika, Africa. They were housed individually in 37.5-liter (50 × 30 × 25 cm deep) glass-sided aquaria such that they could see one conspecific neighbor on each side. The water temperature was 25 ± 0.5 °C, continuously filtered through an inside sponge filter. The light regime was 13 ON:11 OFF. The fish were fed twice daily, once with live brine shrimp and once with *Spirulina* flakes. All experiments were conducted between spring 1999 and summer 2001 in the Valley Life Sciences Building at UC Berkeley.

Experimental procedure

For each contest, a male and a female were selected and measured (standard length (SL) and body mass). We varied the size relationships of the contestants to obtain a range of differences. At the start of the experiment we had 17 males and 22 females, which we sexed by examining differences in the urogenital papilla. The validity of our sex identification method was verified by dissection of a separate set of fish. Twenty-nine fights were conducted, so twelve males and seven females were each re-used once in subsequent trials. To assure independence of data, however, no two fish were ever re-matched, and a period of several months lapsed between the times those individuals were used.

Two subjects were placed into an observation tank that was of the same dimensions as the home aquarium, but lacked a filter. An opaque sheet of dark plastic that divided the tank in half separated the subjects initially. The back and sides of the aquarium were blanketed with the same plastic material, and the bottom was covered with gravel. The fish were allowed to adjust to their aquarium for 1.5 hours before the barrier between them was removed.

Observations

1. First fish to do each of the following:
   a. Approach: Movement toward the other fish. (After removing the barrier, the fish typically stayed relatively still for 3–15 s.)
   b. Roll: Rotation on its long axis, directing its dorsal fin at the other fish.

c. Spread: Fully expanding the median fins. (The long axis of the body at that time was often parallel to that of the other fish.)

d. Tail beat: The caudal fin is expanded and, through a body undulation, the tail is beaten toward the other fish.

e. Bite: In an accelerating dash, the subject swims into the other fish, making contact with its mouth, most likely delivering a bite, though that was difficult to see. We often heard a faint snapping sound at this time.

2. Winner of the contest. The winner was the first fish from which the other fled three times in quick succession. This end point was unambiguous. The fish were immediately removed, and none was injured.

3. Time to end of contest. Time elapsed between removing the barrier and the declaration of one fish as the winner.

Model of fight with escalation

In this generalized account, one or both fish approach, roll, and spread with variable degrees of fin erection. Tail beat often follows and also varies in completeness of expression. After these preliminaries, one fish may bite and the other answer with tail beat. Biting progresses to mouth pushing in which the fish face one another, make contact with their open mouths, and push. That often escalates to mouth locking in which the fish hold on to one another by the mouth. Mouth locking varies in duration, the initiator and controller of the contest, and whether one of the fish continues to hold its lock after the other lets go. The fish that appears to be winning may tip the other fish on its long axis so that it is on its side, and then swing the losing fish from side to side; this was seen only in the most extreme fights.

Statistics

A previous study of fighting in the Midas cichlid (Barlow 1983) indicated that a logistic model was appropriate for this experiment. Relative female body mass, expressed as the proportion of the body mass of the male opponent, was chosen as the independent variable; the dependent variable was fight outcome (0 = lose, 1 = win). From these binary data, we used SAS (Cary, NC) to compute the logistic regression for the relationship between female relative body mass and the probability of winning.

If body mass alone determines the fight outcome, the 50% probability-of-winning point (hereafter denoted as P_{50}) should occur when the body mass of the female, relative to that of the male, equals one. If gender influences the outcome in the direction that we predict, that point should be shifted away from the value of one; P_{50} should occur at some relative size of the female that is less than one. We computed the confidence intervals for the P_{50} relative body mass of the females and determined whether the point for equal body size was excluded.

We tallied the number of times females, as opposed to males, performed a "first to" behavior and compared those ratios to a binomial distribution. The prediction was that females would perform more such behavior and therefore used a one-tail critical region.

To determine whether the winner could be forecast from escalation, we analyzed the "first to" behavior during the course of the fight relative to fight outcome. We compared the data to a binomial distribution to determine statistical significance. Predicting the female would be the escalator, we used a one-tailed critical region.

Results

Effect of size on winning an encounter

Females had a 50% chance of winning fights when their mass was 90% that of their male competitor (Fig. 1). The 99% confidence interval ranged from female weight being 86% to 94% that of the male, so the outcome significantly excluded the point of equal body size.

Does a "first to" behavior predict the winner/loser?

None of the five "first to" acts of behavior predicted the winner (Table 1).

Were females more likely than males to escalate?

Females were more likely than males to be the first to escalate to a late-stage behavior (those that occur further along in the progression of a fight): tail beating and biting ($P < 0.05$; Table 1). No significant differences were found for the three earlier, less physically interactive behavior patterns: approach, roll and spread (Table 1).

Did fight duration correlate with relative body size?

Fight duration ranged from 27 to 793 s, with a mean of 209 s. When duration was tested against relative body size, expressed as its distance from unity, the correlation coefficient was not significant ($r^2 = 0.058$, $P > 0.25$). And, when relative body size was tested against its distance from our P_{50} point, the correlation was also not significant ($r^2 = 0.036$, $P > 0.38$).

Discussion

The issue of sex differences in aggression, independent of body size, has been tested in only one other cichlid, the monogamous Midas cichlid, *Amphilophus citrinellus*, formerly *Cichlasoma citrinellum* (Kullander & Hartel 1997). Using an unusually large sample of Midas cichlids (132 males, 130 females) Holder *et al.* (1991) recorded individual's attacks by the fish at their own mirror images, thereby canceling the effect of body size. Males attacked their images significantly more than did females. Using this measure of behavior, which is readiness to attack, males were judged more aggressive than females. Those results indicated that in a typical pair-bonding cichlid, even when size differences are ruled out, males are more aggressive than females.

We expected females of *J. marlieri* to be more ready to fight, as initiating can confer an advantage in a fight (Barlow *et al.* 1986). But the sexes did not differ significantly in time to initiate, at least under our experimental conditions and sample size. Another behavioral trait
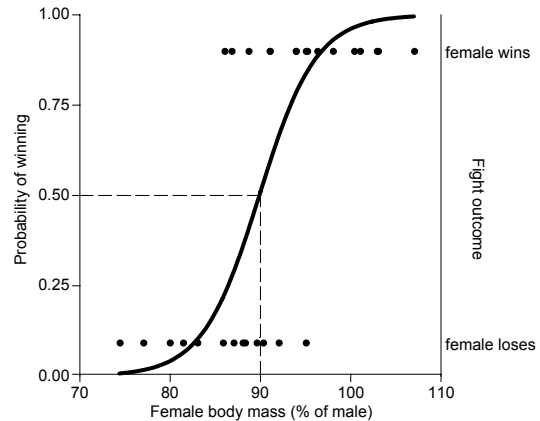
Fig. 1. Probability of female winning as a function of her weight relative to that of the male. The dashed line indicates the relative size of the female at which the probability of winning is equal for the female and the male. The upper row of data points are for females that won; the lower row is for females that lost.

that could promote winning is quicker escalation to more costly stages of the fight. Females were significantly more inclined to escalate than were males. In that sense, they were the more aggressive sex.

Generalizing from our results on *J. marlieri*, females in Lake Tanganyika would consistently win fights with males when the two are equal in size. Following the logistic regression, as the female becomes relatively smaller, her chances of winning diminish. When she reaches 90% the weight of the male, the male and female would

Table 1. Fight outcomes. Five behavioral events and for each, which sex was the more likely to escalate to that behavior first. Also for each behavior, whether the first fish of either sex to perform that event predicted the winner.

First to	Who escalates most? Female:Male	Escalating fish wins? Win:Lose
Approach	10:17	16:11
Roll	11:7	7:11
Spread	11:15	12:14
Tail beat	14:5***	10:9
Bite	13:5***	7:11

*** ratios that are significant at $P \le 0.05$. "Ties", in which both fish simultaneously initiated or escalated, were excluded from the analyses.

have an equal chance of prevailing. Given that males average only 56% the weight of their mates in nature, females should easily dominate their mates.

A mated pair of *J. marlieri* is outwardly peaceful though on occasion the female exerts her dominance through display. Naively, one might assume that the optimum size relationship for a freely formed pair would arise when the female is about 10% smaller than the male. In that case, the cooperating pair would have equally dominant mates. We have seen, on the contrary, that females are almost twice as heavy as their mates. This presents what may be a key insight in understanding the resolution of conflict when two cichlids pair: One member of a pair is so much larger than the other that its dominance is never in question.

In typical cichlids, the obviously larger and dominant mate is the male. In *J. marlieri*, the much larger and dominant mate is the female. The size-effect of dominance is greatly amplified in the larger mate through its higher aggressiveness.

In *J. marlieri*, in contrast to the great number of substrate-brooding monogamous cichlids (Barlow 2000), the female has the capacity to mate with more than one mate (Yamagishi & Kohda 1996). If this translates into a higher potential rate of reproduction for females, our findings that females are more aggressive and can dominate their male mates likely derives from selection for females to compete for access to the limiting sex — males.

Acknowledgments

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