

Is the cichlid fish *Julidochromis marlieri* polyandrous?

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Among the vertebrates, the greatest diversity of mating systems is seen in the fishes, where the mating system is influenced greatly by the parental care pattern (Kuwamura, 1988; Barlow, 1991; Keenleyside, 1991). Within Lake Tanganyika, cichlid fishes of the tribe Lamprologini (ca. 60 species) are substrate spawners which guard their young (Kuwamura, 1986). Many lamprologine fishes are monogamous and show biparental care, but several species are polygynous with maternal care (Kuwamura, 1986; Yanagisawa, 1987). In this tribe, females are usually smaller than males and are more closely tied to the fry (i.e., free-swimming young) (Kuwamura, 1986; Yanagisawa, 1987; Barlow, 1991; Gashagaza, 1991; Keenleyside, 1991). In some species of the genus *Julidochromis* (including 5 species), however, females are larger than males (M. Hori, unpubl.).

Julidochromis marlieri is one of the small benthic fishes resident in the shallow rocky shores of Lake Tanganyika (Brichard, 1989). It forages mainly on sponges and algae on rock surfaces (Hori et al., 1993). While observing

breeding in this fish, we found that monogamous pairs were most common, females being larger than their mates, and that males played a more important role in parental care than females. Our data also suggested that large females may mate with 2 males, although polyandry has not been documented in fishes. The reversed parental roles and mating system of *J. marlieri* are briefly reported herein.

Materials and Methods

This study was conducted at Bemba (Pemba), Zaire, from September to October 1987. We made underwater observations using SCUBA in an 8 m × 10 m quadrat over a rock and pebble substrate in 5–8 m water. Within the quadrat, 28 *Julidochromis marlieri* resided, each easily identified by its individually distinct body colour pattern. Of 8 nests (rock crevices) detected, 7 contained fry 5–30 mm TL (total length), such being either in the nest or on the substrate within 25 cm of the nest entrance. The number of fry per nest varied from 5 to 20. Eggs were de-

Table 1. Total lengths (mm) of members of *Julidochromis marlieri* associated with each nest observed

Members	Nest code							
	a	a'	b	c	d	e	f	g
Females	90.9		81.3	c.80*	78.9	71.8	62.0	60.5
Males	66.9	66.5	58.7	c.60*	62.6	59.1	47.7	40.6
Helpers	c.40 (?)	44.6 (M)	47.9 (F)	—	40.6 (M)	39.1 (M)	—	—

M, male; F, female; *Sex estimated from fish body size and behaviour.

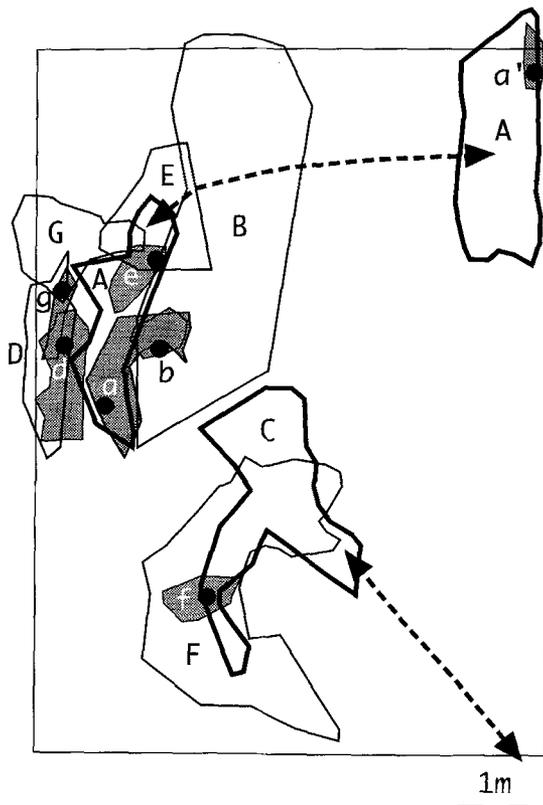


Fig. 1. Arrangement of territories of *Julidochromis marlieri* females (unshaded) and home ranges of males (shaded). Solid circles indicate nest sites. Capitals are female codes and small letters male codes (=nest codes in Table 1). Thick lines show territories of females A and C, and broken lines their routes between their territories. Non-mating fish are not shown.

posited on the inner side of the nests and were not visible from the outside. A female and male, which frequently entered a nest and protected fry from potential predators, were regarded as the parents. Additionally, in each of 5 nests, an individual smaller than the parents played a continuing role in parental care; this individual is here called a helper. A total of 55 30-min observations were conducted during 10:00–16:00 for 7 males, 6 females and 5 helpers, listed in Table 1 (1–10 times per fish). During the observations, swimming routes, time spent around nests, and intra- and interspecific aggression were recorded. At the end of the observations, most resident individuals (86%; 12 females and 12 males) were captured and sexed by gonad examination. Two-tailed statistical tests were used, the

values given being means \pm SD.

Results and Discussion

Females had one or 2 separated territories (Fig. 1), which were defended at the borders against similarly-sized females, but which widely overlapped the territories of different-sized females. Such territories occurred on large rocks and boulders of diameter > 1 m. Males had home ranges around nests located within the female territories. Among a total of 56 aggressive encounters observed between females, most attacks (95%) were initiated by the larger individual, indicating that females were territorial and had a size-dependent dominance relationship.

Five females (B, D, E, F and G in Fig. 1) were monogamous, each having one territory in which they mated with a male. However, the largest female (A) maintained 2 territories, each containing an adult male (a and a') with a nest that was not visited by other females. Female (A) visited each of the nests (always maintaining the same course between the 2 territories [Fig. 1]) 2–4 times per hour, without disturbance of other females. These results suggested that this female was polyandrous. The 2 males (a and a') repelled potential predators from their respective nests, although fry were found in only the nest of male (a) (Fig. 1). Another large female (C) had a territory outside the study area, where she mated with a large male (c). This female also visited a second territory in the study area (Fig. 1), although no mate was present at that site.

In all 8 cases, the mating bond was stable throughout the 2 month study period. In each pair, the female (76.6 mm TL \pm 12.5, $n=6$) was always larger than the male (55.9 mm \pm 9.9, $n=7$), with the larger females mating with larger males ($r=0.935$, $p=0.002$, $n=7$) (Table 1). The 2 males with which the largest female (A) mated were the largest males in the study area. Both mating females ($n=6$) and mating males ($n=7$) were larger than other females (53.8 mm TL \pm 9.4, $n=6$; Mann-Whitney U -test, $U=2.0$, $p=0.01$) and other males (49.1 mm \pm 13.1, $n=5$; $U=1.5$, $p=0.01$), respectively.

In monogamous pairs, the time spent in the nests or within 25 cm of the nests did not differ between males (16.4 min \pm 8.2 per 30-min observation, $n=5$) and females (11.9 \pm 8.4, $n=5$;

Wilcoxon signed-ranks test, $z = -1.48$, $p = 0.13$). However, when not actually in or staying near the nest, males usually remained relatively close, whereas females swam much further away (Fig. 1). At the approach of an observer, females fled sooner than did males. Both parents and helpers repelled other fishes (representing 12 carnivorous species) which approached the fry. Males attacked intruders more frequently (7.5 times ± 2.7 per 30-min observation, $n = 5$) than did females (2.4 ± 1.2 , $n = 5$; Wilcoxon signed-ranks test, $z = -2.02$, $p = 0.04$). The bigamous female (A) stayed for less than 1 min per 30-min observation period at the nest without fry, whereas the male (a') stayed for 12.5 min and attacked predators 3.0 times during the same period ($n = 2$). In the other nest with fry, the male (a) also stayed longer (16.0 min ± 5.2 , $n = 10$) than the female (12.8 min ± 10.3 , $n = 9$; Mann-Whitney U -test, $U = 19$, $p = 0.03$) and attacked intruders more frequently (11.1 times ± 7.7 , $n = 9$; female: 3.4 ± 3.2 , $n = 9$; $U = 12$, $p = 0.01$).

Helpers usually (>98% of observation time) stayed near the nests. Parents with a helper seemed to spend less time near the nest (males: 11.6 min ± 3.1 per 30 min, $n = 5$; females: 7.6 ± 4.9 , $n = 4$) than those without a helper (males: 26.3 min ± 1.4 , $n = 2$; females: 21.0 min ± 6.7 , $n = 2$). Helpers attacked predators 4.4 times (± 6.2 SD, $n = 4$) per 30 min. Males without a helper appeared to attack predators more frequently (10.5 times ± 2.1 , $n = 2$) than those with a helper (6.1 ± 2.8 , $n = 5$).

The observations on the two large females suggested that large dominant female *Juli-dochromis marlieri* may mate polyandrously. Polyandrous mating systems (classical polyandry, sensu Oring, 1986) have been documented in several avian species, in all of which, 1) a female mates with more than one male, each having a nest; 2) the female is larger than her mates and 3) the female conducts less or no parental care. These features are very similar to those observed in *J. marlieri*.

In lamprologine fishes, patterns of parental care largely depend on the spatial distribution of fry, biparental care being essential if a school of fry forages in mid-water, whereas uniparental care occurs if fry are restricted to near the substrate (Kuwamura, 1986; Yanagisawa, 1987). Parental care in *J. marlieri* belongs to the latter

type and can thus be reduced. In this species males played a more important role in brood protection than did the larger-sized females, the latter tending to be less attached to the fry. Furthermore, helpers greatly reduced the degree of parental care by the parents, females with a helper spending only about 25% of their time near the nest, compared to about 70% by those without helpers. These factors may facilitate polyandrous mating in *J. marlieri*.

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