The Social and Mating System of the Maternal Mouthbrooder
Tropheus moorii (Cichlidae) in Lake Tanganyika

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Abstract Territorial behaviour, reproduction and migration of the epilithic algal eater, *Tropheus moorii*, were investigated in Lake Tanganyika, Africa. Adults of both sexes had individual feeding territories which adjoined each other. Males, who occupied higher rocks than females, usually stayed at the same sites for more than 5 months. Females left their territories to pair with males in the males' territories. Paired females actively foraged under the protection of their mates for up to 3 weeks prior to spawning. After spawning, females usually settled in a site unoccupied by territory-holders to mouthbrood the offspring for a month. An examination of the ovaries and a removal experiment of dominant males suggest that females cannot attain fully mature ovaries in their own territories and choose males whose territories can provide enough food to satisfy their nutritive demand. The evolution of a number of local colour morphs in this fish is briefly discussed in relation to social selection.

Cichlid fishes in Lake Tanganyika represent one of the most spectacular examples of adaptive radiation in fishes (Fryer and Iles, 1972; Lowe-McConnell, 1987; Nishida, in press). Rocky shores in this lake are inhabited by a huge variety of cichlid species. Rock-dwelling species, whose habitats are disrupted by sandy beaches, usually include geographical variants within the lake, which may be incipient species. The best-known is *Tropheus moorii*, which is composed of no less than 20 local colour morphs (Marlier, 1959; Matthes, 1962; Nelissen, 1976; Brichard, 1978).

The behaviour and ecology of *T. moorii* have been intensively studied in aquaria by many workers (Wickler, 1969; Nelissen, 1976) and in the field (Kawanabe, 1981; Takamura, 1983, 1984; Yamaoka, 1983; Mbomba, 1986). This fish is an epilithic algal feeder (Takamura, 1983, 1984; Yamaoka, 1983, 1985, 1987), having an individual feeding territory (Kawanabe, 1981). The courtship and spawning behaviour is very similar among colour morphs (Wickler, 1969; Nelissen, 1976). Eggs are mouthbrooded only by females (Wickler, 1969). However, many aspects of social and mating systems of this fish in nature still remain to be investigated. For example, little was known about how long each fish maintains its feeding territory, how consexuals compete for a mate, and whether mating occurs within the male's or female's territory or in a spatially separated spawning site. An understanding of the above for each colour morph is necessary to understand how social factors have affected the evolution of colour morphs.

The 'Bemba orange' morph (see Axelrod et al., 1985, p. 502), which is distributed on the northwestern shore of the lake, was chosen as the subject of this study. Fish of this morph could be recognized individually from an orange band on the body. Their territorial behaviour, reproductive behaviour and migration patterns were observed for 5 months so as to clarify their social and mating system. Moreover, dominant males were removed experimentally from their territories to determine the manner of resource monopolization.

Methods

Field observations and sampling were conducted at Bemba (=Pemba), about 25 km south of Uvira (3°24′S, 29°10′E), Zaire, with the aid of SCUBA. A 30×20 m quadrat, divided into 5×5 m grids, was set on the rock and sand bottom at a depth of 2.8 to 6.1 m, where adult *T. moorii* were abundant. In the quadrat, the configuration of rocks was sketched on a section paper (scale: 3/200) and water depths of the top and base of a rock and the sand floor were

measured at 474 points using a tapeline with a float.

T. moorii larger than 75 mm SL in the quadrat were individually recognized by using a sketch of the profile of a vertical orange band on each side of the body, although the exact identification of wandering fish was often difficult. They were regularly censused during early June and late October, 1987, most intensively (usually at intervals of 2–4 days) during 17 July and 21 September. In each census, their positions and social states (i.e., solitary, paired and mouthbrooding) were recorded.

In the quadrat, behavioural interactions of each fish with conspecifics and other fish species were observed twice for 15 min, once during 9 and 23 June and once during 17 September and 6 October. At the same time, its exact position was plotted on the map every 30 sec. The minimum convex polygon covering all points plotted was regarded as its home range. If the border of a fish's moving area was clearly defined by the substrate (e.g., a cliff of rock) or if a fish moved between two separated areas, we did not adhere to the rule of the minimum convex polygon. The extent of home range overlap of each fish between the two periods is given by $[2c/(a+b)] \times 100$, where c is the overlapped area of home ranges in the two periods (a and b). Sex was determined by gonad examination of fish collected and inferred from mouthbrooding and pairing in fish not caught.

On 9 October, five males whom females had frequently visited were removed. The behaviour patterns of individuals who replaced these males in their territories were observed for 15 min each, 1, 4 and 15 days after removal and for a few minutes 7 days after removal. The behaviour of neighbouring fish was also observed for 2–15 min.

The distribution of *T. moorii* in relation to water depth and substrate was recorded on 14 August. Three parallel lines, about 100 m apart, were set temporarily from the shore to a site 30 m in depth,

and the number of *T. moorii* in areas measuring 10 m long by 2.5 m wide on both sides of each line was recorded along with their approximate body sizes.

Specimens were caught with a small-mesh barrier net and two hand nets. After a small amount of undiluted formalin was injected into their abdominal cavities, specimens were preserved in 10% formalin within 1.5 hours after collection. Adult fish in the quadrat were collected during 26 and 31 October after the removal experiment. Outside the quadrat, mouthbrooding females were collected intensively. In the laboratory, standard length, wet body weight, wet gonad weight, wet weight of fat stored within the abdominal cavity and wet weight of gut contents (total gut weight − vacant gut weight) were measured. Stomach contents were weighed after heating at 60°C for 24 hours (dry weight) and again after heating at 550°C for 4 hours (ash weight), and the fraction of organic matter $\{[(\text{dry weight} - \text{ash weight})/\text{dry weight}] \times 100\}$ was calculated.

Results

Distribution and home range. *T. moorii* inhabited the bottoms of rocks and boulders shallower than 18 m. They also occurred at mixed zones of rocks, boulders and sand, but were never seen on a purely sandy floor. Juveniles smaller than 40 mm SL were almost exclusively found on the bottom of boulders mixed with pebbles at a depth of 0.5–2 m (Table 1). Very small juveniles less than 20 mm SL, which were rarely found in a line census, remained in concealment among boulders and pebbles beneath surface boulders shallower than 1 m. The smallest juvenile collected was 14.0 mm SL, which was of similar size to grown offspring mouthbrooded by the female (the maximum size being 15.9 mm SL), suggesting that the young settle in such shallow habitats after becoming independent from the parent.

Table 1. Population density (per 100 m²) of *Tropheus moorii* in relation to water depth. The data from three line censuses are combined. *, purely sandy area is not included.

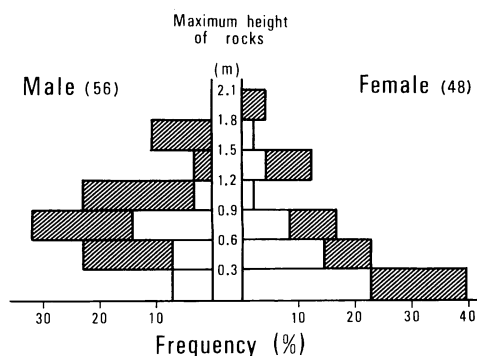| Water depth (m)	Area censused (m²)*	Standard length (mm)					Total
		≤20	21–40	41–60	61–80	81≤	
0– 2	239.5	1.0	27.5	16.4	11.8	10.1	66.8
2– 4	238.5	0	1.6	3.7	5.7	4.3	15.3
4– 6	298.0	0	0	0.8	3.6	6.0	10.4
6– 8	75.5	0	0	1.3	5.3	9.5	16.1
8–10	58.0	0	0	0	0.3	1.7	2.0
10–30	605.5	0	0	0	0.3	0.5	0.8

Fig. 1. The maximum height of rocks in a home range for male and female *Tropheus moorii*. Sample size in parentheses. Data from June and September–October are combined. Striped areas indicate individuals larger than the average body size (97.2 mm SL for males and 87.8 mm SL for females). The height is significantly greater in males (Mann-Whitney U test, $U_1 = 862$, p< 0.01). The female who had the highest value lived in a narrow area at the edge of a big rock occupied by two males.

Adults were abundant in the rocky area up to 8 m depth (Table 1). The sex ratio was nearly 1:1 (29 males and 32 females in June, 26 males and 28 females in September–October, in the quadrat; $\chi^2 = 0.148$, 0.074, df=1, p>0.05). The mean standard length of males was larger than that of females ($\bar{x} \pm$ SD = 97.2±6.3 mm, n=30 vs 87.8±4.1 mm, n=32, t-test, t=6.89, df=60, p<0.001, for specimens in the quadrat; 95.7±6.8 mm, n=47 vs 82.8±5.9 mm, n = 89, t = 11.5, df = 134, p < 0.001, for all specimens). Home ranges of two neighbouring fish adjoined, scarcely overlapping with each other except when belonging to paired individuals. Males inhabited much larger home ranges than females (6.1±2.8 m², n=55 vs 3.4±2.1 m², n=53; t=5.65, df=106, p<0.001, data of June and of September–October combined).

Most of the large and high rocks were occupied by males. Accordingly, the area of rocks in a home range, measured in horizontal projection on the map, was much greater for males than for females (3.92± 2.26 m², n = 50 vs 1.58 ± 1.20 m², n = 46; t = 5.51, df=94, p<0.001) and the average maximum height of rocks in a home range was also greater for males (Fig. 1). The body size of the fish was not correlated with the home range size among either males (r= 0.07, n=50, p>0.05) or females (r=0.10, n=43,

p>0.05). However, it was positively correlated with the area of rocks in the home range of males (r= 0.445, n=50, p<0.01) and nearly so for females (r=0.292, n=43, p≒0.05).

Adults had on average 3.7 neighbours within 1 m of their home range boundaries. The relative frequency of neighbours being of the opposite sex was greater than that expected from random distribution (male– male 89, male–female 228, female–female 43; $\chi^2 = 29.74$, p<0.001). This distribution pattern suggests spacing out between consexuals. Except for one small male (79.8 mm SL) and one small female (78.5 mm), who were often attacked by neighbours and shifted from place to place within a certain area, all adults defended their home ranges against conspecifics and some other cichlid fishes. Their home ranges, therefore, could be regarded as territories.

Territorial behaviour. Aggressive and aggression-inhibiting behaviour patterns between territorial fish were principally the same as those observed in an aquarium (Nelissen, 1976). Attacks by one territorial fish against conspecific territory-holders occurred 6.1 times per hour (in 29.5 h observations) and accounted for 82% (147/180) of all agonistic encounters between them. Other aggressive behaviour patterns were the approaching of one fish (12%) and confrontation at territory borders (3%). The approaching of one fish was often followed by the recipient submissively quivering its tail (82%, 18/22). All observed attacks, except one, between individuals of known body size were made by the larger individual against the smaller (91/92), and 91% (83/91) of the attacks were between individuals with a size difference of more than 5 mm SL. Attacking interactions between sexes were more frequent than those between consexuals (male–male 29, male–female 71, female–female 24). This result may simply reflect the distribution pattern of *T. moorii* in that neighbours were disproportionately of the other sex. In every attacking interaction between sexes, the attacker was a male.

Territorial fish also attacked nonterritorial conspecifics when their territories were invaded. Attacks by males against invaders were more frequent than those by females (2.2 vs 1.3 per hour). The invaders, whose sexes could not usually be identified, were generally smaller than the territorial fish. Some of them were wandering unpaired females. The vertical, orange band of the invaders was usually faded. Tettitory-holders sometimes followed invaders without attacking until the latter had left the territory.

Males sometimes accepted invaders by courtship movements, leading and quivering.

Attacking was also directed to 18 heterospecifics (3.9 per hour), all of which were cichlid fishes. Attacks against a congeneric fish *Tropheus duboisi* (25%) and a scale-eater *Perissodus microlepis* (17%) were often fierce but those against the other fishes were usually mild.

Movement. About half of the adults in the quadrat kept their territories at the same sites throughout the study period between June and September–October and the others moved elsewhere or disappeared (Table 2). The proportion of individuals who maintained their territories at the same sites was much higher in males (83%) than in females (28%), and among these residents the degree of territory overlap between the two periods was greater in males ($68.0\pm16.4\%$, n=23 vs $46.9\pm16.7\%$, n=9; Mann-Whitney U test, $U_1=39$, p<0.01).

Of 5 males who did not stay at the same site, 2 shifted 3 and 10 m, respectively, one occupied a neighbouring territory from which a male had disappeared and the other, which had been on the sandy bottom with small rocks, moved outside the quadrat. The whereabouts of the other 3 males after the disappearance remained unknown. Of 23 females who did not stay at the same site (Table 2), movements of 19 females were related to pairing and brooding (see below). The other 4 females moved 3–15 m to settle into sites from which territory-holders had disappeared (2 cases) or sites which were unoccupied by territory-holders (2 cases).

On the other hand, 63 individuals were new arrivals in the quadrat during the study period. When we found them for the first time, 34 were paired with males in the males' territories, 12 were singly mouthbrooding, and 17 were solitary without mouthbrooding. More than half of them had disappeared from the quadrat by the next census; only 11 stayed in the quadrat for more than 2 weeks.

Reproduction. Social states of the male were categorized as paired or solitary, and those of the female as paired, solitary or mouthbrooding. Pair formation always involved a female's migration to a male's territory where the pair was maintained. Pairs which broke up by the next census or in which the male did not consort with the female (see below) were regarded as tentative. Females carrying fertilized eggs in their mouths always left the males' territories.

Changes of social states for males, who paired with a female at least once, and for females, who are estimated to have reproduced, are shown in Figs. 2 and 3, respectively.

1) Pair formation. Fifty-one individuals were found in male territories at least once during quadrat censuses. Of them, 13 had formerly been solitary in the quadrat, 4 were in male territories from the start of the census, and the other 34 came from outside. Sixteen of the first two groups were finally collected and ascertained to be 14 females and 2 males. The distance between the female's original territory and the male's territory to which she moved ranged from 1 to 15 m (4.7 ± 3.8 m, n=11; distance between the centres of the two territories). In 7 out of 14 cases, the migration was to the neighbouring territory.

Females in the male territory were 'fickle' until they paired stably with one male. Some females returned to their original territories after a short stay in a male's territory and some others visited two or more territories in succession. Two typical cases of successive visits are detailed below.

One female, who came from outside the quadrat, visited three males (M7, M22 and M19) staying in each territory for 2, 20 and 6 min, respectively, during a 35 min observation period. Two days later she again visited these males (6, 25 and 6 min), as well as three other males outside the quadrat (1, 3 and 9 min), in a 75 min observation. Another female (F3), who had been a territory-holder, was found in one of four male (M4, M5, M6 and M7) territories in six successive censuses. These territories were

Table 2. The residence and movement of adult *Tropheus moorii* who were found in the quadrat from June 1987 until September-October 1987. *, 6 returned to their original territories by September-October after having left the territories for reproduction.

	No. individuals	Remained at the same site	Moved in the quadrat	Moved outside the quadrat	Disappeared
Male	29	24	1	1	3
Female	32	9	16*	2	5
Unknown sex	8	2	0	0	6

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M  1    +              +      ▲ ▲ + +    ++   +++ +++ ++++ +++ ++ + + +  ++++      +
M  2    +              +       ∆+ +      +    +++ +++ ++++ +++ ++ + + +  ++++      +    +
M  3       +           +      ∆ ∆ +     +∆    + + ∆++ +++∆ +++ ++ + + +  ++++      +    ∆
M  4  ▲ ▲    +  ∆+ ∆∆∆∆ ++▲ ▲▲ + +      ++   +++ +++ ∆∆++ ++∆ ++ ∆ + +  +▥+      +    +
M  5      ++   + ∆    + ∆∆+ ▲▲ ▲ +      ++   +++ +∆+ +▲▲▲ +++ ++ + + +  +▥+      ∆    +
M  6  +               +      + ∆ +     +∆    +∆+ ++∆ +∆++ ∆+∆ ++ +   +  ∆▥+      +    +
M  7  +     ∆∆ ∆∆ +    ▲ ▲▲▲ ▲▲ ▲ +    ∆+    ∆+∆ ∆∆∆ ++++ +++ +∆ + + ▲  ▲▲▲▲      +    +
M  8       +           +      ∆ + ∆ +    ▲▲   ▲▲▲ ▲+++ +++ ++  ++ + + +  ++++      +
M  9/29 +         ∆    +  ∆+ ▲▲ ▲ ▲    ▲▲   ∆++ +++  +++ +++ ++ + + +  ∆+▲      ▲
M 11   +             ∆+    +    ▲     ▲▲   +++ +++ +∆∆∆ +++ ++ + + +  ++++      ∆
M 12  +    +          +          + +    ++   +++ +++ ++++ ∆++ ++ + ∆ +  ++++      +
M 17      +           +      ∆ + +      ++   ▲▲▲ +++ ++++ +++ ++ + + +  ++++      ∆
M 19     +    ∆       +           ∆ +    ∆+   ++∆ +++ +++∆ ++  ∆+ ∆ + +  ∆+ +      ∆
M 22   +    ∆∆     ∆∆+∆ ∆∆∆ ∆+ + +      ∆∆   −+▲ ▲▲▲ ▲▲▲▲ ▲+  + + + +  ++++      ∆ + +
M 23  + ▲ ▲ ▲ ▲▲ +▲▲▲ ▲▲▲ ++ + ∆     +∆    ▲▲▲ +▲▲ ▲ ▲+ ∆+∆ ++ + + +  +▲▲▲      ∆    +
M 25      + ▲ ▲▲ ▲▲▲+ +++ ++ + +      ++   ++∆ +++ +∆+▲ ▲▲▲ ++ + + +  +++▥      +    +
M 27  +        ∆  ∆▲▲ ▲ +
M 30            ∆ ∆+ +++    + ∆    ▲▲   ▲++ +++ ++++ +++ ++ + + +  ++++      +

         Jun        │      Jul       │      Aug      │      Sep      │   Oct
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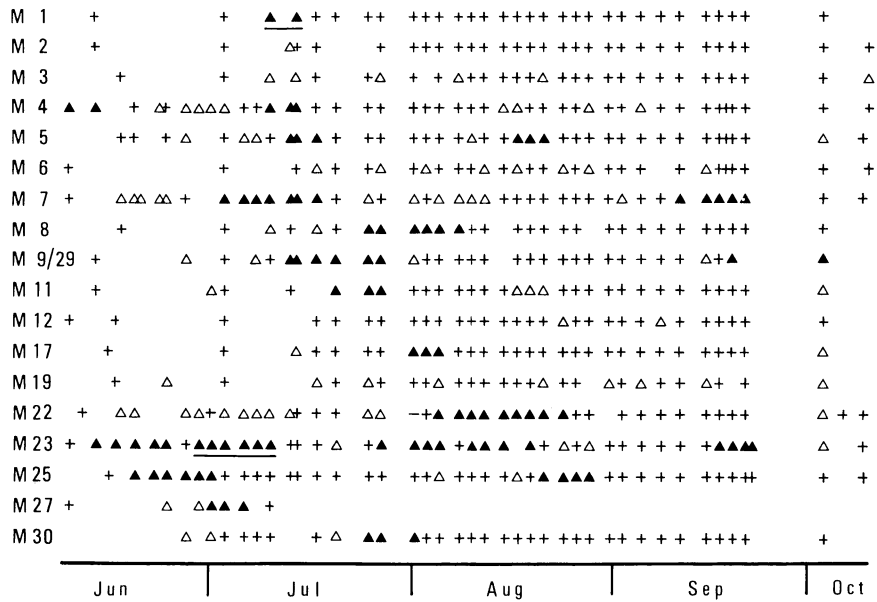
Fig. 2. Changes of social states for male *Tropheus moorii* who have paired with females at least once. Numbers following M are individual numbers. Social states were categorized as: solitary (puls sign), tentatively paired (open triangle) and stably paired (solid triangle). Underlined solid triangles indicate pairing with a male (see text). A minus sign indicates absence from the quadrat. Social states of M9 and M29 are shown on the same line, because we could not specify the exact day on which the latter replaced the former (occurred in the second half of August).

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F  1         ++ +−++ +++ ++ + +    ▲▲   ▲OO OOO OOOO OOO OO + + +  ++++      +
F  3     +  +∆ ∆+ ∆∆∆∆ ∆∆▲ ▲▲ − −    − −   −−O OOO O+++ +++ ++ + + +  ++++           +
F  4      +    + ++++ +++ ++ + +    ++   +++ +++ +▲▲− −−− −− − −− −  −−−−      +    +
F  5     +     + ++++ +++ ++ + +    OO   OOO OOO OOOO O++ ++ + + +  ++++      +
F  6      +    + ++++ +++ ++ + +    ++   +++ +++ ++++ +++ ++ + + ▲  ▲▲▲▲      O    O
F  7       O    O ++++ +++ ++ + +    ++   +++ +++ ++++ +++ ++ + + +  ++++      +
F  9    O O  OOO OOOO OO+ ++ − −    − −   −−− −−− −−−− −−− −− − −− −  −−−−      −
F 10     O    OO ++++ +++ ++ + +    ++   +++ +++ ++++ −−− −− −− −− −  −−−−      −
F 15    O +   ++ ++++ +++ ++ + +    +−   ∆∆∆ −▲▲ ▲▲▲− −−− −− −− −− −  −−−−      −
F 21          ∆∆ −∆∆∆ −−− − − O    OO   O+++ ++− +−−+ −−− −− −− −− −  −−−−      −
F 22    ∆  ∆▲ ▲▲ O−−− −−− − −− −    − −   +++ +++ ++++ +++ ++ + + ++  ++++      +    +
F 24     +    + ++++ +++ ++ + +    ++   +++ +++ +▲▲▲ ▲▲▲ −O O OO  OOOO      O+    +
F 25      ▲ ▲▲ ▲▲▲− −−O ◯O O O    OO   OOO +++ ++++ +++ ++ + + +  ++++      +
F 26   +      + ++++ +++ ++ + +    ++   −++ +++ +++− ∆−O OOO O OO  OOOO      +    +
F 30    ▲O  OOO OOOO OOO ◯O + +    ++   +++ +++ ++++ +++ ++ + ∆ ∆  ∆▲▲▲      −    O
F 33         − −−−−− −−− −O O O    OO   OOO OO+ ++++ +++ ++ + + ++  ++++      +
F 35         − −−−− +−− ++ + −    +−   −−▲ ▲▲▲ ▲▲▲▲ ▲O− −− − −− −  OOOO      + +
F 36         − −−−− −−− − −− −    − −   −O− OOO O++− −+− ++ + + +  ++++      − +

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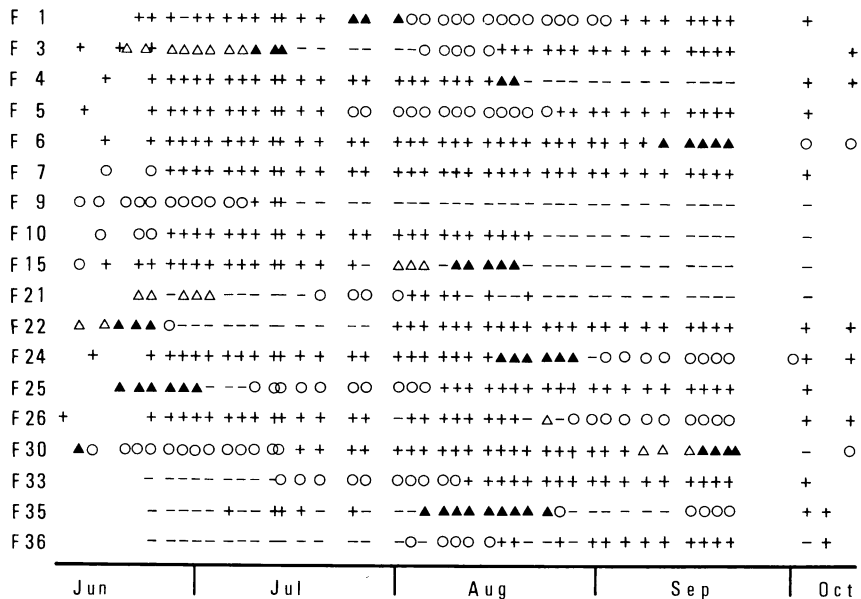
Fig. 3. Changes of social states for female *Tropheus moorii* who are estimated to have reproduced. Numbers following F are individual numbers. Social states were categorized as: solitary (plus sign), tentatively paired (open triangle), stably paired (solid triangle) and mouthbrooding (open circle). A minus sign indicates absence from the quadrat.

within 8 m of her territory. When visiting each male, she was never attacked by him. After a short stay (usually less than 10 min), she returned to her territory or moved to another male's territory.

The male usually received a visiting female with the tail-quivering courtship behaviour. He usually followed her around (usually within 50 cm) wherever she went in his territory (this behaviour is referred to as consortship hereafter), although some males merely tolerated the presence of a female, showing neither aggressive behaviour nor consortship. The female with whom the male consorted devoted herself to foraging, her feeding rate being very high (see the next section).

Of 29 territorial males in the quadrat, 19 were visited by females at least once. However, only 12 of them formed stable pairs with females that lasted more than 2 successive censuses (Fig. 2). The duration of stable pairing varied a great deal among pairs (Fig. 3), ranging from less than 4 days to 21 days. The average body size of males who formed stable pairs was not significantly greater than that of the other territorial males (98.7±4.4 mm SL, n=11 vs 96.5±6.9 mm SL, n=18; t=0.93, df=27, p= 0.36). A male (M23, 94.4 mm) who formed pairs most frequently was a little smaller than the average male body size (97.2 mm), and the largest male in the quadrat (M19, 105.0 mm) never formed a stable pair (Fig. 2). Males who formed stable pairs with females generally held territories including a high rock and a wide rocky area. Neighbouring males, by contrast, never formed stable pairs, even if their territories also included a high rock and a wide rocky area.

Pairs between males appeared on two occasions (between M10 and M1 and between M26 and M23, Fig. 2). In each case, two males had been neighbours, with one subsequently moving to the other's territory. The visitor was smaller in body size in one case (82.5 vs 97.8 mm SL), but larger in the other (101.4 vs 94.4 mm SL). The homosexual pairs continued for 2 and 6 successive censuses, respectively. The resident male consorted with the visitor in the same manner as in a heterosexual pair. After the breakup of the pair, the latter returned to his original territory and remained solitary until the end of study. In both cases, the visitor's own territory included a much smaller rocky area than the territory to which he visited (0.80 vs 3.14, 0.84 vs 7.12 m², and the maximum height of rocks in his territory was lower (10 vs 35, 40 vs 65 cm).

2) Spawning and brooding. In a stable pair, 'pseudo-spawning' (Nelissen, 1976) between the male and female sometimes occurred at a particular part of the territory. Such a site was usually a flat stone or rock whose upper surface was smooth and gently sloped in the shade of a big rock. Actual spawning was observed on one occasion. The sequences of courtship and spawning behaviour were conducted in the same manner as those observed in an aquarium (Nelissen, 1976).

Of 20 females who had been stably paired with males during two or more successive consuses, 12 were found to be mouthbrooding and the other 8 had disappeared in the following censuses. Of the 8 females who had disappeared, 2 (F4, F15) reappeared after an absence of 44 and 67 days, respectively, at the sites of their original territories. They were solitary and not mouthbrooding when they reappeared. Their absence was longer than the mouthbrooding duration (about 33 days, Yanagisawa and Sato, 1990), suggesting that they had mouthbrooded somewhere else in this period. The fact that females who had once stably paired were always found to be mouthbrooding indicates that the formation of a stable pair is followed by spawning.

Mouthbrooding females were always solitary, outside the males' territories, except for one female who was found under a rock in the male's territory in the first census after spawning. She disappeared before the next census. The average distance between the males' territories where females had paired and sites where they were mouthbrooding in or around the quadrat was 4.7 m (range: 2–11 m, n= 12). The actual average distance may be greater, since mouthbrooding females who had gone far away from the quadrat were not considered. Three females (F1, F5, F26) returned to their original territories to mouthbrood. (F5 was solitary without mouthbrooding in her territory until 20 July but was mouthbrooding in her territory in the next census on 25 July. Therefore, the territory in which she spawned is unknown.)

Mouthbrooding females usually settled in a site unoccupied by territory-owners; the sand-rock interface was often used. They were inactive on the bottom and their home ranges were small (0.75± 0.48 m², n=3). They were aggressive only against small fishes such as subadults of *Tropheus moorii* and *T. duboisi*. One exception is a female (F25) who actively defended her territory against intruders. Females took no food into the gut throughout the

mouthbrooding period, although their browsing rate increased with the need to feed the young developing in the buccal cavity (Yanagisawa and Sato, 1990).

Temporal feeding of grown young outside the female's mouth, which commonly occurs in mouthbrooding cichlid fishes (Fryer and Iles, 1972), was never seen in this study, though it was observed in an aquarium. Juveniles soon after independence from the mother were never found in the quadrat, but in shallower water. On 2 occasions, a female mouthbrooding young (more than 30-day old) in the quadrat was absent from her brooding site, and had probably migrated to a shallower area to release the young. After mouthbrooding, females usually remained at the brooding sites (n=14), but a few females moved slightly (1, 2 and 6 m, n=3). They expanded their territories as their feeding activity increased.

Of 32 females who stayed in the quadrat at the start of the study, 18 spawned during the study period (Fig. 3), if females who disappeared after stable pairing were regarded as having spawned. Two (F15, F30) of them spawned twice. The other 14 females never spawned.

Feeding activity and some physical conditions. *T. moorii* spent most of the time browsing epilithic algae within the territory. The feeding rate (the number of browsing actions per 5 min) of a solitary male did not differ from that of a nonbrooding, solitary female ($\bar{x}\pm SD=179.0\pm21.2$, n=8 vs 162.7±49.5, n=23; Mann-Whitney U test, $U_1=63.5$, p>0.05). On the other hand, in a pair wherein a male consorted with a female, the female always fed more actively than her mate (266.4±33.9 vs 149.5±34.9, n=10; Wilcoxon signed rank test, T=0, p<0.01). The feeding rate of such females was higher than that of solitary females (Mann-Whitney U test, $U_1=12.5$, p<0.001), and conversely, that of the consorting males was nearly significantly lower than that of solitary males ($U_1=7.5$, p≒0.05).

Females mouthbrooding early embryos rarely showed feeding actions, but their feeding rate increased with the development of young, as already reported (Yanagisawa and Sato, 1990). Food taken in the mouth was not swallowed, but ingested by the young in the buccal cavity (Yanagisawa and Sato, 1990).

Gut fullness index [(wet weight of gut contents/wet body weight)×100] did not differ between solitary males and females (5.48±1.72, n=38 vs 5.89±1.48, n=39; t-test, t=1.36, df=75, p=0.18). Cor-
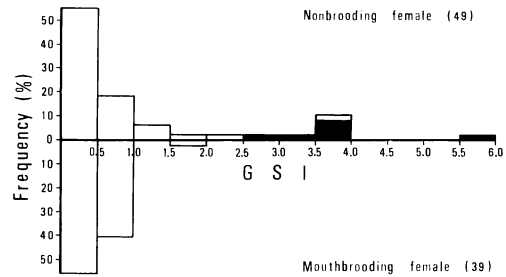

Fig. 4. Frequency distribution of gonadosomatic index (GSI) for mouthbrooding females and nonbrooding females in *Tropheus moorii*. Black areas are for females paired in a male territory. Sample size in parentheses.

responding to the higher feeding rate, females with whom males consorted had higher values of this index than the consorting males (6.63±1.05, n=7 vs 4.87±1.20, n=7; t=3.12, df=12, p<0.01).

The fraction of organic matter in the stomach contents varied greatly between individuals, but did not differ significantly between males (24.8±7.5, n=25) and females (25.8±9.2, n=27). Individuals occupying large rock outcrops protruding more than 1 m had higher values of organic matter than those occupying the lower rocks (30.4±4.8, n=8 males+8 females vs 21.7±8.2, n=17 females+19 females; t=3.79, df=42, p<0.001). Females with whom males consorted usually had larger values than the other females, but the differences were not significant (30.5±9.9, n=7 vs 24.1±8.3, n=20; t=1.61, df=25, p=0.12).

Gonadosomatic index [(wet gonad weight/wet body weight)×100] was high in females with whom males consorted (3.74±0.86, n=7; Fig. 4); they had fully mature ovaries. In contrast, this index was much lower in mouthbrooding females (0.56±0.28, n=39); none had mature eggs in the ovaries with the exception of one individual whose ovary contained a single mature egg. Gonadal recovery of females after mouthbrooding was slow: no females who were known to have passed 25–90 post-mouthbrooding days had fully mature eggs, and their gonadosomatic index remained low (0.54±0.26, n=14). This low gonadosomatic index was common to most solitary females (Fig. 4). These results suggest that the ovaries rapidly develop in females during the period that they are in the male's territory. Gonadosomatic index of males was constantly low (0.13±0.05, n=47).
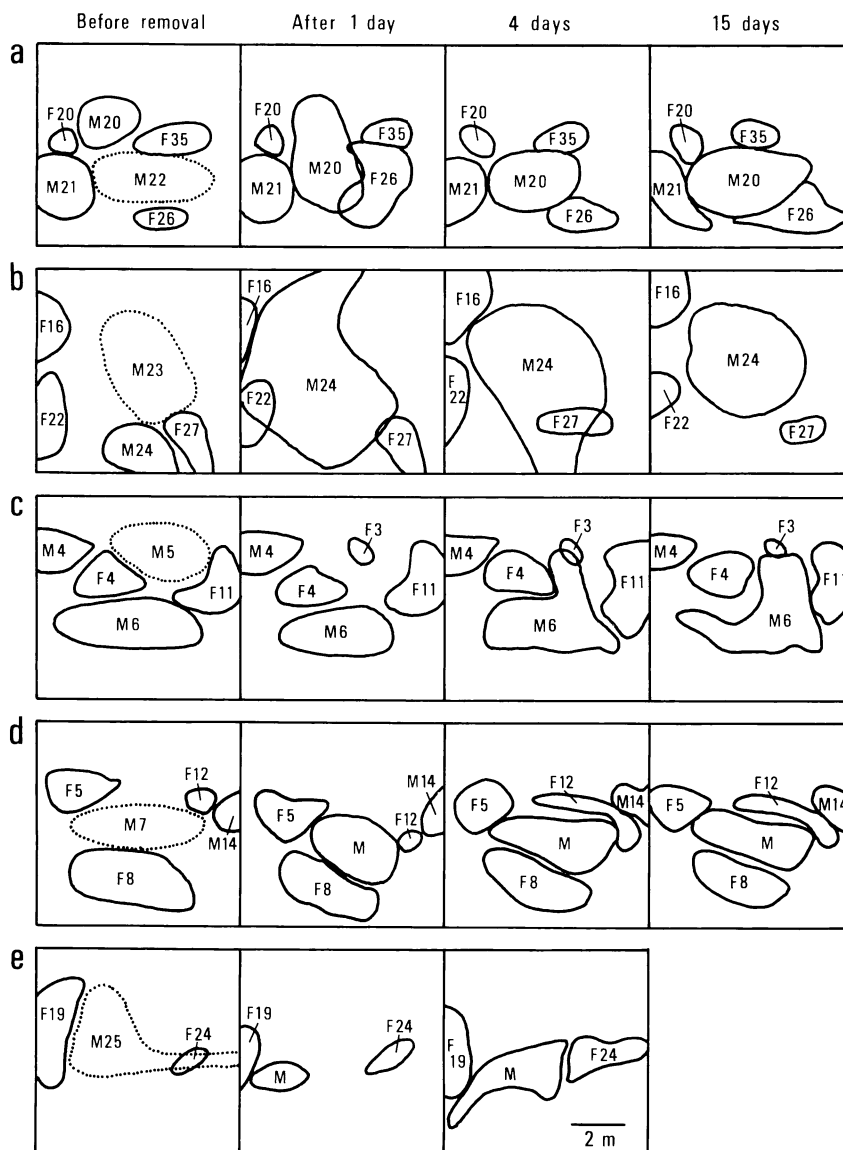
Fig. 5. Positional changes of *Tropheus moorii* 1, 4 and 15 days after the removal of the dominant males, M22 (a), M23 (b), M5 (c), M7 (d) and M25 (e). M not followed by a numeral indicates a male of unknown origin. Each territory was estimated from a 15 min observation of removed and replacement fish and from a 2–15 min observation of other fish.

The condition factor {[(wet body weight−wet weight of gut contents)/(standard length)^3] ×100} of mouthbrooding females was lower than that of nonbrooding solitary females (4.06 g/mm^3 ± 0.24, n=39 vs 4.37±0.23, n=39; t-test, t=5.81, df=76, p<0.001). Females with whom males consorted surpassed nonbrooding solitary females in this factor (4.63±0.23, n=7; t=2.77, df=44, p<0.01). The

condition factor of males (4.32±0.32, n=34) was similar to that of nonbrooding solitary females and did not correlate with their social states.

The amount of fat stored within the abdominal cavity varied greatly between individuals; fat index [(wet fat weight/wet body weight)×100] ranged from 0 to 4.41. The average fat index of males was much higher than that of females (1.07±1.00, n=

37, vs 0.39 ± 0.58, n=65; t=4.27, df=100, p< 0.001), suggesting that surplus nutrition is stored in the form of fat in the male. Among males whose reproductive experiences were known, those who had not spawned throughout the study period had higher values of this index than those who had spawned (Mann-Whitney U test, $N_1 = 15$, $N_2 = 11$, $U_1 = 43$, p<0.05). In the female, fat index did not correlate with the social states.

Removal experiment. After the removal of 5 males (M22, M23, M5, M7, M25) whom females had often visited, all of their territories were replaced by one or two conspecifics. The behaviour of the replacement fish is individually described below.

1) Removal of M22 (104.0 mm, Fig. 5a): Within one day of the removal, two neighbours, M20 (102.6 mm) and F26 (98.1 mm), expanded their territories occupying two thirds and one third of M22's territory, respectively. From the 5th day on, F26, who had withdrawn from M22's territory, stayed within her original territory, whereas, M20, who had left his original territory, managed all of M22's territory. On the 8th day, M20 was paired with a female.

2) Removal of M23 (94.4 mm, Fig. 5b): One day after the removal, a neighbouring male, M24 (97.5 mm), dominated a wide area including both M23's territory and his original territory. F27 (90.6 mm), who had been paired with M23, remained in the territory after the latter's removal. M24 sometimes consorted with her. On the 5th day, M24 still had a large territory at the same site and sometimes consorted with F27 (105 sec during a 15 min period). On the 8th and 16th days, F27 kept still at the border of M24's territory while mouthbrooding, suggesting that she had spawned with M24. By the 16th day, M24's territory had contracted, to almost coincide with the former M23 territory.

3) Removal of M5 (101.3 mm, Fig. 5c): Within a day of the removal, F3 (86.0 mm), who had been lost for a week, appeared in one corner of M5's territory. She remained there until she was collected 20 days later. By the 5th day, a neighbouring male, M6 (101.2 mm), had expanded his territory to include the main part of M5's territory unoccupied by F3. While maintaining a large territory, M6 paired with a female of unknown origin on the 8th day and spawned with her on the 16th day (this is the only spawning we could observe).

4) Removal of M7 (98.0 mm, Fig. 5d): Within a day of the removal, a male (100.0 mm) of unknown origin occupied the greater part of M7's territory

and consorted with a female of unknown origin. From the 5th day onwards, he remained solitary, and his territory nearly coinciding with the former M7 territory.

5) Removal of M25 (100.4 mm, Fig. 5e): A male (91.3 mm) of unknown origin and F24 (87.4 mm), who had been at the verge of M25's territory, each occupied a part of M25's territory within a day of the removal. By the 5th day, both had expanded their territories dividing M25's territory into equal shares. However, at this time the male was accidentally caught with a barrier net. Further expansion of the territory by F24 did not occur thereafter.

Thus territories of removed males were finally occupied by adjacent males (in 3 cases) or males of unknown origin (in 2 cases). These males paired with females within a week of the replacement, except in experiment 5 where the replacement male was captured by accident, and two of them spawned or are thought to have spawned with new mates. Three replacement males whose previous states were known had never paired (M20, M24) or only tentatively paired (M6) with females in their original territories, though they were as large as the removed males.

Discussion

Social and mating system. Most cichlid fishes in African lakes are maternal mouthbrooders, in which the female broods eggs and young in her mouth and the male has no concern with brooding (Fryer and Iles, 1972; Lowe-McConnell, 1987). Such maternal mouthbrooders are common in Lake Tanganyika, although one third of the cichlid species in this lake are substrate brooders (Brichard, 1978) and some of the mouthbrooders are biparental, with both male and female participating in mouthbrooding and/or guarding on the substrate (Yanagisawa and Nshombo, 1983; Yanagisawa, 1986; Kuwamura, 1986, 1988; Kuwamura et al., 1989; Yanagisawa et al., 1990).

The mating system of maternal mouthbrooders of African cichlid fishes so far studied is usually promiscuous: a male and female do not form a lasting pair bond and both breed more than once with different mates. A common feature is that the female visits the male's territory to spawn and leaves carrying fertilized eggs inside the mouth soon after the spawning (Kuwamura, 1986). The male's territory is established for mating in many species, such as

Cyathopharynx furcifer (Nshombo, 1991), *Astatotilapia burtoni* (Fernald and Hirata, 1977) and *Cyrtocara eucinostomus* (McKaye, 1983). Alternatively, the territory is the one which the male has maintained as a feeding site, as seen in *Pseudosimochromis curvifrons* (Kuwamura, 1987) and *Pseudotropheus zebra* (Holzberg, 1978; Ribbink et al., 1983) as well as in *T. moorii.*

Peculiar to *T. moorii* as a maternal mouthbrooder is that a male and female form a pair bond for several days prior to spawning and the female actively forages while the male consorts with her. Ecological conditions which make this behaviour beneficial should be considered.

In *T. moorii*, the gonadosomatic index was low in almost all solitary females (Fig. 4) and the gonadal recovery of solitary females after the termination of mouthbrooding was very slow. These facts suggest that females do not attain fully mature ovaries in their own territories in spite of continuous daytime foraging. Epilithic algae, the primary food item for *T. moorii*, are not homogeneous in distribution as formerly believed (Power, 1983; Reinthal, 1990); their abundance and species composition vary corresponding to depth, and substrate inclination, etc. Furthermore, the efficiency of dietary carbon and nitrogen conversion to growth by some herbivorous fishes is extremely low (Polunin and Brothers, 1989) and deficiency of minerals and trace elements drastically lowers fecundity (Luquet and Watanabe, 1986). We, therefore, infer that the female's territory is a second-grade, feeding site where some nutritive elements are in short supply. Consequently the female makes up for the deficiency prior to spawning by devoting herself to foraging under the male's protection.

The increased feeding rate of a paired female and the attentive defense by her mate, as seen in *T. moorii*, are also known in monogamous butterflyfishes, *Chaetodon multicinctus* and *C. quadrimaculatus*, which feed on corals, also an energetically poor food resource (Hourigan, 1989). The hypothesis regarding the selective advantage of the pair bond for these bufferflyfishes is that fecundity is food limited and pairing increases the time available to females for feeding and enables the paired male to share in his mate's increased fecundity (Hourigan, 1989). This idea may be applicable to *T. moorii.*

Each female usually visited more than one male's territory before the formation of a stable pair. Even if a male received the visiting female with a courtship display, she often left his territory within a few minutes. Eventually, she formed stable pairs with some particular males. Such behaviour suggests that females assess the quality of the territory and/or male during the stay in the male's territory. There was only a weak correlation between the body size of males and their success of pairing, and replacement males in the male removal experiment, who had long been solitary in their old territories, soon got mates. Thus the quality of the territory may be the more important criterion for mate choice by the female, and may depend upon the availability of food.

A remarkable feature of male *T. moorii* is that they are strongly site-attached, irrespective of their reproductive achievement. Most males remained in their territories throughout the study, even if they had never received visits from females. Fat was stored more in bachelor males than in males who experienced stable pairing. From this result we suggest that the bachelor males feed in their territories so as to get as much nutrition as possible until they acquire a territory that attracts females.

The unusual behaviour of two males (M10, M26), who stayed in territories of neighbouring males for several days, may be explained from the standpoint of the improvement in their nutritive conditions. Curiously, the resident males not only tolerated their presence but also consorted with them. Possibly the resident males erroneously regarded the 'changers-on' as females.

Colour morphs and social selection. Colour differences between local populations are a notable feature of cichlid fishes in Lake Tanganyika. This feature is most remarkably represented by *T. moorii*, in which many local morphs have distinct colour patterns (Brichard, 1978; Axelrod et al., 1985; Konings, 1988). For example, the 'Bemba orange' morph, which we studied, has a greatly different body colour from the more northern 'All black' morph, which has no band, although the two populations are separated only by a sandy beach a few kilometers long.

It is unlikely that such colour differences resulted only from natural selection, since great geographical variation in the environmental conditions corresponding to the colour variations apparently does not exist in the habitat of *T. moorii*. However, if body colour is used as a highly significant signal in social interaction and selection for success in the competition using this signal is intense, then a rapid divergence in body colour can be expected between iso-

lated populations, despite a lack of environmental differences (see West-Eberhard, 1983; Dominey, 1984). The possibility that *T. moorii* uses the body colour as a social signal is briefly considered below.

The bright, vertical band on the dark body is conspicuous in the 'Bemba orange' morph, as well as in many other morphs. In this morph, the band is orange in both males and females, though usually a little more yellowish in the latter, with a longer and broader continuation onto the dorsal fin. Since there is little sexual dichromatism and no marked colour changes occur during courtship and spawning, body colour seems to be unimportant in mate choice.

On the other hand, it is clear that the body colour serves as a signal in social behaviour. As this study showed, nearly all of the hard substrates in the habitat were packed with individual territories, each being stably maintained for a long time. The orange band of territory-holders sometimes became brighter when they attacked intruders. In contrast, the band usually faded in fish who left their own territories, unless chasing intruders. Such colour changes may enable each fish to inform others about the level of its aggressiveness and may therefore serve to reduce agonistic encounters. Moreover, body colour may serve for personal acquaintances between neighbouring individuals established through frequent contacts during territorial and extraterritorial activities (C. Sturmbauer, pers. comm.).

Our preliminary observations of the 'All black' morph, whose colour change was not distinct, indicate that it more frequently made one-sided attacks and less frequently performed appeasement displays compared with the 'Bemba orange' morph. The difference in colour pattern between these two morphs may reflect differences in social and mating systems. Comparative studies on the social and mating systems of different colour morphs will be fruitful for understanding of how the body colour is used as a signal in social competition in this fish.

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タンガニイカ湖に生息するカワスズメ科の口内保育魚 *Tropheus moorii* の社会構造と配偶システム

柳沢康信・西田　睦

アフリカのタンガニイカ湖に生息する付着藻類食魚 *Tropheus moorii* のナワバリ行動，繁殖行動および移動パターンを個体識別して調査した．成魚は互いに隣接する採食ナワバリを構えていた．雄は雌よりも背の高い大きな岩を占拠し，長期間同一場所に留まった．雌は，つがいを形成するために雄のナワバリに移動し，産卵に至るまで最長3週間雄に護衛されながら盛んに摂餌活動を行った．産卵後，雌はナワバリを離れ，約1カ月単独で子供を口内保育した．雌の生殖腺の検査および優勢雄の除去実験から，雌は，自分自身のナワバリ内では十分に成熟することができないため，必要な食料を提供できるナワバリをもつ雄を配偶者として選択すると推定した．また，この種の多数の色彩品種の進化について簡単に議論した．

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