

Maintenance of Separate Territories for Mating and Feeding by Males of a Maternal Mouthbrooding Cichlid, *Gnathochromis pfefferi*, in Lake Tanganyika

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Abstract Territorial behavior, feeding habits and breeding behavior of a mouthbrooding cichlid fish, *Gnathochromis pfefferi*, were investigated in the northwestern part of Lake Tanganyika. Males defended feeding territories against conspecifics and females had overlapping foraging areas. Both males and females fed exclusively on shrimps. Males also defended mating territories separately from feeding territories. Males' feeding territories were established over the substrate of sand, pebbles and rocks, while their mating territories were congregated in and near the vegetated patches. The feeding territory was near or adjacent to the mating territory in some cases, but was 80 to 130 m away in others. In the morning males patrolled the whole mating territory to find and mate with females, but in the afternoon they foraged in their feeding territories. Males did not prepare nests for mating, unlike many other maternal mouthbrooders with mating territories. After spawning, mouthbrooding females lurked in or near the vegetated patches. Each male returned to the same mating territory every morning for several months, in spite of competition for mating sites. The long-term occupation of territories suggests that territorial ownership is recognized by competitors while the owner is absent.

Defending a territory is the predominant way of monopolizing resources, e.g., food, mating sites, spawning sites and resting sites, in animals. Generally an individual defends one territory. Territorial behavior is also predominant in cichlid fishes (e.g., Lowe-McConnell, 1959; Fryer and Iles, 1972; Barlow, 1974; Taborsky and Limberger, 1981; Limberger, 1983; Ribbink et al., 1983; McKaye, 1984; Takamura, 1984; Kuwamura, 1986; Kohda, 1991; Yanagisawa and Nishida, 1991), in which an individual seems to defend only one territory for feeding or mating. Among maternal mouthbrooders, not only feeding but also mating is performed in a single territory in some species (Kuwamura, 1987, 1992; Kohda, 1991; Yanagisawa and Nishida, 1991), while only mating occurs in a territory in others (Lowe-McConnell, 1959; Coe, 1966; Loiselle and Barlow, 1978; McKaye, 1983, 1984).

Gnathochromis pfefferi is a maternal mouthbrooding cichlid, occurring in Lake Tanganyika (Brichard, 1978; Poll, 1986). The species feeds on small shrimps, with some individuals forming feeding schools with other benthic animal-feeding cichlids

(Hori, 1987). It has been reported that male *G. pfefferi* defend spawning sites only temporarily (Kuwamura, 1986), but this paper reports that they maintain two separate territories for feeding and mating.

In this paper, territorial behavior, feeding habits and breeding behavior of *G. pfefferi* are described.

Materials and Methods

The field investigation, using SCUBA, was done at Mbemba (3°36'S, 29°10'E), Zaire, on the northwest coast of Lake Tanganyika from October 1988 to April 1989. A 73 m × 28 m study area was established over a substrate of sand, pebbles and rocks, at depths of 1 to 10 m, and divided with string into 2 m × 2 m squares. The study area included 2 vegetated patches composed of two grass species, *Potamogeton schweinfurthii* and *Vallisneria* sp. *Gnathochromis pfefferi* were sexed in the field on the basis of body color, courting, mating and brooding behavior, confirmation being made by subsequent examination of the

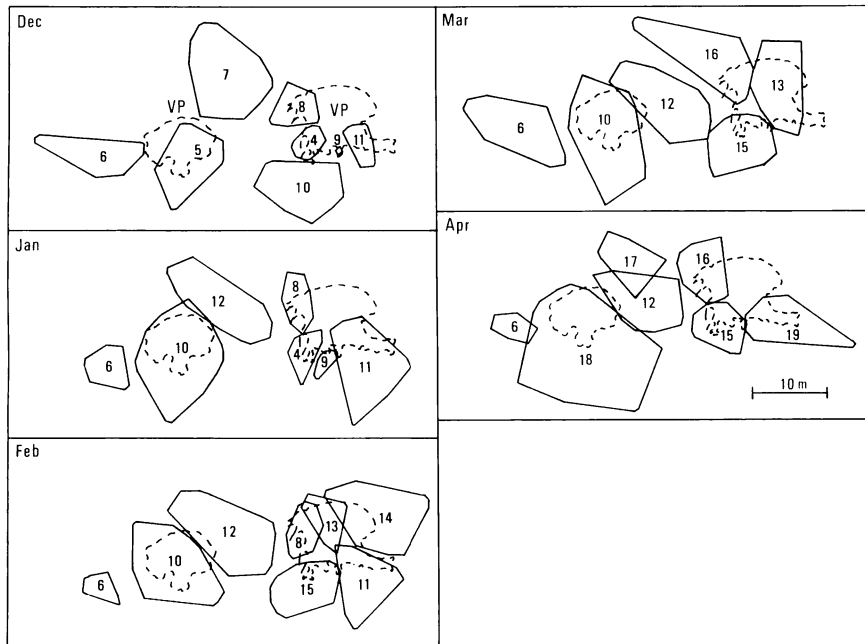


Fig. 1. Mating territories of 17 males, each being the area patrolled during one to three 10-min observations. The area which Male 11 patrolled had been occupied by Male 2 from the beginning to the middle of December. Areas enclosed by broken lines are vegetated patches (VP).

gonads. Nineteen males and 16 females were individually identified by body color, especially the patterns of orange spots on the head.

The whole study area was patrolled once per day, between 10:00 and 16:00, at intervals of 1 to 4 days, to record positions of the identified and unidentified individuals, the number and positions of brooding females, and to locate mating sites. The vegetated patches and their vicinities were repeatedly patrolled between 6:15 and 16:00 every 1 to 3 days to record the positions of territory owners, the times of territorial defense, and the times, positions and participants of matings.

Seventeen males, who defended their territories in and near the vegetated patches in the mornings, were tracked for 10 min to record their movements, social interactions and any occurrence of feeding. The 10 min observations were carried out from 2 to 29 times per male. Five foraging males were tracked for 30 or 60 min to determine their feeding areas and describe feeding behavior and social interactions. The total observation time was from 2 to 9 hrs per male. Six females, which foraged near the vegetated patches, were tracked for 10 min. The 10 min observations were done from 4 to 11 times per female to determine

the feeding area boundaries and record social interactions.

On April 20, 21 and 22, 1989, 49 individuals, including 21 brooding females, were collected with gill and hand nets. In the laboratory, their standard length (SL), body and gonad weights were measured, and their stomach contents examined.

Results

Male territoriality

Six to 8 males gathered in the vegetated patches and actively patrolled their mating territories between 6:30 and 10:00 throughout the observation period (Fig. 1). The patrolled areas, which barely overlapped with one another, varied in size from male to male, ranging from 1 m^2 to 224 m^2 (mean \pm SD = $73 \text{ m}^2 \pm 50$, $n = 16$) estimated from two or three 10-min observations. The males swam around the whole area, which lacked a focal point such as a nest (Fig. 2). When a male encountered other conspecific males in his territory, he attacked them. Fights sometimes occurred on the borders of the territories. The

Separation of Feeding and Mating Territories

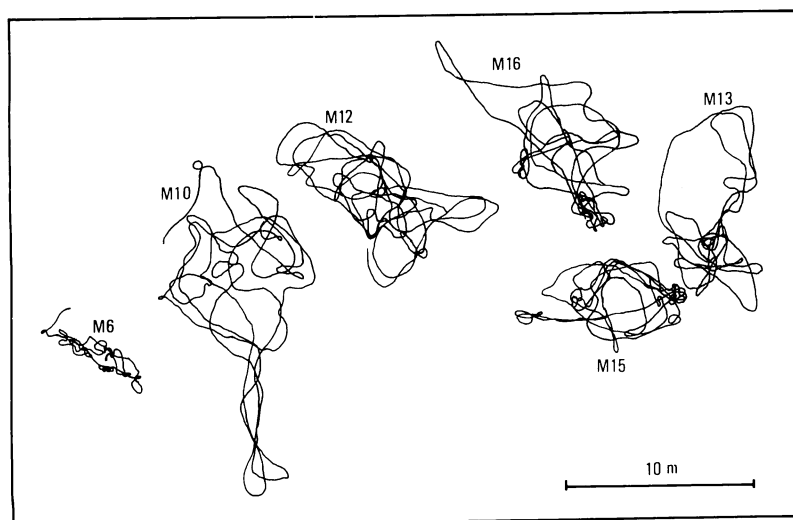


Fig. 2. Tracks of 6 males during a 10-min observation made between 6:30 and 8:10 on March 11.

feeding frequency of the males in the vegetated patches, except one (M6), was low compared to that (number of picks/10 min = 17.5 ± 8.4 SD, $n = 25$) in the foraging areas (Table 1). Sixty-three percent of the males were never observed feeding in 50% or more of the 10-min morning observations made in the vegetated patches.

Seventeen males established territories during a 5 month period, maintaining them on the same sites for 1 to 3 or more months. Only one male (M10) shifted his territory from one place to another (Fig. 1). The size of the males which established mating territories was from 95 to 103 mm SL ($97 \text{ mm} \pm 2.7$ SD, $n = 8$).

Of the 17 territory owners, 11 departed permanently during the study period, their territories being quickly occupied by other males. One change of territory owner occurred, following a fight between the initial owner (M8) and an intruder (M16). After

disappearing from the territories, 3 males (M2, M8 and M11) were found foraging elsewhere.

The males patrolled the mating territories from early in the morning (before 7:00) until usually about 9:00 or 10:00, before going to their foraging areas (Fig. 3). They were found in the same territories the following morning.

While the established territory owners were absent in the territories, other males were found courting females there.

The foraging areas of 14 of the 17 territory owners were located by tracking, and found to be near or adjacent to the mating territories in 9 cases (M2, M4, M5, M8, M11, M13, M16, M17 and M19; see M2, M4 and M5 in Figs. 1 and 5), but about 80 to 130 m distant in the other 5 (M9, M10, M12, M15 and M18; Fig. 4). Males in the former group were often found in their mating territories in the afternoon, but those in the latter were not.

Table 1. Feeding activity of males during 10-min observation periods (10Ms) made in and near the vegetated patches before 10:00

	Males																
	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16	M17	M18	M19	
Total number of 10Ms	6	2	22	2	15	17	24	12	26	11	3	29	8	8	5	7	
% of 10Ms with feeding	0	0	95	100	67	6	0	42	4	45	100	14	62	50	0	86	
Mean number of picks per 10 Ms when feeding occurred*	—	—	23 (8.7)	2 (0)	7 (6.4)	1 (0)	—	9 (8.1)	1 (0)	9 (10.4)	12 (9.2)	3 (2.1)	9 (5.3)	?	—	1 (0)	

* Standard deviations in parentheses.

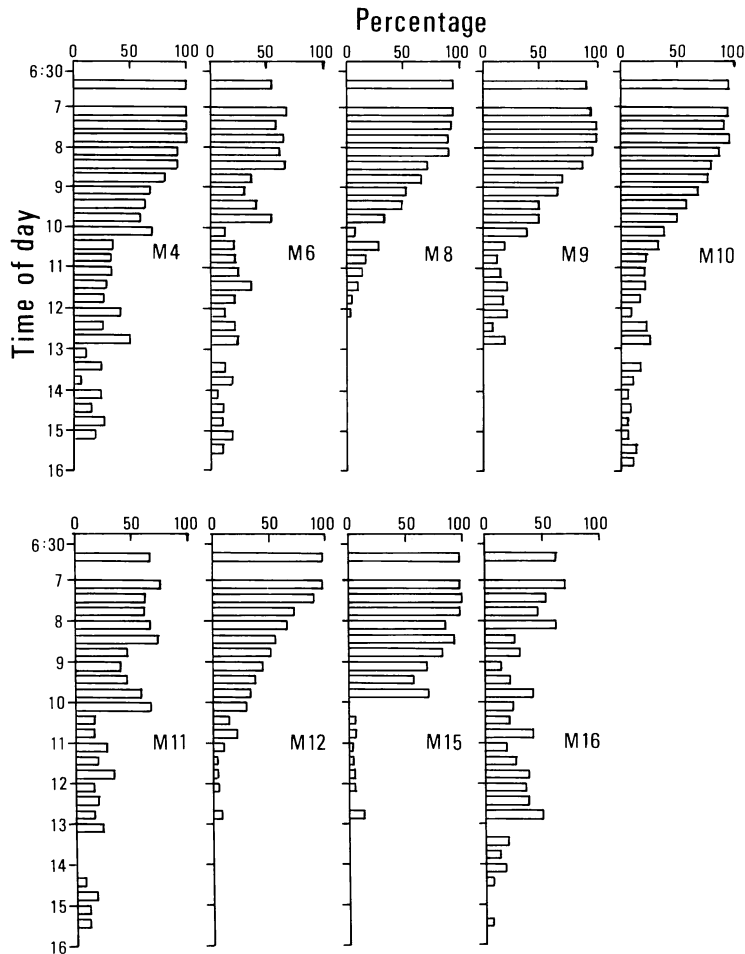


Fig. 3. Percentage of the observation days when males stayed at their mating territories. Data for nine males which were observed on 5 or more days at each time period (20 min) are shown.

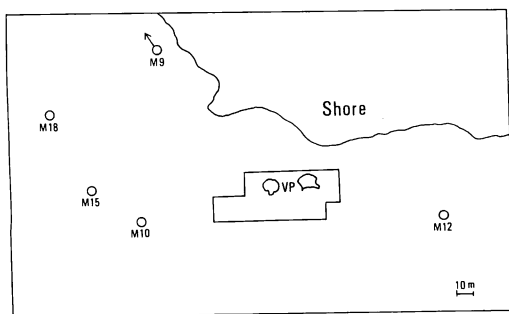


Fig. 4. Five male foraging areas which were relatively distant from their respective mating territories. M9 was lost sight of before reaching his foraging area. VP—vegetated patch.

The foraging areas of 5 males were situated in the study area and its vicinity, 3 (M2, M4 and M5) of the males also possessing mating territories. The males were found in similar areas each observation (Fig. 5), spending almost all of their time in foraging. They picked up shrimps on the pebbles and rocks. Adjacent foraging areas barely overlapped. When a male encountered other conspecific males or conspecifics of unknown sex in his foraging area, he usually attacked them. These results indicate that males defended their feeding territories. The size of the territories ranged from 32 m² to 552 m².

In the feeding territories, of the 5 males, one (M5) always foraged following a large cichlid, *Lobochilotes labiatus*, another (M3) foraged by itself or following a feeding school of the cichlid, *Lamprologus callipt-*

Separation of Feeding and Mating Territories

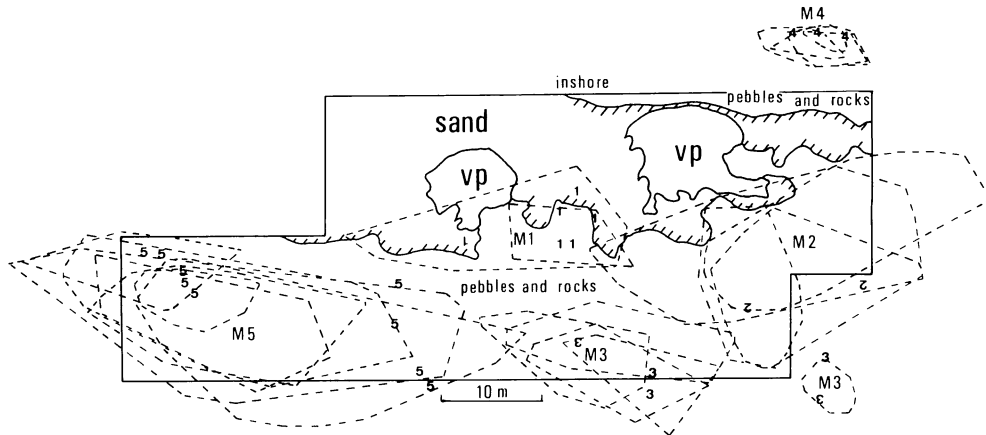


Fig. 5. Feeding territories of 5 males (M1–M5) in November and December. The area within which a male picked during an observation period of 30 or 60 min is enclosed by a broken line. Numerals indicate points where the males attacked other conspecifics. Inverted numerals indicate points where the males were attacked by other conspecifics. The straight solid line indicates the outermost string of the study area. VP—vegetated patch.

erus, and the others foraged by themselves. When the fish followed by M5 left the territory, the latter remained in the area and searched for another of that species. M3 followed a school of *L. callipterus* when the latter passed near by, but also remained in the territory when the school departed.

Home ranges of females

Females foraged on sand, pebble and rock substrates. Six females, which foraged on the sandy bottom near the vegetated patches, were tracked individually (Fig. 6). They remained near the vegetated patches throughout the study period. The female foraging areas overlapped, with encounters between females, resulting in attack of one female against the other.

Mating and spawning sites

Spawnings by 30 females occurred exclusively in the mating territories. Mating was achieved as follows. The male swam around swiftly near the bottom of his territory, searching for a female (swimming distance = $100\text{ m} \pm 31\text{ SD}$ [$n = 10$] in 10 min). When the male found a female, he followed her, repeatedly taking a head-up position and quivering his body by her nose, and tried to lead her to a spawning site.

At the spawning site, the male and female pre-

sented their abdomens to each other, quivering their bodies, and simultaneously one fish brought its mouth into close proximity to the genital area of the other (T-position). The T-position was repeated mutually before spawning, which started between 10 minutes and 3 hours after the male started to follow the female. The female usually laid 1 or 2 eggs (maximum 6) at a bout of T-position, and quickly turned to pick them up in her mouth. The T-position with spawning was usually repeated from 10 to 33 times over an extended period. After the last oviposition, the mutual T-position was repeated.

Mating was interrupted by the intrusion of neighboring territory owners or other conspecific males in 16 cases. The mating males usually repulsed the intruders to resume mating, but lost their mates in 6 cases.

Spawning occurred at 39 sites, all, except one, which was a rock surface, being shallow depressions (1 to 3 cm in depth and 12 to 27 cm in major axis diameter) in the sand, with a boulder situated on one side in 35.9% of cases. Males were not observed preparing the depressions, most of which were probably made by wave action. Sand mounds made by another cichlid, *Cyathopharynx furcifer*, were also used for spawning in 3 cases (7.7%). Males usually changed the sites between spawnings.

Spawning occurred from December to April. During this period, 30 females were observed spawn-

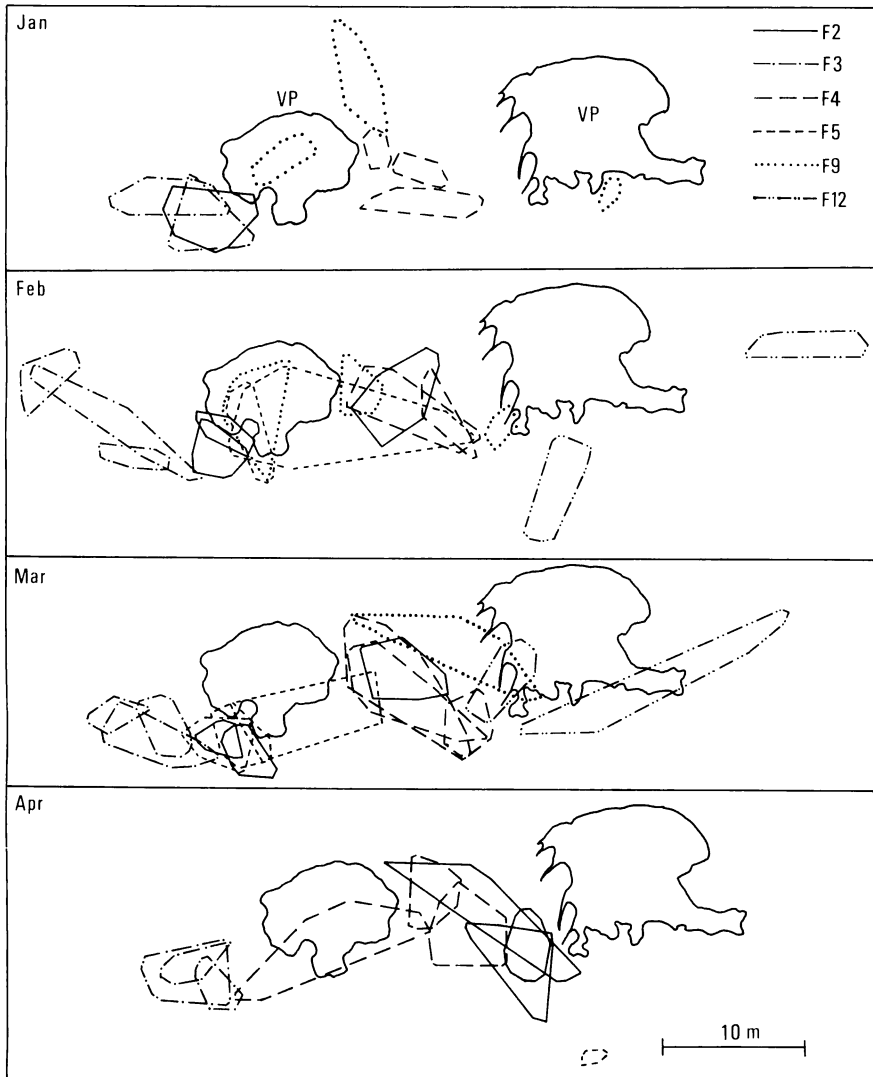


Fig. 6. Home ranges of 6 females, each being the area within which the female moved during a 10-min period. VP—vegetated patch.

ing. Spawning started before 8:00 in 21 females (70%) and finished before noon on all occasions. Spawning time was 30 min on average (15 to 44 min, $n = 17$). Of the 30 females, 26 (86.7%) spawned with one male and the others (13.3%) with two in a day.

The number of females with which the 17 owners of mating territories mated between 6:15 and 10:00 varied from 0 to 8 per male. Except for M6, the number of females with which the males mated was positively correlated with the duration (days) of maintenance of the mating territory (Spearman rank

correlation coefficient: $r_s = 0.818$, $p < 0.01$).

Brooding behavior and breeding cycle of females

Parental care was carried out solely by females who mouthbrooded the eggs and young. Guarding of the young was not observed. Brooding females occurred in the study area throughout the observation period, but the number fluctuated between 5 and 27. The sites where brooding females occurred were restricted mainly to and near the vegetated patches.

They usually lurked in the vegetation or by rocks without feeding.

The size range of brooding females was from 63 to 86 mm SL ($74 \text{ mm} \pm 6.1$, $n=21$). The number of brooded eggs or larvae per female was from 21 to 68 (45.6 ± 12.8 , $n=16$). The egg size was 3.1 mm (0.1 SD) \times 2.4 mm (0.1 SD) ($n=10$). The total length of brooded juvenile at the most developed stage (almost completely absorbed yolk) was $12.7 \text{ mm} \pm 0.12 \text{ SD}$ ($n=10$).

Based on the 16 identified females, the maximum duration of mouthbrooding was 21 days and the females bred from 1 to 3 times during the 4 month period. The spawning interval was estimated to be about 50 to 60 days.

Gut contents

All foraging individuals, which were caught between 9:00 and 11:30, had exclusively small shrimps in their stomachs. The number of shrimps per stomach was $37.3 \pm 20.1 \text{ SD}$ (range=6 to 74, $n=11$) for males (SL= $86 \text{ mm} \pm 9.9 \text{ SD}$) and $17.7 \pm 11.3 \text{ SD}$ (range=4 to 37, $n=9$) for females (SL= $73 \text{ mm} \pm 10.4 \text{ SD}$).

Of the six males (M12, M15, M16, M17, M18 and M19), which were caught in their mating territories between 7:00 and 8:00, three had empty stomachs and the others contained 1, 3 and 45 shrimps, respectively.

All of the mouthbrooding females caught ($n=21$) had empty stomachs, except one which had been caught just after spawning and contained 16 shrimps.

Discussion

Defense of two separate areas by a male

The results indicated that male *Gnathochromis pfefferi* maintain two separate territories for mating and feeding. An individual which establishes two separate territories is forced to neglect the defense of one while staying in the other. The degree of neglect will depend upon a distance between the two territories. The shorter the distance, the more easily an individual can move between the two territories. In *G. pfefferi*, males whose mating territories were near or adjacent to their feeding territories repeatedly came and went between the two territories in the course of a day, but males whose two territories were

distant did not do so. In either case, the neglect of territorial defense may have resulted in loss of resources in the territory, but did not in loss of the territory.

Food resources (shrimps) in the feeding territory must have been eaten by intruders while the male *G. pfefferi* stayed in his mating territory. However, the possibility of his losing a mating opportunity while visiting the feeding territory must have been low because matings occurred at that time of day when males remained in their mating territories.

Loss of a territory resulting from the neglect of territorial defense occurs in the mouthbrooding cichlids, *Cyrtocara eucinostomus* (McKaye, 1983) and *Sarotherodon grahami* (Coe, 1966). In these species, males lose their mating territories when they leave to forage. In contrast, males did not lose territory ownership in *G. pfefferi*. Each male repeatedly returned to the same mating territory every morning although other males appeared in the territory during the owner's absence. Competition for mating sites between males must exist in *G. pfefferi*, because the area of the mating territories, the vegetated patch, was limited (Fig. 5) and recruitment of a new territory owner following the disappearance of the former owner was observed several times during the observation period. Nevertheless, fighting between males for a mating territory was observed only once and wounds from such conflicts were not noticed on the bodies of any mating territory owners. These observations suggest that long-term occupation of the same mating territory was possible because the ownership was recognized by competitors even during the owner's absence. Observations of events following an owner's return to his mating territory are necessary for an understanding of the mechanism by which a male can occupy the same site day after day, in spite of competition.

Many cichlids defend feeding territories (e.g., Fryer and Iles, 1972; Kawanabe, 1981; Ribbink et al., 1983; Takamura, 1984), but there are no reports of males leaving their feeding territories for the purpose of mating in those species. In some of the species, males have been reported mating with females visiting the males' feeding territories (Kuwamura, 1987, 1992; Kohda, 1991; Yanagisawa and Nishida, 1991). This raises the question of why male *G. pfefferi* defends separate territories for feeding and mating. Theoretically, separation of feeding and mating territories will occur if places suitable for these activities are different, and the gain from one

territory exceeds the cost of leaving the other. It is possible that the density of fishes which disturb mating, including predation on both parents and the eggs, is lower in the vegetated patches than in the foraging area, and that the vegetation is a useful shelters. This may also explain why many brooding females rested in and near the vegetated patches.

The other only cichlid which is known to spawn chiefly in vegetated patches in Lake Tanganyika is the mouthbrooder, *Ctenochromis horei* (Ochi, 1993), which also forages mainly in the patches unlike *G. pfeffer*. *C. horei* feeds on various benthic animals (mainly oligochaetes), whereas *G. pfeffer* feeds only on shrimps. This feeding specialization may be one factor responsible for the separation of mating and feeding territories in the latter.

Occupying a mating territory in the morning and a feeding territory in the afternoon was in tune with the diel change of wave action by wind. Three other mouthbrooders, *Pseudosimochromis curvifrons* (Kuwamura, 1987), *Tanganicodus irsaca* (Kuwamura et al., 1989) and *C. horei* (Ochi, 1993), which spawn in shallow waters in the northwestern part of Lake Tanganyika also limit their spawning time to the morning. In that part of the lake, wind increases wave action considerably in the afternoon throughout the year (H. Ochi, pers. obs.), resulting in the churning of bottom sediments and consequent disturbance of spawning and collection of the eggs by mouth.

Mating system characteristics

Defense of mating territories by males has been reported in many maternal mouthbrooders (Lowe-McConnell, 1959; Coe 1966, 1969; Fryer and Iles, 1972; Brichard, 1975; Eccles and Lewis, 1981; McKaye, 1983, 1984, 1991; Kuwamura, 1986; Konings, 1988). The mating systems in these species are usually polygamous, without paternal care and with a relationship between male and female only at mating (Barlow, 1991). The congregation of mating territories at a certain place, with males not feeding in the mating territories, is known for some of the maternal mouthbrooders (Fryer and Iles, 1972; Loisselle and Barlow, 1978; McKaye, 1983, 1984, 1991). *G. pfeffer* also showed these characteristics. Although the number of mating territories in and near the vegetated patches was relatively small in *G. pfeffer*, observation of movements between the feeding and mating territories showed that male *G.*

pfeffer gather on the mating ground.

In mating territory-defending, maternal mouthbrooders, species-specific sand nests or bowers for spawning are usually constructed by males in their territories (Fryer and Iles, 1972; Brichard, 1975; McKaye, 1983, 1984; Kuwamura, 1986). Such nests are focal points of territorial behavior of the males, which spend much time in maintaining and repairing the nests, while waiting for visiting females (Fryer and Iles, 1972; McKaye, 1983; H. Ochi, pers. obs.). It has been suggested that the nest itself may function to attract females in these species (McKaye et al., 1990; McKaye, 1991). In contrast, male *G. pfefferi* did not prepare nests for spawning and had no focal point in their mating territories.

The mating ground of *G. pfefferi* may be unsuitable for nest preparation, so as to attract females, because of the grass cover, which would necessitate weeding of the site. Such an activity is probably difficult for *G. pfefferi*, although male *Oreochromis tanganyicae*, which are much larger than the former, construct the nests in the grass zone in such a manner (H. Ochi, pers. obs.). Under these conditions, rather than spend time and energy in nest construction and maintenance, male *G. pfefferi* appear to patrol the whole territory searching for mates.

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カワスズメ科魚類 *Gnathochromis pfefferi* の雄による繁殖なわばりと摂餌なわばりの維持と繁殖形態
越智晴基

タンガニカ湖に生息し、小えびを専食するカワスズメ科の口内保育魚 *Gnathochromis pfefferi* のなわばり行動、摂餌習性、および繁殖行動を個体識別して調査した。雌の摂餌範囲は互いに重なっていたが、雄は重ならない摂餌なわばりを持っていた。繁殖なわばりは水草場とその周辺に集合して作られ、雄はそこで午前中雌を求めて活発に泳ぎ回った。雄は午後には、摂餌なわばりに戻った。繁殖なわばりと摂餌なわばりは隣接している場合もあれば、100m以上はなれている場合もあった。本種の繁殖形態は、繁殖なわばりを作る他の多くの口内保育をするカワスズメ科魚類のそれとにているが、産卵のための巣を作らないという点で異なっていた。それぞれの雄は、競争があるにもかかわらず

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ず、数カ月の間毎朝同じ繁殖なわばりに戻っていた。このことから、所有者がいない時にもなわばりの所有権が競争相手から認められていることが示唆された。

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