

Parental Care in a Monogamous Mouthbrooding Cichlid *Xenotilapia flavipinnis* in Lake Tanganyika

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Abstract Breeding pairs of *Xenotilapia flavipinnis* held their territories on the sandy bottom and repeated several breeding cycles. Females mouthbrooded the eggs and early larvae but afterward males took over the mouthbrooding role. When the young became free swimming, they were guarded by both parents and remained in the spawning territory. Males played a leading role in the guarding, while females were more active in foraging during the guarding period. It was concluded that males' active participation in the parental care could accelerate the gonadal recovery of females and consequently could maximize the fecundity of serially monogamous pairs.

Fishes in the family Cichlidae take care of their eggs and young. Their parental care has two distinct types: substrate brooding (or guarding) and mouthbrooding (Fryer and Iles, 1972; Keenleyside, 1979). Care is usually provided by both parents in the former but females alone in the latter. It is generally accepted that biparental substrate brooding is more primitive and maternal mouthbrooding has evolved from it (Breder, 1934; Myers, 1939; Lowe, 1959; Timms and Keenleyside, 1975; Baylis, 1981). The few species of cichlids that have patterns of parental care different from the two types are often considered to be at intermediate stages between them (Reid and Atz, 1958; Lowe, 1959; Myrberg, 1965; Oppenheimer, 1970; Fryer and Iles, 1972).

While conducting surveys of Lake Tanganyika, I found several cichlid species in this lake that have such unusual care patterns. In a scale-eating species *Perissodus microlepis*, for example, eggs and yolk-sac larvae ("wrigglers") are mouthbrooded by females alone, but free-swimming young are guarded on a rock by both parents (Yanagisawa and Nshombo, 1983). *Xenotilapia flavipinnis*, which inhabits shallow sandy bottoms (Poll, 1985), is other example; females mouthbrood the eggs, males mouthbrood the larvae, and both parents guard free-swimming young. In the present study, I describe in detail the parental behaviour of *X. flavipinnis* under natural conditions. Foraging activity of parents during the brooding period was investigated closely, since it was hypothesized that food availability could affect parental fecundity and differentiation of parental roles.

Methods

The field observation was carried out at Luhanga, 12 km south of Uvira (3°24'S, 29°10'E), Zaire, from August to December 1983. SCUBA was used in all observations. *X. flavipinnis* was abundant on the sandy substrate ranging from 1 to 30 m deep. Juveniles and non-breeding adults formed schools in the water close to the substrate. Brooding pairs usually established territories on the sandy bottoms, though occasionally they were found on flat rocks. Two types of brooding sites could be readily distinguished: those where territories were aggregated and contiguous with each other, and those where territories were isolated. The former (referred to as colonial brooding sites; C-sites) were the norm for the species and were usually located on horizontal or gently sloping bottoms at depths less than 5 m. Isolated brooding sites (I-sites), in contrast, were found on sloping bottoms where sand areas were not extensive and were usually in areas deeper than 5 m.

A 12 m × 10 m quadrat was established in C-sites. About 50% of the bottom of the quadrat was covered with rocks and gravel. The bottom sloped gently offshore, at a depth from 1.4 to 4.1 m. Brooding conditions (i.e. maternal mouthbrooding, paternal mouthbrooding, biparental guarding and non-brooding) of pairs in the quadrat were censused 31 times between 10 August and 23 September (the first half of study period) and 31 times between 8 October and 10 December (the second half). The time of these censuses was between 0830 and 1530 hours. To estimate the duration of each

brooding condition, it was assumed that any change between two consecutive censuses occurred at the middle point between them. When a pair was guarding the young, the number of young was counted two or three times at every census and the counts were averaged to estimate brood size. I tried marking adult fish for identification in the earliest period of this study but stopped it soon since they often left their original sites once they were caught and anesthetized for marking. Two pairs were lost from the quadrat because of marking. Thereafter, individual fish were recognized based on body size, coloration and scars on the bodies.

During the censuses, the behaviour of the male and female in each pair in the quadrat and that of their young, if present, were observed for 10 min each. In observing the adults, the numbers of their feeding bouts and the frequency of their agonistic encounters with other fishes were recorded. In the observations on young, the following were recorded: (1) the amount of time each parent spent in close proximity to the school of young, (2) the amount of time the young spent settling on the substrate, (3) the sex of the parent which approached the young before they rose back into the water, and (4) the amount of time the young spent taking refuge in a parent's mouth. These observations were conducted 72 times for 9 pairs in various brooding conditions.

The mobility of each adult was measured by plotting its position every 10 sec on the map for a 10 min period. Its moving-area was expressed as the minimum convex polygon covering all dots plotted. This measurement was conducted 5 times for each adult in both the first and second halves of the study period. The combined moving-area of the male and female in a pair in 5 plottings was defined as the range of their territory. Growth rates of young were measured by collecting 1–5 individuals from each school in the quadrat at intervals of 1–4 days during the second half of study period. At the end of field study, all paired individuals in the quadrat were caught and their sex and size determined in the laboratory.

Additional specimens of paired adults and their offspring were collected at Mpemba, about 30 km south of Uvira, in August to October 1983. Mouthbrooding parents were caught with a hand net and were transferred quickly into a plastic bag underwater, so as not to miss any eggs and larvae.

A gut fullness index (wet weight of gut contents/wet weight of body $\times 100$) was calculated for full adults and stomach contents were examined for 10 adults (200 prey were counted for each). A gonadosomatic index (wet weight of gonad/wet weight of body $\times 100$) was calculated for females. Oocytes whose diameter exceeded 1 mm were regarded as matured, judging from their shape and coloration.

Results

Territories of breeding pairs. In the quadrat, 10 pairs (Pairs A–J in Fig. 1) were found at the start of census (10 August), of which nine were territorial and one was nomadic. After two territorial pairs (Pairs B and G) were lost in the process of marking on 18 August (see Methods), a nomadic pair (Pair J) took over one of the vacant territories. After that time, positions of the eight pairs rarely changed except for about 3 m shift of Pair J between 23 September and 8 October. Disruption of pairs occurred on only two occasions during the study period; the male of Pair A disappeared (13 September) and the female of Pair J was replaced by another female (5–8 November). The female in Pair A abandoned the territory 7 days after the male disappeared. In the second half of study period, two pairs (Pairs K and L) established territories in areas which were previously unoccupied (Fig. 1).

Territory size averaged $6.8 \text{ m}^2 \pm 0.5 \text{ SE}$ ($N=14$) and the distance between the centres of two neighbouring territories averaged $3.1 \text{ m} \pm 0.2 \text{ SE}$ ($N=20$). Neighbouring territories were nearly contiguous (Fig. 1). Pairs held their territories selectively in sandy areas; 65% (40–90%) of bottom surface of territories was sand, while only 50% of the total bottom surface in the quadrat was sand. Pairs that occupied less sandy areas tended to have larger territories; territory size was negatively correlated with percent of sand area in the territory ($r = -0.507$, $N=14$, $P \approx 0.05$).

Breeding cycle. The sequences of brooding conditions for 9 pairs (Fig. 2) showed that in all cases ($N=20$) females mouthbrooded the eggs after spawning and that males subsequently mouthbrooded until the larvae were released on the substrate. Parents never performed the mouthbrooding jointly. The mean durations of maternal and paternal mouthbrooding were 9.4 and 5.7 days, respectively, and the mean total duration of



Fig. 1. Territories of pairs (Pairs A-L) in the 12 m×10 m quadrat during the period from 10 August to 23 September (solid lines) and from 8 October to 10 December (broken lines) in 1983. Pairs B and G disappeared after marking on 18 August. Ranges of territories of Pairs J and L were not measured. Hatched areas are covered with rocks and stones.

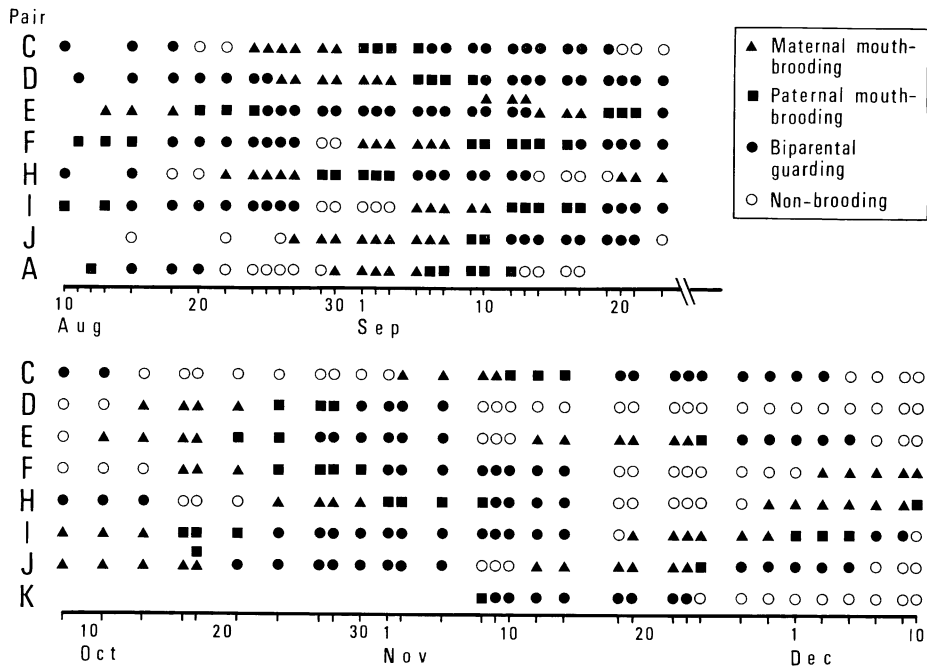


Fig. 2. The sequences of brooding conditions for nine pairs.

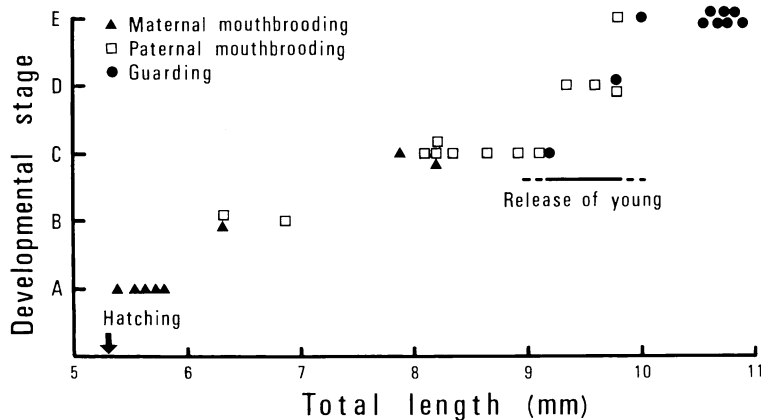


Fig. 3. Brooding conditions of pairs in relation to the total lengths and developmental stages of their offspring after hatching. Morphological features of the developmental stages: A, pectoral fin bud; B, caudal rays; C, pectoral, dorsal and anal rays; D, pelvic rays; E, segments in dorsal and anal rays.

mouthbrooding was, therefore, 15.1 days (Table 1). Thereafter, the free-swimming young were guarded by both parents in the territory for an average of 13.3 days. This guarding duration varied widely between pairs, ranging from 3.5 to 24.5 days. The time interval between disappearance of young from the territories and next spawning also varied widely; at one extreme, parents spawned a second brood 4 days before the first brood departed the territory; at the other extreme, the next spawning did not occur for at least 33 days after disappearance of young. The interval between broods was usually less than 8 days in the first half of the study period but was longer in the second half (Fig. 2). Stable pairs had 3–5 breeding cycles ($\bar{x}=3.9$, $N=7$) during the study period.

Examination of specimens revealed that eggs and yolk-sac larvae smaller than 6.3 mm in total length (TL) were always mouthbrooded by females, larvae between 6.3 and 8.2 mm TL by either males or females, and those larger than 8.2 mm TL always

by males (Fig. 3). Observations in the aquarium indicated that eggs hatched 3 days after spawning and larvae reached sizes of 6.3 and 8.2 mm TL in 4 and 8 days after hatching, respectively, when water temperature in the aquarium was similar to that in the field (24–27°C). Consequently, duration of maternal mouthbrooding was estimated to be about 7–11 days, which matched closely the figure estimated from quadrat censuses (7–12.5 days).

Spawning and brood size. Neither spawning nor courtship behaviour of this cichlid was seen during the observation period (0830–1530 hours). Since this cichlid was inactive at night as were other cichlids, it was assumed that spawning occurred in the early morning or in the late afternoon.

The smallest male and female in pairs were 49.6 and 48.5 mm in standard length (SL), respectively. Body sizes of brooding males ranged from 54.6 to 70.6 mm SL ($\bar{x}=64.5$, $N=58$) and

Table 1. Duration (days) of maternal mouthbrooding, paternal mouthbrooding and biparental guarding in *Xenotilapia flavipinnis*. Means are followed by standard errors.

Period	Mouthbrooding			Guarding
	Maternal	Paternal	Total	
Aug. and Sep.	8.4±0.7 (N=8)	5.9±0.6 (N=9)	14.4±0.4 (N=8)	13.3±1.5 (N=6)
Oct. to Dec.	10.2±0.7 (N=9)	5.5±0.8 (N=10)	15.8±0.4 (N=8)	13.2±1.8 (N=11)
Total	9.4±0.5 (N=17)	5.7±0.5 (N=19)	15.1±0.3 (N=16)	13.3±1.3 (N=17)

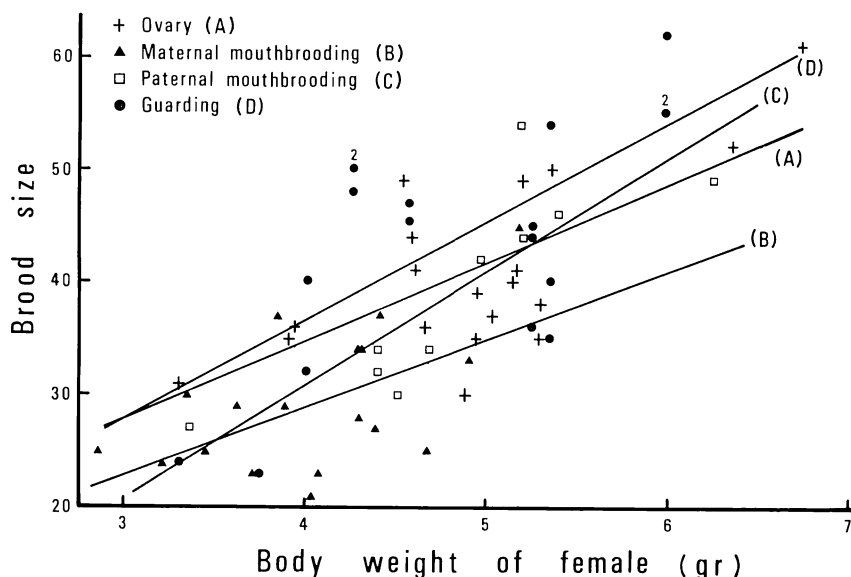


Fig. 4. The number of oocytes in the mature ovaries and brood sizes at the stages of maternal mouthbrooding and paternal mouthbrooding and at the start of guarding stage in relation to the body weight of females. (A) $y = 6.80x + 7.49$, $r = 0.688$, $N = 19$, $P < 0.01$; (B) $y = 5.79x + 6.08$, $r = 0.546$, $N = 18$, $P < 0.05$; (C) $y = 9.95x - 8.90$, $r = 0.840$, $N = 10$, $P < 0.01$; (D) $y = 8.67x + 1.82$, $r = 0.663$, $N = 18$, $P < 0.01$.

those of brooding females from 54.2 to 69.1 mm SL ($\bar{x} = 60.6$, $N = 62$). Males were usually larger than their mates (in 56 of 68 pairs) and larger males tended to pair with larger females ($y = 0.69x + 16.77$, x : SL of males, y : SL of females, $r = 0.773$, $N = 68$, $P < 0.001$).

Eggs were orange-yellow and were $2.95 \text{ mm} \pm 0.03 \text{ SE}$ ($N = 15$) long with a diameter of $1.98 \text{ mm} \pm 0.02 \text{ SE}$. The number of oocytes in the mature ovaries (prespawning stage) and brood sizes at the stages of maternal and paternal mouthbrooding and at the start of guarding stage were all significantly correlated with the body weight of the females (Fig. 4). Slopes of four regression lines showing the relationships between the body weights of female and the brood sizes were not significantly different from one another. The adjusted means of the brood sizes were generally not significantly different among the four stages; the exceptions between prespawning and maternal mouthbrooding (ANCOVA, $F_H = 6.77$, $P < 0.05$) and between maternal mouthbrooding and guarding ($F_H = 9.32$, $P < 0.01$) are probably accidental, since there is no logical reason why brood size at the stage of maternal mouthbrooding is smaller than at the later stage. Overall, it appears that the loss of brood during the period from spawning to the

earliest guarding stage is not remarkable, if any.

Mouthbrooding. Mouthbrooding parents usually hovered about 10 cm above the bottom sometimes settling on the substrate in the central part of their territory, while their mates foraged about within the territory.

Attempted transfer of larvae from female's to male's mouth was observed on two occasions. In one case, a female spat a brood onto the substrate when her mate approached within 20 cm from her. He immediately rushed up to the larvae and positioned his mouth near to them. In response to this action, the larvae dashed into his mouth. These actions were completed within 2 sec. In another case, a female put the larvae on the substrate when her mate moved towards her, but the male passed by without reacting to the larvae. The female then rapidly retrieved them into her mouth. The next day, however, the male had taken over the mouthbrooding role.

Young were released for the first time from the male's mouth at the sizes of around 9.5 mm TL ($= 7.9 \text{ mm SL}$) (Fig. 3). Young at such sizes still had a remnant of yolk. Small young within a few days of their first release sometimes took refuge in the parents' mouths instead of on the substrate. Of 15 such cases observed, young took

refuge in the male's mouth in 13 cases and in the mouths of both parents in 2 cases.

Guarding. Guarding parents stationed themselves in close proximity to the school of young, which were hovering up to 20 cm above the substrate while feeding on planktonic organisms. The school was usually situated in the central part of the territory. As the young grew, it spread horizontally within the territory. Guarding time of males was much longer than that of females throughout the guarding period (Fig. 5). About two thirds of the males' time was spent guarding when the young were very small, but this proportion decreased as the young grew. On the other hand, guarding time of females was consistently brief irrespective of the size of young. From about the 10th day onwards, both parents rarely stayed in the proximity of the young.

Young settled on the substrate in response to sudden movements of their parents, which rushed at intruders, and the young remained on the bottom while parents were absent. In the first three days, young settled on the substrate about 8 times per 10 min and stayed there 27% of their time (Fig. 5). Both the frequency and percent time of settling of young decreased as they grew, and young more than 9 days old were never observed hiding on the bottom (in 270 min). Set-

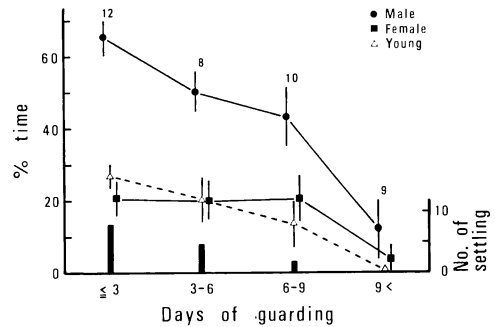


Fig. 5. Percent times that males and females spent guarding and that young were settling on the substrate, with the numbers of the settling per 10 min, in relation to days of the guarding stage. The numbers of the settling are shown by vertical bars. Vertical lines and numbers just above them are ranges of standard errors and sample sizes, respectively.

ting young usually returned to the water column after one of the parents approached them. The first parent to approach the young was usually the male (117 out of 136 observations).

Mixing of broods. The number of young in a school rarely changed in the first eight days (Fig. 6). Afterwards, however, the number increased in some territories owing to mixing of foreign

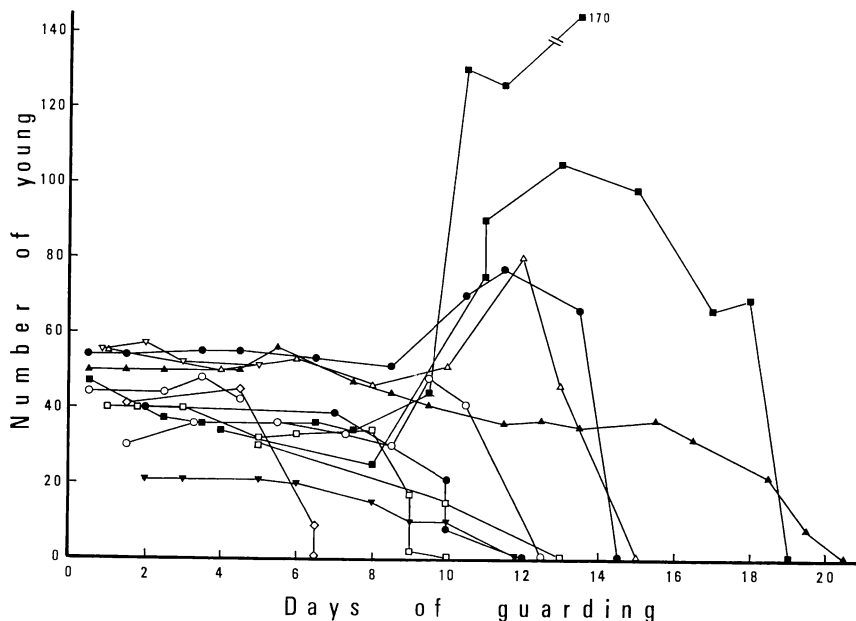


Fig. 6. Daily fluctuations of the number of young in one school.

young and decreased in some others. Based on the number and size of the young observed, it was not difficult to determine the origin of foreign young. Obvious mixing of foreign young was observed 28 times in a total of 15 schools in the quadrat. In 18 cases these foreign young appeared to have originated from other schools in the quadrat, 14 from the neighbouring territories and 4 from the next territories but one, and in 10 cases the young came from schools outside of the quadrat. Schools received 1–90 individuals of foreign young between consecutive censuses. Body sizes of the foreign young were between 9 and 18 mm SL and were smaller, as large as, and larger than those of the native young in 13, 3 and 12 cases, respectively. In two cases, mixed broods that included more than 100 individuals stretched over two neighbouring territories. Broods which remained in the natal territories for more than 12 days ($N=11$) all received foreign young sooner or later. Guarding time of parents whose broods included foreign young was minimal; percent time of guarding was 9.6% for males and 3.5% for females (in 70 min). Spawning intervals of pairs were not correlated with the duration of their guarding period (Kendall's rank correlation coefficient, $\tau=0.04$, $N=7$, $P>0.05$).

There are two ways young have been observed to join a foreign school. Yanagisawa (1985) first reported brood farming-out in the cichlid *Perissodus microlepis*, in which a parent carried young in its mouth and placed them under the care of other brooding parents. Such farming-out was observed once in *X. flavipinnis*. On 8 October, an adult of unknown sex was seen to invade a territory of other guarding parents. It was attacked several times by the latter but remained nearby and finally spat its young near the substrate on which the native young had been taking refuge since its approach. After this, it returned to its territory some 6.5 m away. The invaded parents were agitated for a while, but ultimately guarded the mixed brood. The body sizes of the young farmed out and the native young were nearly equal (both about 9 mm SL). On 4 other occasions, I witnessed males of guarding pairs leave their territories for 1–10 min carrying some of their young (9–11 mm SL) in the mouths and returned to the territories still carrying them. During the trips, the males invaded several territories of other guarding pairs, but each time

they were attacked by the pair. In all cases, by the next censuses, the young of these invading males had completely or partially disappeared from their territories and, correspondingly, foreign young were found in some broods of these pairs.

Mixing of brood can also occur when young in one territory invade the neighbouring territory by themselves and join with the resident young. This was observed once in a mixed brood of young whose body sizes were 12–17 mm SL. When the young invaded the neighbouring territory, the adults in this territory attacked them many times but finally accepted them. Mixing of broods in this way seems to occur mainly when invading young are relatively large (probably larger than 12 mm SL).

Growth of young. Growth of young, estimated from specimens collected during the period from 21 October to 1 December, was nearly linear when measured in standard length, with mean growth rates ranging from 0.20 to 0.40 mm/day ($\bar{x}=0.32$, $N=9$). These rates were slightly less than those measured in the aquarium, where young were well fed with the nauplii of *Artemia* (0.43 mm/day).

Foraging activity of adults. Foraging adults thrust their mouths lightly into sand, mouthed a small amount of sand, and then spat it out from the mouths or gill-openings. They also picked up prey from the surfaces of rocks and gravel. Copepods, ostracods and nematods were abundant in their stomachs (Table 2). Paired adults at the brooding stage always moved within their territory, and those at the non-brooding stage did so in all but two cases. In Pairs F and I (Fig. 1), the male and female sometimes left their territory to forage together on a sand slope 4–10 m distant from the territory.

Feeding rates of adults, measured as the number of feeding bouts per minute, were highest at the

Table 2. Number percents of stomach contents of adult *Xenotilapia flavipinnis*.

Item	%	Item	%
Nematods	9.2	Copepod nauplii	0.6
Hydrachnellas	0.3	Copepodid	0.2
Ostracods	16.2	Atyid shrimps	0.1
Cyclopoid copepods	24.0	Chironomids	2.7
Harpacticoid copepods	46.4	Other dipteras	0.2
		Gastropods	0.1

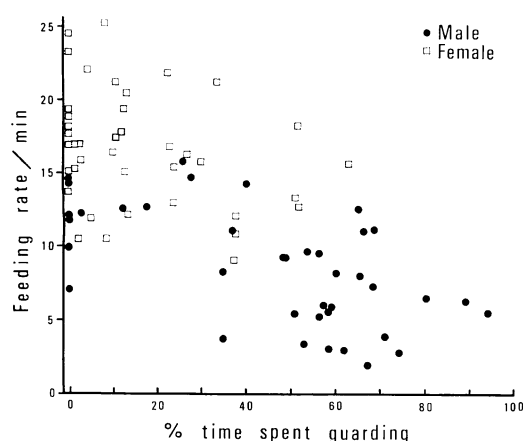


Fig. 7. Relationships between percent times males and females spent guarding and their feeding rates.

non-brooding stage (Table 3). Parents that were mouthbrooding never fed, whereas their non-brooding mates foraged as actively as adults without offspring. Foraging activity of males guarding the young was low, especially when the

young were small. Their feeding rates increased as time went by. In contrast, foraging activity of guarding females was not greatly affected by the presence of the young (Table 3). Feeding rates of both males and females were negatively correlated with percent time of guarding (Fig. 7) ($r = -0.57$, $N = 39$, $P < 0.001$ for males; $r = -0.36$, $N = 39$, $P < 0.05$ for females; $r = -0.49$, $N = 78$, $P < 0.001$ for both combined).

Areas that adults moved within the territories in 10 min were related to their foraging activities and consequently to their brooding conditions (Table 3). Mouthbrooding parents were apt to stay in the central part of the territory, while their mates moved as widely as adults without offspring. The size of areas covered by guarding males was positively correlated with age of the young ($r = 0.704$, $N = 37$, $P < 0.001$), but that of guarding females was not so ($r = 0.256$, $N = 37$, $P > 0.05$). Both males and females guarding the young for more than 9 days moved a little more widely than those with no offspring, though the difference was significant only for females ($t = 3.11$, $df = 31$, $P < 0.01$). This probably reflects the tendency of

Table 3. Feeding rates of males and females in *Xenotilapia flavipinnis* and areas that they moved in 10 min, in relation to their brooding conditions. Means are followed by standard errors. The numbers of 10 min observations in parentheses.

Brooding condition	Feeding rate (/min)		Moving area ($m^2/10$ min)	
	Male	Female	Male	Female
Number of offspring	17.2 ± 1.4	18.7 ± 1.1 (10)	3.29 ± 0.48	2.79 ± 0.28 (21, 22)
Maternal mouthbrooding	16.8 ± 2.6	0 (11)	2.51 ± 0.40	0.98 ± 0.14 (19)
Paternal mouthbrooding	0	15.3 ± 0.9 (11)	1.04 ± 0.15	2.34 ± 0.21 (9)
Guarding				
≤ 3 days	5.2 ± 0.5	15.4 ± 1.1 (12)	0.89 ± 0.22	2.38 ± 0.36 (9)
3–6 days	9.3 ± 1.2	16.8 ± 1.2 (8)	1.44 ± 0.29	2.86 ± 0.37 (9)
6–9 days	10.8 ± 1.4	16.1 ± 1.5 (10)	2.18 ± 0.40	3.02 ± 1.02 (6)
> 9 days	11.7 ± 0.9	18.7 ± 1.2 (9)	4.37 ± 0.47	4.34 ± 0.42 (11)

Table 4. Index of gut fullness for males and females and gonadosomatic index for females in relation to their brooding conditions. Means are followed by standard errors. Sample sizes in parentheses.

Brooding condition	Index of fullness of gut		Gonadosomatic index of female
	Male	Female	
Number of offspring	0.88 ± 0.09 (14)	0.75 ± 0.08 (14)	2.00 ± 0.37 (14)
Maternal mouthbrooding	0.89 ± 0.36 (9)	0 (16)	0.22 ± 0.01 (15)
Paternal mouthbrooding	0.01 (13)	0.83 ± 0.10 (11)	0.27 ± 0.02 (11)
Guarding			
≤ 10 mm SL young	0.21 ± 0.06 (16)	0.65 ± 0.09 (14)	0.76 ± 0.14 (14)
> 10 mm SL young	0.48 ± 0.07 (10)	0.70 ± 0.09 (9)	1.20 ± 0.36 (9)

parents to forage in the outer parts of the territory, avoiding the central area occupied by the school of young.

Gut fullness of adults was related to their brooding condition (Table 4), as would be expected from their feeding rates. The guts of mouthbrooding parents were almost completely empty, but the index of fullness for their mates was nearly equal to that for adults with no offspring. This index was positively correlated with the size of their young for guarding males ($r=0.589$, $N=26$, $P<0.001$), but not for guarding females ($r=-0.001$, $N=23$, $P>0.05$). The index for guarding males was almost always less than that of their mates (21 of 23 pairs).

Agonistic behaviour. Paired adults most frequently attacked conspecific juveniles that approached the periphery of their territory. They also frequently attacked a paedophagous cichlid *Lamprologus elongatus* and two cichlids *Lamprologus callipterus* and *Gnathochromis pfefferi* which moved about in groups (Table 5). Males performed more attacks than females nearly

throughout the brooding period (Table 6). Conversely, adults were attacked by two cichlids *Cyathopharynx furcifer* and *Lamprologus modestus* which held territories in the same areas (Table 5). The frequency of being attacked did not differ between the sexes (Table 6). Mouthbrooding parents, which usually stayed in the central part of the territory, were rarely attacked.

Agonistic encounters between pairs were relatively rare; an average of only 1.45 agonistic encounters were observed per hour (in 3540 min). These encounters were relatively frequent between Pairs F and I (30% of the total), between Pairs D and F (15%) and between Pairs E and F (12%), where the distances between the centres of their territories were less than for other pairs (see Fig. 1). Such encounters consisted of a few brief chase near territory boundaries.

Gonadosomatic index of females. Paired females at the non-brooding stage usually had mature oocytes in the ovaries (13 of 14 females) and had higher gonadosomatic index (G.S.I.) than those at the brooding stage (Table 4), suggesting that

Table 5. Relative frequencies of attacks which paired adults of *Xenotilapia flavipinnis* made on other fishes and which they suffered from other fishes. Attacks between the paired adults are not included. Total observation time was 1420 min. Relative densities of fishes were calculated from their numbers counted twice in the quadrat.

Species	Relative density (N=555)	<i>Xenotilapia flavipinnis</i>	
		Attacking on (N=337)	Being attacked by (N=99)
<i>Xenotilapia flavipinnis</i>	9.5	48.4	0
<i>Lamprologus callipterus</i>	0.4	15.4	1.0
<i>Lamprologus elongatus</i>	10.1	10.3	0
<i>Gnathochromis pfefferi</i>	0.7	8.6	0
<i>Lamprologus modestus</i>	10.8	3.0	51.5
<i>Lestradea perspicax</i>	0	2.4	1.0
<i>Grammatotria lemairei</i>	0	2.4	0
<i>Telmatochromis bifrenatus</i>	7.0	2.1	0
<i>Xenotilapia</i> sp.	0	2.1	0
<i>Cyathopharynx furcifer</i>	7.5	1.8	43.4
<i>Perissodus microlepis</i>	0.7	0.6	1.0
<i>Telmatochromis temporalis</i>	5.7	0.6	1.0
<i>Lamprologus fasciatus</i>	0.4	0.6	0
<i>Aulonocranus dewindti</i>	31.6	0.3	1.0
<i>Lamprologus brichardi</i>	5.9	0.3	0
<i>Lamprologus profundicola</i>	0.2	0.3	0
<i>Tropheus moorei</i>	1.5	0.3	0
<i>Lamprichthys tanganicanus</i>	0.2	0.3	0
<i>Synodontis</i> sp.	0	0.3	0
others	7.8	0	0

All species belong to Cichlidae except for *L. tanganicanus* (Cyprinodontidae) and *Synodontis* sp. (Mochokidae).

they were already or nearly ready to spawn. On the other hand, females at the maternal and paternal mouthbrooding stages never had mature oocytes and their G.S.I. was very low. Subsequently, when guarding the young, 13 of 23 females had mature oocytes. The G.S.I. of such females tended to increase with the age of their young (correlation between G.S.I. and the body sizes of the young, $r=0.393$, $N=23$, $P\approx 0.05$).

Pairs in the isolated brooding sites. The behaviour of adults described so far is that of adults in the colonial brooding sites (C-sites). That of adults in the isolated brooding sites (I-sites) was considerably different from that in C-sites. Body sizes of brooding pairs in I-sites were smaller than those in C-sites ($\bar{x}=60.1$ mm SL, $N=3$, for males; $\bar{x}=56.1$ mm SL, $N=8$, for females). In I-sites, just before spawning pairs settled at particular sites but did not defend their sites. After spawning, eggs and yolk-sac larvae were mouthbrooded sequentially by females and then by males, as in C-sites. Unlike pairs at C-sites, however, parents at the mouthbrooding stage rarely defended their sites and often left the sites to join with the nearby

schools of non-breeding adults and juveniles. They became aggressive toward intruders after they started guarding the young at their sites. Frequency of the attack was much higher when compared to parents guarding the young of the equivalent body sizes in C-sites (Table 7). The amount of time males guarded the young in I-sites was slightly less than in C-sites, apparently owing to the frequent absence of males from vicinity of the young to drive off intruders. The proportion of time female spent guarding, in contrast, was higher in I-sites. Consequently, the difference in guarding time between the sexes was smaller in I-sites. Since they spent more time guarding, parents in I-sites had less time available for foraging (Table 7). All broods of young observed in I-sites completely disappeared from the natal sites within 10 days ($N=9$), suggesting that the parents either failed to raise them or that they had been farmed out to other guarding parents.

Discussion

Monogamous mouthbrooders. Of the over 700 species of the family Cichlidae, nearly 30% are

Table 6. Frequencies of attacks (per 10 min) which paired adults of *Xenotilapia flavipinnis* made on other fishes and which they suffered from other fishes, in relation to their brooding conditions. Attacks between conspecifics are not included.

Brooding condition	No. of 10 min observations	Attacking		Being attacked	
		Male	Female	Male	Female
Number of offspring	10	0.8	0.5	0.4	0.6
Maternal mouthbrooding	11	1.2	0.3	0.8	0
Paternal mouthbrooding	11	1.4	0.5	0.2	0.8
Guarding					
≤ 3 days	12	2.0	1.3	0.6	1.3
3–6 days	8	0.9	1.3	0.8	0.8
6–9 days	10	1.4	1.2	1.0	0.6
> 9 days	9	3.4	1.1	0.9	1.0
Total	71	1.6	0.9	0.6	0.7

Table 7. Behavioural differences between guarding parents of *Xenotilapia flavipinnis* in the colonial brooding sites and in the isolated brooding sites. Means are followed by standard errors.

Behaviour	Colonial brooding sites		Isolated brooding sites	
	Male	Female	Male	Female
Guarding time (%)	59.0 ± 9.3	20.5 ± 3.6 ($N=20$)	48.5 ± 7.0	33.7 ± 6.0 ($N=11$)
Attacks (/10 min)				
on conspecifics	0.6 ± 0.3	0.5 ± 0.2 ($N=20$)	11.7 ± 6.6	7.5 ± 4.0 ($N=13$)
on other species	1.6 ± 0.4	1.3 ± 0.4 ($N=20$)	4.9 ± 1.1	3.7 ± 0.9 ($N=13$)
Feeding rate (/min)	6.8 ± 0.7	16.0 ± 0.8 ($N=20$)	4.6 ± 1.4	7.5 ± 0.8 ($N=13$)

estimated to be biparental substrate brooders and about 70% maternal mouthbrooders (Keenleyside, 1979). Most other species are monogamous mouthbrooders, in which parents stay together through at least one brooding cycle and each assumes mouthbrooding and/or guarding roles, e.g. *Chromidotilapia guentheri*, *Geophagus jurupari* and *Aequidens paraguayensis* (Reid and Atz, 1958; Myrberg, 1965; Timms and Keenleyside, 1975; Dupuis and Keenleyside, 1982). Unlike other monogamous mouthbrooders, *X. flavipinnis* always exhibits maternal mouthbrooding followed by paternal mouthbrooding; parents never mouthbrood jointly. Prolonged guarding of the young in this fish is also exceptional. Parental care by *Perissodus microlepis* in Lake Tanganyika is similar to that of *X. flavipinnis*, except that the mouthbrooding role does not change between parents; rather females alone mouthbrood the eggs and larvae and afterwards both parents guard the young for more than one month (Yanagisawa and Nshombo, 1983). In the recent surveys of Lake Tanganyika, several other species have also been confirmed to be monogamous mouthbrooders. In *Asprotilapia leptura*, maternal mouthbrooding of eggs and early larvae is followed by paternal mouthbrooding and the free-swimming young are guarded by both parents for a long time, like in *X. flavipinnis* (in preparation). Specimens of mouthbrooding individuals collected show that in *Xenotilapia longispinis*, *Xenotilapia boulengeri*, *Eretmodus cyanostictus* and *Tanganicodus irsacae*, eggs are mouthbrooded by females and afterward males take over the mouthbrooding role (T. Kuwamura, personal communication). In *X. longispinis* both parents subsequently guard the young; such guarding behaviour has not been observed in the other species.

Determinants of parental care pattern in *X. flavipinnis*. In monogamous cichlids, one parent generally can defend immobile offspring as effectively as two, whereas two parents are necessary to defend a school of free-swimming young against predators (Barlow, 1974; Perrone and Zaret, 1979). The brooding activity of *X. flavipinnis* suggests that this general rule applies to it as well. In this species, while one parent mouthbroods eggs or larvae, the other is completely freed from the caring duty. In this circumstance, the latter might have an opportunity for access to other potential mates and might be tempted to desert

its partner. Nevertheless, such desertion has never been observed. The proportion of time spent guarding by parents (Fig. 5) indicates that two parents are especially necessary when they are guarding the small young. This constraint may be one factor preventing polygamy in this fish. When young become more than 9 days old or so, the parents are, however, scarcely involved in guarding and, therefore, either parent might be tempted again to desert its partner. No occurrence of such desertion is probably due to difficulties in getting a new territory of good quality, or perhaps because the female can soon spawn again.

Among monogamous cichlids, there is generally appreciable differentiation of parental roles. The tendency is for females to do more direct care, while males are more active territory-guarders and are less intimately associated with the brood (Barlow, 1974; Keenleyside, 1979). The parental care pattern of *X. flavipinnis* is obviously inconsistent with this tendency. In this fish, males play a leading role in direct care except for the period of maternal mouthbrooding of eggs and early larvae. This is probably related to serial spawnings of a pair within one breeding season. In species in which a pair spawn serially, fecundity of a pair should be limited by the rate of gametogenesis of the female because oogenesis is a slower process than spermatogenesis (Baylis, 1981). This rate is, of course, affected by her nutritive condition during the brooding period. Her emancipation from the parental duties, due to the male's active participation in it, can promote her foraging activity and therefore may increase the fecundity of the pair.

Differentiation of parental roles in fishes which spawn serially has not been considered extensively. In *P. microlepis* in which pairs usually separate after independence of their young (personal observation), females alone mouthbrood and consecutively play a leading role in guarding (Yanagisawa and Nshombo, 1983). By contrast, in the anemonefishes (Pomacentridae) in which one pair breeds several times in one breeding season, brood care is almost exclusively carried out by males (Allen, 1972; Bell, 1976; Moyer and Bell, 1976; Ochi, 1985; Yanagisawa and Ochi, 1986).

If males of *X. flavipinnis* are indeed selected to assume the parental roles as much as possible in order to maximize the fecundity of the pair, one may ask why males do not undertake mouth-

brooding role soon after spawning. In cichlids, it is unknown for males to take eggs into the mouth immediately after each bout of egg-laying; in a few species males or both parents begin taking up the eggs after the whole clutch has been laid (Aronson, 1949; Myrberg, 1965; Timms and Keenleyside, 1975). On the other hand, in all typical maternal mouthbrooders eggs are collected by females immediately after each bout of egg-laying. This behaviour has been regarded as an adaptation to high predation pressures on eggs on the substrate (Fryer and Iles, 1972). It is conceivable that in cichlids rapid mouthing by females has been more effective than that of males for avoiding predation of eggs, though the reason for this is uncertain. Greenwood (1983) considers *Xenotilapia* to be closely related to a number of genera, which practice lek-forming and maternal mouthbrooding (e.g. *Cyathopharynx*). G.F. Turner (personal communication) suggests that *X. flavipinnis* may be descended from species with such behaviour. If so, it is possible that this fish retains initial mouthing by females as a phylogenetic constraint.

In this fish, change from maternal mouthbrooding to paternal mouthbrooding occurred around 9 days after spawning, when the larvae had developed the caudal rays (Fig. 3); in aquarium observation such larvae were able to swim up a few centimetres from the bottom. Immobile offspring may be as vulnerable to predators as the newly spawned eggs on the substrate and accordingly females may be forced to keep the offspring until they have some motility. If so, parents of this fish are using the earliest opportunity for the safe transfer of offspring, and males are in fact assuming nearly all possible responsibility for caring for the young.

Mixing of broods. Mixing of broods in *X. flavipinnis* was caused either by farming-out of young by the parents or by their own immigration. Although mixing of broods, either conspecific or heterospecific, is not rare in cichlids (Ward and Wyman, 1975, 1977; McKaye and McKaye, 1977; Ribbink, 1977; Ribbink *et al.*, 1980, etc.), these ways of mixing have been reported only in *P. microlepis* under experimental conditions (Yanagisawa, 1985). One possible benefit to parents whose young were put under the charge of other parents is to emancipate themselves from parental duties and consequently to accelerate the gonadal

recovery for the next spawning. In fact, however, no correlation was found between spawning interval of pairs and the durations of their guarding period, suggesting that earlier emancipation from parental duties does not necessarily result in the acceleration of the next spawning. This result is probably attributed to the fact that mixing of broods usually occurred in the second half of the guarding stage when the young had grown larger and the parents guarding such young scarcely sacrificed foraging activity. At present, it is not clear what advantage is gained by parents that farm out their young. But, it is certain that this behaviour is of benefit to parents that are guarding the young in the isolated brooding sites where raising the young is not easy.

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タンガニイカ湖に生息する一夫一妻制のマウス・ブルードー *Xenotilapia flavipinnis* (カワスズメ科) の育児様式
柳沢康信

Xenotilapia flavipinnis の繁殖ペアは砂底にナワバリを構え、1繁殖シーズンに数回繁殖サイクルを繰り返す。子供は、産卵直後から前期仔魚期の途中まで雌によって口内保育され、その後、卵黄の吸収がおわる時期まで雄によって口内保育される。遊泳期の稚魚は平均13日間ナワバリ内にとどまり、両親によって保護される。この期間中、雄が主に保護活動を行ない、雌は大部分の時間を摂餌活動にあてた。育児に対する雄の積極的な係わりは雌の生殖腺の回復を早め、その結果、1繁殖シーズンのペアの産卵数を高めることができると推察した。

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