Mate Monopolization by a Dominant Male in a Multi-male Social Group of a Mouthbrooding Cichlid, Ctenochromis horei

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Abstract Spacing behavior, feeding habits, social interactions and breeding behavior of a mouthbrooding cichlid, $Ctenochromis\ horei$, were investigated in Lake Tanganyika. About 60–70 individuals found in a $15\ m \times 9\ m$ vegetated patch had a nearly equal sex ratio. Most fish remained for more than 3 months, limiting movements, foraging, mating and brooding, to the patch. They formed a stable group with well-overlapping home ranges and foraged in schools. Attack and avoidance behavior among large males indicated a dominance order positively correlated with body size. Replacement of the most dominant male in group occurred twice during the 6-month observation period. All observed matings were monopolized by the dominant male, although apparent sneaking behavior by other males occurred during mating. Mating monopolization was accomplished by the dominant male defending a female from rivals for several hours before and during spawning. These observations suggested that the mating system of C. horei is polygynous. Only females mouthbrooded the eggs and larvae, and later guarded the juveniles. The spacing behavior of C. horei appears to be responsible for its mating system, which contrasts with those so far reported for other mouthbrooding cichlids.

The family Cichlidae has two ways of brooding young; either substrate-brooding or mouthbrooding (Breder and Rosen, 1966; Fryer and Iles, 1972; Keenleyside, 1979; Kuwamura, 1986). In most mouthbrooding cichlids, females are care-takers and males are emancipated from brood care (Keenleyside, 1979, 1991; Kuwamura, 1988). Consequently, males are inclined to mate with as many females as possible (Trivers, 1972). A polygamous mating system is therefore expected to prevail in maternal mouthbrooders. In maternal mouthbrooders whose mating behavior has been reported, males or individuals of both sexes defend their territories. Males mate with visiting females in the males' territories, the females subsequently departing with the eggs (Lowe-McConnell, 1959; Fryer and Iles, 1972; Loiselle and Barlow, 1978; McKaye, 1983, 1984; Kuwamura, 1986, 1987; Yanagisawa and Nishida, 1991). Their mating system is considered to be polygynandrous because males mate with plural females (polygyny) and females also with plural males (polyandry) (Barlow, 1991).

Ctenochromis horei is a maternal mouthbrooder, which inhabits the vegetated zone of Lake Tangan-

yika (Konings, 1988). During invetigations of the social organization of Tanganyikan maternal mouth-brooders, multiple males and females of *C. horei* were found residing in the same area, with a dominant male defending a female which was ready to spawn, against other males. Such a mating system in maternal mouthbrooders has not been previously reported (see Kuwamura, 1986; Barlow, 1991).

In this paper, spacing behavior, feeding and breeding habits, and social relationships are described so as to elucidate the mating system of *C. horei*, inhabiting the vegetated patch. Factors which allowed a male to control access to females are discussed.

Materials and Methods

The field investigation, using SCUBA, was done at Mbemba ($3^{\circ}36'S$, $29^{\circ}10'E$), Zaire, northwest coast of Lake Tanganyika from June 1989 to January 1990. A $73 \text{ m} \times 28 \text{ m}$ study area was outlined on a substrate of sand, pebbles and rocks at depths of 2–10 m (Fig. 1). In the study area, two vegetated patches, A $(15 \text{ m} \times 9 \text{ m})$ and B $(15 \text{ m} \times 11 \text{ m})$, oc-

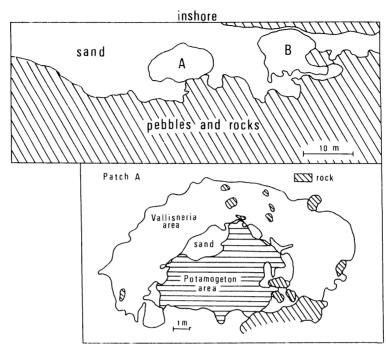


Fig. 1. Substrata of the 73 m×28 m study area with two vegetated patches A and B, and distribution of two grass species in Patch A.

curred. Patch A consisted of two grass species, Potamogeton schweinfurthii and Vallisneria sp., and Patch B, P. schweinfurthii only. In Patch A, the area of Potamogeton was almost completely surrounded by Vallisneria (Fig. 1). Potamogeton was tall (max. 80 cm) and sparsely distributed, whereas Vallisneria was short (max. 30 cm) and densely distributed. Patch A was divided into $1 \text{ m} \times 1 \text{ m}$ squares with string. The whole study area was patrolled twice (on 7 and 10 December) to confirm which substratum C. horei inhabited.

Large individuals (>60 mm total length: TL) in Patch A were identified by their body size and distinct patterns of black spots on the head. Forty-nine individuals were identified by the end of July. Their TL was measured underwater with a ruler while the fish remained still, and their sexes were determined by courtship, mating and brooding behavior during underwater observations, and later confirmed by gonad examination.

Underwater observations were made between 06:20 and 16:00 throughout the investigation period, mainly at Patch A. During the observations, data on home ranges, social interactions between males, foraging behavior, mating behavior and brooding

behavior were collected as follows. Movements of the 10 largest males, 5 females and 3 unsexed individuals belonging to Patch A were recorded on the field map for 10 min. The 10-min observation was conducted 6 to 9 times per male, 6 or 7 times per female and 3 times per unsexed individual. The whole area, which each individual patrolled during the 10-min observations, was regarded as its home range. Social interactions, including attack and avoidance, between large individuals were recorded by following a known fish. The total observation time per male varied from 120 to 480 min. C. horei often foraged in schools, and the number of individuals in a school was counted in Patch A at various times on 6 days. Preliminary observations indicated that mating started early in the morning and finished before noon. Accordingly, observations for mating behavior started before 7:00 on 61 days from August to January. When mating behavior was seen, observation continued until completion. The number and location of brooding females and patterns of brooding were recorded in Patch A at intervals of 1 to 4 days. At that time, the number of guarded young was also counted. While six guarding females were each observed for 10 min, fishes attacked by them were

recorded and attacking distance from the guarding female to the attacked fish measured.

Recognized individuals in Patch A were censused 46 times at intervals of 2 to 7 days from July 20, 1989 to January 5, 1990, so as to determine the duration of their residence. On January 7 and 12, 1990, 67 individuals, including 39 recognized, were collected in Patch A with a gill and hand nets. In the laboratory, their TL, standard length (SL), and body and gonad wet weights were measured, and sex and stomach contents examined.

Results

Habitat, duration of residence and home range overlap

Ctenochromis horei were observed exclusively in the vegetated zones during the two patrols of the study area. During the investigation period, 60 to 70 individuals inhabited Patch A and about 30 inhabited Patch B. In Patch A, more than 90% of the fish occurred among the *Vallisneria*.

Of 67 fish collected in Patch A, 32 were males, 33 were females and the sex of the other two was undetermined. Males were 42 to 115 mm SL (mean \pm SD=80 \pm 18.3), females 51 to 97 mm SL (67 \pm 10.2), and unsexed 31 and 68 mm SL (Fig. 2). Males grew much larger than females (t=3.40, P<0.01).

Of 49 individuals, which were identified before the end of July, 45 (91.8%) stayed in Patch A for more than 1 month, 42 (85.7%) for more than 2 months, 38 (77.6%) for more than 3 months, 32 (65.3%) for more than 4 months and 28 (57.1%) for more than 5 months. Of the 26 individuals, which stayed in Patch A throughout the observation period (169 days), 14 (53.8%) were males, 11 (42.3%) were females and 1 (3.8%) was unsexed. The 3 largest males, M1, M2 and M3, occasionally left Patch A, on 10, 7 and 1 day, respectively. M1 visited either Patch B or another vegetated patch, which was about 130 m distant from Patch A, courting and threatening conspecifics. M3 also visited Patch B, but the destinatin of M2 was not found. Besides the usual residents, there were several fish which appeared intermittently in Patch A.

In Patch A, about 60 residents foraged exclusively in the *Vallisneria* area and about 5 in *Potamogeton*; home ranges of 9 individuals are shown in Figure 3. The residents in the *Vallisneria* area sometimes vis-

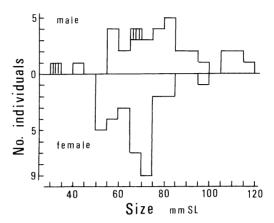


Fig. 2. Size distribution of males and females. Lined columns represent unsexed individuals.

ited the Potamogeton area to rest.

Large males moved extensively about the *Vallisneria* area, and their home ranges overlapped considerably with each other and with those of females (Table 1). Female home ranges also overlapped considerably (Table 2).

Foraging behavior and food

Ctenochromis horei foraged only in the vegetated zones. Among residents in Patch A, most fish limited their feeding to the *Vallisneria* area and only 5 to the *Potamogeton* area.

Residents in Patch A foraged either solitarily or in schools. A school usually consisted of 10–40 fish swimming in the same direction and stopping to forage at the same spot. Often, almost all residents in the Vallisneria area, irrespective of body size and sex, joined in school foraging. The school tended to decrease in size in the afternoon (Fig. 4).

C. horei snapped up benthic animals from the vegetation, or captured them on the sandy bottom in the grass patch. In the latter case, the fish often plunged the mouth into the sand, filling it with sand which was later spat out. Of the 28 fish whose stomachs contained food, 17 (60.7%) had ingested oligochaetes (1–350 individuals per fish), 13 (46.4%) shrimps (1–18), 8 (28.6%) nematodes (1–6), 2 (7.1%) copepodes (1–6), 1 (3.6%) caddisfly larva (1) and 1 (3.6%) fish fry (1).

Dominance order among large males

The following behavior patterns occurred fre-

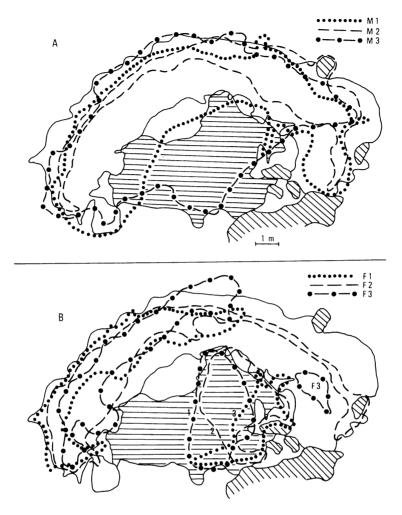


Fig. 3. Home ranges of 9 individuals in Patch A. A) Home ranges of the largest 3 males (M1-3); B) home ranges of 3 females (F1-3) in the *Vallisneria* area and 3 unsexed fish (numerals without letter) in the *Potamogeton* area. Observation time was 60-90 min for each male and female, and 30 min for each unsexed fish. See Figure 1 for distribution of the grass species.

quently following large male encounters; either attack, i.e., rushing at the other fish which then escapes, or avoidance, i.e., moving away from an approaching fish before it attacks. Based on these two behavior patterns, which were recorded on the days when mating was not observed, the dominance order was determined for the 12 largest residents (11 males and 1 unsexed), which stayed together in Patch A for more than 4 months (with one exception) (Table 3). Attack or avoidance occurred oneway between any two of the 12 fish, indicating a linear dominance order: M1>M3>M2>M5>M4 (>M6, M12)>M8 (>M11)>9 (>M7)>M10

(the exact positions of the males in parentheses could not be determined as each had had no aggressive interactions with those in the succeeding order). The dominance order was positively correlated with total lengths (Kendall's τ =0.857, n=8, excluding M 6, M7, M11 and M12, P<0.01).

After M1 had disappeared from Patch A, on December 3, the second-ranked fish, M3, became the most dominant. After about a month, however, M3 fought against M48 (>M3 by 3 mm TL), which had often been observed in Patch B. The fight continued for 10 min, each protagonist biting the other on the trunk or about the mouth. Finally M3 fled to the

rocky area, being chased by M48. The latter subsequently settled in Patch A, being dominant over all the remaining large males.

Courtship, spawning and male mating success

On non-spawning days, large males occasionally made a courtship display, taking a head-up position while quivering the body and displaying an orange spot on the anal fin to a female (Head-up display) between bouts of foraging. On the day of spawning, the most dominant male foraged infrequently, being engaged in following the female for 1 to 4 hours before spawning occurred (Table 4). The male displayed repeatedly, either making "Head-up display" (18.7 times \pm 3.5 SD per 10 min, n = 7) or quivering its tail to lead the female to the spawning sites (2.9 times ± 2.7 SD per 10 min, n=7). The female did not respond readily to the courtship display, instead continuing to forage. Other large foraging males avoided the most dominant male, which attacked the former when they approached the female. The dominant male sometimes lost sight of the female while attacking subordinate males, but quickly sought her out among the other females and resumed courting behavior.

Eventually, the dominant male succeeded in leading the female to the spawning site, which was a sandy space in the grass or on the edge of the grass patch. There he took a head-up position, while quivering his body, and the female brought her mouth into close proximity with the male's genital area for a few seconds. The two fish then reversed their positions, Such mutual "T-position" behavior was repeated from 0 to 24 min before the start of spawning.

The female performed 5 to 18 ovipositions (1 to 4 eggs each time) in the head-up position over 4 to 73 min. Immediately after picking up the eggs from the bottom with her mouth, she nuzzled the genital area of the male. The female spawned at several different sites (2.4 sites ± 2.2 SD, n = 5) with the same mate.

After the final oviposition, the female continued mutual "T-position" behavior with her mate or another male, intermittently for 2 to 24 min. Afterwards the male resumed foraging, while the female remained motionless in the grass zone.

Mating behavior of six females (65–83 mm TL) was observed from September to December, all in the morning (Table 4). All the females mated with the most dominant males at the time (M1, M3 and M

48). Three females mated with M1 in Patch A on different days. One female, which had been followed by M1 in both Patches A and B before spawning, mated with M48 in Patch B while M1 chased off another male, and later with M1 in the same patch,

Table 1. Overlap* of home ranges between the 10 largest males and between them and 5 females in Patch A

Males	with other males mean±SD (%)	with 5 females mean ±SD (%)
M 1	40.7 ± 19.3 77.2 ± 14.3	27.0± 9.0 82.7± 9.0
M2	52.4 ± 16.7 35.7 ± 12.1	24.6 ± 8.6 28.2 ± 3.0
М3	29.5 ± 13.9 80.7 ± 8.8	21.2 ± 7.2 87.7 ± 10.5
M4	60.1 ± 20.3 57.2 ± 12.8	39.9 ± 14.5 61.9 ± 10.4
M5	46.2 ± 25.6 33.8 ± 12.0	20.2 ± 13.9 24.2 ± 14.7
M6	64.2 ± 24.3 33.7 ± 12.3	50.1 ± 12.0 48.9 ± 14.9
M7	53.6 ± 20.7 56.7 ± 14.5	34.1 ± 10.8 59.5 ± 3.5
M8	53.5 ± 15.0 55.6 ± 17.2	38.7 ± 12.4 65.4 ± 11.1
M10	56.2 ± 22.7 38.6 ± 8.6	44.5 ± 21.2 51.4 ± 16.1
M11	45.4 ± 15.7 32.7 ± 11.2	36.0 ± 15.8 44.3 ± 14.3

^{*} Degree of overlap (A) of each male's home range (B) with that of another fish (C) was calculated as follows: upper, 100 A/B (%) and lower, 100 A/C (%).

Table 2. Overlap of home ranges between 5 females in Patch A (see footnote of Table 1 for the method of calculation of degree of overlap)

Females	with other females mean±SD (%)					
F1	41.8±15.1 43.9±10.9					
F2	44.9± 7.1 65.2±12.7					
F3	41.7 ± 17.4 39.8 ± 5.7					
F4	33.5 ± 14.6 40.1 ± 5.9					
F5	52.4 ± 21.8 25.3 ± 8.4					

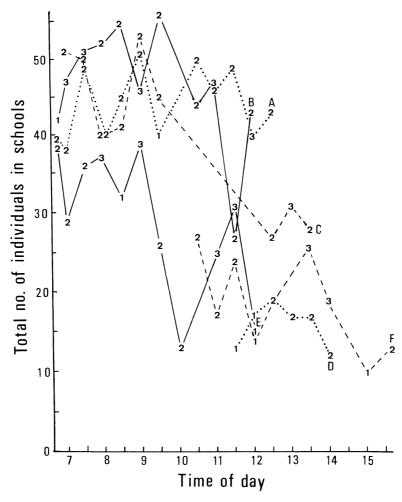


Fig. 4. Diel changes in total number of individuals in feeding schools in Patch A. Numerals represent the number of schools. A—October 20; B—October 23; C—October 26; D—November 2; E—November 7 and F—November 14.

after M1 had driven M48 away. After the disappearance of M1 from the study site, two females mated with M3 in Patch A and Patches A and B, respectively.

A second male or sex-unknown fish (60–134 mm TL) dashed into the spawning site (and quivered in parallel with the dominant male, taking a head-up position in one case) 5 and 4 times respectively, during 2 matings of M3. Such dashing occurred when the female nuzzled the dominant male's genital area, and is therefore suggested to be 'sneaking', although whether or not the 'sneakers' succeeded in fertilization is unknown.

Brooding behavior and female breeding cycle

Parental care carried out by the female consisted of mouthbrooding eggs and larvae, and guarding free-swimming juveniles. Guarding females could take the juveniles into the mouth, if necessary. Mouthbrooding was usually done in the *Potamogeton* area and guarding, exclusively in the *Vallisneria* area. Locations of mouthbrooding females sometimes changed from day to day, but those of guarding females were almost always fixed. Guarding females attacked other cichlids, i.e., *Lamprologus callipterus*, *Lepidiolamprologus elongatus*, *Neolamprologus mon-*

dabu, Cyathopharynx furcifer, Gnathochromis pfefferi, Limmnotilapia dardennii, Perissodus microlepis, Simochromis sp. and Xenotilapia flavipinnis, and also conspecifics, including the males with which they had mated. Guarding females were the most cautious toward the piscivorous Lepidiolamprologus elongatus, the attacking distance from the female to the latter $(1.2 \,\mathrm{m} \pm 0.6 \,\mathrm{SD}, \, n = 8)$ being significantly longer than to any other species $(0.5 \,\mathrm{m} \pm 0.4 \,\mathrm{SD}, \, n = 43)$ (Mann-Whitney U-test, Ucal = 318.5, P < 0.001). Mouthbrooding duration was from 15 to 23 days $(19.1 \pm 3.1, \, n = 8)$ and guarding duration from 0 to

Table 3. Dominant-subordinate* relationships among the 12 largest individuals in Patch A

Tows		M1 152	M3 135	M2 147	M5	M4 135	M6 120	M8 102	9 100	M7 106	M10 95	M11 95	M12 93	Total
Ву														
M 1	A** B***		18 0	27 0	8	31 0	8 0	15 0	13 0	9 0	1	3 0	19 0	152 0
М3	A B	0 81		1 0	1 0	2 0	4 0	4 0	0 0	5 0	0 0	1 0	0 0	19 81
M2	A B	0 125	0 69		6 0	23 0	4 0	5 0	0 0	2 0	0 0	7 0	1 0	48 194
M5	A B	0 58	0 8	0 24		6 0	4 0	0 0	5 0	0 0	3	0 0	2	20 90
M4	A B	0 128	0 14	0 26	0 7		0 0	2 0	2 0	0 0	2 0	0 0	1 0	7 175
M6	A B	0 42	0 5	0 5	0 15	0 2		0 0	0 0	0 0	0 0	0 0	0 0	0 69
M8	A B	0 28	0 9	0 0	0 0	0 10	0 0		2 0	0 0	1 0	3 0	0 0	6 47
9	A B	0 27	0 1	0 4	0 2	0 2	0 0	0 0		0 0	3 0	0 0	0 0	3 36
M7	A B	0 36	0 2	0	0 1	0 1	0 0	0 0	0		0 0	0 0	0 0	0 46
M 10	A B	0 8	0 1	0 0	0 0	0	0 0	0 1	0 4	0 1		0 0	0 0	0 18
M11	A B	0 7	0 4	0 1	0 0	0	0 0	0 10	0 0	0 1	0 0		0 0	0 26
M12	A B	0 55	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0		0 55

^{*} Numbers of attacks (A**) and avoidances (B***) (see text for details), which were recorded on the days when mating was not observed, are given. Eleven males and an unsexed fish which are numbered in order of body size were observed for 430, 420, 480, 470, 420, 120, 160, 190, 160, 160, 180 and 160 min, respectively.

Table 4. Courtship, spawning time and mates of 6 females

Female	TL (mm)	Date	Observation time	Following by mate	Mutual T-position	Spawning	No. of ovipositions	Mate
F44	67	13 Sept.	0640-1005	0705-1005	0936-0946	0936-0940	5	M 1
F40	70	7 Oct.	0622-1109	0622-1104	1010-1101	1034-1057	7	M 1
F45	83	30 Oct.	0637-1005	0658-1001	0850-0932	0907-0918	11	M 1
F58*	_	9 Nov.	0658-0926	0658-0926	0848-0857	0848-0857	3+	M1 & M48
F57	65	8 Dec.	0650-0838	0650-0830	0728-0825	0739-0812	18	M3
F59	83	11 Dec.	0645-0911	0645-0854	0736-0852	0737-0850	14	M3

^{*} See text.

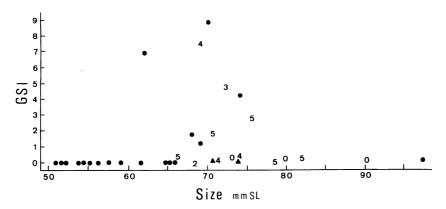


Fig. 5. Relationship between gonadosomatic index (GSI) and female size with its last spawning day. GSI = (wet weight of gonad/wet weight of body) × 100. Females whose last spawning day was known are represented by 0 (spawned within 1 month), 2 (2-3 months previously), 3 (3-4 months previously), 4 (4-5 months previously) and 5 (>5 months previously). Dots and triangles represent females for which the last spawning day was unknown and which did not spawn during the study period, respectively.

30 days (6.8 \pm 10.0, n=11). Thus the total brooding period differed from female to female, varying from 15 to 47 days (27.1 \pm 11.7 SD, n=7).

The number of mouthbrooded eggs or young was 27, 28 and 57 in females of 80, 73 and 90 mm SL, respectively. The number of guarded juveniles (15–30 mm TL) was smaller, and usually decreased day by day; from 13.4 juveniles \pm 5.7 SD (n = 12, range: 5–22) (maximum) to 8.8 \pm 6.9 SD (range: 1–19) (minimum).

Mouthbrooding and guarding females occurred in Patch A throughout the observation period from June 1989 to January 1990, the number being higher in July and August than in the other months (Table 5). The number of breedings occurring during the observation period (from July or August to December) was once in 9 females (81.8%) and twice in 2 (18.2%). The gonadosomatic index (GSI) was near zero in all females smaller than 62 mm SL, but varied in larger individuals (Fig. 5). GSI was nearly zero in females which spawned within the previous 3 months, and higher in other females which had

Table 5. Seasonal changes in number of brooding females per census in Patch A

	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.
Average	5.0	5.1	2.3	2.0	1.1	1.1	1.7
SD	1.6	1.2	1.0	0.9	1.3	0.8	0.6
Range	3-7	3-7	1-5	0-3	0-4	0-2	1-2
No. of censuses	4	20	18	22	16	12	3

spawned more than 3 months previously.

Discussion

Numerous males and females of Ctenochromis horei together inhabited a grass patch and had overlapping home ranges. A dominance order, which was established among males, was correlated with male mating success, as reported in many animals (see Wilson, 1975). All of the observed matings were achieved by the most dominant males, although apparent sneaking behavior by other fish was observed. In general, males may monopolize matings by monopolizing critical resources for females (e.g., feeding, spawning and brooding sites) or by controlling direct access of other males to females (Emlen and Oring, 1977). Dominant male C. horei did not defend critical resources, instead concentrating efforts toward the female about to spawn, by following the said female for several hours before spawning commenced. Such defense of females must be difficult for males other than the most dominant, especially when there are many rivals with overlapping home ranges.

A male can control access to females more easily if he is recognized as dominant by other males. Constant application of pressure on the other males by the dominant male even on non-spawning days may have been useful to defend females on the spawning days. The magnitude of monopolization of matings by a male is dependent on the temporal pattern of availability of sexually receptive females (Emlen and Oring, 1977). If sexual receptivity among females is asynchronous, there is a high potential for a dominant male to monopolize matings. The long breeding season (Table 5), variation in ovary maturation (Fig. 5) and frequency of observed matings during this study indicated asynchronous sexual receptivity of the females.

Two methods of displacing the most dominant male were observed during the study; the rise of a second-ranking male to the top rank after the disappearance of the most dominant male, and the intrusion of a male from another vegetated patch. This indicated that large, subordinate males may either wait for the dominant position to be vacated or search for a group in which they can be dominant. The occasional absenses of M2 and M3 from Patch A may have been related to the latter.

The mating system of C. horei contrasts with that of most maternal mouthbrooders for which mating behavior has been reported so far. In the latter, males or individuals of both sexes defend their territories and males mate with visiting females in the males' territories (Lowe-McConnell, 1959; Fryer and Iles, 1972; Loiselle and Barlow, 1978; McKaye, 1983, 1984; Kuwamura, 1986, 1987; Yanagisawa and Nishida, 1991). Female mate choice may operate on male mating success in these species, as suggested by some authors (McKaye et al., 1990; McKaye, 1991; Yanagisawa and Nishida, 1991), but is unlikely in C. horei. Sexual dichromatism is usually remarkable in the former (Fryer and Iles, 1972; McKaye, 1984; Kuwamura, 1986), but not so in C. horei, a difference which may depend upon whether or not female mate choice operates.

Sexual dimorphism in body size was observed in *C. horei*; males were much larger than females. Such sexual dimorphism can be explained by inter-male competition for mates (see Halliday, 1978). In *C. horei*, competition for sexually receptive females is intense between males, male mating success being determined according to the dominance order among the males, which is positively correlated with body size.

In this study, one male, the most dominant, seems to have almost completely monopolized matings in the multi-male and multi-female groups. However, the magnitude of mate monopolization generally depends on the size and isolation of the group.

Because the vegetated patches in the study site were relatively small and well isolated from one another by sandy and rocky areas, one dominant male may have succeeded in mate monopolization. In a large vegetated area, such would be impossible for one male, as opportunities for other males to mate would increase. *C. horei* also inhabit much larger vegetated areas elsewhere in Lake Tanganyika. Investigation of the species in different-sized areas is necessary to elucidate the influence of habitat size on its mating system.

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- 口内保育をするカワスズメ科魚類 Ctenochromis horei の 複数の雄と雌からなるグループにおける優位雄による 繁殖の独占

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タンガニイカ湖において水草地帯に生息し, 雌が口内保育を するカワスズメ科魚類 Ctenochromis horei の社会構造を婚姻形態 を中心に調査した. 調査した 15 m×9 m の水草のパッチには、ほ ぼ同数の雌雄が60から70尾生息し、ほとんどの個体が3カ月 以上そこに滞在した。彼らはそのパッチで摂餌し、産卵し、子育 てをした.彼らの行動圏はよく重なり、彼らはよく群れをなして 摂餌した. 攻撃行動と回避行動から, 大きい雄の間でほぼ体の大 きさに一致した優位性が認められ、観察された繁殖全てに最優 位の雄がかかわっていた。スニーキングのような行動も観察さ れた. 産卵日の朝, 最優位雄は, 産卵の始まる前から終わるまで 数時間, 雌を追尾し, 他の雄から守ることによって独占的に繁殖 しようとした。6ヵ月の調査期間中に最優位雄の交代が2度起 こった.このような一夫多妻的な婚姻形態は,口内保育をするカ ワスズメ科魚類では初めての報告であり, 本種に特有な空間利 用の仕方が他の種と異なる婚姻形態を持つ原因であると推察さ れた.

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