Social Organization of a Polygynous Cichlid
Lamprologus furcifer in Lake Tanganyika

Yasunobu Yanagisawa

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Abstract *Lamprologus furcifer* inhabited vertical or overhanging rock surfaces. Females persistently stayed at particular sites and singly guarded the offspring there. Males also stayed at particular sites but often left them to visit females. A dominant male controlled the territories of several breeding females at a time. Schools of young under maternal care spread horizontally on the rock surface as they developed and fed mainly on benthic organisms such as atyid shrimps. It is suggested that the emancipation of males from brood care is attributed to the benthic life of young.

Of the over 700 species of the family Cichlidae, about 30% are estimated to be substrate brooders (Keenleyside, 1979). They usually have a monogamous mating system, in which a male and female form a pair bond and jointly protect the offspring on the substrate. In some species of substrate brooders, however, one male keeps mating relationships with two or more females at the same time. Such polygyny in cichlids has been observed in *Apistogramma trifasciatum* (Burchard, 1965) and *Lamprologus congolensis* (Wickler, 1965) in aquarium studies and in *Aequidens coeruleopunctatus* (Barlow, 1974) and *Cichlasoma nigrofasciatum* (Keenleyside, 1985) under natural or semi-natural conditions. Recent surveys in Lake Tanganyika are revealing that the genus *Lamprologus*, the largest group in the littoral fish community of this lake, includes a number of polygynous species. For example, in *L. furcifer*, *L. modestus* and *L. savoryi* one dominant male patrols widely and gains access to brooding sites of more than one female (Hori, 1983; Nagoshi, 1983; Kondo, 1986). Also, in *L. attenuatus*, *L. brichardi*, *L. tetracanthus* and *L. toae*, which have been considered to be monogamous, one male occasionally establishes a large territory including two brooding females (Limberger, 1983; Kuwamura, personal communication).

L. furcifer has the most strict bond toward a special type of habitat among the cichlids of Lake Tanganyika; it stays in the dark against vertical or overhanging rock surfaces (Brichard, 1978; Hori, 1983; Nagoshi, 1983). In the present study, brood care by females and social interactions between males and between males and females were observed. The growth, survival and food habits of offspring protected by the parent were also surveyed since these were considered to be important determinants of the mating and social system.

Methods

The field work was conducted at Luhanga, 12 km south of Uvira (3°24′S, 29°10′E). SCUBA was used in all observations and collections. A 20 m × 20 m quadrat, divided into 2 m × 2 m grids, was set on a rocky bottom with an average inclination of about 35°. It covered the bottom from the shore line down to the depth of 12 m. Positions of adult male and female *L. furcifer* were censused in the quadrat every 3 to 7 days from August to November, 1981. For identification, their body sizes, scars on the bodies and frags of the elongated caudal rays were recorded and some adults were tagged. When females were guarding the broods, their developmental stages (eggs, yolk-sac larvae and free-swimming young), numbers and approximate body sizes were recorded. In one census (on 10 October), a careful examination was carried out, in which I tried to find juveniles as well as adults and measured the inclinations and areas of rock surfaces where they occurred. Five adult males in the quadrat were followed individually for 14 to 50 min, usually 20 min, on 5 to 10 different days to determine their mobility. While following them, their positions were plotted on a map every
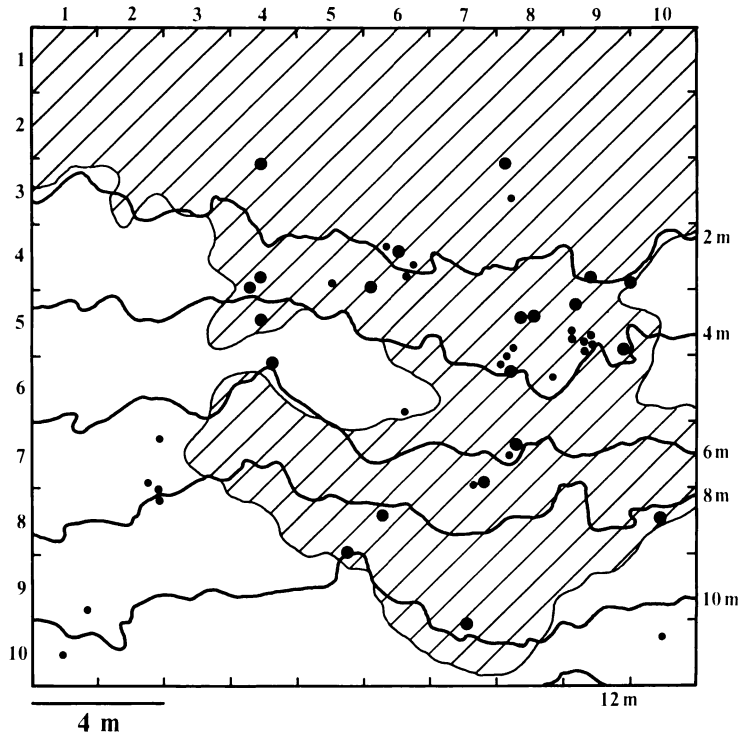
Fig. 1. Bathymetric map of the quadrat and occurrence of *Lamprologus furcifer* in it on 10 August 1981. Hatched area is rocky bottom and the remaining area rock-rubble-sand bottom. Small dots indicate individuals smaller than 75 mm SL and large dots the larger ones.

30 sec and their social interactions with other adults were recorded.

To measure the growth of free-swimming young, several individuals were collected from 21 broods outside of the quadrat at intervals of about 10 days. All adults and some of the young observed were sampled at the end of the field work, using hand nets and gill nets. After measurements of standard length (SL) and total length (TL), specimens were used for the examination of food habits and age-determination. For the examination of food habits, the numbers and approximate sizes of prey in the stomach and anterior intestine up to the first bend were recorded. For age-determination, 'check marks' on scales were counted. These marks were regarded as annual rings for the following reasons: (1) they were marked at regular intervals in the same way as annual rings seen in many other fishes, and (2) the age at maturity (2 years) and the maximum age (7 years) that were estimated from these marks approximated that of the medium-sized cichlid (see Fryer and Iles, 1972). However, it

remains unsolved which environmental or biological factors are related to the formation of these marks. Formation of annual rings is exceptional in tropical cichlids (Fryer and Iles, 1972).

Results

Distribution and home range. Twenty-one adults (larger than 75 mm SL) and 26 juveniles of *L. furcifer* were found in the quadrat (400 m²) (Fig. 1). Adults were distributed only on the rocky bottom, while juveniles on both rocky and rock-rubble-sand bottoms. Both adults and juveniles were situated close to rock surfaces whose inclinations exceeded 80° (Table 1), such as the undersides of rocks and shelves and the vertical surfaces of overhanging rocks and crevices. Rock surfaces inhabited by this fish were usually not rugged, covering an area of up to about 5 m². Breeding females selectively occupied extensive surfaces (Table 1) such as the undersides of shelves and vertical surfaces of overhanging rocks. Males, non-breeding females and juveniles were usually
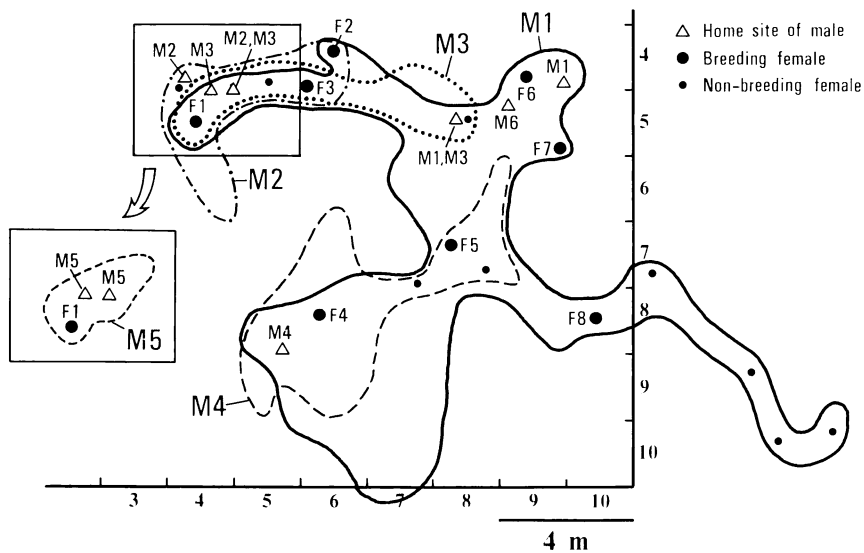
Fig. 2.　Home sites of males (M1–M6), breeding females (F1–F8) and non-breeding females and cruising areas of males (M1–M5).　Cruising areas are shown with lines.　Home sites and cruising area of M5 are shown in the margin.

more cryptic than breeding females and occupied the smaller rock surfaces.　Some of them were found in the inmost recesses of the underside space of complicate rocks or in deep crevices.　Probably many other individuals must have been past unnoticed due to their cryptic life.

Eight breeding females that occurred in the quadrat at the start of the census (F1–F8 in Fig. 2) stayed persistently at particular sites; six did throughout the study period (=96 days) and the other two for 87 and 75 days respectively until they disappeared from the study site.　Guarding of offspring, feeding and other activities of females were all conducted within their territories except for short moments when they chased away intruders.

Of six males in the quadrat, four (M1, M3, M4 and M6) were seen throughout the study period. One male (M2) disappeared between 8 and 11 September and was replaced soon by a slightly smaller male (M5) of unknown origin (Fig. 2).

Males also stayed at particular sites but, unlike breeding females, each occupied 1 to 3 sites during the study period (Fig. 2).　Some sites were occupied successively by two or three males on different days.　Males often left their home sites to cruise along rock surfaces.　The largest male (M1) most frequently left his home sites and his cruising area during the whole observation time (263 min) covered nearly 100 m² (Table 2).　On the other hand, cruising areas of the other males were smaller and were nearly completely included within that of M1 (Fig. 2).　The home range of M3 partially overlapped those of M2 and M5.

Social interaction.　During cruises, males often dropped into the territories of females (Table 3). M1 was observed to visit seven breeding females in the quadrat and nine non-breeding females in the quadrat and just outside of it.　On the other hand, the other males visited only 1 to 3 breeding and a few non-breeding females.　At the moment

Table 1.　The inclinations and areas of rock surfaces which *Lamprologus furcifer* occupied. Breeding females in parentheses.

Inclination (°)	<80	–100	–120	–140	–160	–180	Total
No.	1	6 (2)	5 (3)	5	7 (2)	6 (1)	30 (8)
Area (m²)	<0.1	–0.2	–0.4	–0.8	–1.6	>1.6	Total
No.	6	10	5 (1)	6 (4)	2 (2)	1 (1)	30 (8)

of their encounter, a male sometimes circled a few times around a female or both circled each other, head to tail. Males stayed at one female territory for up to 20 min but more than half of their visits (55%) were shorter than 30 sec. Their departure from the territory was sometimes triggered by the nudging of the female at the belly. Females showed no essential differences in their responses to visiting males.

Males occasionally encountered each other when they were cruising or visiting females. Of the nine such encounters observed, the larger male chased off the smaller ones in six cases and the smaller sneaked away from the larger before being attacked in three cases. Females were never observed to leave their territories and therefore no interactions were seen between them in this study. However, M. Hori (personal communication) once observed a prolonged fight between a brooding and an intruding female at Luhanga. It intermittently continued for at least two hours, sometimes involving mutual oral biting. This observation suggests that competition for breeding territory is intense among females. Actually, when breeding females were removed from their territories, females of slightly smaller size filled them up soon (within one day in 3 of 4 removals).

Reproduction and brood care. Eggs were found attached to rock surfaces in the central area of the female territory. They were olive green and 1.83 mm $\pm$ 0.02 SE (N=6) long with a diameter of 1.34 mm $\pm$ 0.03 SE. It took at least three days after spawning for the eggs to hatch. After hatching, the yolk-sac larvae adhered to the rock surface with their head glands and became free swimming young in four days at a size of 5.2 mm SL (=5.85 mm TL). Free-swimming young were in contact with the rock surface at the spawning site and the school of young spread horizontally on the surface as they developed. When they grew larger than 10 mm SL or so, they spaced out from one another. This repelling behaviour frequently occurred among them. They usually stayed in the territory for over one month and the next brood was often produced before their independence (Fig. 3). In the territory with two successive broods, the grown young situated themselves along the outer areas of the territory and were sometimes attacked by the female. If the new brood perished early, they were again

Table 2. Percent time of cruising, cruising speed and cruising area of males in the quadrat. Cruising area is expressed as the number of 1 m × 1 m grids which a male passed.

Male	Standard length (mm)	Observation time (mm)	Percent time of cruising (%)	Average cruising speed (cm/min)	Cruising area (m²)
M1	124	263	68 3	143	98
M2	ca. 120	135	57.8	82	18
M3	113	222	20 0	73	18
M4	106	189	21 4	180	32
M5	105	105	17.1	103	9

Table 3. Visits of males to breeding females. The number of visits is in the upper row and the total visiting time (sec) in the lower row. Standard lengths of fish in parentheses.

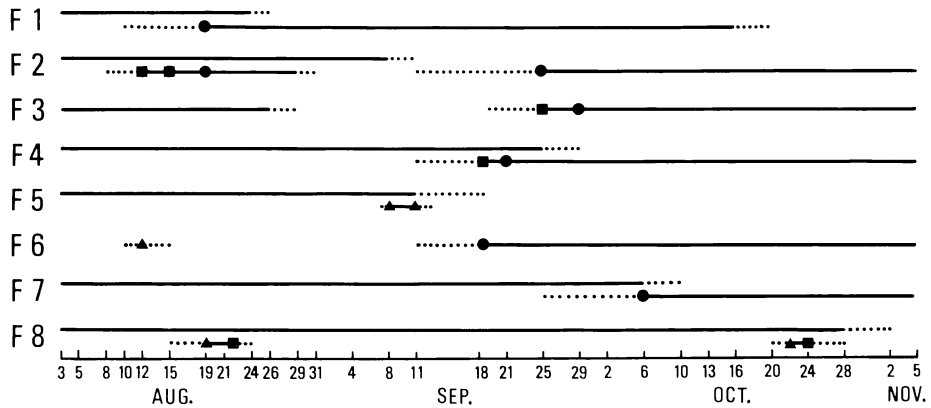| Male	Observation time (min)	F1 (85)	F2 (92)	F3 (98)	F4 (92)	F5 (91)	F6 (96)	F7 (107)	F8 (94)	Total
M1	263	1	1	0	3	8	2	1	11	27
(124)		10	20	0	90	640	10	10	190	970
M2	135	11	3	3	0	0	0	0	0	17
(ca. 120)		520	110	80	0	0	0	0	0	710
M3	222	3	0	1	0	0	0	0	0	4
(113)		70	0	20	0	0	0	0	0	90
M4	189	0	0	0	2	1	0	0	0	3
(106)		0	0	0	20	20	0	0	0	40
M5	105	7	0	0	0	0	0	0	0	7
(106)		100	0	0	0	0	0	0	0	100

Fig. 3. Duration of guarding in eight females during the period from 3 August to 5 November, 1981. Solid and dotted lines indicate actual and possible guarding periods, respectively. Triangles, squares and circles indicate the stages of eggs, yolk-sac larvae and free-swimming young, respectively.

tolerated in the central area of the territory by the female.

Brood size at the egg stage was 87.0 ± 6.5 SE (N=9) if one exceptionally small (=12) brood was neglected. Of nine broods found at this stage, eight perished within six days and only one persisted for more than one month. The brood size of yolksac larvae was 26.1 ± 6.4 SE (N=7). This indicates that brood size decreased by 70% or more on the average during the egg and larval stages even in broods which had not perished. Of six broods which were first found at the larval stage, three persisted for over one month but two perished within 3 and 16 days each. In the remaining one, only one individual survived until the 13th day, when it was sampled. These results clearly indicate that a greater portion of the eggs produced suffer death before they become free-swimming young.

Broods at the early free-swimming stage (less than 7 mm SL) contained 5 to 17 individuals ($\bar{x}=9.9$, N=15). These values, however, may be a little underestimated, since some young may have been unnoticed by the observer: their greyish body colour well melted into a shady background. Of 15 broods censused from the early free-swimming stage, only two became extinct within one month. In the others, the number of young scarcely reduced in the first one month; for instance, in five intact (not being sampled) broods the reduction of brood size was 10% on the average. As the young grew still larger, their number gradually decreased. But it was not

rare that a few young were found just outside of the territory. They were probably forced out from the territory by their fellow young. When some young were removed from the territory in one survey, they were sometimes replaced by others in the next survey, suggesting that such expelled young came back to the territory. Young were estimated to become independent of the mother at the sizes between about 25 and 35 mm SL: the largest individual collected in a female territory was 36.2 mm SL and the smallest outside of the territory was 27 mm SL.

Growth rate of young, measured in standard length, slightly decreased with development (Fig. 4). The mean growth rate was 0.34 mm/day until they attained 20 mm SL but 0.26 mm/day afterwards.

Females guarding the eggs, yolk-sac larvae or early free-swimming young attacked intruders 7.8 times per 10 min (in a 163 min observation). Two cichlid species, Lamprologus brichardi and Asprotilapia leptura, were most frequently attacked (24 and 12% of the total, respectively). Aggressiveness of females tended to decrease with the growth of young, though not measured quantitatively. The behaviour of guarding females was not very different from that of non-brooding females except for attacking on intruders: both kept still most of their time in the central area of the territory. Males that were visiting the territory of a female were unconcerned with the brood.

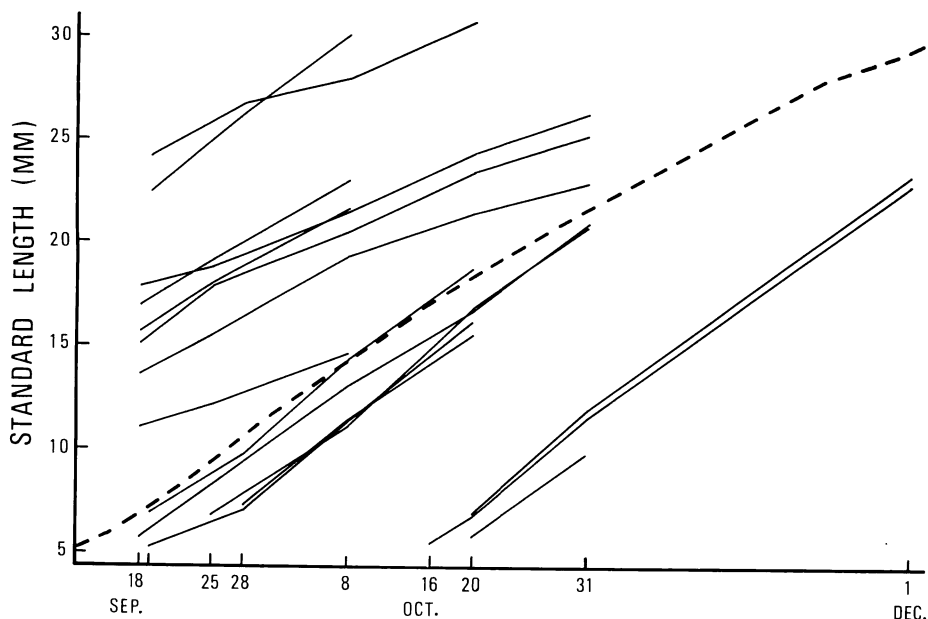**Food habits.** Free-swimming young less than 10 mm SL mainly fed on copepods (Table 4).

Fig. 4. Growth curve of free-swimming young under parental care. The mean is shown with a broken line.

About half of them were nauplii. Percent volume of copepods in the guts of young, however, decreased with growth. On the other hand, atyid shrimps occurred abundantly in the guts of young over 11 mm SL and were the primary food of the larger young, juveniles and adults (Table 4). The number of shrimps eaten by a young were usually one and occasionally two. A gut containing shrimp bulged out, since the shrimp was usually larger than 3 mm in body length. While, adult guts contained up to 120 shrimps. The number of shrimps in one gut tended to be higher in females than in males, though not statistically significant (Mann-Whitney U test, $p > 0.05$, Table 5). This number was not related to the brooding conditions of females (Kruskal-Wallis analysis of variance of ranks, $H = 5.21$, $P > 0.05$). Shrimps were abundant in the habitat of *L. furcifer*; the

Table 4. The numbers and relative volumes of prey eaten by *Lamprologus furcifer*.

Standard length (mm)	No. of sample	Number of prey per individual					Percent volume of prey				
		Ostracods	Copepods	Atyid shrimps	Insects[1]	Others	Os.	C.	A.S.	I.	Ot.
5.5–10	7	0.71	32.57	0	0.14	—	8	89	0	3	0
10–15	20	1.05	20.80	0.80	0.05	—	1	11	88	*	0
15–20	14	0.07	6.86	0.36	0.71	—	*	10	73	17	0
20–30	29	0.03	13.14	0.59	0.21	Nematods	*	13	84	2	*
30–40	10	0.20	3.20	1.10	0.30	Fish scales	*	4	94	1	*
40–50	5	0	0.60	1.00	0	Fish scales	0	*	99	0	*
50–70	3	0	0.67	8.00	0.67	—	0	*	99	*	0
70–90	4	0	0	8.25	1.50	—	0	0	91	9	0
90–124	28	0	0.04	12.46	0.46	Fish scales Fish eggs[2] Fish	0	*	91	*	8

* less than 1%; 1) Ephemeroptera, Plecoptera, Trichoptera, Diptera and Coleoptera; 2) Eggs of *Lamprichthys tanganicanus*.
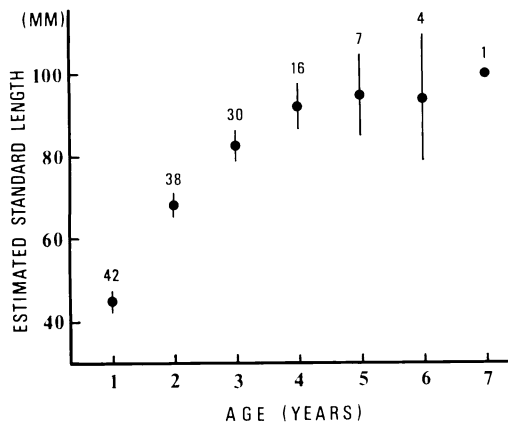
Fig. 5. Estimated standard length of *Lamprologus furcifer* when each annual ring was formed on the scale. Vertical lines and numbers just above them are ranges of standard errors and sample sizes, respectively.

mean abundance of shrimps in the territory of a female was 50.3/200 cm² on rough surfaces (N=6), though it was only 3.5/200 cm² on smooth surfaces (N=2). Shrimps concealed themselves in small depressions of the rock surface in the daytime and swam up into the water at night. They are probably more available to *L. furcifer* at the moment when they migrate between the rock and open water.

Age. The largest juveniles whose scales showed no annual ring was 51.6 mm SL, whereas the smallest whose scales showed an annual ring was 48.6 mm SL. From back-calculation, body sizes at the formation of the first annual ring were estimated to be between 27.2 and 65.8 mm SL, with a mean of 45.0 mm SL (Fig. 5). Estimated body sizes of the fish steadily increased as their annual rings increased up to 4 but reached a plateau thereafter. Males and breeding females

had 2 to 7 and 2 to 6 annual rings, respectively. Positive correlation was recognized between the body sizes and the number of annual rings in breeding females (r=0.489, N=21, P<0.05). Incidentally, the largest male M1 (124 mm SL) had four annual rings but a smaller male M5 (106 mm SL) had seven.

Discussion

Mating and social systems. Polygyny is defined as prolonged association and essentially exclusive mating relationship between one male and two or more females at a time (see Keenleyside, 1985). In *L. furcifer*, most breeding females were visited by more than one male and they showed no essential difference in the responses to visiting males. So, it was not possible to absolutely determine with which they mated. However, dominance of the largest male over other males in his home range and his frequent visits to females suggest that he could defend access to females ready to spawn and, therefore, could monopolize matings. Accordingly, *L. furcifer* must be an essentially polygynous species. Probably, a dominant male of this fish tolerates other males in his home range simply because it is impossible for him to expel them. Innumerable refuges are available in their habitat.

In this study, a dominant male had access to 16 females, of which seven were breeding. And, M. Hori (personal communication) observed at Luhanga that a large male visited six females. The number of females to which a dominant male had access is also known in other polygynous species of the genus *Lamprologus*: 2 in *L. attenuatus*, *L. brichardi*, *L. tetracanthus* and *L. toae* and up to 4 in *L. savoryi* and up to 6 in *L. modestus* (Limberger, 1983; Kondo, 1986;

Table 5. The numbers of atyid shrimps in the guts of adult *Lamprologus furcifer* in relation to their sexes and brooding conditions.

	No. of sample	Average standard length (mm)	No. of shrimps ($\bar{x} \pm SE$)
Females without offspring	9	92.9	9.1± 5.2
Females guarding the eggs, larvae or small young (<13.6 mm SL)	7	96.7	15.4± 3.5
Females guarding the large young (>17.6 mm SL)	8	96.2	18.8±14.5
Males	8	107.1	5.5± 2.5

Kuwamura, personal communication). The first four species are principally monogamous in which both parents guard the offspring and even bigamous males of these species make substantial contributions to brood care. By contrast, in the latter two species, polygyny is the rule and males have no or little concern with brood care as in *L. furcifer*. Thus, the mating system is closely correlated with the brooding pattern.

Uniparental care. Monogamy is predominant in substrate brooders (Fryer and Iles, 1972; Keenleyside, 1979). It has been suggested that in these cichlids an inclination toward polygyny is counteracted by selection pressure from predation, requiring two parents for protecting their offspring (Barlow, 1974). In general, two parents are more necessary to defend the free-swimming young than to defend the immotile offspring (eggs and yolk-sac larvae) (Perrone and Zaret, 1979; Yanagisawa, 1986). However, the necessity of two parents to defend young seems to vary according to the microdistribution of young. Two types are discriminated in the microdistribution of young: the hovering type and the benthic type. In the former, the school of young expands its area into the water as they develop, but in the latter it spreads horizontally on the substrate. Generally, young of the hovering type will be more vulnerable to predation and therefore protection by two parents will be more necessary in this type. This prediction agrees well in the genus *Lamprologus* (Nagoshi, 1985; Kuwamura, personal communication). For example, in the species of the hovering type, such as *L. attenuatus*, *L. brichardi*, *L. elongatus*, *L. toae* and *L. tretocephalus*, both parents guard the young. On the other hand, in the representative species of the benthic type, such as *L. furcifer*, *L. modestus* and *L. savoryi*, females alone guard the young. As a matter of course, typical polygyny occurs only in the benthic type. In the hovering type, only a facultative bigamy occurs, as seen in *L. attenuatus* and *L. brichardi*.

Microdistribution of young is closely related to their food habits (Gashagaza and Nagoshi, 1986). Young of the hovering type live on planktonic copepods. On the other hand, young of the benthic type mainly feed on benthic organisms such as shrimps and insects except for the earliest free-swimming stage. In general, planktonic prey must be more renewable, since they are con-tinuously being carried by water currents. Benthic prey must be more exhaustible for young which move within a small area. In fact, atyid shrimps, which are the primary food for young of *L. furcifer* and some other species of the benthic type (Gashagaza and Nagoshi, 1986), are not eubenthic but planktobenthic: they show diel migration between the water and bottom. Thus, the young will be supplied with shrimps in their sites on a daily basis. It seems that a stable supply of benthic prey in the brooding sites is a prerequisite for the occurrence of the benthic type and the emancipation of one parent from brood care.

Mortality of offspring under parental care. The present study indicates that mortality of offspring at the egg and larvae stages is very high in *L. furcifer*. In a rough estimation from the data on the extinction rate of broods and reduction of brood size with development, less than 1 % of the eggs produced can survive to the time of independence. Mortality of offspring under parental care has been surveyed in a few cichlids (McKaye, 1977; Yanagisawa and Nshombo, 1983; Nagoshi, 1985; Yanagisawa, 1986). In four species of *Lamprologus* (*L. elongatus*, *L. modestus*, *L. toae* and *L. tretocephalus*), the number in one brood decreased by 63 to 96 % during the period from the egg stage to independence. In addition, some broods at the egg and larvae stages completely perished (Nagoshi, 1985). Nagoshi suggests that such reduction and extiction of broods were mainly caused by predatory fishes at night. The destruction of broods in *L. furcifer* also seems to have occurred mainly at night, since broods of this fish were never attacked by predators during the daytime observations. Thus, high mortality of offspring at the early stage in this fish is probably not attributed to uniparental care in the daytime but to no brood care in the night. Intensive field research at night is needed.

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(Department of Biology, Ehime University, 2-5 Bunkyo-cho, Matsuyama 790, Japan)

タンガニイカ湖に生息する一夫多妻制のカワスズメ科魚類 *Lamprologus furcifer* の社会構造

柳沢康信

Lamprologus furcifer は特異的に岩の下面や垂直面に生息していた．雌は長期にわたり特定の場所にとどまり，単独で子供の保護を行った．雄も特定の場所にとどまる傾向にあったが，しばしばそこを離れて雌のナワバリを訪れた．優位な雄は同時に数個体の繁殖雌のナワバリを支配した．親に守られている稚魚はエビなどの底生動物を主な餌とし，その群れは岩面に沿って平面的に広がった．この種において雄の育児活動が不要になったのは，稚魚が底面に密着して生活しているためであると推察した．

(790 松山市文京町 2-5　愛媛大学理学部)