

## Brood Defence and Parental Roles in a Biparental Cichlid Fish *Lamprologus toae* in Lake Tanganyika

Shigeru Nakano and Makoto Nagoshi

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**Abstract** Brood defence of a cichlid fish, *Lamprologus toae*, was investigated in its natural habitat in Lake Tanganyika. Both parents guarding a brood attacked both conspecific and heterospecific intruder fishes at different locations. The heterospecific intruder fishes could be classified into three groups on the basis of the locations at which the attacks against each species took place. The distinction of groups by the parents seemed to be primarily based on food habits and feeding behaviour of the intruder fishes. The piscivorous species which were more dangerous for the brood were attacked by both parents at more distant locations from the brood. Parental defence of breeding territory changed with the development of the young. The frequency of attacks against each group decreased after the young reached the size too large for the fishes of the group to prey on. Division of labour in the territorial defence was recognized between male and female. The male parent mainly defended the peripheral region of the territory and the female parent defended the inner region. Significance of the selective attack against intruders and the division of labour between the two sexes in brood defence is discussed.

Selective defence of interspecific territory is known in many reef fishes (Clarke, 1970; Fishelson, 1970; Keenleyside, 1972; Myrberg and Thresher, 1974; Ebersole, 1977; Kohda, 1984) and cichlid fishes (McKaye and Hallacher, 1973; Baylis, 1974; Perrone, 1978; McKaye, 1984).

Males of the damselfish, *Eupomacentrus altus*, selectively attack potential egg predators, food competitors and conspecific males at different locations during the breeding season (Kohda, 1984). In this instance, the territory holder seems to protect several kinds of resources by selective defence. Cichlidae are well known for their variety of parental behaviour which generally extends over a long period (Fryer and Iles, 1972; Keenleyside, 1979). Perrone (1978) and McKaye (1984) reported that the parents of cichlid fishes form a territory around a breeding site and selectively attack intruder fishes at different distances from a brood and at different frequencies. Perrone (1978) showed that the parents of *Cichlasoma maculicauda* attack fry predators at a point where the predators can get access to the fry and ignore them otherwise.

It is considered that selective defence enables territory holders to maximize defensive effect without a large increment of costs that accompany territorial defence. For parental cichlid fishes, defence of the breeding territory is expected

to change gradually with development of the young. However, only a few papers have been published on this subject (McKaye, 1984).

Among many biparental substrate-brooding cichlid fishes, the division of parental labour is widely known. Generally, the female is mainly concerned with direct care of the young, whereas the male is primarily involved in territorial defence (Barlow, 1974; Keenleyside, 1978, 1979). However, there has been scarcely any attempt to examine the division of labour in parental care in terms of the efficiency of brood protection. In addition, the relationship between selective defence and the division of labour has been little studied.

A Tanganyikan cichlid *Lamprologus toae* seems to be one of the good examples for the study of this subject because of its typical biparental care (Nagoshi, 1983, 1985, 1987). The purpose of the present paper is to examine how effectively the parents of *L. toae* defend their breeding territory by selective defence and sexual labour division.

### Materials and methods

**Study area.** This study was carried out at a rocky shore of Luhanga (03°31'S, 29°09'E), 12 km southward from Uvira (03°24'S, 29°07'E), located near the north-western end of Lake Tanganyika.

There are no inlet streams around the station. Water transparency was more than 10 m during the study period. The substratum consists mainly of rock and boulders with a few sandy patches. The bottom slope is markedly steep at depths over 3 m, with a gradient of one in two. Eighty-seven fish species, of which more than 70% belong to the Cichlidae, were observed in the study area. Some additional observations of breeding behaviour and collections of breeding pairs of *L. toae* were made at Mbemba, 15 km farther south from Luhanga.

**Breeding biology.** An outline of the breeding habits of *L. toae* was given by Nagoshi (1983, 1985). The breeding sites of *L. toae* are distributed at a depth of 1 to 5 m in slightly sloping rocky areas. The female lays 100–200 eggs in a mass on a rock surface. As the eggs hatch, the female transfers wrigglers (yolk-sac larvae) with her mouth to a nearby small rock crevice or hole which she has previously cleaned. Only the female is involved in the direct care, fanning and mouthing, of the eggs and wrigglers. The parents usually hover near the center of the breeding site. Both parents attack intruder fishes during breeding. The free-swimming fry aggregate in the water column just above the spawning site. The aggregation gradually expands vertically and horizontally with growth of the young. Fry over 25 mm SL leave the breeding site.

**Observations.** The territorial behaviour of parental *L. toae* guarding their brood was observed from August to September 1985. A line 400 m long was placed on the bottom of 5 m depth to record the positions of the breeding sites. Prior to the observations, topographic maps of the bottom around each breeding site were drawn on a scale of one tenth. Direct observations were conducted underwater with SCUBA. In the daytime, 1,020 min of observations (units of 60 min), were performed for 17 breeding pairs whose young were at various developmental stages. The hovering positions of the parents, the locations where their attacks took place, the species names of intruders and the intruding courses of all intruders were recorded on the map. Vertical distance from the bottom was measured by a graduated rope with a float set near the breeding sites.

A few young under parental care were collected

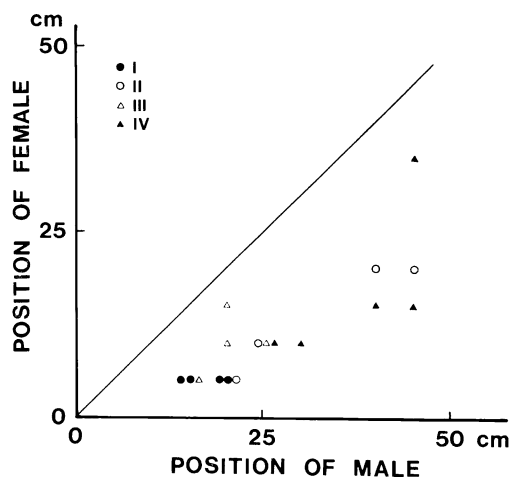


Fig. 1. Relation between hovering points (cm above the substrate) of male and female parents of *Lamprologus toae*. I, II, III, and IV represent the developmental stages of young under parental care (see text for detail).

by hand net after each observation to assess their size and developmental stage. In this study, developmental stages of the young were divided as follows: I—egg and prolarva under 4.5 mm (wriggler); II—free-swimming fry under 10 mm; III—from 10 to 20 mm; and IV—over 20 mm SL. The parents were collected by spearing to check their sex and size, just after the observation of their hovering positions.

## Results

Males ranged from 63 to 69 mm ( $\bar{X}=65.9$ ,  $SD=1.8$ ,  $N=17$ ) and females from 58 to 75 mm ( $\bar{X}=65.2$ ,  $SD=5.0$ ,  $N=17$ ) in standard length. There were no significant differences between the two sexes in body size (t-test,  $p>0.1$ ), body shape or colouration. The parents usually occupied fixed positions near the center of the breeding site. From 17 samples of parents collected after the observation, we found that the female always stayed closer to the bottom than her mate, regardless of the developmental stage of the young (Fig. 1). Therefore, we could easily distinguish male and female parents underwater by their positions.

**Selective territorial defence.** Both parents guarding the young were aggressive to conspecific and heterospecific fishes approaching

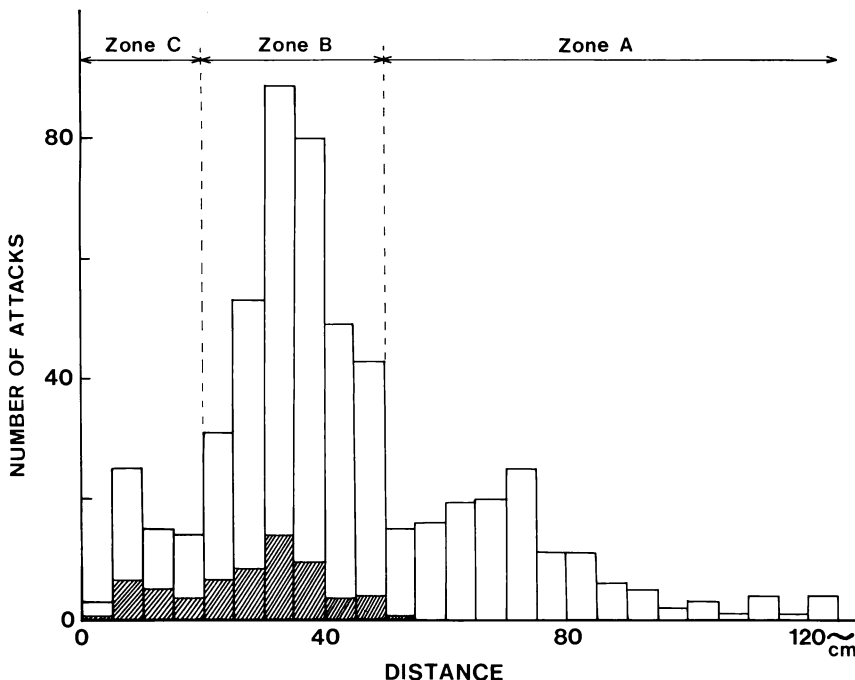


Fig. 2. Frequency distribution of the distance between the center of egg mass or fry aggregation and the point at which the attacks against intruders took place (attack distance). White and shaded bars represent male and female, respectively.

their breeding site. About 30 species (25 cichlids and 5 non-cichlids), which account for nearly one third of the total fish species found in the study area, were attacked by the parents during observations of 17 pairs.

The frequency distribution of the distances between the central point of the egg mass or fry aggregation and the point at which intruders were attacked (attack distance) is shown in Fig. 2. The histogram has three peaks and we divided the surrounding area of the breeding site into three zones as shown in Fig. 2.

Attack distances against each intruder species are shown in Table 1. Conspecific intruders were classed as Group 1 for convenience. Heterospecific intruders were classifiable into three groups (2-4) on the basis of the attack distance (Table 1). The frequencies of the intrusions of the fishes in each group and the attacks of parents against them are represented in Table 2.

Conspecific adults were attacked mainly in Zone A (distance,  $\bar{X}=76.6$  cm,  $SD=39.7$ ,  $N=23$ ). The attack distances hardly changed throughout the developmental stages of the young

(ANOVA,  $p>0.05$ ). However, the attack distances were considerably different between the two sexes (t-test,  $p<0.01$ ). Males attacked conspecific intruders at a distance of 60-130 cm ( $\bar{X}=91.6$ ,  $SD=29.1$ ,  $N=19$ ), while females did so at a distance of 6-34 cm ( $\bar{X}=19.6$ ,  $SD=11.5$ ,  $N=5$ ). The male often allowed some conspecific individuals to intrude into the territory without aggression and displayed courtship behaviour toward them, whereas the female attacked all intruders allowed by her mate. Although it was impossible to distinguish the sex of the conspecific intruders, both parents seemed to attack intruders of their own sex.

Four species of the Cichlidae, attacked also in Zone A (distance,  $\bar{X}=69.2$  cm,  $SD=16.2$ ,  $N=120$ ), were placed in Group 2. The attack distances did not differ among the developmental stages of the young (ANOVA,  $p>0.05$ ) or between male and female parents (t-test,  $p>0.05$ ). The frequency of intrusions of the fishes in Group 2 increased with development of the young, but it decreased as the fry reached 20 mm SL (Table 2). Intruders were always pursued for a long distance,

except for *Perissodus microlepis* which could approach the brood closer than other fishes in Group 2 (see below).

Fifteen cichlid species and three fishes of three other families were attacked mainly in Zone B (distance,  $\bar{X}=33.9$  cm,  $SD=8.7$ ,  $N=366$ ) and placed in Group 3 (Table 1). Their attack distance slightly decreased (16.6%) after the fry grew over 10 mm SL (t-test,  $I>II$ ,  $p>0.05$ ;  $I>III$ ,  $p<0.05$ ;  $I>IV$ ,  $p<0.05$ ;  $II>III$ ,  $p<0.05$ ;  $II>IV$ ,  $p<0.05$ ,  $III>IV$ ,  $p>0.05$ ). As the fry grew over 20 mm SL, 90 of 148 (60.8%) intruding individuals were not attacked in Zone B and 21 of 24 individuals were not attacked even in Zone C (Table 2). The attack distances of the male were slightly larger (about 9.0%) than those of the female

(t-test,  $p<0.05$ ). Of the 372 attacks against fishes of Group 3, 276 were directed toward the following three species: *Telmatochromis temporalis* (127), *Lamprologus brichardi* (75), and *Telmatochromis bifrenatus* (74), which were abundant in the study area (Hori et al., 1983).

*Tropheus moorei* and *Petrochromis* spp., which were mostly attacked in Zone C (distance,  $\bar{X}=10.5$  cm,  $SD=7.3$ ,  $N=33$ ), were included in Group 4. The attack distances against them scarcely changed with the development of the young (ANOVA,  $p>0.05$ ). The difference in the attack distance between the two sexes was not significant (t-test,  $p>0.05$ ). The frequency of the attacks against them decreased with the development of the young (Table 2). Parents

Table 1. Attack distance (cm) against each intruder species and its body size (L: SL>10 cm; M:  $5\leq SL\leq 10$  cm; S: SL<5 cm), body depth rate (BDR): body depth/body length $\times 100$  (l: >40; m: 30–40; s: <30) and food habit (C, carnivorous; H, herbivorous; O, omnivorous; f, fish; p, plankton; b, benthos; s, scale).

Group	Species	Attack distance		Size	BDR	Food habit
		N	mean $\pm$ SE			
1	<i>Lamprologus toae</i>	23	76.6 $\pm$ 15.9	M	m	C (b)
2	<i>L. profundicola</i>	10	86.8 $\pm$ 11.7	M	s	C (f)
	<i>L. fasciatus</i>	1	78.0	M	s	C (f)
	<i>L. elongatus</i>	53	71.9 $\pm$ 3.6	M	s	C (f)
	<i>Perissodus microlepis</i>	56	63.2 $\pm$ 4.0	M	s	C (f)
3	<i>Synodontis</i> spp.	1	46.0	M	s	C
	<i>Hapochromis pfefferi</i>	5	39.2	M	m	C (b)
	<i>Lamprologus callipterus</i>	17	38.1 $\pm$ 3.5	M	s	C (b)
	<i>Lamprichthys tanganicanus</i>	2	37.5	M	s	C
	<i>Lamprologus compressiceps</i>	4	37.5	M	m	C (b)
	<i>L. modestus</i>	11	37.5 $\pm$ 4.9	M	s	C (b)
	<i>Mastacembelus</i> spp.	2	37.5	L	s	C
	<i>Plecodus straeleni</i>	2	37.5	M	m	C (s)
	<i>Telmatochromis caninus</i>	2	36.5	M-L	m	C
	<i>Lamprologus savoryi</i>	3	35.7	M	m	C (p)
	<i>L. lemairi</i>	5	35.4	M	m	C (f, b)
	<i>Lobochilotes labiatus</i>	7	34.9	M-L	m	C (b)
	<i>Lamprologus brichardi</i>	75	34.3 $\pm$ 2.2	M	m	C (b)
	<i>Telmatochromis bifrenatus</i>	127	33.8 $\pm$ 1.4	S	s	O
	<i>Julidochromis marlieri</i>	10	33.7 $\pm$ 3.9	M	s	C (b)
	<i>Asprotilapia leptura</i>	6	32.8	M	s	H
	<i>Lamprologus tredocephalus</i>	2	32.5	M	m	C (b)
<i>Telmatochromis temporalis</i>	74	32.4 $\pm$ 2.1	S-M	s	O	
<i>Lamprologus leleupi</i>	16	30.4 $\pm$ 5.6	M	s	C (b)	
<i>Julidochromis transcriptus</i>	2	29.0	S	s	C (b)	
4	<i>Tropheus moorei</i>	23	11.6 $\pm$ 3.3	M-L	m	H
	<i>Petrochromis</i> spp.	8	7.5	M-L	m-l	H

guarding their fry over 10 mm SL did not attack the intruders except for one case when *T. moorei* dashed into the territory.

An example of the breeding territory of *L. toae* is shown in Fig. 3. As intruder fishes, especially in Group 2, approached the breeding site from above, the parents sometimes attacked them in an upward direction from the bottom. Therefore, the forms of breeding territories were not plane but dome-shaped.

Several characteristics of the intruding fish species of each group are shown in Table 1. Body depth rate of the fishes was measured from the figures in Poll (1956). Information about their diet was taken from Brichard (1978), Hori (1983), Gashagaza and Nagoshi (1985), Nshombo et al. (1985) and from our observations.

Three species, *Lamprologus elongatus*, *L. profundicola* and *L. fasciatus* of Group 2 are piscivorous fishes with slender body shapes. However, one species, *Perissodus microlepis*, is a scale-eating fish which preys rarely on fish larvae.

Group 3 includes many species with several kinds of food habits. Of the 20 species, 17 are carnivorous, 2 omnivorous and 1 herbivorous. All but two of the carnivorous species are benthos- or plankton-feeders. Most of them are regarded

as potential predators of eggs, wrigglers and small fry. Of the two exceptions, one is a piscivore and another is a scale-eater.

*T. moorei* and *Petrochromis* spp. of Group 4 are representative herbivores around the breeding site of *L. toae*, which are expected to eat immovable eggs and wrigglers if available.

There was no relation between body size of the intruding fishes and the attack distance.

**Division of male-female roles in territory defence.**

Division of male-female parental roles was recognized in the behaviour of territorial defence (Table 3). In Zone A, males attacked the intruding fishes far more frequently than females until independence of the young (Mann-Whitney's U-test,  $p < 0.05$  for stages I-IV). Of the 138 attacks in Zone A, only one was performed by a female.

When the young were under 20 mm SL, the male parent attacked the fishes in Zone B three to five times as frequently as his mate did (Mann-Whitney's U-test,  $p < 0.05$  for stages I-III). However, the frequency of male attacks decreased as fry reached 20 mm SL, while that of female attacks increased. The female took over about half of all attacks in Zone B at stage IV.

The attacks in Zone C were primarily per-

Table 2. Frequencies of intrusion (I) of fishes in each group and attack (AT) by parents of *L. toae* against them.

Intruder	Stage of young	Zone						Observation period (min)	Number of broods
		A		B		C			
		I	AT	I	AT	I	AT		
Group 1	I	8	4	2	1	1	1	240	4
	II	11	8	3	1	2	2	240	4
	III	6	6	0	0	0	0	300	5
	IV	1	0	1	1	0	0	240	4
Group 2	I	12	10	2	2	0	0	240	4
	II	30	24	3	3	0	0	240	4
	III	68	61	6	6	0	0	300	5
	IV	14	13	1	1	0	0	240	4
Group 3	I	174	3	87	77	1	1	240	4
	II	218	7	111	104	5	3	240	4
	III	215	2	132	101	15	13	300	5
	IV	272	0	148	58	24	3	240	4
Group 4	I	98	0	64	0	23	23	240	4
	II	86	0	45	0	13	7	240	4
	III	99	0	66	0	18	0	300	5
	IV	109	0	62	1	17	0	240	4

formed by the female when the offspring were eggs or wrigglers (Mann-Whitney's U-test,  $p < 0.05$ ). The difference in attack frequency between the sexes was not significant after the young had developed into free-swimming fry (Mann-Whitney's U-test,  $p > 0.05$  for stages II–IV).

### Discussion

From the present study, the territory of *L. toae* in the breeding period may be regarded as a brood- and mate-guarding territory. In the defence of territory, the parents apparently discriminated among four groups of intruder species. The discrimination of heterospecific fishes was primarily based on the food habits of the intruder fishes. However, there were few exceptions.

*P. microlepis* in Group 2 is a scale-eating fish which rarely preys on fish larvae, while the other three species are piscivorous. The latter usually cruise above the bottom or in open water and lunge at prey fish from a distance (about 50–100 cm) (Hori, 1983 and our observation). *P. microlepis* dashes at its prey from a distance of 20–200 cm to eat scales (Nshombo et al., 1985). The common characteristic of Group 2 species is the dashing at the prey from a distance. *Lamprologus lemairei* and *Perissodus straeleni* which are a piscivore and a scale-eater, respectively, are classified in Group 3. They have a compressed body. *L. lemairei* may be an ambushing hunter (Hori, 1983). *P. straeleni* usually attacks prey fish from a distance of about 10 cm (Nshombo, pers. comm.). It is likely that these two species can hardly dash at prey from a long distance. The reason why the parents of *L. toae* regarded *Asprotilapia leptura*, which is herbivorous, as a potential predator like other fishes of Group 3 is not clear.

It is concluded that parents strictly classify the heterospecific intruders on the basis of not only food habits, but also the feeding behaviour of the intruders. The attack distance of the parents probably corresponds to the usual predatory behaviour of the intruder species.

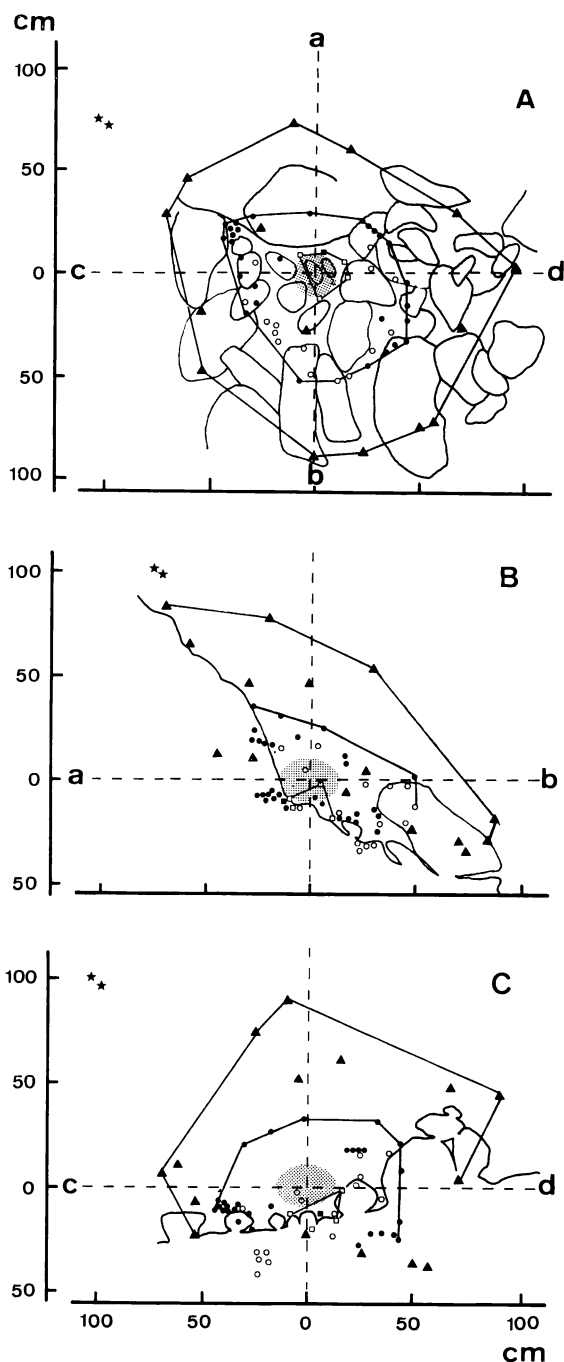


Fig. 3. Example of a breeding territory at stage II of young. A is a plane figure; B and C show cross sections through a–b and c–d, respectively. Solid and open symbols indicate the attacking points of male and female, respectively. Asterisk, triangle, circle and square represent the attacking points against Groups 1, 2, 3 and 4, respectively. The shaded area in the center of each figure represents the range of fry distribution. The solid lines show outlines of substrata.

The young seem to be in danger of predation by many fish species unless their parents guard them. However, the distance at which each intruding fish can damage the young is different among the species and the extent of the damage changes with the development of the young. Therefore, from the view point of economical and effective brood defence, selective attacks against the predators seems to be significant.

The same distinction of intruding fishes in defence of the breeding territory is recognized for some other species of the genus *Lamprologus* inhabiting the study area (our observation) and other cichlid fishes (Perrone, 1978; McKaye, 1984). Selective territorial defence is known also for many reef fishes (Clarke, 1970; Fishelson, 1970; Low, 1971; Keenleyside, 1972; Kohda, 1981, 1984). They selectively attack potential egg predators, food competitors and so on. However, it has been little known that the selective territorial defence changes with the development of the young.

Some tropical lakes and coral reefs have a great diversity of fish species (Fryer and Iles, 1972; Barbour and Brown, 1974; Greenwood, 1974; Lowe-McConnell, 1987). For example, more than 250 fish species are known from Lake Tanganyika (Brichard, 1978). Especially in the littoral zone, the species composition of the fish community is complicated and the density is exceedingly high (Kawabata and Mihigo, 1982; Hori et al., 1983; Kuwamura, 1987). Selective defence seems to be indispensable to the parental cichlids and some territorial reef fishes in such an environment.

Among many biparental substrate-brooding cichlid fishes, division of parental labour is widely known. Generally, in biparental cichlid fishes, the female parent is mainly concerned with direct care of the young, whereas the male parent is primarily involved in territorial defence. This

division of labour declines with the development of the young (Barlow, 1974; Smith-Grayton and Keenleyside, 1978; Keenleyside, 1978, 1979; Itzkowitz and Nyby, 1982; Itzkowitz, 1984).

In parental *L. toae*, the division of labour between male and female is shown in territorial defence. The male mainly defends the peripheral area of the breeding site while the female defends the inner area. During egg or wriggler stage, the division of labour between the two sexes seems to be related to the female's direct care of the young in the central part of the breeding territory. After the young develop into free-swimming fry, the female attacks intruders in the intermediate area. However, the male defends the outermost area alone throughout the developmental stages of the young. The experimental removal of the male parent (Nagoshi, 1987) caused the female to share the male's duties. It is suggested that the male was influencing her behaviour or vice versa and the division of labour is decided by the relationship between the two sexes.

Dupuis and Keenleyside (1982) demonstrated that in egg-care behaviour of *Aequidens paraguayensis*, increasing predatory density led to greater division of labour between the two sexes. They also stated that it is presumably more effective in keeping predators away from the eggs than having all parental care duties shared evenly by both parents, since males are generally larger than females.

Also in *L. toae*, it is thought that the division of labour in territorial defence is significant in terms of efficiency of brood protection. However, the suggestion mentioned above does not seem to apply to the parents of *L. toae* because there are no significant differences between their body size.

On the other hand, another interpretation is possible: if both parents leave the central part of the territory to attack intruder fishes at the same

Table 3. Frequencies of attacks (mean+SD/hr) by male (M) and female (F) parents in Zones A-C.

Stage of young	A		B		C	
	M	F	M	F	M	F
I	4.50+3.11	0	16.00+3.16	3.00+1.63	1.75+1.26	4.75+2.80
II	9.00+6.68	0.25+0.50	19.00+4.69	6.50+3.00	0.75+0.96	2.25+1.50
III	13.80+6.34	0	15.80+6.69	5.40+2.41	2.20+1.64	0.60+0.89
IV	3.25+1.71	0	7.25+6.70	8.25+6.60	0.50+0.58	0.25+0.50

time, this may give other intruder fishes a chance of predation. The division of aggressive labour possibly enables one parent, the female, to stay always near the young and enhances the effect of brood protection.

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- (SN: Nakagawa Experimental Forest, Faculty of Agriculture, Hokkaido University, Otoineppu-mura, Nakagawa-gun 098-25, Japan; MN: Faculty of Science, Nara Women's University, Kitauoya-nishimachi, Nara 630, Japan)
- タンガニーカ湖のカワスズメ科魚類 *Lamprologus toae* における両親による子の防衛と両親の役割
- 中野 繁・名越 誠
- タンガニーカ湖のカワスズメ科魚類 *Lamprologus toae* の両親による子の保護様式を潜水調査した。子の保護は岩場に形成されたなわばりで雄と雌の双方によって行われ、両親は同種と他種の両方の侵入者を攻撃した。親の攻撃距離により他種の侵入者は3つのグループに分けられた。親によるグループ分けは主に侵入者の食性と摂餌行動に基づくと考えられ、子に対する捕食の危険が高いと考えられるグループほど遠い地点で攻撃された。それぞれのグループに対する攻撃の頻度は子の成長とともに変化し、子にたいする捕食の危険性が小さくなったグループに対する攻撃の頻度は減少した。また、雌雄間での分業が見られ、雄がなわばりの周辺部を防衛するのに対して、雌はより内側の防衛に携わった。子の保護における侵入者にたいする選択的な攻撃と雌雄間に見られる分業の重要性について考察した。
- (中野: 098-25 中川郡音威子府村 北海道大学農学部中川地方演習林; 名越: 630 奈良市北魚屋西町 奈良女子大学理学部)