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Interspecific brood-mixing in Tanganyikan cichlids

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Synopsis

We collected schools of young, guarded by parents, of six common cichlid species to investigate the frequency and origin of interspecific brood-mixing. The main host species were a piscivore *Lepidiolamprologus elongatus* and a scale-eater *Perissodus microlepis*; more than half of their schools included heterospecific young, accounting for 20–40% of the total young. Most of the foreign young belonged to four biparental mouthbrooders whose parents have a habit of carrying their young in their mouths. Many of these young were smaller than the largest young brooded by their own parents. We concluded that adoption of young before independence results from farming-out, a behavior by which parents actively transfer their young to foster parents.

Introduction

Foreign conspecific or heterospecific young have often been found mixed in broods of many cichlid species in Africa, Southeast Asia and Central America (e.g., McKaye 1977, 1985, McKaye & McKaye 1977, Ribbink 1977, Ward & Wyman 1975, 1977, Ribbink et al. 1980, 1981, Yanagisawa 1985, 1986, Sato 1986, Kuwamura 1988, McKaye et al. 1992, Wisenden & Keenleyside 1992, also see Keenleyside 1991). Because they are guarded by foster parents together with their own young, this brood-mixing has attracted much attention as parasitism or mutualism (see Taborsky 1994). Much controversy has arisen over who are the beneficiaries, foreign young, their parents or foster parents, and which benefits they receive (McKaye 1977, 1981, 1985, Ribbink 1977, Coyne & Sohn 1978, Lewis 1980, McKaye & Oliver 1980, Yanagisawa 1985, Mrowka 1987a, McKaye et al. 1992, Wisenden & Keenleyside 1992). Information on who initiates the transfer of young may provide some clue to understanding the ultimate causation of this behavior. However, the chances are small of witnessing the process of mixing under natural conditions.

Two or more broods that are guarded close to each other may fortuitously mix by turbulence from predators or from fights between guarding parents (family conflux; McKaye & McKaye 1977, Lewis 1980). Brood-mixing may also originate from a voluntary act of the young, e.g., intrusion of independent young into other broods (independent offspring inclusion; Ribbink 1977, Ribbink et al. 1980). In these two cases, benefit to parents of foreign young or foster parents, if any, may be incidental. Recently, two patterns of parental behavior that cause brood-mixing have been observed. One is transportation of offspring by their parents to other broods (farming-out; Yanagisawa 1985, 1986, McKaye et al. 1992, Wisenden & Keenleyside 1992, Ochi et al.

1995). The other is active adoption of foreign young by foster parents (kidnapping; McKaye & McKaye 1977, Mrowka 1987b). In these cases, we may expect that the initiating parents benefit from brood-mixing.

Lake Tanganyika harbors more than 170 cichlid species, of which about one third guard free-swimming young after guarding or mouthbrooding embryos (Brichard 1978, Kuwamura 1986, Poll 1986, Konings 1988). Intraspecific brood-mixing has been reported in some of these species (Yanagisawa 1985, 1986, Kuwamura 1988, Ochi et al. 1995). Its occurrence is attributed mainly to farming-out. However, no extensive study has been made on interspecific brood-mixing. In the present study, we collected young guarded by parents of six common cichlid species to determine the frequency of interspecific brood-mixing, the composition and the size of guest species. Possible origins of interspecific brood-mixing are discussed in relation to behavioral traits of host and guest species.

Materials and methods

Collection of young

Collection of young was done with a 4.1 m ×1.8 m or 5.2 m × 2.1 m haul net (made of mosquito netting) at the rocky shore of Nkumbula Island (1–20 m deep), Mpulungu, Zambia, in October and November 1992 and at the rocky shore of Pemba (3–30 m deep), Zaire, in November 1992–January 1993. At Nkumbula Island, 21 schools of young guarded by *Lepidiolamprologus elongatus* (*Le*), 7 by *L. attenuatus* (*La*), 9 by *Neolamprologus caudopunctatus* (*Nc*), 22 by *N. moorii* (*Nm*), 12 by *N. tetracanthus* (*Nt*), and 28 by *Perissodus microlepis* (*Pm*) were collected. At Pemba, 28 schools guarded by *L. elongatus,* 7 by *L. attenuatus* and 33 by *P. microlepis* were collected. All the schools were guarded by a pair of parents, except one *Nt* school was guarded by a single parent. For the *Le* school, only a part of the young was caught because the school, consisting of numerous young (usually > 800), spread too widely in midwater to be enfolded whole in the net. Schools of other species were entirely enfolded. The young in the net were gathered on shore and fixed in 10% formalin solution. The average numbers of young collected were 314 (± 223 SD) for *Le* schools, 56 (± 39) for *La* schools, 26 (± 15) for *Nc* schools, 39 (± 35) for *Nm* schools, 19 (± 13) for *Nt* schools and 215 (± 135) for *Pm* schools. The proportion of young estimated to have escaped from collection was 17% (± 19 SD, n = 13), 17% (± 19, n = 9), 15% (± 20, n = 21), 14% (± 17, n = 12) and 2% (± 4, n = 58) for *La, Nc, Nm, Nt* and *Pm* schools, respectively. The collected young were identified and their standard lengths (SL) were measured in the laboratory with a sliding calliper to the nearest 0.1 mm.

Parental species

L. elongatus, L. attenuatus and *P. microlepis* were common at both sampling sites. *N. caudopunctatus, N. moorii* and *N. tetracanthus* were common at Nkumbula Island, but the former two were not found and the third was rare at Pemba.

L. elongatus is a piscivore (Hori 1983) and the largest (up to 170 mm SL) among the six species. Schools of free-swimming young guarded by the parents expand in midwater (up to 5 m) as they grow (Nagoshi 1985, Gashagaza 1991). The guarding period extends over 12 weeks (Nagoshi 1985).

L. attenuatus feeds on benthic animals and young fish and grows up to 115 mm SL (Hori 1983, unpublished data). As in *L. elongatus*, schools of free-swimming young guarded by the parents expand in midwater (up to 3 m) as they grow (Nagoshi & Gashagaza 1988, Gashagaza 1991). The guarding period is between 8–12 weeks (Nagoshi & Gashagaza 1988).

N. caudopunctatus is a small fish (up to 50 mm) feeding on zooplankton. Free-swimming young guarded by the parents form a school less than 1 m from the bottom.

N. moorii and *N. tetracanthus* are middle-sized fishes (up to 90 and 100 mm) feeding on epilithic algae and benthic animals, respectively (unpublished data). Free-swimming young of both species are guarded within the parents' territories for several weeks; they stay near the bottom and are aggressive against each other, resulting in spacing out.

P. microlepis is a middle-sized fish (up to 100 mm) that strips scales from other fishes (Nshombo et al. 1985, Nshombo 1994). In contrast to the above 5 species being substrate brooders, this fish is a biparental mouthbrooder (Yanagisawa & Nshombo 1983). Eggs and embryos are mouthbrooded solely by the female for 9 days and then free-swimming young are guarded by both parents for 5–7 weeks. Schools of young expand in midwater (up to 5 m) as they grow.

Results

Interspecific brood-mixing

At Nkumbula Island, most of *Le* and *Pm* schools and half of *La* schools contained heterospecific young (Table 1). If only mixed schools are considered, the mean proportion of heterospecifics to the total number of young in a school was the highest (41%) in *Le* schools and the second highest (23%) in *Pm* schools. Brood-mixing was rare in *Nt* and *Nc* schools and never occurred in *Nm* schools. At Pemba, *Le* and *Pm* schools less frequently included heterospecific young than at Nkumbula Island. The

Table 1. Mixing of heterospecific young in schools of host species.

Host species	n	Guest species	% schools with heterospecific young	Mixed young ratio (%)* (mean ± SD)
Nkumbula Island				
Lepidiolamprologus elongatus	21	*Xenotilapia spilopterus*	86	15 ± 15
		Microdontochromis tenuidentatus	86	21 ± 19
		Perissodus microlepis	57	9 ± 11
		Lepidiolamprologus attenuatus	33	7 ± 6
		Haplotaxodon microlepis	10	1 ± 1
		Cyprichromis sp.	5	27
		Total	95	41 ± 32
Perissodus microlepis	28	*Xenotilapia spilopterus*	71	13 ± 10
		Microdontochromis tenuidentatus	50	10 ± 13
		Haplotaxodon microlepis	18	13 ± 11
		Cyprichromis sp.	4	0.3
		Total	75	23 ± 19
Lepidiolamprologus attenuatus	7	*Xenotilapia spilopterus*	57	11 ± 7
Neolamprologus caudopunctatus	9	*Microdontochromis tenuidentatus*	11	5
Neolamprologus tetracanthus	12	*Xenotilapia spilopterus*	8	3
		Microdontochromis tenuidentatus	8	2
		Total	17	3 ± 1
Neolamprologus moorii	22		0	–
Pemba				
Lepidiolamprologus elongatus	28	*Perissodus microlepis*	32	16 ± 22
		Haplotaxodon microlepis	7	1 ± 0.4
		*Microdontochromis tenuidentatus***	4	64
		Total	36	21 ± 26
Perissodus microlepis	33	*Haplotaxodon microlepis*	55	24 ± 21
		Cyprichromis sp.	9	6 ± 4
		Lepidiolamprologus elongatus	3	1
		Total	55	25 ± 22
Lepidiolamprologus attenuatus	7		0	–

* The ratio of heterospecific young to the total young in a school. Only schools that contained members of the guest species were considered.

** Only large young and adults were mixed. They are not included in Table 2 and Figs 2 and 3.

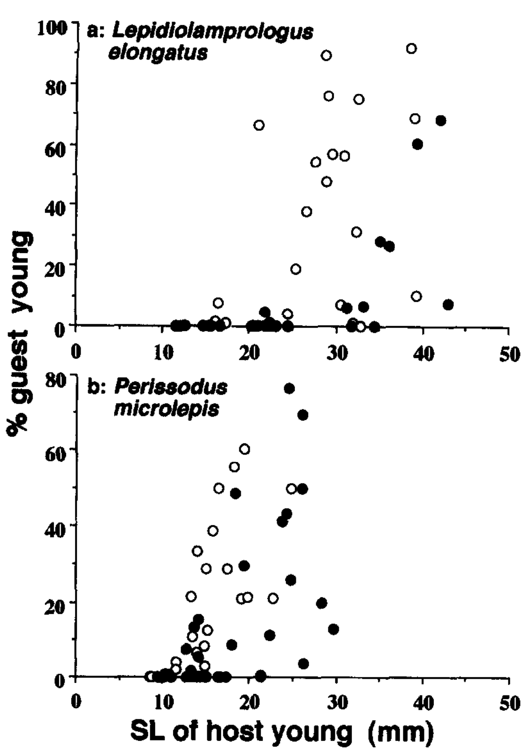

Fig. 1. Percent of guest young in schools of *Lepidiolamprologus elongatus* and *Perissodus microlepis* young against the mean standard length of host young. Open and solid circles indicate schools collected at Nkumbula Island and Pemba, respectively.

mean proportion of heterospecifics in *Le* schools (21%) was as high as that in *Pm* schools (25%). *La* schools never included heterospecifics. The fact that most of *Pm* schools contained different size classes of conspecific young (Ochi et al. 1995) indicated that intraspecific brood mixing in *Pm* schools was a common occurrence (but conspecific foreign young were not treated as foreigners in this paper because the absolute distinction between host and foreign young was not possible).

The proportion of heterospecifics in *Le* and *Pm* schools increased with growth of host young (Fig. 1). They first appeared when SL of host young was 16 mm in *Le* schools and 11 mm in *Pm* schools. They were almost always found in *Le* and *Pm* schools whose young exceeded 25 and 15 mm, respectively, and often outnumbered host young.

Heterospecific young found at Nkumbula Island belonged to six cichlid species, *Xenotilapia spilopterus, Microdontochromis tenuidentatus, Haplotaxodon microlepis, P. microlepis, Cyprichromis* sp. and *L. attenuatus* (Table 1). The former four are biparental mouthbrooders, the fifth a maternal mouthbrooder and the last a substrate brooder (Yanagisawa & Nshombo 1983, Kuwamura 1988, Nagoshi & Gashagaza 1988, Gashagaza 1991, unpublished data). Guest young in a *Le* school were composed of up to 5 species and those in a *Pm* school composed of up to 4 species. The commonest were *X. spilopterus* and *M. tenuidentatus*, each of which occurred in schools of 4 host species, abundantly in *Le* and *Pm* schools (Table 1). *H. microlepis* young were mixed in *Le* and *Pm* schools, but rarely in the former, *Cyprichromis* sp. young were also mixed in *Le* and *Pm* schools, and *L. attenuatus* young only in *Le* schools.

At Pemba, guest young belonged to 5 species, *H. microlepis, P. microlepis, Cyprichromis* sp., *M. tenuidentatus* and *L. elongatus* (Table 1). One school included young of 1 or 2 guest species. The commonest was *H. microlepis* young, which were mixed abundantly in *Pm* schools, and the second commonest *P. microlepis* young. *T. elongatus* and *Cyprichromis* sp. young were found in *Pm* schools. The difference of guest species and their mixing rate between the study sites were mainly due to the fact that *X. spilopterus* and *M. tenuidentatus* were common at Nkumbula Island, but the former did not occur and the latter was rare at Pemba.

Size of guest young

Size-frequency distributions of guest young at the two sampling sites combined are shown in Fig. 2. *X. spilopterus* and *M. tenuidentatus* young were remarkably smaller in *Pm* schools than in *Le* schools (Fig. 2a, b): the mean SL of *X. spilopterus* young was 13.2 mm (± 2.7 SD, n = 694) in *Pm* schools and 27.9 mm (± 5.7, n = 504) in *Le* schools (t-test, t_s = 59.66, $p < 0.001$), and the mean SL of *M. tenuidentatus* young was 16.5 mm (± 2.7, n = 416) in *Pm* schools and 24.6 mm (± 5.3, n = 796) in *Le* schools (t_s = 29.13, $p < 0.001$). Young of *Cyprichromis* sp. in *Pm* schools (21.3 mm ± 2.4 SD, n = 44) were also smaller than those in *Le* (26.0 mm ± 2.8 SD, n = 36) (Fig. 2c, t_s = 8.126, $p < 0.001$).

Offspring are known to be brooded by their par-

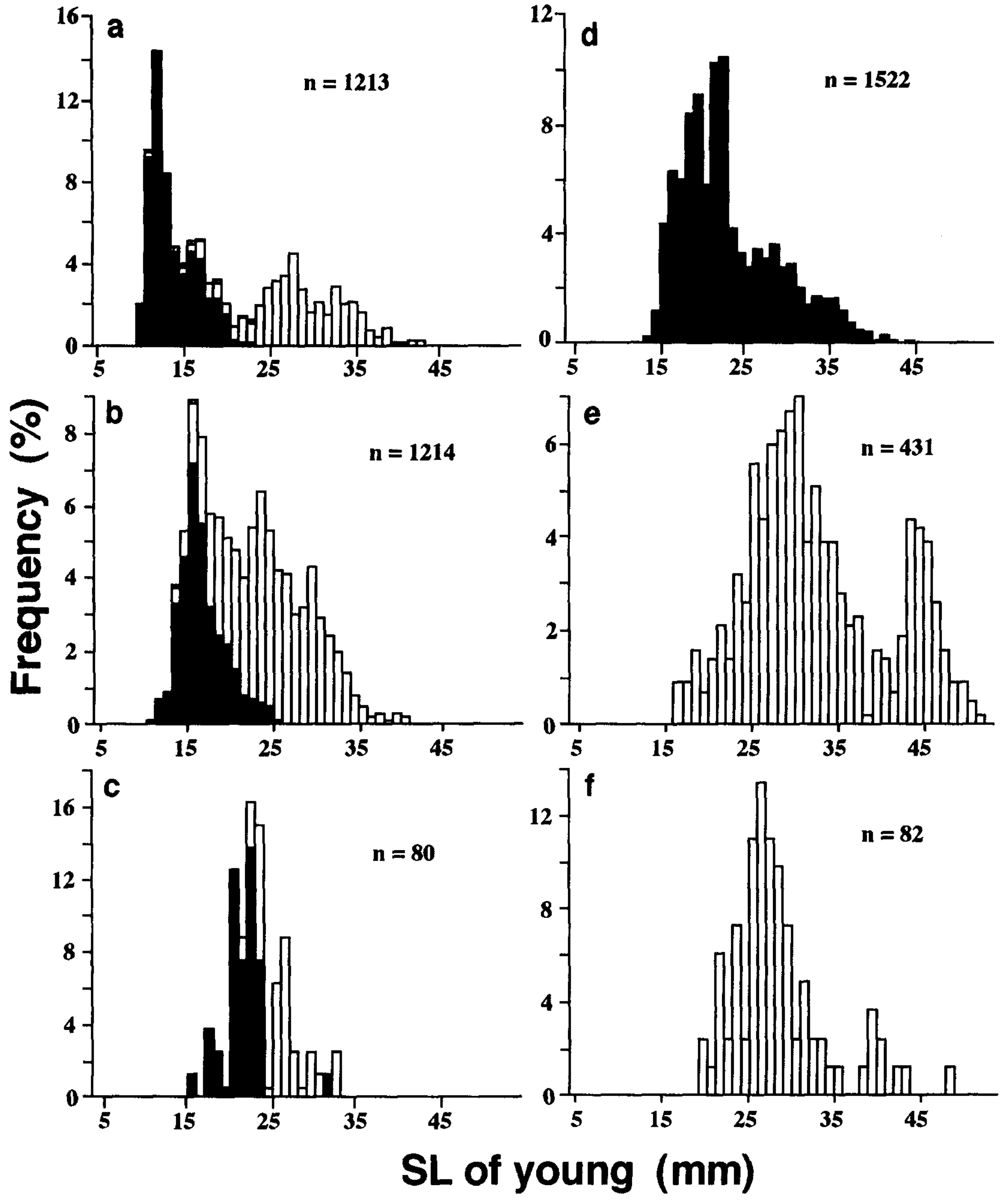

Fig. 2. Size-frequency distributions of guest young in schools of *Lepidiolamprologus elongatus* (open), *Perissodus microlepis* (solid) and others (dotted): a-*Xenotilapia spilopterus*, b-*Microdontochromis tenuidentatus*, c-*Cyprichromis* sp., d-*Haplotaxodon microlepis*, e-*Perissodus microlepis*, and f-*Lepidiolamprologus attenuatus*.

ents until they attain at least 13 mm SL in *X. spilopterus*, up to 17.4 mm in *M. tenuidentatus* (unpublished data), up to 28–31 mm in *P. microlepis* (Yanagisawa & Nshombo 1983), up to 20–24 mm in *H. microlepis* (conversion from total length in Kuwamura (1988)) and up to 18.1–34.1 mm in *L. attenuatus* (Nagoshi & Gashagaza 1988). Comparison between these sizes and size-frequency distributions of young in host schools (Fig. 2) indicate that a large number of young in these species, especially in *Pm*

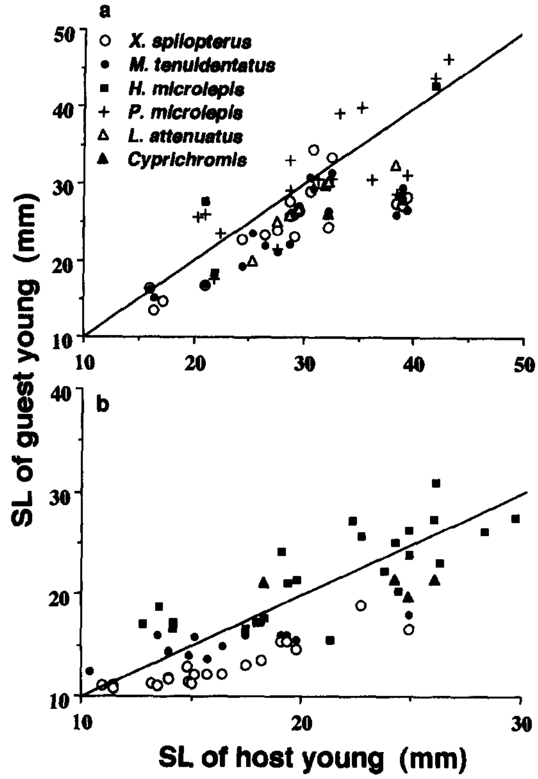

Fig. 3. Size (mean standard length) relationship of guest young to host young in a *Lepidiolamprologus elongatus* (a) and *Perissodus microlepis* (b) school. Line indicates equal size of host and guest young.

schools, were adopted before they became independent from their parents.

Body size of guest young positively correlated with that of host young (Fig. 3, $r = 0.774$, $F = 99.885$, $n = 69$, $p < 0.001$ for *Le* schools and $r = 0.809$, $F = 111.831$, $n = 61$, $p < 0.001$ for *Pm* schools). *X. spilopterus, M. tenuidentatus, L. attenuatus* and *Cyprichromis* sp. young were usually smaller than host young (Table 2). In contrast, *P. microlepis* and *H. microlepis* young were larger than host young in nearly half of schools.

Discussion

Origin of interspecific brood-mixing

This study demonstrated that interspecific brood-mixing commonly occurs in Tanganyikan cichlid fishes. A wide size range of guest young and their great size differences according to host species (Fig. 2) suggest that they mixed in host schools at various life stages; some must have mixed before independence from their own parents and the others after independence.

For mixing of young before independence, three possible ways have been proposed: farming-out, kidnapping and family conflux (for review see Taborsky 1944). Farming-out is known as the origin of intraspecific brood-mixing of two Tanganyikan cichlid species, *P. microlepis* and *Xenotilapia flavipinnis* (Yanagisawa 1985, 1986, Ochi et al. 1995): parents transfer young in their mouths to foster parents.

Performers of farming-out, either intraspecific or interspecific, should satisfy at least the two following requirements: (1) parents should have a habit of carrying young in their mouths to transport them to foster parents, and (2) young under parental care should have the same feeding habit as those of host

Table 2. The number of schools in which the body size difference between young of host and guest species was significant at the level of $p < 0.05$ (t-test).

Guest species	n	Significant difference		No significant difference
		Host > Guest	Host < Guest	
Microdontochromis tenuidentatus	34	21	2	11
Xenotilapia spilopterus	43	31	2	10
Lepidiolamprologus attenuatus	7	5	0	2
Perissodus microlepis	21	9	8	4
Haplotaxodon microlepis	27	11	14	2
Cyprichromis sp.	5	3	1	1

species, namely zooplankton feeding, to support themselves after being fostered. The first requirement is satisfied by all four main guest species, *X. spilopterus, H. microlepis, P. microlepis* and *M. tenuidentatus*. The parents of the former three collect their guarded young in the mouths when disturbed, and parents of the last species always keep their young in the mouths (unpublished data). The second requirement is also satisfied by these fishes. Young of the former three feed on zooplankton while guarded by the parents (Yanagisawa & Nshombo 1983, Kuwamura 1988, personal observation), and those of *M. tenuidentatus* do so within the parent's buccal cavity (i.e., intra-buccal feeding of young).

In contrast, maternal mouthbrooders, which account for more than half of Tanganyikan cichlids, do not satisfy the second requirement, although they satisfy the first: young of these fishes never take zooplankton under parental care. Conversely, the other major group, substrate brooders, which amount to about one third of Tanganyikan cichlids, do not satisfy the first requirement: parents have never been observed to carry the free-swimming young in the months.

This evidence suggests that farming-out is the probable way of mixing for young of the main guest species before independence. The broad size overlap of their young in *Pm* schools with young brooded by their own parents indicate that these young were mostly adopted by farming-out (including intraspecific farming-out of *P. microlepis*), although some of large young may have mixed after independence rather than having grown in the host schools after being fostered. On the other hand, young in *Le* schools were rarely smaller than young brooded by their own parents (in *M. tenuidentatus* and *P. microlepis*) or distinctly larger (in *X. spilopterus*). Most or all of the young probably mixed in *Le* schools after they became independent from their parents. The most probable scenario is that they were first farmed out by their parents into *Pm* schools and after growing up there they found their way into *Le* schools.

Kidnapping is a possible way of brood-mixing when guest species have a guarding phase. This may be accomplished by a foster parent in two ways: herding a part of foreign young into a school of its own young (see McKaye & McKaye 1977) or intruding into a school to collect foreign young in the mouth. The first way is practicable when the two schools are in close proximity (see Wisenden & Keenleyside 1992), but it cannot be a common way in Lake Taganyika where guarded schools are rarely near. The second way is less likely to occur, because host species other than *P. microlepis* are substrate brooders, which do not have the habit of carrying young. For *P. microlepis,* we observed the parental behavior in great detail (Yanagisawa & Nshombo 1983, Yanagisawa 1985) but did not notice any actions related to kidnapping.

Family conflux can also occur when two schools are near. *L. attenuatus* young occasionally found in *Le* schools may have mixed in this way. Both *L. elongatus* and *L. attenuatus* are substrate brooders whose young extend into the water column with growth (Nagoshi 1985, Nagoshi & Gashagaza 1988). Because the parents of *L. elongatus* are larger than those of *L. attenuatus*, the former are likely to be a winner when repulsive behavior occurs between them.

Young of *Cyprichromis* sp. found in host schools were as large as young forming a big school of their own species after separation from their mother (unpublished data). They seem to have originated from the schooling independent young.

Selectivity of hosts

Ribbink et al. (1980) suggested that in Lake Malawi all cichlids that have a phase of guarding free-swimming young are potential hosts. In Lake Tanganyika, however, host selectivity was apparent. Which species are selected as hosts may depend on the behavior of guarding parents and their young.

Two major host species, *L. elongatus* and *P. microlepis*, have a common feature in guarding: schools of their young expand three-dimensionally in the water column with their growth (Nagoshi 1983, Yanagisawa & Nshombo 1983). This geometric pattern undoubtedly makes these schools conspicuous and accessible to guest fishes. This microdistribution contrasts with a confined distribution of young within the parents' brooding territory in many substrate brooders (Nagoshi 1983, 1985, Kuwamura 1986, Yanagisawa 1987). This feature is attributable to a protective ability of parents. *L. elongatus* is a large piscivore with a lightning attack (Hori 1983), and *P. microlepis* is a scale-eater that dashes against a prey (Nshombo et al. 1985, Hori 1987, Nshombo 1994). Therefore, guarding parents of these species can repulse intruders from afar.

Host selectivity may also be influenced by the food habit of host young. The minimum size of guest young in *Le* schools is larger than that in *Pm* schools (Fig. 2) and, as mentioned above, *Le* schools are not the main target of farming-out. One condition of these results may be that large *L. elongatus* young under parental care have a piscivorous habit, although they ordinarily feed on zooplankton. In a field experiment in which *P. microlepis* young were introduced to *Le* schools, they were devoured by the natal young when the former were considerably smaller (unpublished data). On the other hand, *Le* schools are frequently exploited by independent young. Probably, this is because *L. elongatus* young are guarded for a long time (up to > 40 mm SL) and their survival rate is high (Nagoshi 1983, 1985).

Nt and *Nm* schools were rarely or never exploited by foreign young (Table 1). Young of these fishes are benthic and aggressive against each other, resulting in spacing out, like young of *N. mondabu* and *N. furcifer* (Nagoshi 1983, Yanagisawa 1987). These young would similarly be aggressive against heterospecific foreigners if introduced. Fishes whose young show aggressiveness would be least likely to be selected as hosts.

Relative body size of foreign young to host young has been considered to be an important determinant of host parents' acceptance (Noakes & Barlow 1973). In some Central American cichlids, parents accept only foreign young of similar body size or smaller than their own young (Noakes & Barlow 1973, Baylis 1974, Wisenden & Keenleyside 1992). Because smaller young are more vulnerable than large young, host parents may benefit by small foreign young serving as predation targets (McKaye & McKaye 1977, McKaye et al. 1992, Wisenden & Keenleyside 1992). In Lake Tanganyika, however, foreigners larger than host young were often accepted (Fig. 3, Table 2). This may indicate that host parents of this lake do not benefit from being particular in their choice of foreigners. Since a great disturbance in guarded young attracts many predators, host parents may refrain from excluding foreigners from their schools. This may explain why brood-mixing is so common in Lake Tanganiyka.

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