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Intraspecific brood adoption in convict cichlids: a mutual benefit

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Summary. Convict cichlids (*Cichlasoma nigrofasciatum*) are biparental, substrate brooding cichlid fish which have extended care of their eggs, larvae (wrigglers) and free-swimming young (fry). Field observations indicate that intraspecific brood adoption of fry occurs frequently under natural conditions. Of 232 broods 29% contained foreign fry and of 232 broods 15% were identified as fry donors. Foreign fry were usually of similar size to or smaller than the host brood fry. Experimental fry transfers showed that parents accept foreign fry smaller than their own but immediately reject or eat foreign fry larger than their own. A predation experiment showed that within a mixed brood, smaller fry are eaten more often than larger fry. Thus, accepting foreign fry may benefit parents through the dilution effect and through a differential predation effect. In comparison with intact families, broods from which the male parent was removed were less likely to reach independence, had fewer fry surviving to independence, and had a greater probability of having some fry transferred to neighbouring broods. We propose that intraspecific brood adoption in convict cichlids is mutually beneficial to the adult donors and recipients.

Introduction

A well-known feature of fish in the family Cichlidae is the parental care of their eggs and free-swimming young (fry) for several weeks (Fryer and Iles 1972; Keenleyside 1991). Such high levels of parental care are a large parental investment and are thought to be necessary to compensate for high potential brood predation (Barlow 1974).

In laboratory experiments, parental cichlids can be induced to adopt and care for eggs and fry from other conspecific and heterospecific broods (Noble and Curtis 1939; Greenberg 1963; Burchard 1965; Myrberg 1964; Noakes and Barlow 1973; Baylis 1974; Mrowka 1987a, c). These findings are supported by field observations (McKaye and Hallacher 1973; Lewis 1980; McKaye 1977, 1985; McKaye and McKaye 1977; Ward and Wyman 1975, 1977; Ribbink 1977; Ribbink et al. 1980; Yanagisawa 1985).

Laboratory experiments (Greenberg 1963; Myrberg 1964; Noakes and Barlow 1973; Baylis 1974; Mrowka 1987b) and field observations (McKaye and McKaye 1977; Ribbink 1977; Carlisle 1985; Yanagisawa 1985) have shown that among cichlid fishes an important criterion for acceptance of foreign fry (inter- or intraspecific) by foster parents is the size of those fry relative to their own. The general conclusion from these studies is that cichlid parents readily accept foreign fry of the same size or smaller than their brood, but reject larger fry. The adaptive significance of this phenomenon has received little attention.

Brood adoption in cichlids has attracted attention because parental investment in non-related young appears to be maladaptive. However, if predation on host fry is reduced by diluting the brood with foreign fry (the "dilution effect"), then natural selection will promote brood adoption (McKaye and McKaye 1977).

If the dilution effect benefits host parents that adopt foreign fry, can this benefit be enhanced if the hosts selectively adopt only certain fry? Some authors observing interspecific brood adoption have suggested that a greater vulnerability of adopted young to predators may increase the benefit to host parents (McKaye and Oliver 1980; Goff 1984). One hypothesis tested in this paper is that host parents can increase the potential benefit of adoption by accepting fry smaller than their own. If smaller fry are more easily taken by predators than larger fry, then when a predator attacks the brood, the smaller, foreign fry will suffer a disproportionate amount of mortality. Thus, survival of the host fry would be increased above what would be predicted by the dilution effect alone.

The convict cichlid (*Cichlasoma nigrofasciatum*) is a Central American, substrate brooding species which has

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biparental care of its eggs, wrigglers (larvae) and fry. This paper documents field observations of intraspecific fry adoption by convict cichlids in Costa Rican streams. Preliminary work indicated that adopted fry were usually smaller than host fry. Experimental fry transfers between broods were conducted in the field to investigate the possibility that parental discrimination explains the size difference between foreign fry and host fry. A laboratory experiment was designed to test whether or not fry of different sizes differ in their vulnerability to brood predators. Parental male convict cichlids occasionally desert the brood and female before fry independence (Keenleyside et al. 1990). Deserted females may not be as effective at defending a brood from predators as two parents. We hypothesized that when faced with reduced prospects of fry survival, deserted females should show a higher incidence of fry transfer to neighbouring broods than biparental families do. A male removal experiment was conducted to determine the contribution of male parental care to fry survival and to assess the effect of male desertion on fry adoption.

Materials and methods

Observations of convict cichlid reproductive ecology were made within the species' natural range (Bussing 1987) in Guanacaste province, northwest Costa Rica, during two breeding seasons, January to June 1990 and December 1990 to June 1991. The study sites were located in small streams at Lomas Barbudal Biological Reserve, 10°30′N, 85°23′W. Four study sites were used, representing two habitat types. Two sites were in the Rio Cabuyo and two were in the Quebrada Amores, a tributary of the Rio Cabuyo. In each stream, one site was a relatively deep, wide pool ("pool site") and the other was a series of small, shallow, interconnected pools ("stream site").

Convict cichlid breeding activity was monitored at each site. Spawning locations were marked with flagging tape (1990) or painted stones (1991). Parents were marked as follows when their brood became free-swimming. Parents and young were surrounded with a fine-mesh black seine. The male was captured first because he was the most likely to flee. Next, all fry were captured using hand nets. The female parent always remained close to the fry while they were being captured, and any fry that strayed, quickly returned to her. The female was then captured. Each parent was anaesthetized with MS222 (tricaine methanesulfonate), weighed, measured, and given a unique identifying mark by excising two dorsal spines. Detailed sketches were made of the body markings of each parent for later identification. Fifteen fry were randomly chosen, anaesthetized with MS222 and their standard length (SL) measured to the nearest 0.5 mm. The total number of fry in the brood was recorded. When all fish had recovered from the anaesthetic, the parents were gently returned to their capture site, which was still surrounded by the seine to exclude potential fry predators. Upon release, the male often fled and hid. However, the female soon began to search the area for her fry. The fry were then reintroduced using a clear plastic tube. When the tube was lifted the female approached the fry and resumed normal brood defence behaviour. The male usually joined the female in brood defence soon after the fry and the female were reunited. Controls testing for mortality caused by handling showed a loss of 0.78 fry per sample.

Individual families were identified by their location in the stream, the stage of fry development, and the body markings of the parents. At regular intervals (usually 7 days) each brood was recaptured as before. The parents were left in the water with some fry (<10) to keep the adults from wandering in search of missing fry. A visual count of the remaining fry was made using face mask and snorkel. The captured fry were counted and 15 were randomly chosen, anaesthetized and measured. When clearly different size groups appeared in a brood, the mean length and number of each size group was recorded. The fry were then returned to the adults as described above.

When two or more size groups were found in a brood, or when the number of fry in a brood increased over time, that brood was considered to be a fry receiver or host brood. We knew which size group was the host fry and which was foreign because we followed each brood for the duration of fry development. For each mixed brood, an attempt was made to match the size of the foreign fry to those of a neighbouring brood, which was then labelled as the fry giver or donor brood. When there were no neighbouring broods matching the foreign fry size, no brood was ascribed as the donor. On three occasions the size of foreign fry in a mixed brood matched more than one neighbouring brood. In these cases, other factors such as proximity and fry number were used to label one as the donor brood.

Fry transfer experiment. Altogether 25 experimental fry transfers were made to determine if the size difference between host and foreign fry was maintained by discrimination on the part of host parents. Transfers were made by capturing fry from one brood and placing them directly into another, using a clear plastic tube. The mean SL of added fry was either larger (mean size difference $\pm$SE$=2.13 \pm 0.28$ mm, $n=9$) or smaller (mean size difference $=1.92 \pm 0.14$ mm, $n=16$) than the mean fry SL of the receiving brood. These size differences (2.13 and 1.92) were not significantly different from each other ($t=0.73$, $P<0.47$). Host broods were observed for 15 min to determine if the introduced fry were accepted or rejected.

The number of fry introduced varied within and between the two treatments of smaller and larger transferred fry. Foreign fry represented 13–75% of the total brood after transfer, with a mean of $33.0\% \pm 4.8$ and $18.8\% \pm 2.3$ for the smaller and larger foreign fry transfers respectively. The mean number of fry transferred in the small foreign fry transfers was significantly greater than the mean number of fry transferred for the large transfers ($t=20.46$, $P<0.014$).

Predation experiment. A prey size selectivity experiment was conducted in the laboratory to test the relative vulnerabilities of different-sized convict cichlid fry to two of their most effective natural predators. Mixed size-group broods were simulated by creating schools of 20 fry, consisting of 5 fry from each of 4 different size groups: 5 mm, 6 mm, 7 mm and 8 mm SL. These size groups were chosen because field observations of fry mortality rates showed predation to be most intense on small fry (unpubl. data). Mortality rates of fry sized 8–10 mm (fry independence) were relatively low. The experiments were carried out in a 110-l test aquarium ($93 \times 35 \times 30$ cm high) which contained 5 cm of beige-white gravel, a transparent partition dividing the tank in half, and a large (20 cm diameter) stone in the centre of each side. For each trial the 20 fry were placed in one side of the test aquarium, chosen randomly. One of two predator species was placed in the other side. After 15 min the partition was removed. After another 15 min the predator(s) were removed and the number of surviving fry from each size group was counted. A new predator(s) was used for each trial. The two predator species tested were juvenile wild-caught *Cichlasoma dovii*, $n=1$ per trial, (mean SL$=30.8 \pm 0.92$ mm, $n=10$), and juvenile convict cichlids, $n=3$ per trial, (mean SL$=28.87 \pm 0.38$ mm, $n=30$). Predators were starved for 12 h before testing. Ten trials were run with each predator species. Juvenile convict cichlids and juvenile *C. dovii* were the only predators observed to successfully take fry from undisturbed convict broods in 140 h of field observations. Juvenile convict cichlids received 15.6% of attacks by guarding parents. Juvenile *C. dovii* only accounted for 4.7% of parental attacks but were attacked from a greater distance from the brood than other potential brood predators (unpubl. data). The size of predators used in the experiment

Table 1. Occurrence of fry adoption by convict cichlids at four sites in Lomas Barbudal Biological Reserve during 1990 and 1991

Site	Broods	Adoption detected		Gave		Received	
		n	%	n	%	n	%
Amores Pool	64	25	39	13	20	12	19
Amores Stream	44	8	18	1	2	8	18
Cabuyo Pool	65	27	42	12	18	18	28
Cabuyo Stream	59	37	63	9	15	30	51
Total	232	97	42	35	15	68	29

Some broods both gave and received fry

Table 2. Percentage of broods with access to neighbouring broods and mean distance to nearest neighbouring broods at each site, for all samples combined

Site	With accessible neighbouring brood		Distance to nearest neighbouring brood (m)[†]		
	n	%	$\bar{x}$	SE	n
Amores Pool	185	99.5	4.53[a]	0.24	173
Amores Stream	169	71.6	3.64[ab]	0.21	112
Cabuyo Pool	225	98.7	2.97[b]	0.02	217
Cabuyo Stream	302	91.1	1.97[c]	0.35	262
Total	881	91.0	3.08	0.15	764

[†] Differences among sites are significant ($F = 14.49$, $P < 0.001$)
Shared superscripts indicate no significant difference ($P < 0.05$) using a Student-Newman-Keuls multiple range test

approximated the size of fish preying on convict cichlid broods in the field.

Male removal experiment. Male parents were removed from 21 randomly chosen broods. Brood age was standardized to be approximately half way through the fry stage of development (mean fry SL $= 7.41 \pm 0.10$ mm, $n = 21$). Parental males were removed as before, by surrounding the brood and parents with a seine and capturing the male with a hand net. The fate of each brood following the male's removal was recorded.

Data were analyzed using PC SAS or SPSS. Variation about mean values is always expressed as the standard error of the mean.

Results

Prevalence of fry adoption

Intraspecific brood transfers involved 42% of the 232 broods examined and occurred at all study sites (Table 1). Foreign fry were detected in 68 (29%) of the 232 broods and 35 (15%) of the 232 broods were considered to be fry donors. Six (3%) broods both gave and received fry. These are conservative estimates because broods containing foreign fry were only detected when there were two or more obvious size groups within a brood, or when the number of fry within a brood increased with time.

The relatively low rate of detected fry adoption at Amores stream site (Table 1) is consistent with the relatively low proportion of pairs breeding at that site with access to other breeding pairs (Table 2). Many Amores stream site pairs reproduced in detached pools with restricted or blocked access to neighbouring pairs. Fry transfer between broods would have been difficult or impossible for such pairs. The highest fry adoption rate occurred at the Cabuyo stream site (Table 1). A high density of breeding pairs at that site produced the lowest mean interbrood distance of all sites (Table 2) and fry were relatively easy to transfer between broods.

Some parents adopted fry on two ($n = 13$), three ($n = 2$) or four ($n = 1$) occasions. In total, 84 instances of brood adoption were recorded ($n = 68$ broods). Distinct size groups were apparent in 73 of these cases ($n = 62$ broods). When this occurred, it was possible to separate foreign fry from host fry by their relative sizes.

Mixed broods (not including fry transfers resulting from experimental male removals) contained an average of 11.3 ± 1.6 percent foreign fry. The proportion of foreign fry was less than 5% of the brood in almost half (49.3%) the cases (Fig. 1).

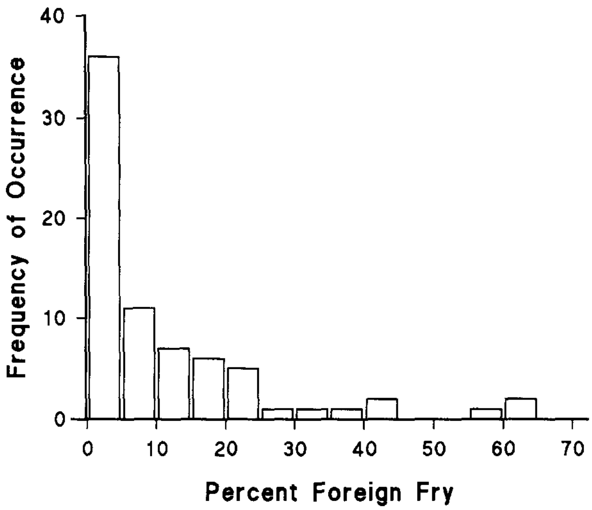

Fig. 1. Frequency distribution of the number of foreign fry, expressed as percent of total brood, in broods with more than one size group ($n = 84$ adoption events in 68 broods)

When adoption resulted in more than one size group within a brood, the mean SL of foreign fry was equal to or less than that of the host fry in 68 of 84 cases (Fig. 2). In most cases where adopted fry were larger than the host fry ($n = 16$), the foreign fry were 10 mm SL or larger. Convict cichlid fry began dispersing from their parents after reaching 10 mm SL; therefore, the large foreign fry were probably newly independent juveniles.

Fry transfer experiments

The results of these experiments were consistent across a range of fry sizes. The fate of foreign fry was usually apparent within 15 s of the transfer. When the introduced fry were larger than the host fry, they were immediately rejected, either chased away or eaten by the parents. When the introduced fry were smaller than the host fry, they were accepted (Fig. 3). We conclude that parents can detect the presence of a new size group of

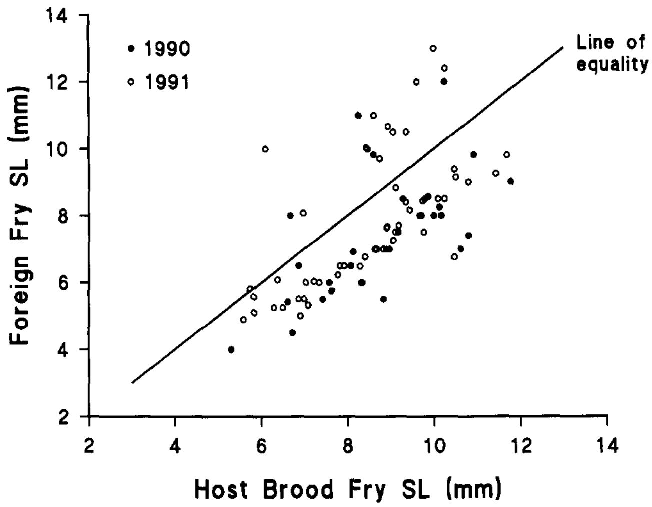

Fig. 2. Mean size (SL in mm) of foreign fry and host fry in mixed broods ($n = 84$ events in 68 broods). Male removal and fry transfer manipulations not included. *Line of equality* indicates equal size of host and foreign fry. *Filled circles*, 1990; *open circles*, 1991

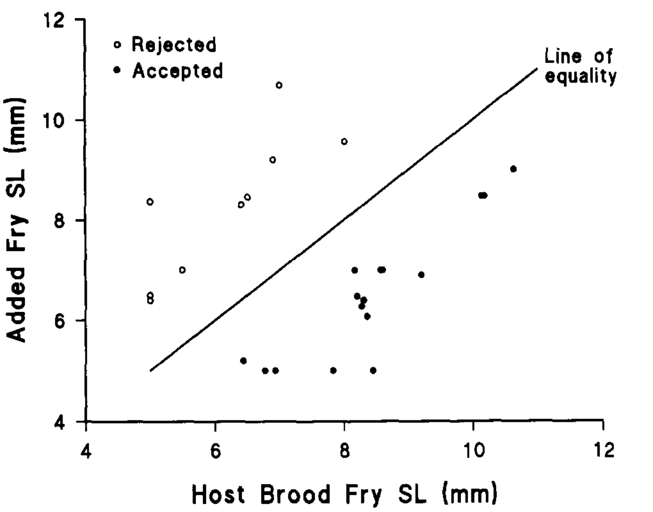

Fig. 3. Response by parents to added foreign fry that were larger or smaller than their own ($n = 25$). *Open circles*, rejected; *filled circles*, accepted

conspecific fry in their brood, yet only reject foreign fry larger than their own.

Predation experiment

ANOVAs using fry size group as a class variable showed that the size classes of convict cichlid fry significantly differed in their vulnerability to juvenile *C. dovii* ($P < 0.031$) and to groups of three juvenile convict cichlids ($P < 0.001$) (Fig. 4). Pairwise comparisons revealed that the smallest fry were eaten significantly more often then other fry sizes by *C. dovii* (5 mm > 8 mm) and juvenile convict cichlids (5 mm > 6 mm = 7 mm = 8 mm) (Student-Newman-Keuls, $P < 0.05$).

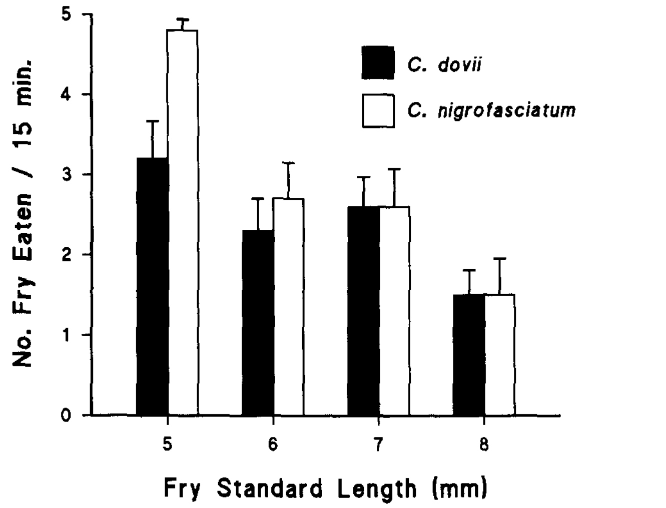

Fig. 4. Number of *Cichlasoma nigrofasciatum* fry of each size group within a mixed school that were eaten by single *C. dovii* ($n = 10$) (*solid bars*), or groups of 3 juvenile *C. nigrofasciatum* ($n = 10$) (*open bars*) in 15 min. *Bars* represent mean + SE

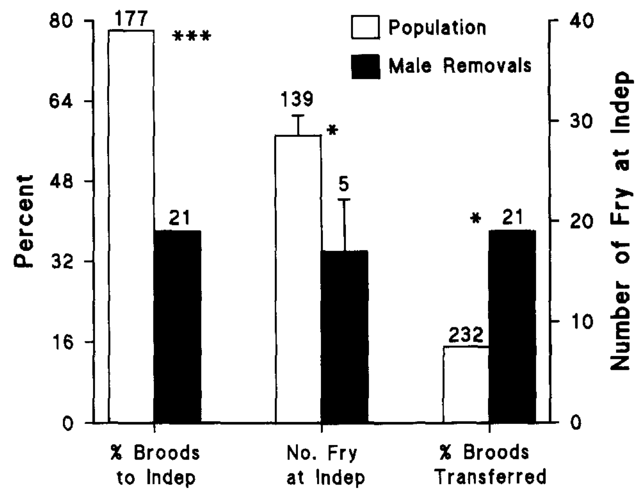

Fig. 5. A comparison of two measures of reproductive success and rate of fry transfer among broods in the unmanipulated population (*open bars*) with broods from which the male parent had been removed (*solid bars*). For comparison purposes, percentage of broods to independence in the unmanipulated population was calculated from broods surviving from 7 mm SL to independence (10 mm fry SL). *Numbers* above bars represent sample sizes. * indicates a significant difference at $P < 0.05$, *** indicates a significant difference at $P < 0.001$

Male removal experiment

Eight male-removal broods reached independence. Females either stayed with the brood ($n = 3$), or transferred fry to other broods ($n = 5$). Of unmanipulated broods in which fry had grown to 7 mm SL (fry size at male removal in male removal broods), 78% successfully reared fry to independence, compared with 38.1% (8 of 21) of the male removal broods ($\chi^2 = 15.41$, $P < 0.001$; Fig. 5).

The mean number of fry per brood surviving to independence (> 10 mm fry SL) in the general population

Table 3. The fate of broods from which the male parent was removed half way through the free-swimming fry stage ($n=21$)

Relative size of fry in neighbouring broods	Fry transferred	Female remained with brood	Brood failed
Larger, similar and smaller	5[a]	1	2
Larger only	3	1	1
Similar size only[b]		1	
Smaller only			5
No neighbours		2	
Total	8	5	8

[a] Three broods and part of a fourth brood were transferred to broods with larger fry, one brood and part of a second brood were transferred to broods with fry of similar size (host fry were smaller than adopted fry by 0.60 mm and 0.88 mm SL)
[b] Two neighbouring broods were nearby containing fry larger than the male removal brood by 0.04 mm and 0.17 mm SL

was 28.57 ± 2.01 ($n=139$), over 1.5 times the mean number of fry surviving to independence for male-removal broods (17.00 ± 5.19, $n=5$). This difference is significant (1-tailed $t=2.08$, $P<0.046$) (Fig. 5).

Fry from 8 of the 21 male-removal broods were later discovered in neighbouring broods (Table 3). When a male removal resulted in fry transfer, fry were always transferred to neighbouring broods whose fry were either of similar size of larger than the transferred fry (Table 3). This is consistent with the natural population adoption data (Fig. 2).

The incidence of fry transfer among male removal broods (8 of 21) was signifiantly greater than the incidence of fry donation detected in the unmanipulated population (35 of 232) (Fisher's exact test $P<0.013$) (Fig. 5).

If no neighbouring broods with similar size or larger fry were present ($n=7$), removal of the male parent resulted in brood failure or in an attempt by the female to rear the brood alone (Table 3). When only younger broods were present ($n=5$), fatherless broods failed before fry independence. In the two cases when there were no neighbours, the female stayed and reared the brood to independence (Table 3).

It was noted that brood dispersal occurred when host fry were about 10 mm SL, even if smaller foreign fry were also in the brood. Foreign fry were therefore disadvantaged in a mixed brood because they became independent at a size less than 10 mm SL.

On one occasion, a transfer of fry was observed. On January 12 1991, Cabuyo pool pair #3 and #14 were sampled and male #3 was removed. On January 13, female #3 led her fry (mean fry SL = 7.17 mm, $n=44$) directly toward nearby pair #14 (mean fry SL = 8.67 mm). When female #3 was about 50 cm from brood #14, the three parents began to fight. After about 30 s female #3 withdrew with a school of fry. We then resampled brood #14 and found two fry corresponding to the fry SL of brood #3 (fry SL = 7.0 mm, 7.5 mm) which had not been there the day before. The 18 other fry in brood #14 (January 13) ranged from 8.5 mm to 9.5 mm. The next sample was taken on January 19. Female and brood #3 were gone. Brood #14 contained two groups; one with a mean SL 8.59 mm ($n=17$) (corresponding to the expected size of brood #3), and the other (host fry) with a mean SL 10.47 mm ($n=21$, gaining three newly independent fry since the previous sample). Blood #14 dispersed before the next sample.

Discussion

Although some field workers have not reported seeing any evidence of brood adoption in their cichlid study species (Perrone 1978a; Carlisle 1985), others document widespread occurrence of mixed broods. Ribbink et al. (1980) found foreign fry in 34% of broods of 13 cichlid species in Lake Malawi. Multiple size groups within a brood were noted in Central American cichlids (McKaye and McKaye 1977) and African cichlids (Ribbink et al. 1980; Yanagisawa 1985). Yanagisawa (1985) presented length frequency distributions of fry from nine broods of *Perissodus microlepis* in Lake Tanganyika, showing the presence of discrete size groups in seven of them. Assuming the largest mode in each graph to represent the host fry, four of the seven mixed broods contained foreign fry smaller than the host fry, two broods contained foreign fry smaller and larger than the host fry, and one mixed brood contained only larger foreign fry.

Ribbink et al. (1980) showed that the proportion of foreign fry in mixed cichlid broods in Lake Malawi was usually <5% of the total. Our results were similar (Fig. 1), where mixed broods (not including fry transfers resulting from male removals) averaged 11.3% foreign fry.

Other than the one observation of fry transfer in Cabuyo pool, we are uncertain exactly how fry moved from brood to brood. Fry transfers are probably brief and sporadic events, thus the changes of observing one are small. Proposed mechanisms of fry transfer are: (1) kidnapping (McKaye and McKaye 1977; Mrowka 1987b); (2) active transfer of young by their parents into another brood ("farming out") (Ribbink 1977; McKaye 1985; Yanagisawa 1985); and (3) dislocation of fry resulting from territorial skirmishes between two sets of parents ("parent displacement") (Lewis 1980), or fry separated from their parents finding their way independently to another brood (Baylis 1974; McKaye and McKaye 1977; Coyne and Sohn 1978; Perrone 1978a; Ribbink et al. 1980). Each mechanism implies a different set of conditions. Method (1) implies that parents actively seek foreign fry to increase their brood size; (2) suggests that parental care is a burden that parents pass off to foster parents; and (3) implies that there is inefficiency and/or indifference in cichlid parental care.

On the face of it, hypotheses (1) and (2) appear to be mutually exclusive; various circumstances may cause parents to favour either one. In other words, under the right conditions fry transfer in convict cichlids can be mutually beneficial to both the fry donor and the fry recipient. These conditions are considered below.

Conditions benefitting fry recipient

McKaye and Hallacher (1973) and McKaye and McKaye (1977) proposed that parents accepting foreign fry benefit through the "dilution effect". A strike by a brood predator results in the loss of one or a few fry, not an entire brood. Given that brood predators will take *some* fry, parents can reduce the probability of their own young being taken by diluting their brood with foreign fry. Accepting foreign fry should benefit parents as long as the addition of foreign fry does not result in significant increases in brood defence, increased predator attack rate (Pitcher 1986) or increased competition for food among fry (Perrone 1978b).

Foreign fry and host fry may not be equally vulnerable to predators. Accepting foreign fry may be advantageous to the host if adopted fry are sufficiently different from host fry that they are singled out more easily by a predator (Ribbink et al. 1980). The presence of adopted fry benefit host fry in interspecific cichlid-catfish broods where adopted cichlid fry remain on the periphery of the brood and receive a disproportionate number of predator attacks, sparing the host catfish fry (McKaye and Oliver 1980; McKaye 1985). Similarly, Goff (1984) observed eggs and larvae of longnose gar (*Lepisosteus osseus*) on the periphery of smallmouth bass (*Micropterus dolomieui*) nests and hypothesized that gar fry receive many of the attacks by brood predators. Perrone (1978b) tested vulnerabilities of different sizes of *Cichlasoma maculicauda* fry to a *Gobiomorus* sp. predator and found the rate of capture to be highest in small fry.

In our study, smaller convict cichlid fry were more vulnerable than larger fry to two important brood predators (Fig. 4). Host parents can benefit in two ways when they accept foreign fry smaller than their own. Predation on their young is reduced by diluting their brood with foreign fry (the "dilution effect") and it is further reduced by adopting small foreign fry which serve as predation targets (the "differential predation effect"). It follows that for parents to accept fry larger than their own would put their fry at a disadvantage. Therefore, it could be predicted that parents accepting foreign fry should be vigilant and not accept fry larger than their own, but readily accept fry of similar size or smaller than their fry. The greater the size advantage of the host fry over the foreign fry becomes, the greater the differential predation effect.

Conditions benefitting fry donor

Parental care is an energetically costly endeavour which depletes body energy reserves, delays remating opportunities and increases predation risk to the caring parent (Gross and Sargent 1985). It is an obvious benefit to reduce these costs, provided that the parent(s) can be confident that their offspring have a reasonable chance of survival with foster parents. However, in a mixed brood, smaller foreign fry suffer from proportionately higher risk of predation and become independent at a smaller size than host fry. Under normal conditions, parental convict cichlids should be better off raising their own young. If prospects of successfully rearing fry to independence are reduced, as was shown for broods without male parents (Fig. 5), then fry transfer to foster parents may become advantageous.

Mate desertion by male convict cichlids has been documented in experimental ponds and in the field (Keenleyside et al. 1990; Keenleyside and Mackereth 1992) and occurred in 7.8% of all broods during this study (unpublished data). When one parent of a biparental species leaves the family, the burden of parental care is increased for the remaining parent (Mrowka 1982; Keenleyside et al. 1990). Thus, when a male deserts, the probability of rearing fry to independence is reduced (Keenleyside 1978; Keenleyside and Bietz 1981). Faced with possible brood failure, a deserted female parent should be inclined to compromise and accept the disadvantaged status her fry may have in a foster brood.

The male removal experiment simulated male desertion and resulted in the transfer of fry to neighbouring broods (Table 3; Fig. 5). Aspects of our results are comparable to those of Yanagisawa (1985). He removed either the male or female parent from the Lake Tanganyikan cichlid *Perissodus microlepis*, a biparental mouthbrooder, where both sexes defend the fry. The removal of one parent resulted in increased brood predator attack rates and higher predation losses. He found evidence of "farming out" by single males and females in 14 (54%) of 26 test broods. Single parents of 7 (27%) of his 26 test broods remained with their broods for at least 7 days after mate removal. In our study 8 (57%) of 14 male removal broods where neighbouring broods of same size or larger fry were present transferred fry, and 5 females (24%) of 21 broods remained with their brood (Table 3).

Experimental fry transfers were only successful in our study when fry of the receiving brood were larger than the foreign fry (Fig. 3). Some researchers have succeeded in transferring similar-sized fry between conspecific cichlid broods in the field (McKaye and McKaye 1977; McKaye and Hallacher 1973; Carlisle 1985), while others observed that all attempts to experimentally introduce foreign fry into broods were rejected by the parents when the foreign fry were similar in size (Ribbink et al. 1980; Yanagisawa 1985), or were smaller and larger than host fry (Perrone 1978a).

It is unclear how much of the size distribution in fry seen in Fig. 2 is also attributable to discrimination on the part of the fry donor. Male-removal broods whose only neighbouring broods contained fry smaller than their own failed 5 out of 5 times (Table 3). Perhaps fry transfers were attempted by these lone females and rejected by the receiving parents. When a choice was available, success was mixed, perhaps as a result of attempting to transfer large fry to a foster brood of smaller fry.

Conclusions

Intraspecific brood adoption involved at least 97 broods (68 broods were fry receivers, 35 were fry donors) of the 232 broods monitored in this study. The argument most frequently put forward to explain how natural selection could favour fry adoption is the dilution effect hypothesis. The dilution effect could be potentially greatly enhanced by parents accepting only fry of similar or smaller size while rejecting larger fry. Small fry are more vulnerable to brood predators; thus when brood predators attack, small foreign fry have a greater probability of being taken, which serves to further deflect brood predation away from host fry (the differential predation effect).

Further experimentation showed that intraspecific fry adoption in convict cichlids is beneficial both to the fry donor and the fry recipient. Survival of foreign fry is lower than that of fry being cared for by their own parents (Fig. 5), and often their period of parental protection ends at a younger age of development. Therefore, parents should generally be expected to care for their own young when possible. When prospects for successfully rearing their young to independence are low, such as when the male parent deserts, then fry transfer to another brood becomes advantageous.

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