The Dilution Effect and Differential Predation Following Brood Adoption in Free-ranging Convict Cichlids (*Cichlasoma nigrofasciatum*)

BRIAN D. WISENDE& MILES H. A. KEENLEYSIDE


**Abstract**

Parental investment in unrelated offspring is potentially maladaptive but may be promoted by natural selection if the presence of foreign young enhances the survival of the parents' own young. We experimentally augmented broods of free-ranging convict cichlids (*Cichlasoma nigrofasciatum*) to test whether survival of the adopting parents' young (fry) increases, in relation to that of control broods, after the addition of smaller foreign fry, and whether such an increase can be attributed to the effect of brood dilution acting alone or to a combination of brood dilution and the effect of differential predation on adopted young. Total fry survival did not differ between experimental (E) broods and control (C) broods, but E broods had significantly more large (host) fry after 5 days and 10 days than C broods did. In E broods, small (foreign) fry suffered higher rates of predation than large fry, indicating differential predation. In E broods starting at 7.0 and 7.5 mm standard length (SL), observed fry mortalities did not differ significantly from mortalities expected from the effect of brood dilution. However, E broods starting at 8.0 mm SL had significantly lower mortalities than expected, indicating that parents that adopt smaller foreign fry can increase the survival of their own fry by the combined effects of brood dilution and differential predation. Within E broods, growth of smaller foreign fry was significantly slower than that of larger host fry, suggesting that intra-brood agonistic behaviour affects access to food for smaller fry. Therefore, increased predation and reduced growth are two negative effects that act on fry of donor parents.

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**Introduction**

Alloparental care, that is, the care of genetically unrelated conspecific young (WILSON 1975), has been documented in a wide range of birds and mammals.
Alloparental care presents an interesting evolutionary problem because investment in unrelated young appears to be an act of altruism and therefore maladaptive by conventional evolutionary theory (Hamilton 1964). However, there is growing evidence that alloparental care is not a true example of altruism, but a predictable outcome of natural selection (McKay 1981; Constanz 1985; Eadie et al. 1988; Cooper & Miller 1992; Wisenden & Keenleyside 1992). Parents that adopt unrelated young can benefit if predation on their own (genetically related) young is reduced by the effect of brood dilution (Baylis 1974; McKay & McKay 1977; Eadie et al. 1988) and/or adopted (genetically unrelated) young suffer a disproportionate amount of predation and thereby deflect predation away from the foster parents' own young (Eadie & Lumsden 1985; McKay et al. 1992; Wisenden & Keenleyside 1992). These two hypotheses are not mutually exclusive.

The convict cichlid, Cichlasoma nigrofasciatum, is a small freshwater fish native to Central America. Males and females form monogamous pairs and jointly excavate, defend and spawn in a small cave. Care of the eggs and non-mobile hatchlings lasts about a week, after which free-swimming young (fry) emerge as a compact school hovering above the substrate. At this time they measure about 5 mm in standard length (SL). For the next three or four weeks, until the young grow to approximately 10 mm SL and begin to disperse, both parents actively defend the brood from potential predators (Wisenden & Keenleyside 1992).

A study of four breeding populations of free-ranging convict cichlids in Costa Rica showed that intraspecific brood adoption is widespread (Wisenden & Keenleyside 1992). Adopted fry were usually (81% of 84 cases) similar in size or smaller than the adopting parents' fry, especially when the latter were less than 8 mm SL.

In the present study we explore two questions about brood adoption in convict cichlids: (1) does the survival of the adopting parents' offspring increase after the addition of smaller foreign fry? and (2) can such an increase be attributed either to the effect of brood dilution acting alone or to the combined effects of brood dilution and differential predation on adopted young?

Study Site and Methods

We studied breeding convict cichlids from 23/3—2/5 1993 at two sites: Quebrada Amores and Rio Cabuyo, located in Lomas Barbudal Biological Reserve, Guanacaste province in northwest Costa Rica (10° 30'N, 85° 23'W). Quebrada Amores is a headwater stream and a tributary of Rio Cabuyo. Both streams are supplied by ground water during the dry season (Dec.—May). Some physical characteristics of the two sites are described in Table 1.

Although the parents used in this experiment were not measured, the mean size of breeding convict cichlids used in a concurrent experiment was significantly larger in Quebrada Amores than in Rio Cabuyo (females: t = 7.31, df = 43, p < 0.001; males: t = 5.68, df = 42, p < 0.001). The mean SL ± SE of breeding females and males was 52.0 ± 0.8 mm (n = 14) and 63.7 ± 0.9 mm (n = 13) in Quebrada Amores and 42.2 ± 0.8 mm (n = 31) and 56.1 ± 0.8 mm (n = 31) in Rio Cabuyo. These site differences in size of brood-guarding fish are consistent with those found at the same sites in 1990 and 1991 (Wisenden 1994).
Table 1: Physical characteristics of the study sites on 27, 28 Apr. 1993. Temperature data were collected from 28 Feb.—3 May 1993. Data are presented as X ± SE (n).

<table>
<thead>
<tr>
<th></th>
<th>Quebrada Amores</th>
<th>Rio Cabuyo</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean width (m)</td>
<td>3.07 ± 0.17 (76)</td>
<td>10.56 ± 0.39 (28)</td>
</tr>
<tr>
<td>Mean depth (cm)</td>
<td>17.52 ± 0.6 (519)</td>
<td>44.76 ± 2.4 (157)</td>
</tr>
<tr>
<td>Flow volume (l·s⁻¹)</td>
<td>6.2</td>
<td>231.7</td>
</tr>
<tr>
<td>Current speed (cm·s⁻¹)</td>
<td>0.96</td>
<td>4.90</td>
</tr>
<tr>
<td>Water temperature (°C)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daily maximum</td>
<td>28.8 ± 0.1 (17)</td>
<td>29.3 ± 0.1 (18)</td>
</tr>
<tr>
<td>Daily minimum</td>
<td>25.3 ± 0.2 (17)</td>
<td>26.1 ± 0.2 (18)</td>
</tr>
</tbody>
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In 1990 and 1991, broods in those streams with mean fry size between 6 and 8 mm SL contained a median of 44 fry (X ± SE = 50.8 ± 2.2, n = 200) (WISENBEN, unpubl. data). For the present study we altered the size of 24 broods in Quebrada Amores and 22 broods in Rio Cabuyo to 40 fry each. In each case we captured all but a few fry using hand nets, face mask and snorkel. Some fry were left with the parents in the stream to ensure that the parents stayed there until the captured fry were returned to them. We anaesthetized the fry with a dilute solution of tricaine methanesulfonate (MS222) and measured the SL of each to the nearest 0.5 mm. We sorted fry by size intervals of 0.5 mm to ensure that the 40 fry returned to the parents were uniform in size. The few fry remaining with the parents were captured and removed, using hand nets, before the group of 40 uniform-sized fry was given to the parents. We returned fry to their parents using a clear plastic tube and made detailed sketches of the body markings of the parents for later identification (WISENBEN & KENNEDY 1992). The entire sampling procedure lasted approximately 30 min per brood.

We standardized the initial size of the 40 fry to either 7.2, 7.5 or 8.0 mm SL, equally balanced between control and experimental treatments, between Quebrada Amores and Rio Cabuyo and, as far as possible, between different sections of each stream. These initial sizes made it possible to add smaller fry and still follow them for 10 days before the larger fry reached independence from parental care.

Control (C) broods were left with 40 uniform-sized fry. To experimental (E) broods we added an additional 20 fry that were 1.5 mm shorter in SL. The added fry were usually obtained from broods outside the study area, however, due to the precise size requirements of each manipulation we sometimes took fry from nearby broods. We chose a size difference of 1.5 mm because a previous study on the same populations of convict cichlids had shown that the mean size difference between host and adopted fry within a brood was 1.38 ± 0.07 mm (n = 64) (WISENBEN & KENNEDY 1992). E broods were thus composed of 33% 'foreign' (and smaller) fry. In the previous study the percent of foreign fry in mixed broods was 11.9 ± 1.5 (range 0.9—43.9, n = 64).

All broods were resampled after 5 days and 10 days. In each sample, we captured all but a few fry, anaesthetized a subsample of 10, measured their SL, and counted the number of fry in the brood including those that were left in the water with the adult pair. The captured fry were then returned to the adults. We did not collect data on fry behaviour or predation events directly, because, from a distance that did not disturb the parents, it was impossible to distinguish between the size groups of fry.

Results

There was no obvious pattern to whether or not E and C broods remained intact until the day-10 sample was taken (Table 2). The experimental treatment had no significant effect on the frequency of complete brood failure ($\chi^2 = 0.164$, df = 1, $p = 0.685$). Some broods which started at 8.0 mm SL dispersed before day 10. Other $\chi^2$ tests were inappropriate due to small sample sizes. Further analyses
Table 2: The number of intact broods on days 0, 5 and 10 for each starting size of fry at Quebrada Amores and Rio Cabuyo

<table>
<thead>
<tr>
<th>Initial size of fry</th>
<th>7.0 mm</th>
<th>7.5 mm</th>
<th>8.0 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td>10</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td><strong>Amores E Broods</strong></td>
<td>3</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td><strong>C Broods</strong></td>
<td>3</td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td><strong>Cabuyo E Broods</strong></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td><strong>C Broods</strong></td>
<td>5</td>
<td>4</td>
<td>3</td>
</tr>
</tbody>
</table>

*one brood adopted fry naturally between day 5 and day 10 making it impossible to determine the effect of the experiment*

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Fig. 1: Mean percentage fry survival (+SE) for control (C) broods (open bars), the combined total of large and small fry in experimental (E) broods (cross hatching), and large (ascending hatching) and small (descending hatching) fry in E broods. *t-tests p < 0.05; ns, p > 0.05

Analysis of percentage survival among large and small fry in E broods (Fig. 1) showed that small fry had suffered higher predation than large fry in the same brood by day 5 (t = 5.31, df = 15, p < 0.001) and by day 10 (t = 7.95, df = 15, p < 0.001). There was no significant difference between percentage fry survival in C broods and the combined total of large and small fry in E broods on day 5 (t = 0.66, df = 31, p = 0.512) or on day 10 (t = 1.02, df = 23.3, p = 0.307). Thus, higher survival of large fry in E broods than of fry in C broods (Fig. 1) was not
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7.0 7.5 8.0
SL
hml
of Large Fry at Day 0
FI~.
2: Difference between mean number of large fry in E broods and mean fry number in C broods plotted against starting fry SL of large fry at day 0. Squares: Quebrada Amores; circles: Rio Cabuyo; solid lines and solid symbols; day-5 samples; dashed lines and open symbols: day-10 samples

Starting fry size (i.e., 7.0, 7.5 or 8.0 mm SL) had a strong influence on the increase in survival of large fry in E broods relative to fry in C broods (Fig. 2). For broods starting at an SL of 7.0 mm and 7.5 mm, there was no significant difference in fry survival between C and E broods by day 5 (7.0: t = 0.18, df = 10, p = 0.862; 7.5: t = 1.23, df = 10, p = 0.246) or by day 10 (7.0: t = 0.04, df = 10, p = 0.967; 7.5: t = 1.48, df = 10, p = 0.169). However, for broods starting at 8.0 mm SL, there were significantly more large fry in E broods than fry in C broods on both sample days (day 5: t = 4.87, df = 7, p = 0.002; day 10: t = 6.51, df = 7, p < 0.001).

If brood dilution was solely responsible for the increased survival of large fry in E broods compared to the fry in C broods, then mortality of large fry in E broods should have been 4:6 of fry mortality in C broods. If observed mortality of large fry in E broods was less than this expected value, then it would probably be due to brood dilution enhanced by differential predation.

We calculated fry mortalities expected from the dilution effect alone by multiplying the observed mortalities in C broods by the dilution factor of 4:6 and compared these with observed mortalities of host fry in E broods (Fig. 3). These mortalities were not significantly different for E broods starting at 7.0 and 7.5 mm SL on day 5 (7.0: t = 1.21, df = 10, p = 0.254; 7.5: t = 0.07, df = 10, p = 0.943) or on day 10 (7.0: t = 1.64, df = 10, p = 0.133; 7.5: t = 0.09, df = 10, p = 0.928). However, for E broods starting at 8.0 mm SL, observed mortalities of large fry were significantly lower than expected on day 5 (t = 3.61, df = 7, p = 0.009) and on day 10 (t = 3.70, df = 7, p = 0.008), indicating that survival of large fry in these E broods was increased by the combined effects of brood dilution and differential predation (Fig. 3).

There was no apparent site-effect on fry mortality for any combination of treatment, day, and starting size except for the day-10 sample of broods starting
Fig. 3: Mean mortality (+SE) of host fry in E broods (solid bars) compared to mortality expected from the effect of brood dilution (dashed bars) for broods starting at 7.0, 7.5 and 8.0 mm fry SL. 5, day-5 sample; 10, day-10 sample. Expected fry mortalities were calculated by multiplying observed fry mortalities in C broods by the dilution factor of $4:6$. *t-tests, $p < 0.05$.

Fig. 4: Mean (+SE) growth increment (mm) over 5 days for fry starting between 7.0 and 8.0 mm SL. Growth of C broods and large fry of E broods was measured between day 0 and day 5. Growth of small fry of E broods was measured between day 5 and day 10. Number above bar: sample size; *Control = Large E fry > Small E fry (Student Newman Keuls multiple range comparison $p < 0.05$)

at 8.0 mm SL (ANOVA treatment: $F = 44.65$, df = 1, 8, $p = 0.001$; Site: $F = 24.9$, df = 1, 8, $p = 0.004$). However, this may have been a result of small sample sizes. Mean ($\pm$ SE) fry mortality observed on day 10 in large fry, for E broods starting at 8.0 mm SL, was $10.75 \pm 0.85$ (n = 4) in Quebrada Amores and 5.0 (n = 1) in Rio Cabuyo.

Overall, growth rates were lower for both size groups of fry in E broods than for fry in C broods. Mean growth of large fry in E broods was not significantly different from that of C fry ($t = 0.93$, df = 31, $p = 0.358$). The growth of small fry could not be compared directly to the growth of large fry because the absolute growth increment may be confounded by body size (i.e. a change of 1 mm SL for small fry represents more growth relative to their size than it does for large fry). Therefore we took those E broods for which the mean size of small fry was
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between 7.0 and 8.0 mm SL in the day-5 sample (n = 10), and calculated their growth over the next 5 days (i.e. day 5–day 10). We then compared this with the growth of fry in C broods and that of large fry in E broods from day 0 (when mean SL was from 7.0 to 8.0 mm) to day 5 (Fig. 4). Growth of fry in C broods and of large fry in E broods was faster than that of small fry in E broods (ANOVA F = 4.29, df = 2, 40, p = 0.021; Student Newman Keuls: C fry = large E fry > small E fry, p < 0.05).

Discussion

This experiment has demonstrated that brood-guarding pairs of convict cichlids that adopt foreign young smaller than their own young can benefit both from the effect of brood dilution and from differential predation acting on two size classes within the brood. The overall number of large fry in E broods was significantly greater as a result of the presence of small fry (Fig. 1). Percentage fry survival in E broods (small and large fry combined) did not differ from that in C broods, yet small fry in E broods suffered a significantly greater proportion of predation than large fry in E broods (Fig. 1). However, these effects depended on the size of the host fry when foreign fry were added. Mean numbers of fry in C broods and large fry in E broods starting at 7.0 mm SL were almost identical on both day 5 and day 10 (Fig. 2). There was no increase in fry survival in E broods due to the effects of dilution or to differential predation (Fig. 3). This suggests that parents of 7.0 mm SL fry may not benefit by adopting smaller foreign young. However, mortality of large fry in E broods starting at 7.5 mm SL was slightly reduced in comparison to C broods, especially at the Quebrada Amores sites (Fig. 2), and very closely matched the expected values based on the dilution effect (Fig. 3). For E broods which started at 8.0 mm SL, mortality of large fry was significantly lower than was expected by the effect of brood dilution alone (Fig. 3). Therefore, the beneficial effect of brood adoption on host fry survival appears to be dependent on the size of the host fry. These results concur with the results of Fraser et al. (1993) where a threshold of host fry size of about 8.0 mm SL was found, above which adopting parents no longer rejected larger foreign young. This suggests that an important element of fry development occurs when fry reach about 8.0 mm SL that renders them less vulnerable to brood predators than smaller fry, and similar in escaping abilities to fry larger than 8.0 mm SL.

We have shown that, at least in some cases, foreign fry that are smaller than host fry incur greater losses due to predation than the host fry do. This may occur because: 1. small foreign fry generally have weaker predator escape abilities than larger host fry (Skagen 1988; Stouffer & Power 1991; Wisenden & Keenleyside 1992; Fraser et al. 1993); 2. foreign young are pushed to the periphery of the brood where predator attacks are most likely (McKay & Oliver 1980; Goff 1984; McKay 1985; Eadie et al. 1988; McKay et al. 1992); or 3. brood predators select odd-sized prey from within a mixed brood (Ribbink et al. 1980; Eadie et al. 1988). These hypotheses are not mutually exclusive and, since
we did not monitor predator attacks directly, we cannot determine which was the more likely cause in our study. Our experience with convict cichlids in the laboratory (Wisenden & Keenleyside 1992) suggests that the first hypothesis is the most likely.

Within E broods, the growth rate of large fry was significantly higher than that of small fry (Fig. 4). This suggests that large fry can use their size advantage, in combination with agonistic behaviour, to gain greater access to food resources than smaller fry (Valerio & Barlow 1986). A size difference of 1.0 mm SL between fry in the same brood is enough to produce intra-brood aggression (Fraser et al. 1993). Convict cichlid fry feed almost exclusively on the substrate. If parents can effectively defend only a limited area, then an increase in fry number may result in an increase in fry density within a brood and thereby increase competition for food (Perrone 1978).

Although this study involved the experimental transfer of fry between broods, the rationale for the work was the evidence that alloparental care by convict cichlids is common at our study sites (Wisenden & Keenleyside 1992). The mechanism of fry transfer between convict cichlid broods is unknown, but several mechanisms have been proposed for other cichlids. Fry transfer may be active: they are either kidnapped by foster parents (McKaye & McKaye 1977) or deposited (‘farmed out’) by their own parents (Ribbink 1977; Yanagisawa 1985). Alternatively, fry transfer may be passive when fry become separated from their parents and independently find their way into other broods (Coyne & Sohn 1978; Lewis 1980). Parents can benefit from adopting fry through reduced predation on their own young, often at the expense of the adopted young. Therefore active fry donation to other broods is a last resort of parents (Eadie et al. 1988; Lank et al. 1989), and may occur only when the probability of rearing their own young to independence is low, such as when the male parent in a biparental species deserts his mate (Yanagisawa 1985; Wisenden & Keenleyside 1992).

The most economical explanation for the mechanism of fry transfer between convict cichlid broods would be a three-step process. Firstly, fry become separated from their genetic parents during skirmishes between their parents and predators, or between their parents and neighbouring breeding pairs (Lewis 1980). Secondly, separated fry are strongly attracted to an adult with the characteristic black and white parental markings and that is exhibiting parental ‘calling’ behaviour, even if that fish is not their own parent (Lavery et al. 1990; De Gannes & Keenleyside 1992). Thirdly, convict cichlid parents accept stray fry that are similar in size or smaller than their own (Myrberg 1964; Wisenden & Keenleyside 1992), either because they cannot distinguish between foreign fry and their own (Coyne & Sohn 1978) or because natural selection has promoted the survival of adults that behave this way (McKaye 1981).

Factors that predispose convict cichlids to alloparental care are similar to those for least sandpipers, Calidris minutilla (Cooper & Miller 1992): 1. the cost of providing parental care for a small number of additional fry is negligible; 2. they display strong ‘broodiness’ tendencies, where young are attracted to parental adults and parental adults are strongly motivated to care for any young
near them; 3. they breed in high densities and the home ranges of mobile families of convict cichlids are shared (prevalence of natural brood adoption was highest at the site where mean interbrood distance was the shortest [WISENDE & KEENLEYSIDE 1992]); and 4. their breeding is synchronised (WISENDE 1994).

In conclusion, we have shown that convict cichlid parents that adopt foreign young can increase the survival of their own young, and thereby increase their reproductive success, by the effects of brood dilution and differential predation on the foreign young. If adopting parents discriminate against foreign young larger than their own, and in favour of those the same size or smaller than their own, they stand a good chance of increasing their survival rate at little or no risk of additional parental investment.

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