

Factors affecting reproductive success in free-ranging convict cichlids (*Cichlasoma nigrofasciatum*)

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This study examines the effect of parent size, fry growth rate, and habitat-related brood predation pressure on two measures of reproductive success (percent brood survival and fry number at independence from their parents) of free-ranging convict cichlids (*Cichlasoma nigrofasciatum*). Four populations in Costa Rican streams were studied, two in "pool" habitat and two in "stream" habitat. The number of fry that emerged from the spawning site (as free-swimming young) was positively correlated with female standard length (SL) for sites with a relatively wide size range of breeding females. SL of males had no effect on fry number at emergence, nor did size of either parent affect the probability of a brood reaching fry independence. Large parents reared more fry to independence than small parents in stream habitat but not in pool habitat. There was a significant difference among sites in fry number at emergence but not at independence (mean = 27 fry), suggesting a maximum number of fry that two parents can economically defend. Fry growth rate had no effect on either measure of reproductive success. Reproductive success was largely determined by the effect of habitat. Adult *Cichlasoma dovii* in pool habitat may have reduced mean brood survival from 47% ($n = 126$ broods) in stream habitat to 14.9% ($n = 141$ broods) in pool habitat. Predators such as juvenile *C. dovii* may be more effective in the dim ambient light in pool habitat, overwhelming the effect of parent size on brood defence.

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On trouvera ici les résultats de l'étude de l'influence de divers facteurs (taille des parents, taux de croissance des alevins, pression de prédation exercée sur la progéniture en fonction de l'habitat) sur deux mesures du succès de la reproduction (survie de la progéniture exprimée en pourcentage, nombre d'alevins au moment de la séparation d'avec les parents) chez des Cichlides à bande noire (*Cichlasoma nigrofasciatum*) en liberté : il s'agissait de quatre populations d'eau courante de Costa Rica, deux en eau lente et deux en eau rapide. Le nombre d'alevins issus des sites de ponte (jeunes à nage libre) s'est avéré en corrélation positive avec la longueur standard des femelles (SL) aux sites où les tailles respectives des femelles reproductrices s'étaient sur une échelle relativement grande. La longueur SL des mâles n'influait pas le nombre d'alevins à l'émergence et la taille de l'un ou l'autre parent n'affectait pas non plus la probabilité que la progéniture atteigne le stade d'indépendance. Les parents de grande taille ont réussi à rendre un plus grand nombre d'alevins jusqu'au stade de poissons indépendants en eau rapide, mais pas en eau lente. Il y avait des différences significatives entre les sites quant au nombre d'alevins au moment de l'émergence, mais pas au moment de l'indépendance (moyenne = 27 alevins), ce qui indique que les parents peuvent être économiquement responsables d'un nombre maximal d'alevins. Le taux de croissance des alevins est resté sans effet sur les deux mesures du succès de la reproduction, lequel était en grande partie sous l'influence de l'habitat. La présence d'adultes de *Cichlasoma dovii* en eau lente est peut-être responsable de la survie moyenne plus faible de la progéniture dans ce milieu (14,9%, $n = 141$ portées comparativement à 47%, $n = 126$ portées en eau rapide). Il est possible aussi que les prédateurs tels que les *C. dovii* juvéniles soient plus efficaces dans l'eau un peu trouble des zones lentes, inhibant l'effet de la taille des parents sur la défense de la progéniture.

[Traduit par la Rédaction]

Introduction

Parental care is unusual among fishes; it is found in only 20.1% of fish families (Blumer 1982). Biparental care in fishes is rarer still, being found in only 2.4% of all fish families that have been studied. Most Neotropical species of the freshwater family Cichlidae have biparental care of their eggs, free embryos (wrigglers), and free-swimming larvae (fry) over a total of about 6 weeks (Keenleyside 1991). During the fry stage of development (3–4 weeks) both parents guard the brood from potential predators. Biparental care in Central American cichlids is thought to be maintained by the need to defend the young against intense predation pressure (Barlow 1974).

Convict cichlids (*Cichlasoma nigrofasciatum*) are small freshwater fish native to Central America (Bussing 1987). They breed during the long dry season (December to June) and have

biparental care of their young. Convict cichlids form monogamous pair bonds and jointly defend and spawn in small caves that they excavate under solid objects (usually rocks) on the substrate. The eggs hatch in about 3 days and emerge from the cave as fry about a week after the spawning event. At this time, the fry measure slightly less than 5 mm standard length (SL). Fry become independent from their parents soon after they reach about 10 mm SL (Wisenden and Keenleyside 1992).

In this study three factors that may affect reproductive success in convict cichlids were examined: (1) parent size; (2) fry growth rates; and (3) habitat. Two measures of reproductive success of free-ranging convict cichlids were used as dependent variables: the probability of at least one fry from a brood surviving to independence, and the number of fry surviving to independence.

Parent size

Parent size has been singled out in a number of studies as an important factor influencing reproductive success in fishes

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(Turner 1993). Large fish achieve higher reproductive success than small fish in a wide range of taxonomic groups (e.g., salmonids, Hanson and Smith 1967; cyprinodontids, Kodric-Brown 1977; sticklebacks, Li and Owings 1978; Dufresne et al. 1990; sculpins, Brown 1981; gobies, Magnhagen and Kvarnemo 1989; cichlids, Perrone 1978b). Laboratory studies of mate choice in convict cichlids have indicated that females prefer large males over small males (Noonan 1983; Keenleyside et al. 1985) and that males prefer large females over small females when both are gravid, and ignore size when choosing gravid females over nongravid females (Nuttall and Keenleyside 1993). The benefits associated with large size in males are that they are often more successful than small males in acquiring high-quality territories, nest sites, and feeding areas for the young (Perrone 1978a) and they may be more effective defenders of the young (Keenleyside et al. 1985). Large females are more fecund than small females (Bagenal and Braum 1978; Townshend and Wootton 1984) and may also be more successful at defending fry from predators. As a consequence of intersexual selection, size-assortative mating occurs in cichlid fishes in Lake Jiloá, Nicaragua (Barlow 1986; McKaye 1986), and in Costa Rican streams (Wisenden 1994b). In this study, I predicted that larger parents would be more likely to rear their brood to fry independence than small parents, and that broods reared by large parents should contain more fry at independence than broods reared by small parents.

Fry growth

Small fry are poor swimmers and are potential prey for many other fishes, including juvenile conspecifics (Perrone 1978b; Carlisle 1985; Townshend and Wootton 1985; Keenleyside et al. 1990; Wisenden and Keenleyside 1992). Predation losses during the fry stage are high, even when two parents guard the brood (McKaye 1977). Fast-growing fry develop effective antipredator behaviour and outgrow gape-limited predators sooner than slow-growing fry and thus are subjected to predation for a shorter time period (Perrone 1978a). Brood survival and the number of fry surviving to independence should be higher for broods with fast growth rates of fry than for those with relatively slow fry growth.

Habitat

Predation pressure can change in two ways: the number of predators and the type of predators (species, size, and time of day when they are actively foraging). Either of these factors may vary with habitat type. Differences in predation pressure potentially mask or overwhelm the influence of parent size or fry growth rate.

Methods and materials

Study sites

I monitored the breeding activity of convict cichlids in Costa Rican streams during the long dry season from January 1990 to June 1990 and from December 1990 to June 1991. The study sites were in and adjacent to Lomas Barbudal Biological Reserve in Guanacaste Province, northwestern Costa Rica (10°30'N, 85°23'W). Four sites were used, two each in "pool" and "stream" habitat. A description of the physical and chemical characteristics of the study sites is given in Wisenden (1994b) and Wisenden and Keenleyside (1994). Two sites were in the río Cabuyo: one was a wide, deep pool referred to as "Cabuyo pool" (CabP) and the other was a section of the río Cabuyo where the stream forms a series of small, shallow interconnected pools, referred to as "Cabuyo stream" (CabS). The two other sites were in the Quebrada Amores, a tributary of the río Cabuyo. These

sites are referred to as "Amores pool" (AmP) and "Amores stream" (AmS) for the pool and stream habitat, respectively.

Sampling procedure

The location of each spawning site (cave) was noted and marked with flagging tape or a painted stone. All brood-guarding adults were captured, anaesthetized with tricaine methanesulfonate (MS 222), measured to the nearest millimetre, and marked by excising two dorsal spines in a unique code so that individuals could be distinguished (Rinne 1976). Because reading the mark required capturing the fish and inspecting the dorsal fin at close range, sketches of adult body markings were made to minimize stress caused by the sampling procedure. In subsequent samples individual families could be identified using the sketches, the location of the family in the stream, and the stage of brood development. The fry in each brood were counted and the SL of a sample of 15 fry was measured at intervals of 5–7 days as described in Wisenden and Keenleyside (1992).

Parent size

Parent size was tested against fry number soon after the fry emerged from the spawning cave (fry SL < 6 mm) and again just before fry independence (fry SL > 10 mm) to examine the effects of parent body size on fecundity and defence efficiency separately. Convict cichlids paired size assortatively; thus, within pairs, SL of males and females were correlated (Wisenden 1994b). To test for the effect of each sex separately I regressed fry number (LnFryNo) at emergence and at independence against parent size:

$$\text{LnFryNo} = b_0 + b_1 \text{Ln (SL for males)}$$

$$\text{LnFryNo} = b_0 + b_1 \text{Ln (SL for females)}$$

Fry growth

I calculated fry growth rates by regressing mean fry SL against day for each brood. Fry growth was linear (mean $r^2 = 0.987 \pm 0.002$; $n = 117$) for all broods sampled at least three times. Fry numbers at emergence and at independence were regressed against fry growth rate (mm/d) using

$$\text{LnFryNo} = b_0 + b_1 \text{Ln (growth, mm/d)}$$

Habitat

Pool and stream habitats do not contain the same constellation of brood predators. Common at all sites were adult and juvenile convict cichlids, the poeciliids *Poecilia gillii* and *Brachyrhaphus rhabdophora*, and the schooling characin *Astyanax fasciatus*. In addition, the río Cabuyo contained the poeciliids *Alfaro cultratus*, *Poeciliopsis turribarensis*, and *Phallichthys amates*, and the characin *Rhoboides guatemalensis*. Adult and juvenile *Cichlasoma alfarei* occurred in the río Cabuyo only, where they commonly inhabited the deeper (pool) sections of the river with a sand substrate. Adult *Cichlasoma dovii* occurred only in pool habitat in each study stream. These are piscivorous fish that grow to 45 cm in length (Bussing 1987). *Cichlasoma dovii* and *C. alfarei* bred in pool habitat during the long dry season at the same time as convict cichlids. Juvenile *C. dovii* dispersed to all parts of the study streams. *Rhamdia guatemalensis*, a nocturnal pimelodid catfish, occurred at all sites.

Parental brood defence behaviour was monitored to estimate predation pressure on broods at each site. The shallow, nonturbulent, and clear water made it possible to record parental behaviour while sitting quietly on shore or wading to within a few metres of the family. I made observations with the aid of polarized sunglasses to reduce surface reflection. I allowed a 5-min acclimation period before beginning recordings. A 10-min focal sample of brood defence behaviour was recorded for each parent. I recorded the number of attacks per 10 min directed at each species (and in some cases size class) of brood predator, and the approximate distance of the predator from the brood when the parent initiated an attack.

To measure the amount of fry predation that occurred during the day and during crepuscular or nocturnal periods, 11 broods were repeatedly sampled for 3–6 days (mean 3.5 ± 0.3 d). The fry in each

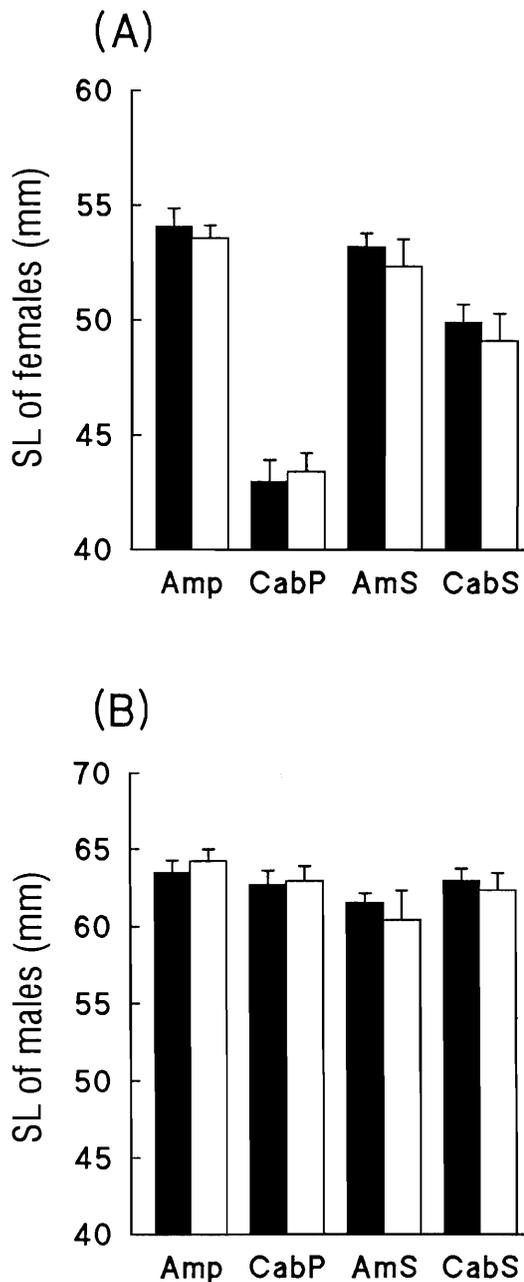


FIG. 1. Mean (+ SE) standard lengths (mm) of parents at four study sites guarding broods that reached fry independence (solid bars) or failed before reaching fry independence (open bars). (A) Females. (B) Males. AmP, Amores pool; CabP, Cabuyo pool; AmS, Amores stream; CabS, Cabuyo stream.

brood were counted early in the morning (as soon as ambient light levels permitted) and again at dusk. Diurnal and nocturnal changes in fry number were recorded.

Throughout the results, variation is always expressed as the standard error of the mean.

Results

Parent size

There were no significant differences in SL of parental females or parental males between broods that succeeded in rearing some fry to independence and those that did not (ANOVA, $p > 0.05$; Fig. 1). The number of fry at emergence increased with female size up to about 50 mm SL, but not for

TABLE 1. Regressions of fry numbers at emergence and at independence against SL of parental males and females within each site

Site	SL of males			SL of females		
	df	r^2	p	df	r^2	p
At fry emergence						
AmP	20	0.03	0.436	19	0.04	0.402
CabP	35	0.07	0.125	35	0.11	0.041
AmS	8	0.06	0.507	9	0.00	0.878
CabS	37	0.05	0.195	37	0.23	0.002
At fry independence						
AmP	10	0.17	0.190	10	0.00	0.978
CabP	16	0.00	0.897	15	0.07	0.311
AmS	20	0.13	0.097	20	0.22	0.028
CabS	23	0.26	0.010	23	0.16	0.046

NOTE: For explanation of abbreviations see text. All slopes are positive.

breeding females larger than 50 mm (Fig. 2). Fry number at emergence increased with SL of females at sites in the río Cabuyo, where many females were < 50 mm SL, but not at the two sites in Quebrada Amores, where most breeding females were > 50 mm SL (Table 1). SL of males had no significant effect on fry number at emergence (Table 1).

SL of females was significantly correlated with fry number at independence at stream sites but not at pool sites (Table 1). Fry number at independence increased significantly with SL of males at Cabuyo stream and weakly at Amores stream ($p = 0.097$), but did not increase at the sites in pool habitat ($p > 0.19$).

Variation among sites in fry number at emergence was near-significance (ANOVA, $p = 0.088$; Fig. 3). However, fry number at independence did not differ among sites (ANOVA, $p = 0.241$), with a grand mean of 27.4 ± 1.9 fry ($n = 81$). There was no effect of habitat or the number of fry at emergence on the number of fry at independence (ANCOVA, habitat: $p = 0.812$; emergence: $p = 0.165$; habitat \times emergence: $p = 0.715$).

Fry growth

There was a significant difference in fry growth rates among sites and between years. Fry growth was significantly faster at sites in Quebrada Amores than at sites in the río Cabuyo in both years of the study (Student–Newman–Keuls multiple-range test, $\text{AmP} = \text{AmS} > \text{CabS} = \text{CabP}$; $p < 0.05$). Within sites, there were no significant differences in growth rates between fry in broods from which at least one fry reached independence and fry from broods from which no fry survived to independence (ANOVA, $p > 0.05$; Fig. 4).

Fry number at emergence was not correlated with fry growth at AmP, CabP, and AmS, but fry growth was negatively correlated with fry number at emergence at CabS (Table 2). Fry growth rates did not explain a significant proportion of the variance in fry number at independence (Table 2).

Habitat

Brood survival to fry independence in stream habitat was 46.8% ($n = 126$ broods) compared with 14.9% ($n = 141$ broods) in pool habitat ($\chi^2 = 32.3$; $p < 0.001$). Brood survival to fry independence was not a result of intersite differences in fry growth rates. Fry growth was fastest at the Quebrada Amores sites in both pool and stream habitat, and

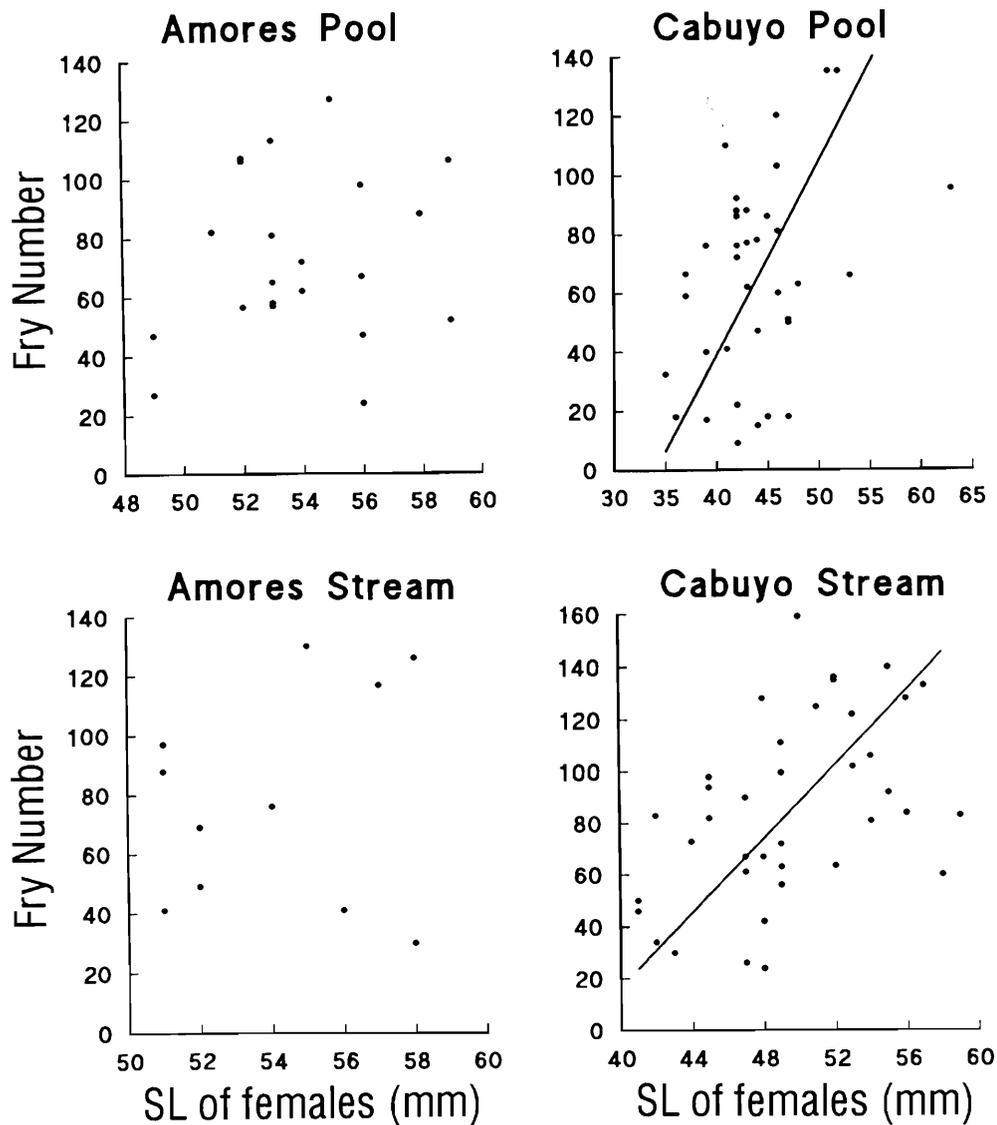


FIG. 2. Number of fry at emergence from the spawning cave plotted against SL of females for broods reared at each site.

TABLE 2. Regressions of fry numbers at emergence and at independence against fry growth rates (mm/d) within each site

Site	df	r^2	p
At fry emergence			
AmP	37	0.03	0.330
CabP	47	0.22	0.130
AmS	37	0.18	0.269
CabS	57	0.44	<0.001
At fry independence			
AmP	10	0.05	0.488
CabP	12	0.00	0.878
AmS	20	0.00	0.826
CabS	22	0.03	0.406

NOTE: Data were combined from both years of the study. All slopes are positive except for CabS at emergence.

culated as the product of the number of fry surviving to independence in each brood and the average probability of a brood at each site surviving to fry independence. The average overall reproductive success of convict cichlids breeding at each site was as follows: AmP, 4.7 ± 0.9 fry ($n = 12$); CabP, 3.9 ± 0.5 fry ($n = 18$); AmS, 15.9 ± 2.0 fry ($n = 26$); and CabS, 11.8 ± 1.7 fry ($n = 25$). A Student–Newman–Keuls multiple-range test of overall reproductive success among sites revealed significant differences between habitats, as follows: AmS = CabS > AmP = CabP ($p = 0.005$).

Females attacked potential brood predators significantly more often than males did (Wisenden 1994a), and parental attacks occurred more frequently at sites in stream habitat than in pool habitat (Tables 3, 4). Thus, frequent parental attacks did not correspond to patterns of brood mortality as expected.

The minimum distance from the brood at which a potential predator was tolerated by a parent should reflect the relative threat posed to the brood. Parents attacked juvenile and adult *C. dovii* at significantly greater distances from the brood than other predators (Fig. 5). Parental attack distances to adult and juvenile convict cichlids were intermediate between those of *C. dovii* and non-cichlids, i.e., *A. fasciatus* and poeciliids (Fig. 5). Analyses of the parental attack data should be treated

slowest at the río Cabuyo sites in both pool and stream habitat (Fig. 4).

The overall reproductive success of convict cichlids was cal-

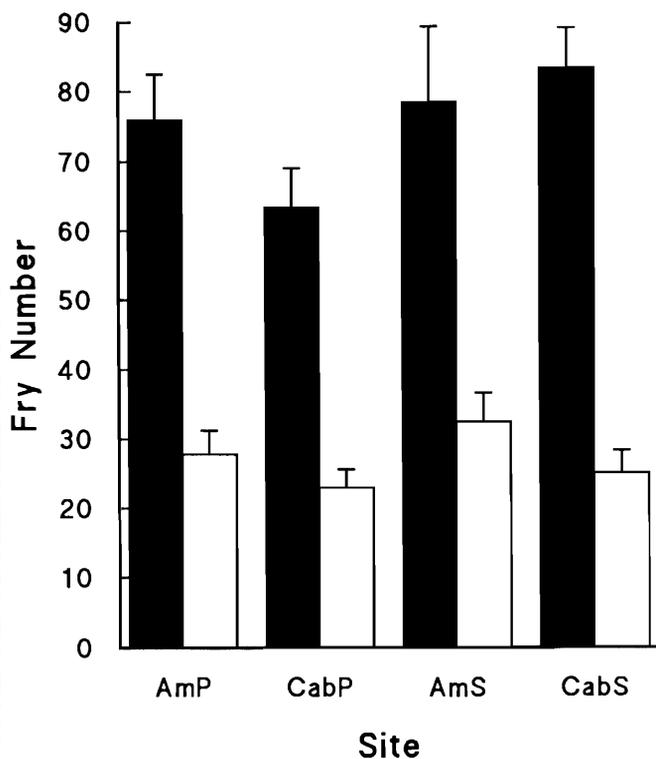


FIG. 3. Mean (+ SE) fry numbers at emergence (solid bars) and fry independence (open bars) at each site.

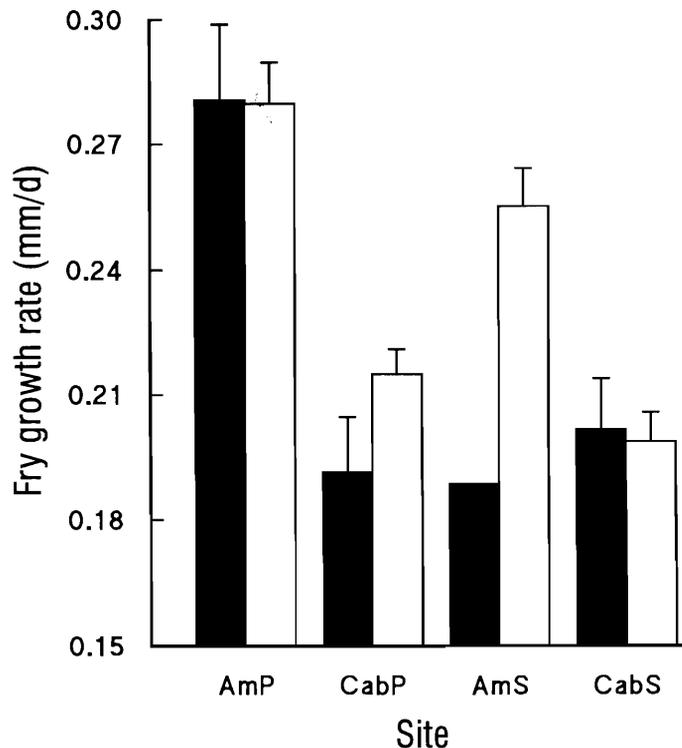


FIG. 4. Mean (+ SE) fry growth rates of broods that failed before fry independence (solid bars) or reached fry independence (open bars).

an interpretive guide rather than strong statistical tests because the data were unbalanced and there were repeated measures from many fish. These statistical irregularities were unavoidable given the rates of brood survival and logistical constraints on data collection.

During the day, convict cichlid parents travelled along the stream bottom with their broods. At dusk and dawn convict cichlid families were always found near the entrance to their spawning cave. At night (complete darkness) convict cichlid families used their spawning caves for shelter. Fry losses during the day were equal to fry losses at night (including both crepuscular periods; Fig. 6). Fry losses per brood during daylight hours averaged 2.7 ± 1.0 fry ($n = 35$ brood-days) compared with 2.3 ± 1.0 ($n = 24$ brood-nights) at dusk, night, and dawn ($t = 0.25$, $p = 0.802$). Loss of fry was zero on 13 out of 35 (37%) brood-days compared with 10 out of 24 (42%) brood-nights. There were no differences among sites in fry loss during the day (ANOVA, $p = 0.735$) or at night (ANOVA, $p = 0.535$). The effect of habitat on day and night predation was not significant (ANOVA, day/night, $p = 0.940$; habitat, $p = 0.849$).

Discussion

Parent size

In studies of mate choice, large size is commonly assumed to represent high quality in a mate (Halliday 1983). The data presented here show that these assumptions are justified for convict cichlids under some, but not all, ecological conditions. Breeding adults of all sizes at each site in this study were equally capable of rearing at least some fry to independence (Fig. 1). In contrast, in Lake Jiloá, with a relatively harsh predation environment, large (> median SL) parental males and females were more likely than smaller parents to be found

guarding a brood containing fry more than 3 weeks old, suggesting that large parents were better brood defenders than small parents (McKaye 1986).

Large parents at sites in stream habitat successfully reared more fry to independence than small parents did (Table 1). Therefore, in stream sites, both sexes potentially improved their reproductive success by pairing with a large mate. The effect of parent size on fry number at independence was not apparent in pool habitat. SL of the parents was not correlated ($p > 0.05$) with either time spent away from the brood or the total number of attacks on brood predators for any of the study sites (B.D. Wisenden, unpublished data). Therefore, in stream habitat, the higher success of large parents at brood defence relative to small parents may be through intimidating brood predators without attacking them, or through access to high-quality brood-rearing areas (Perrone 1978b) rather than greater parental investment in brood defence as proposed by Williams (1975).

Significant size-assortative pairing occurred at CabP, CabS, and AmS (Wisenden 1994b). Large females had more fry at emergence than small females at sites in the río Cabuyo, where the size range of breeding females included those smaller than 50 mm SL (Fig. 2, Table 1). In the río Cabuyo (CabP, CabS), fry number at emergence is probably closely linked to size-related differences in female fecundity (Townshend and Wootton 1984). Females that bred at Quebrada Amores were almost all > 50 mm SL. Males do not gain fecundity-related fitness benefits by choosing large females from among females larger than 50 mm SL (Fig. 2), reflected by nonsignificant size-assortative pairing at AmP. However, males in stream habitat (i.e., AmS) benefit from large mates (among those > 50 mm SL) as a result of more effective defence (Table 1). Size-assortative pairing was observed at the three sites where

TABLE 3. Number of parental attacks per 10 min (mean + SE) by females during defence of broods of all ages against 8 potential brood predators in each site

Predator	AmP		CabP		AmS		CabS	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
JCon	1.71	0.52	3.22	1.55	1.48	0.33	3.20	0.43
ACon	2.23a	0.25	1.05b	0.16	2.51a	0.36	3.21a	0.53
JAlf	—	—	0.39	0.10	—	—	0.41	0.10
AAIf	—	—	0.15	0.05	—	—	0.09	0.03
JDov	0.44ab	0.09	0.38ab	0.13	0.15a	0.05	0.69b	0.13
ADov	0.09	0.04	0.06	0.03	0.09	0.03	0.01	0.01
Ast	1.81a	0.33	1.20a	0.26	4.22b	0.68	3.94b	0.93
Poec	0.64	0.12	0.36	0.16	1.17	0.53	1.10	0.22
Tot	7.21a	0.52	7.32a	1.53	10.64ab	1.19	13.84b	1.33

NOTE: JCon, juvenile convict cichlids; ACon, adult convict cichlids; JAlf, juvenile *Cichlasoma alfar*; AAIf, adult *C. alfar*; JDov, juvenile *C. dovii*; ADov adult *C. dovii*; Ast, *Astyanax fasciatus*; Poec, poeciliids; Tot, total attacks (including "unknown" and "miscellaneous"). Sample sizes are 65 for AmP, 54 for CabP, 37 for AmS, 39 for CabS. *Cichlasoma alfar* occurred in the río Cabuyo only. Values followed by the same letter are not significantly different across sites (Student–Newman–Keuls, $p > 0.05$).

TABLE 4. Number of parental attacks per 10 min (mean + SE) by males during defence of broods of all ages against 8 potential brood predators in each site

Predator	AmP		CabP		AmS		CabS	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
JCon	0.43a	0.09	0.97b	0.20	0.34a	0.07	1.50b	0.39
ACon	1.59a	0.21	0.92a	0.16	1.46a	0.24	2.94b	0.41
JAlf	—	—	0.23	0.09	—	—	0.27	0.09
AAIf	—	—	0.25	0.08	—	—	0.15	0.06
JDov	0.16	0.06	0.24	0.06	0.14	0.04	0.19	0.05
ADov	0.06a	0.03	0.18b	0.05	0.02a	0.02	0.00a	0.00
Ast	1.05	0.30	1.55	0.42	1.26	0.35	1.31	0.34
Poec	0.17	0.05	0.20	0.10	0.20	0.08	0.43	0.16
Tot	3.66a	0.44	4.70a	0.56	3.65a	0.51	7.29b	0.93

NOTE: For other details see Table 3. Sample sizes are 63 for AmP, 53 for CabP, 35 for AmS, and 35 for CabS. *Cichlasoma alfar* occurred in the río Cabuyo only. Values followed by the same letter are not significantly different across sites (Student–Newman–Keuls, $p < 0.05$).

either small females (<50 mm SL) bred (fecundity effect) or the abilities of large females in brood defence increased fry number at independence. The lack of an increase in fry number at emergence for females >50 mm SL was unexpected. It may indicate that there is a maximum number of fry that a female and its mate can rear to emergence (Wisenden and Keenleyside 1994b), or it may result from bet-hedging, where females adjust their fecundity in the face of high predation risk to their young (Wisenden 1993).

The reason for the small mean size of breeding females at CabP (Fig. 2) is unknown. One possibility is that large females breed in the best sections of the river (stream habitat), forcing smaller females to marginal areas (pool habitat). At AmP, which was closed to immigration and emigration, resident large females excluded small females from breeding altogether (Wisenden 1994b). In Lake Jiloá, Nicaragua, small female convict cichlids bred predominantly during the peak breeding time of the large, dominant cichlid species, *Cichlasoma citrinellum* (McKaye 1986). Large female convict cichlids bred when *C. citrinellum* were not breeding. However, the reproductive success of convict cichlids breeding at these two times is not known.

Fry growth

At the onset of the long dry season, many of the deciduous trees in Lomas Barbudal Biological Reserve drop their leaves (Frankie et al. 1974). Leaves accumulated in the study streams, particularly at the sites in Quebrada Amores, because this is a small headwater stream with a small flow volume (Wisenden and Keenleyside 1994a). The río Cabuyo is a higher order stream than the Quebrada Amores and much of the allochthonous material was flushed downstream beyond the study sites. Leaf litter constitutes a major influx of nutrients and can greatly increase stream productivity (Vannote et al. 1980). This may have contributed to the significantly faster rates of fry growth at sites in Quebrada Amores than in the río Cabuyo (Fig. 4). Despite these site differences in growth, there was no effect of fry growth on the probability of a brood reaching fry independence or on fry number at independence within or among sites (Fig. 3, Table 2). The effect of fry growth on fry survival may be subtle relative to the overwhelming effect of habitat. For fry growth rates to affect fry survival in this context, a much greater range in growth rates may be required than those measured for the broods in this study.

At CabS, there was a negative correlation between fry num-

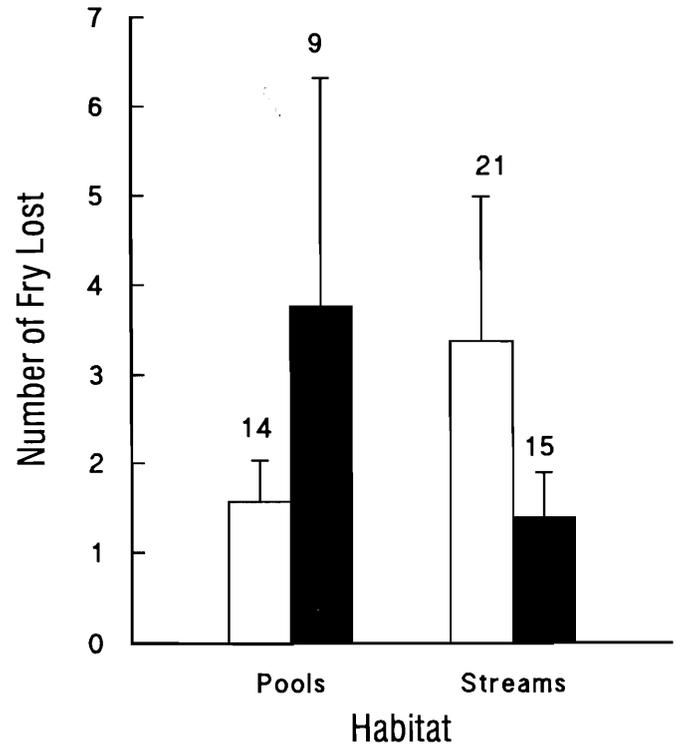
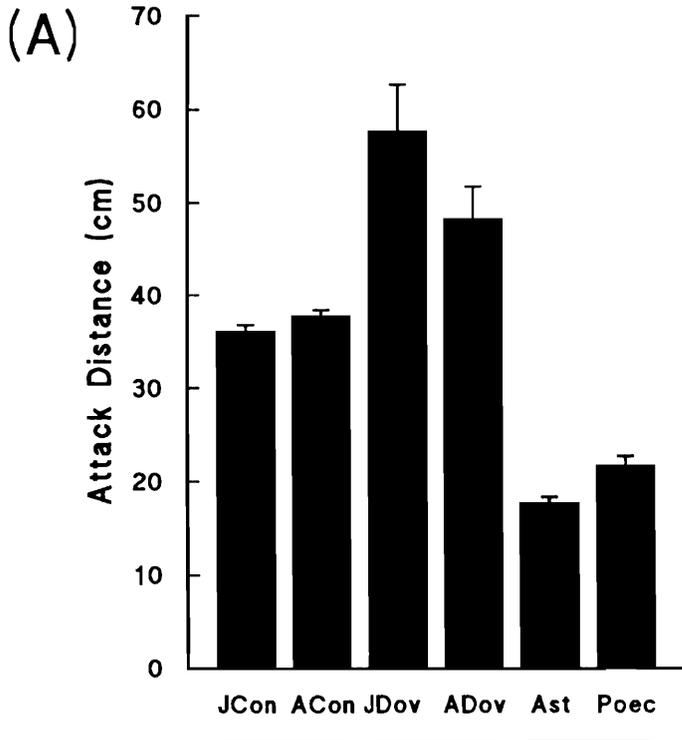


FIG. 6. Mean (+ SE) numbers of fry lost during the day (open bars) and from dusk to dawn (solid bars) in pool and stream habitats. The numbers above the bars are sample sizes.

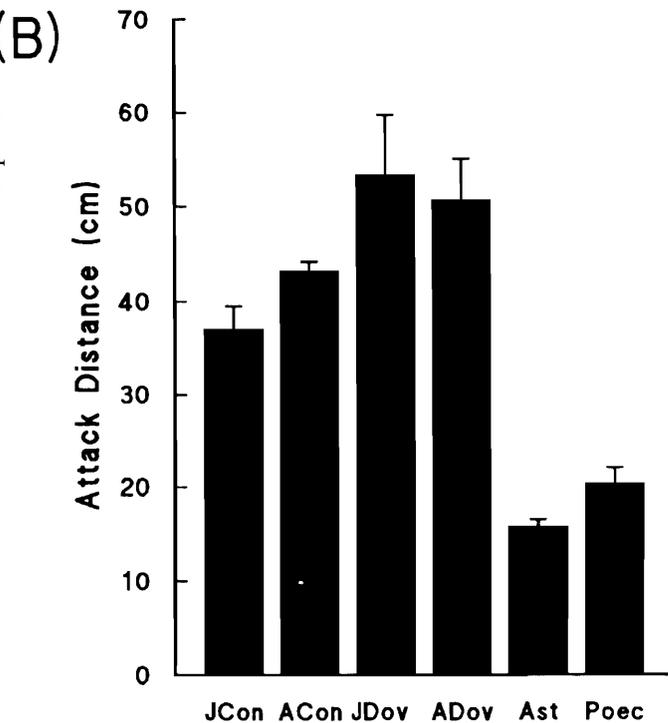


FIG. 5. Mean (+ SE) distances at which parent convict cichlid females (A) and males (B) attacked six potential brood predators: JCon, juvenile convict cichlids; ACon, adult convict cichlids; JDov, juvenile *Cichlasoma dovii*; ADov, adult *C. dovii*; Ast, *Astyanax fasciatus*; Poec, poeciliids. *Cichlasoma alfarei* do not occur in Quebrada Amores and were excluded from this figure to allow multiple-range testing among attack target species. The lines below the labels on the x axis connect values that are not significantly different (Student–Newman–Keuls, $p > 0.05$).

ber at emergence and fry growth, indicating that fry growth may be suppressed at high fry density. This was also found in broods that were experimentally augmented to the upper limit of the range of natural brood sizes (Wisenden and Keenleyside 1994b). There may be a trade-off between foraging efficiency and predation risk for fry that stray to the fringe of the area protected by the parents. Because convict cichlid fry are demersal, density increases within the area of maximal parental protection as fry number in a brood increases, resulting in increased fry–fry competition for food and suppressed growth (Wisenden and Keenleyside 1994b). Fry numbers at independence averaged 27.4 (Fig. 3) and did not differ significantly among sites despite significant site differences in fry growth rates, SL of females, and rates of total brood loss. This could result from a behavioural constraint acting during the early stages of brood development on the number of fry that two convict cichlid parents can economically defend (Wisenden and Keenleyside 1994b).

Habitat

Habitat was the single most important factor determining reproductive success of convict cichlids in these streams, overriding any effect of parent size. Survival of convict cichlid broods in Lake Jiloá, Nicaragua, was 9% (McKaye 1977) compared with the 15% found in pool habitat in this study, indicating that broods in these two populations face intense predation pressure. Among my study sites, brood survival was not linked to frequency of parental attacks on diurnal predators in any obvious way (Tables 3, 4). Attack data were collected at midday, when visibility (for the human observer) was best; thus, important periods of brood predation may not be well represented by these data. If parental attack rates reflect predator density, then it would be expected, from the rates of brood

survival and the effect of parent size on fry number at fry independence, that attack rates would have been higher in pool habitat than in stream habitat. This was not the case, which calls into question the reliability of parental attack frequency in estimating predator abundance or predation pressure on cichlid broods (e.g., Townshend and Wootton 1985). It could also be argued that for other unknown reasons, high brood survival at stream sites was a consequence of high parental aggression in stream habitat. Experimental manipulation of predator densities is needed to resolve this question.

Few broods in the present study contained fewer than six to eight fry at any stage of brood development, suggesting that this may be the lower limit of brood size at which parents give up and abandon their brood. Alternatively, parents may transfer their fry to the care of a neighbouring pair (Yanagisawa 1985; Wisenden and Keenleyside 1992).

Clearly, the reproductive success of breeding convict cichlids was greater in stream habitat than in pool habitat. Stream habitat may represent a predation refuge for breeding convict cichlids in the same way that *Herotilapia multispinosa*, sympatric with the large piscivorous cichlid *Cichlasoma managuense*, migrate from the río Frío during the rainy season to breed in ponds where *C. managuense* do not occur (Baylis 1974).

Attrition versus absolute predation

Over the period of parental defence of fry, broods typically followed one of two patterns: fry gradually declined in number or the entire brood abruptly disappeared. Broods that failed (completely disappeared) did not contain significantly fewer fry in the sample taken before failure than surviving broods, indicating a catastrophic predation event (Wisenden 1994a). There may be two forms of brood predation on convict cichlid broods: (1) predation by attrition, where an individual brood predator attacks a brood and, if successful, eats only one or two fry before the guardian parent(s) chases it away; (2) absolute predation, where the entire brood, or most of it, is consumed during a single encounter with one or more predators.

The number of fry surviving to independence may be determined by predation by attrition and the probability of a brood reaching independence may be determined by the probability of its encountering absolute predators.

Candidate attrition predators

Juvenile *C. dovii* produced in pool habitat disperse and feed in the shallower sections of the stream (including "stream" habitat). They are efficient predators of convict cichlid fry (Wisenden and Keenleyside 1992), as reflected in parental attack distances (Fig. 5). In contrast to attacks on other potential brood predators, parent convict cichlids chased juvenile *C. dovii* for up to 2 or 3 m from the brood (personal observation). Juvenile *C. dovii* and other attrition-style predators, such as juvenile convict cichlids, may be aided by the lower ambient light levels in deep water in pool habitat when attacking convict cichlid broods (McKaye et al. 1979; Helfman 1993). Greater effectiveness of attrition predators in pool habitat than stream habitat may explain the interaction between the effects of habitat and parent size on the number of fry at independence (Table 1). Any initial advantage in egg number gained by large females over small females in Cabuyo pool was cancelled by the effect of habitat by the time the fry reached independence. Although the size of males did not contribute to fry number at emergence, large males in stream habitat were associated with higher numbers of fry at inde-

pendence. Large females in sites at Quebrada Amores (pool and stream) did not start with more young at emergence than small females, but large females had more fry at independence than small females in the stream site.

Possible absolute predators

Adult *C. dovii* are potential absolute brood predators, found only in pool habitat, and are the most likely cause of low brood survival in pool habitat. Parental convict cichlids attacked adult *C. dovii* that approached their brood by swimming in a wide circle around the fish and nipping its caudal fin, clearly avoiding its head. On one occasion I observed a large *C. dovii* consume a whole brood of convict cichlid fry with huge gulps at the substrate. Attempts by the parents to drive it away were met with open-mouthed lunges by the larger cichlid, causing the parental convict cichlids to retreat momentarily.

Other possible absolute predators are the characin *A. fasciatus* and the nocturnal catfish *Rhamdia guatemalensis* "Avalanching" behaviour by *A. fasciatus* has been observed in Costa Rican streams (Meral 1973) and a Mexican lagoon (Neil 1984), where large schools of these fish attacked cichlid broods, overwhelming the defensive abilities of the parents with their numbers, and consumed all the fry. I never observed avalanching in the río Cabuyo or Quebrada Amores while the parents were undisturbed. *Astyanax fasciatus* were abundant at all four sites. Thus, avalanching behaviour is not a likely explanation for the habitat differences in brood survival.

Similarly, the nocturnal pimelodid catfish *R. guatemalensis* occurred at all sites and therefore does not seem likely to have been responsible for the relatively low brood survival in pool habitat. However, this species is potentially an absolute brood predator (K.R. McKaye, personal communication), particularly at night, when fry are gathered into a small area. Perhaps in response to nocturnally active brood predators, a number of biparental cichlid species use crevices or holes for nocturnal shelter (McKaye and Hallacher 1973; Baylis 1974; Neil 1984; McKaye et al. 1979; Wisenden 1994a). The efficacy of sheltering in cavities against nocturnal predators is not known. Clearly, more research is needed on the behavioural ecology of fishes in this system.

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