

Does parental fin digging improve feeding opportunities for offspring in the convict cichlid?

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Synopsis

The function of the fin digging behaviour in increasing food availability for the offspring was analysed in the convict cichlid, *Cichlasoma (Archocentrus) nigrofasciatum*. Consistent individual differences in the frequency of fin digging were found in the parental fish. Examination of the gastrointestinal tract of young revealed that higher frequency of parental fin digging was associated with higher consumption of large and more profitable prey (Diptera larvae), which inhabited deep horizons of the bottom substrate and possibly were difficult to access without parental assistance. Thus, parental fin digging was initially associated with a significant increase of the offspring growth rate. However, at later brood intervals, when parental care ceased, the young of the high-digging parents were characterised by a poorer consumption of small larvae that were most accessible for them without parental aid and represented an increasingly more important component of their ration than large larvae. Offspring of the low-digging parents, on the other hand, presumably as a result of their individual experience, showed a considerably better consumption of small larvae, increasing their growth rate. As a consequence, prior parental fin digging did not affect the offspring body size after independence. Thus, there exist pronounced individual differences and alternative parental styles in the convict cichlid.

Introduction

Many vertebrate species exhibit parental care, which often includes protection of the young from predators and providing them with food. Because parental care typically involves a high investment of time and energy, its existence poses many important evolutionary questions (Clutton-Brock 1991). Although parental care is relatively uncommon among fishes, it is an important characteristic feature of the cichlid family (Teleostei: Cichlidae, see Keenleyside 1991). Guarding the eggs and young from brood predators and egg fanning are the most typical forms of parental behaviour in these fishes. Nonetheless, some species exhibit various forms of parental food provisioning (Keenleyside

1991). However, food provisioning has received relatively less attention than other forms of their parental behaviour, the data are often anecdotal and scattered in the aquarist literature.

One example of such poorly understood patterns of parental behaviour in New World cichlids is fin digging. Fin digging occurs when the adult fish settles its body onto the substrate and stirs up loose bottom material by a short bout of rapid, vigorous beating of its pectoral fins and undulating movements of the body. In response, the young immediately rush in and begin feeding (Keenleyside 1991, Wisenden et al. 1995, Zworykin 1998). Even though this form of parental behaviour was known long ago (see Keenleyside 1991 for a review), only Wisenden et al. (1995) and

Zworykin (1998) have analysed fin digging in some detail. However, the evidence for food provisioning function of fin digging obtained so far still remains indirect and somewhat ambiguous.

The main aim of the present investigation was to assess the function of fin digging behaviour in the convict cichlid, *Cichlasoma (Archocentrus) nigrofasciatum*. Whenever it is hardly possible to manipulate the parents to artificially make them to reduce the frequency of fin digging, while not affecting other aspects of their behaviour, one can presumably exploit the natural individual differences which can be often expected within populations (Magurran 1993). The possible existence of individual differences in parental behaviour is extremely interesting on its own. If under the same environmental conditions some parents reduce food provisioning for their offspring, what is the benefit of this seemingly maladaptive behaviour? Thus, the second aim of this study was to determine whether individual differences exist in parental fin digging, and what is their stability and adaptive function. Direct assessment of the adaptive value of parental food provisioning as increasing food availability for the young was possible by comparing the growth rate and stomach content.

Materials and methods

Subjects, maintenance and behavioural observations

The convict cichlid is a biparental substrate nesting and guarding species inhabiting Central American streams and lakes. Our stock was descended from fish obtained from an aquarium breeder. Prior to experiments, all fish used as parents were maintained in a large tank (1.2 m³), containing about 80 same-age conspecifics, where they were allowed to freely choose their mates. As such, they did not differ much in their experience. Fourteen pairs (standard length 65–76 mm in males, 54–66 mm in females) and their young were used in the study. Each pair was spawned and further maintained in a 50-l aquarium (46 × 28 × 39 cm) with half a clay flowerpot as a potential spawning substrate and about 3 cm layer of natural gravel. The photoperiod was a 10:14 h light : dark cycle. Water temperature was maintained at 26 ± 1°C. Both adults and young were fed moderately (0.7–0.9 g of food per pair with brood) with commercial dry flakes five times per week. Before spawning, adults were also occasionally fed with common bloodworms (8–12 mm in length).

As in previous studies of parental fin digging (Wisenden et al. 1995, Zworykin 1998, Budaev et al. 1999), the brood development was classified into five intervals: egg, free embryo (wiggler), 3 days as larvae (fry), 10 days as juvenile and 17 days as juvenile. The differences between brood size of different pairs did not exceed 25% (assessed through areas occupied by the clutches), and it is known (see Lavery & Keenleyside 1990) that parental fin digging in the convict cichlid does not depend on the clutch size. We recorded the number of parental fin digs during 10-min observation periods once at each brood interval. The recording sessions were carried out between 12:00 and 16:00 h, before the fish were fed (see Zworykin 1998, Budaev et al. 1999 for details).

Substrate analysis

Substrate analysis was conducted to assess its quality in terms of food availability for the young, and it was carried out when the offspring were at 20 days as juveniles. We took samples of surface and deep layers of the bottom gravel using a glass cylinder with an aperture diameter of 42 mm and a length of 115 mm, operated by a long handle. To collect surface samples, a portion of gravel occupying approximately 1/2 of the cylinder volume was ladled into it. To sample deep layers, approximately 1/2 of the gravel depth was cautiously removed with a small shovel, and the material laying directly on the glass bottom of the aquarium was scooped. Subsequently, both gravel and water were transferred to a 0.5-l glass vessel, vigorously shaken, and the suspension obtained was poured into another glass vessel to settle for one hour.

The front walls of the experimental aquariums were regularly cleaned to enable behavioural observations. Three other walls, however, remained undisturbed. We sampled the fouling that covered these walls using a small plastic scraper 47 mm in width. When taking samples, the scraper was gently, but with sufficient effort, dragged over the wall upwards from the bottom to the water surface. All substrate samples were taken from 12:00 to 16:00 h before the fish were fed.

The samples of the loose organic material were transferred into test tubes (1.5 cm³ volume) and fixed in 5% formaldehyde. After fixation and final settling for one day, the sediment volume in all cases was about 0.3 cm³. Finally, the samples were placed on mounts and examined under a microscope. Six samples were taken from randomly chosen locations in every aquarium: two

from surface, two from deep gravel layers and two from the aquarium walls.

Dissection and measurements of the young

Two samples of young were taken from each aquarium. The first one was taken when the offspring reached the age of 20 days as juveniles. At this time, the parents displayed parental care, including fin digging, and the young were large enough for examination (average standard length 6.23 ± 0.14 mm).

Ten individuals were randomly caught from each brood and fixed in 5% formaldehyde. Their standard length was measured under a microscope using an eyepieces micrometer. Each was then dissected with flatly sharpened dissecting needles. First, the wall of the body cavity was cut from head to the anus. The gastrointestinal tract was then pulled out onto the mount, separated from the body (cut at pharynx and anus) and dissected longitudinally. Its content was spread as a thin layer on the mount and the number of Diptera larvae was counted under microscope. Only head segments were taken into account when partially digested larvae were observed.

The second sample was taken at the brood age of 45 days as juvenile, when they reached the average standard length 12.18 ± 0.34 mm. No parents exhibited clear parental care at this time and fin digging has already disappeared. The measurements, dissection and examination of specimens was carried out as described above.

Statistical analysis

Summary statistics are expressed as mean \pm standard error. In some cases of repeated measures ANOVA, where the sphericity and compound symmetry assumptions were violated (as assessed by the Mauchly W test), we used the Huynh-Feldt adjustment for the degrees of freedom (Crowder & Hand 1995). In addition, when the assumption of variance homogeneity was violated, we used the Welch t-test (Wilcox 1987) and the arcsin-transformation in ANOVA. Because of relatively small sample size, Spearman and gamma correlation and Kendall concordance coefficients were used for correlational analysis. Gamma correlations are typically computed in cases of multiple zero frequencies to take account of such tied observations (Krauth 1988).

Results and discussion

The frequency of fin digging was affected (see Figure 1) by both the offspring age ($F_{1,56,20,27} = 24.7$, $p < 0.001$ with the Huynh-Feldt adjustment, Mauchly test: $W = 0.006$, $p < 0.001$) and the parent sex ($F_{1,13} = 25.06$, $p < 0.001$). The interaction term was also significant (Wilks lambda = 0.26, $p = 0.006$, Mauchly test: $W = 0.002$, $p < 0.001$). Contrast analysis evidenced that fin digging in both sexes increased linearly with the offspring age (linear trend contrast: $F_{1,13} = 22.28$, $p < 0.001$ in males and $F_{1,13} = 28.84$, $p < 0.001$ in females). Furthermore, females were characterised by a higher overall frequency of fin digging than males ($F_{1,13} = 25.06$, $p < 0.001$, contrast analysis).

Individual differences in the frequency of fin digging consistent over the brood intervals were found in males (Kendall's concordance coefficient $W = 0.73$, $p < 0.001$). Such individual differences were even more stable in females (Kendall's concordance coefficient $W = 0.90$, $p < 0.001$). In addition, there were significant correlations in the frequency of fin digging between males and females within pairs (Table 1). That is, the parents within a given pair tended to show similar level of fin digging activity. Previous studies have demonstrated that various cichlids (Francis 1990, Budaev et al. 1999), guppies (Budaev 1997) and pumpkinseed sunfish (Coleman & Wilson 1998) have stable behavioural profiles similar to individual temperaments. Furthermore, our recent investigation (Budaev et al. op. cit.) evidenced that convict cichlids pair assortatively according to their 'temperament' traits. There might also be a link with physical condition of the parental fish.

This consistency and between-sex correlation allowed us to collapse the five scores of males and females together, which yielded a single composite measure, reflecting the overall tendency of a particular pair to exhibit fin digging. Such data aggregation decreases measurement error and leads to more parsimonious description of individual differences (e.g. Budaev 1997, Budaev et al. 1999).

The substrate analysis revealed two kinds of Diptera larvae, which largely differed in size and were easily discernible by simple visual inspection. The small specimens length ranged from 0.4 to 1 mm with the mean 0.7 mm, whereas the large larvae ranged from 2 to 4.5 mm with the mean length 3.3 mm (t-test with the Welch adjustment: $t_{15,46} = 12.34$, $p < 0.0001$, $N = 30$, note that there was no overlap between their distributions). Because these organisms have not been



Figure 1. The frequency of fin digging exhibited by the parents at various brood intervals. Median values, 25–75% quartiles, and the minimum and maximum values are shown.

Table 1. Gamma and Spearman correlation coefficients between the frequency of fin digging in male and female at various brood intervals.

Brood interval	Correlation	p
Eggs	0.92 ^a	<0.001
Free embryo	0.96 ^a	<0.001
3 days as larvae	0.51 ^a	<0.005
10 days as juveniles	0.66 ^b	<0.01
17 days as juveniles	0.56 ^b	<0.05

^aGamma correlation.

^bSpearman correlation.

deliberately introduced into our experimental aquariums, their origin is unknown. They might have got there with the bloodworms, which were previously given to the adult parents, or emerge from eggs laid directly into the aquariums by the imago. However, their presence created the basis for our study concerning the adaptive function of fin digging behaviour.

The distribution of these small and large larvae differed substantially. The percentage of different specimens of larvae (arcsin-transformed scores) was affected by the substrate layer (surface versus deep, $F_{1,13} = 75.70$, $p < 0.0001$) but not by the sampling repetition and location ($F_{1,13} = 0.30$, $p = 0.59$), and the interaction was also non-significant ($F_{1,13} = 3.11$, $p = 0.10$). Specifically, the percentage of small larvae was greater in the surface layer (77.7%) than in the bottom layer (10.3%). Thus, small Diptera larvae predominantly occurred within the surface layer of the substrate, whereas large ones strongly preferred deep horizons, and the procedural alterations were unimportant. Only small larvae were observed on the aquarium walls.

Both small and large Diptera larvae were represented in the gastrointestinal tract of the young. Furthermore, the total amount of large and small larvae differed significantly between the two samples taken at the 20 and 45 days as juvenile brood intervals. The overall average number of small specimens increased from 1.59 ± 0.20 to 6.89 ± 0.61 ($t_{168,94} = 8.31$, $p < 0.0001$), whereas

the number of large Diptera rose in a much smaller extent, from 1.44 ± 0.19 to 1.82 ± 0.14 ($t_{258.43} = 1.67$, $p = 0.096$, the power to detect such difference at the alpha level of 0.05 is equal to 0.38). This indicates that the large larvae were relatively unavailable to the young after independence and they were forced to switch to the small larvae.

To correlate the frequency of fin digging made by the parents with the young characteristics, we aggregated the standard length of the young as well as the number of large and small Diptera larvae in their stomachs within the 14 pairs, that is, calculated average values for each pair. The aggregated fin digging score closely correlated with several young characteristics. However, the patterns of correlations were different at 20 and 45 days as juvenile brood intervals (Table 2). At 20 days, fin digging showed a positive correlation with the standard length of the young and the number of large Diptera larvae in their gastrointestinal tract. However, at 45 days as juveniles, fin digging showed negative correlations with the number of small Diptera larvae in the tract. At both ages, the frequency of parental fin digging correlated positively with the percentage of large larvae in the gastrointestinal tract.

To check, whether the frequency of fin digging and the young growth depend on various aspects of substrate quality, we correlated the aggregated fin digging score, young body length and all the above stomach content characteristics with four substrate quality measures (the number of small and large Diptera larvae in the surface and deep layers of bottom gravel). The aggregated fin digging score was not correlated with the substrate quality ($p > 0.1$ in all cases). Also,

substrate quality had no relationship with the body length and stomach characteristics of the young at 20 days ($p > 0.1$ in all cases). However, at 45 days, the young body length correlated positively with the number of large Diptera larvae in both surface and deep substrate layers ($R_s = 0.58$, $p = 0.029$ and $R_s = 0.73$, $p = 0.003$, respectively), as well as with the number of small larvae in the deep layer ($R_s = 0.68$, $p = 0.008$). The number of large larvae in the young gastrointestinal tract tended to correlate with the number of large larvae in the surface layer ($R_s = 0.48$, $p = 0.08$) and small larvae in the deep layer ($R_s = 0.50$, $p = 0.07$) of the substrate (the power to detect such correlations with $\alpha = 0.05$ is equal to 0.4). However, the number of small Diptera in the young stomachs did not depend on the abundance of these organisms in the deep and surface layers of the substrate ($p > 0.1$ in all cases).

These results indicate that substrate quality had no effect on the frequency of parental fin digging and did not affect the young growth at 20 days. Yet, it tended to exert significant effects on young growth and stomach content at 45 days. It seems self-evident that growth rate and stomach content of the young after independence significantly depend on the substrate quality.

General discussion

The results of the present study agree with those obtained by Wisenden et al. (1995) and Zworykin (1998) in that the frequency of fin digging increases with brood interval, and is higher in females than in males. Such a pattern is consistent with the hypothesis that this behaviour serves to increase food availability for the young. Indeed, nutritive requirements of the young increase as they grow and females are more involved in direct parental behaviour in many cichlid species (Keenleyside 1991, Wisenden et al. 1995).

More importantly, our study revealed a close link between the frequency of parental fin digging and the offspring growth: higher frequency of fin digging correlated with significantly higher amount of large, presumably more profitable, specimens of Diptera larvae, which tended to hide in deep layers of the bottom substrate and therefore were not easily accessible by the small young. As a result, the total quantity of food material was significantly higher in the offspring of frequently digging parents, ultimately increasing their growth rate.

The most important fitness benefit of high growth rate of the young is certainly associated with avoiding

Table 2. Spearman correlations between the overall aggregated fin digging score and juvenile stomach contents characteristics at two brood intervals.

Characteristics of young	R_s	t_{12}	p
<i>20 days as juveniles</i>			
Standard length of the young	0.90	7.19	0.000
Number of small larvae	-0.08	0.27	0.795
Number of large larvae	0.92	8.21	0.000
Total number of larvae	0.93	9.11	0.000
Percentage of large larvae	0.79	4.51	0.001
<i>45 days as juveniles</i>			
Standard length of the young	0.33	1.20	0.252
Number of small larvae	-0.59	2.51	0.027
Number of large larvae	-0.06	0.20	0.844
Total number of larvae	-0.53	2.17	0.051
Percentage of large larvae	0.74	3.84	0.002

brood predators. For example, predation on young cichlids is often very intense, even though they are constantly guarded by the parents. Furthermore, small young have significantly higher vulnerability to brood predators than just a few millimetres larger (Wisenden & Keenleyside 1992, 1994). In addition, large body size would bestow a significant benefit in competitive and agonistic interactions. We conclude, therefore, that parental fin digging really functions to increase food availability for the offspring and would also significantly increase the offspring survival.

However, an unexpected pattern was found at the offspring age of 45 days as juveniles, when the parents ceased to display parental behaviour. At this time, higher level of previous parental fin digging was associated with a significant reduction of the total amount of food organisms in the gastrointestinal tract of their offspring. Whereas there was no association between parental fin digging and the number of large dipteran larvae eaten, the young of the frequently digging parents were characterised by a significantly poorer consumption of small larvae. These small larvae, however, become an increasingly more important component of the offspring ration than large larvae at the age of 45 days (note that the mean number of large larvae eaten by the young did not exceed two and did not increase from 20 to 45 days). Furthermore, the correlation between prior fin digging and the offspring body length become non-significant.

This seemingly counterintuitive pattern may point to a possible trade-off between parental food provisioning and the offspring individual experience. On the one hand, higher level of provisioning would increase the availability of more profitable prey for the young, leading to their initially higher growth rate. But on the other hand, the offspring of parents who do not dig much, are likely to gain an important individual experience in searching and hunting for smaller and inconspicuous prey, which are accessible for them even without assistance. The 45 days old juveniles (12 mm) are still too small to dig out large larvae from the deep substrate layers (3 cm of gravel). Thus, to the end of the parental period, the former young would become inexperienced and less capable to obtain more available small food organisms, which reduce their growth rate. Ultimately, the differences in growth between the offspring of parents employing various food provisioning styles disappeared.

Furthermore, previous investigation (Budaev et al. 1999) indicated that more aggressive individuals tend

to exhibit lower level of direct parental behaviour and spend more time away from the brood. It was suggested that such aggressive parents may trade-off brood defence against parental provisioning. Thus, a wide variety of parental styles appear to exist in the convict cichlid. Some parents may devote time and energy to active brood provisioning, thereby increasing the offspring food availability, initial growth rate and survival. More aggressive parents could invest more in active defence of their territories at some distance for the expense of direct brood provisioning, which would also increase the young survival.

However, a potentially important limitation of the present results is that they are correlational rather than truly experimental. Therefore, they do not, strictly speaking, provide a conclusive evidence for these adaptive explanations. Further experiments under more natural conditions manipulating parental fin digging and offspring individual experience are necessary.

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