

# Parental Brood Provisioning as a Component of Parental Care in Neotropical Cichlid Fishes (Perciformes: Cichlidae)

D. D. Zworykin and S. V. Budaev

Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninskii pr. 33, Moscow, 117071 Russia

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**Abstract**—This paper reviews a series of studies of fin digging, one of the least studied forms of parental behavior in cichlid fishes (Cichlidae). It was found that the main adaptive function of this behavioral pattern is parental brood provisioning. The fin digging intensity increased with the offspring age. The parental satiation state regulates the intensity of this behavior. For the first time, we studied the relationships between parental temperament (consistent individual differences in behavior), patterns of their parental care, and assortative mating. In addition, we observed several previously undescribed patterns of division of parental efforts in *Archocentrus nigrofasciatus* and *A. octofasciatus*. It was found that these fishes display alternative tactics of parental investment. On the basis of the original and literature data it was hypothesized that the parental brood provisioning evolved as an evolutionary extension and change of function from the adults own foraging activity to parental brood provisioning.

## INTRODUCTION

It is well known that parental brood provisioning is very efficient in increasing the offspring fitness (Alexander, 1974; McFarland, 1985; Clutton-Brock, 1991; Dawkins, 1989). It is one of the most evolutionarily advanced forms of parental care, which, in addition to protection from predators, parasites and unfavorable environmental conditions, facilitates the survival and subsequent reproductive success of the offspring. (Trivers, 1972; Maynard Smith, 1984). Unlike many other animals, this behavior is relatively uncommon in fishes, even in species with active parental care (Maynard Smith, 1984; Perrone and Zaret, 1979). Nonetheless, various forms of parental brood provisioning can be observed in several species of teleosts. For example, some neotropical cichlid fishes increase the food availability for their offspring by means of fin digging. Fin digging usually occurs when the adult fish settles its body onto the substrate and stirs up loose bottom material, such as mud and detritus, by a short bout of rapid, vigorous beating of its pectoral fins and undulating movements of the body. This apparently increases the availability of food for the offspring. The number of these movements per unit time is the intensity or frequency of digging.

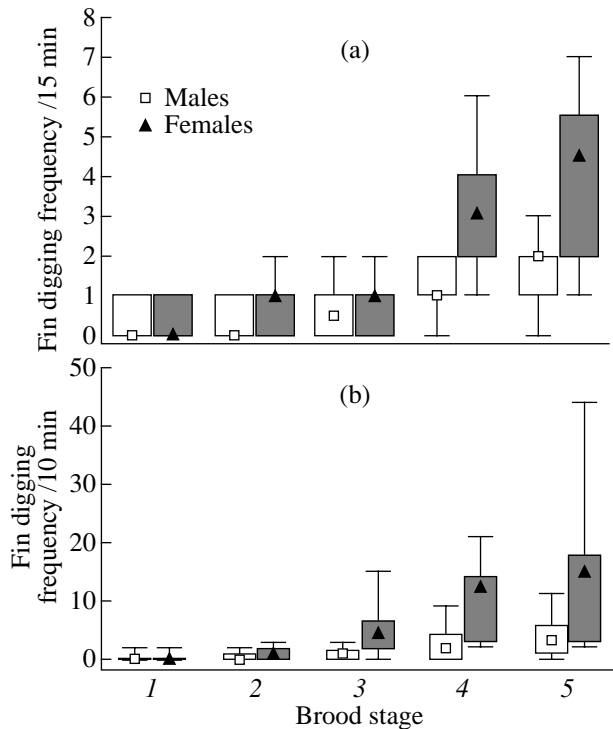
Even though such behavioral activity of fish is documented in the literature from the 1970s (Williams, 1972; Krischik and Weber, 1974; Keenleyside *et al.*, 1990), these references are rather formal. In fact, there has been only one investigation specially devoted to fin digging (Wisenden *et al.*, 1995). Moreover, even the brood provisioning hypothesis of parental fin digging is usually accepted a priori and has never been experimentally confirmed. Thus, fin digging is one of the least known components of parental behavior in fishes.

Thus, the aim of this investigation was to study the adaptive function of parental fin digging as a mechanism increasing the availability of food for the offspring, as well as some other aspects of reproductive behavior in cichlid fishes. We examined two Central American species: the convict cichlid (*Archocentrus nigrofasciatus*) and *A. octofasciatus*. Several studies have been conducted and published in a series of publications (Zworykin, 1998, in press; Zworykin *et al.*, 1998, 2000; Budaev *et al.*, 1999).

These species are the most widespread in studies of cichlid fish behavior, and thus represent model species. They are monogamous, substrate-breeding, eurybiont, fishes. The partners cooperatively care for the offspring, which is obligatory. Simultaneous with the beginning of exogenous feeding, the larvae begin swimming, and form a family group with the parents, which exists for about 5 weeks. The study consisted of several smaller tasks, each accomplished using specific methods. The frequency of fin digging was recorded at five brood stages: eggs, prolarvae, 3, 10 and 17 days of exogenous feeding. The use of just these stages is most convenient for analysis of cichlid parental care and is typically adopted in similar studies.

## THE BASIC PATTERNS OF PARENTAL BROOD PROVISIONING BY FIN DIGGING. REGULATION OF DIGGING INTENSITY

Both the literature data (Williams, 1972; Artigas Azas, 1992) and our observations suggest that adult cichlids use fin digging for feeding not only during the parental care period, but also during the non-reproductive period. This is why we hypothesized that the basic factor, affecting the digging frequency is the level of the



**Fig. 1.** The frequency of fin digging per 15 min in males and females of *A. octofasciatum* (a) and per 10 min in males and females of the convict cichlid (*A. nigrofasciatum*), (b) at five brood stages. The data before and after feeding the parents are collapsed. The figure presents median, 25 and 75% quartiles, as well as the minimum and maximum values. The brood stages are as follows: (1) eggs, (2) prolarvae, (3) 3rd day of exogenous feeding, (4) 10th day of exogenous feeding, (5) 17th day of exogenous feeding.

parents' satiation. This hypothesis seems plausible for several reasons. First, if fin digging is used by the adult fish as a form of their foraging behavior, it should by definition depend on the feeding motivation. Second, the feeding strategy of these species is at any age based on benthos and drift (Konings, 1989; Wisenden *et al.*, 1995). Therefore, digging of the bottom substrate would increase the availability of food for both the adult fish and their fry. Therefore, satiation levels of the parents and their offspring should correlate. We attempted to verify this hypothesis, and, in addition, determine how the frequency of fin digging depends on the parent sex and the offspring age (Zworykin, 1998; Budaev *et al.*, 1999).

The results of this analysis revealed a high similarity of the basic patterns of fin digging in the two species of cichlids studied. In both species this behavior was observed significantly more frequently in females than in males (Fig. 1). This agrees with the common pattern of parental role division, characteristic of most cichlid fish species (Keenleyside, 1991). The specialization of parental investment, associated with sex, can be observed in many other animals, for example in birds

(Carere and Alleva, 1998; Woodard and Murphy, 1999; Sejberg *et al.*, 2000).

The number of digs significantly increased with age in males and females of both *A. nigrofasciatum* and *A. octofasciatum*. This increase in the parental brood provisioning, caused by increased food requirements of the growing offspring, is one of the most general and obvious predictions of the parental investment theory, documented in many animal species (Clutton-Brock, 1991). For example, various bird species increase the quantity of food brought to the nest as the young grow (Haggerty, 1992; Conrad and Robertson, 1993; Westneat, 1995). The statistical interaction between such variables as the parent sex and the offspring age was significant in both species of fish studied. This, most probably, was caused by a higher increase of the digging frequency in females than in males.

It is worth noting that in females the median value of the fin digging frequency exceeded zero not just after the beginning of the offspring exogenous feeding, which is clearly expected and indeed occurs in males, but earlier, at the prolarvae stage. In part this may be explained by the fact that fin digging is displayed by the adult fish in the non-reproductive period. However, in aquariums, its use for foraging is rarely observed, even in hungry fish. Therefore, many differences between the pattern of fin digging in reproductive and non-reproductive periods (Wisenden *et al.*, 1995) requires an explanation, which should involve consideration of parental care. We believe that this pattern may be associated with the "precocious activity" of the female.

Moreover, the most significant increase of the digging intensity took place not at the offspring transition to the exogenous feeding (Fig. 1, stages 2–3), but somewhere between the 3rd and 10th days of exogenous feeding (stages 3–4). This pattern may be associated with the fact that in cichlids (Ishibashi, 1974; Balon, 1991) as well as in other teleost fishes (Iwai, 1972; Makeeva, 1992; Balon, 1999), the transitions to free swimming and exogenous feeding occur prior to the complete resorption of the yolk sac and complete formation of the gastrointestinal system. Accordingly, the offspring food requirements are likely to increase significantly from 3rd to the 10th day of exogenous feeding, as compared with the transition from prolarval to larval stages.

One of the most important results is that the parents' satiation state acts as an important factor, regulating the intensity of provisioning (Zworykin, 1998). To assess the effect of satiation on the fin digging intensity, the frequency of digging was recorded twice at each stage. The feeding procedure, the food composition and the recording methods were organized in such a way as to minimize the time interval between the recording sessions. Thus the only significant difference was the satiation level of the parents (hungry during the first recording session, and satiated during the second recording session). Neither the satiation state nor any

other parameters were changed. It was found that the digging frequency in hungry parents of both sexes was significantly higher than in satiated fish (Fig. 2). In addition, the interactions between the satiation level and the parents sex, between the ontogenetic stage of the offspring and the parents' satiation state, as well as between all these three factors were not significant. This indicates that, first, the digging intensity in hungry males and females is higher than in hungry individuals of the same sex. Second, the digging intensity increases in both hungry and satiated females as well as hungry and satiated males. At first glance, one can think that satiation induces a transient effect, only involving reduction of general activity in satiated fish. However, it was observed (Zworykin, 1995), that neither overall locomotor activity nor the intensity of various forms of parental behavior in satiated parents were reduced.

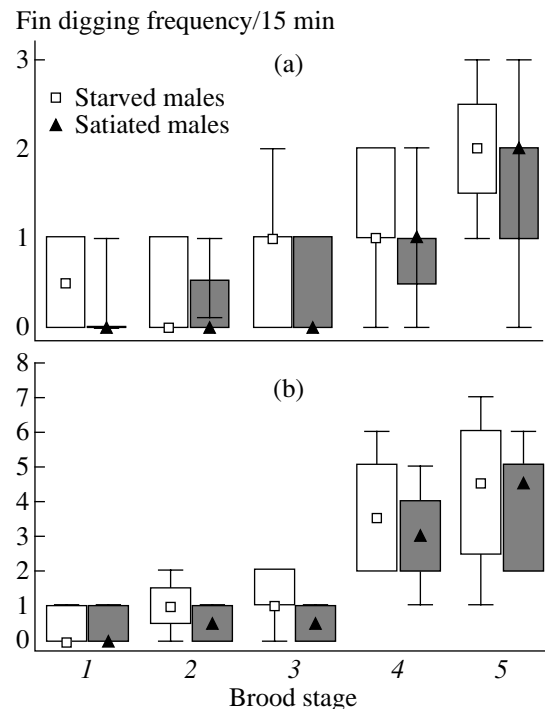
If the satiation levels of adult cichlids and their offspring really correlate, one can expect a single physiological mechanism, motivationally governed by the parents' satiation, and regulating both the digging intensity of adult fish and parents during parental brood provisioning. Natural selection could probably retain such a relatively simple mechanism, instead of the development of a new mechanism, specially devoted to the assessment of the offspring food requirements.

#### THE EFFECT OF PARENTAL BROOD PROVISIONING ON CHARACTERISTICS OF THE OFFSPRING FEEDING AND GROWTH

Both the literature and original data on parental fin digging in cichlids clearly point to a close relationship between this behavior and the strategy of parental care. For example, during parental care the intensity of digging significantly increases, whereas the associated feeding of parents decreases. During almost 30 years, parental fin digging in cichlids was a priori considered as a means of increasing the food availability for the offspring. However, this has never been corroborated experimentally. Therefore, the function of fin digging behavior in cichlids requires validation.

This is why we conducted a special study aimed at determining the function of parental fin digging in cichlids. It seems obvious that, if this behavior really increases the food availability for offspring, its higher intensity should bring about higher quantity of food in the gastrointestinal tract of the young as well as promote faster a growth rate. The frequent existence of pronounced individual differences in fish behavior inspired another aim of this study, namely, to determine whether individual differences exist in the parental fin digging, and if so, what their stability and adaptive value is.

The data obtained (Zworykin *et al.*, 2000) confirmed the existence of consistent individual differences in the frequency of parental fin digging in cichlids. The parents, which exhibited a high or low



**Fig. 2.** The effect of the parents' satiation state on the frequency of fin digging in males (a) and females (b) of *A. octofasciatum*. For further explanation of the symbols, see Fig. 1.

level of this behavior at one brood stage tended to retain a similar tendency at all other stages. In addition, there was a significant correlation in the frequency of fin digging between the male and the female within the pair. That is, both parents within the pair showed similar tendencies to either a high or low intensity of parental fin digging.

To assess the effect of the digging intensity on the characteristics of feeding and growth of the young, the food was introduced into the experimental aquariums in a minimum quantity, only necessary for normal offspring development. The young obtained additional food by means of the parental fin digging, which enabled the discovery of common aquarium inhabitants, such as Chironomidae larvae, from lower layers of the bottom substrate. Two size categories of these larvae were found in the aquariums. The differences between them were quite high, so that there was no overlap in their size distributions. They differed even more, by a factor of two, in their volume.

To assess the number of the larvae in various microhabitats of the aquariums, differing in their availability to the fry, we conducted an analysis of surface and deep layers of the bottom substrate, as well as the inside walls of the aquariums. This revealed that the small larvae predominantly occurred in the surface layers of the aquarium (77.7% of their total number in this microhabitat) and the walls of the aquarium (100%), where they were available for the young without parental

**Table 1.** Relationships between the overall frequency of fin digging and characteristics of the gastrointestinal tract and standard length (SL) of fry of the convict cichlid (20th and 45th days of exogenous feeding)

| Measure                                 | 20th days |       | 45th days |       |
|---|-----------|-------|-----------|-------|
|   | $R_S$     | $p$   | $R_S$     | $p$   |
| Standard length (SL) of the fry         | 0.90      | 0.000 | 0.33      | 0.252 |
| The number of small Chironomidae larvae | -0.08     | 0.795 | -0.59     | 0.027 |
| The number of large Chironomidae larvae | 0.92      | 0.000 | -0.06     | 0.844 |
| Total number of larvae                  | 0.93      | 0.000 | -0.53     | 0.051 |
| Proportion of large larvae              | 0.79      | 0.001 | 0.74      | 0.002 |

assistance. However, the energetically more profitable large larvae inhabited deep layers of the bottom substrate (89.7%), and were therefore almost inaccessible to the young without some help from their parents.

To investigate the contents of the offspring gastrointestinal tracts and body length at the 20th and 45th days of exogenous feeding (i.e., during the parental care period as well as after it was finished), 10 individual fry were caught, measured and dissected from each brood. In both cases, the gastrointestinal tract analysis revealed small as well as large Chironomidae larvae. A correlational analysis showed that a higher intensity of parental fin digging caused a higher proportion of large larvae specimens as well as the total quantity of the food material and its total volume, which ultimately brought about a significantly higher growth rate of the offspring (Table 1). Thus, we conclude that parental fin digging really increased the food availability for the young and, therefore, represents a form of parental brood provisioning.

An important pattern was discovered after the end of the parental care period, however, when the offspring did not obtain any additional food from the parents. At this stage, the total digging intensity had no relationship with the offspring body length. Moreover, its higher level was associated with a reduction in the total number of food organisms in the gastrointestinal tracts of the fry. The percentage of large Chironomidae larvae was still higher in the offspring of intensely digging parents. However, this was not caused by higher foraging abilities of these individuals, because the absolute number of large larvae was the same in all offspring. It is especially important that the offspring of the intensely digging parents were characterized by a significantly lower ability to hunt for small Chironomidae larvae (Table 1).

These patterns point to an extremely interesting trade-off between parental brood provisioning and the individual experiences of the offspring. On the one hand, higher level of provisioning would increase the availability of more profitable prey for the young, lead-

ing to their initially higher growth rate. On the other hand, they are likely to gain relatively little individual experience in searching and hunting for smaller and inconspicuous prey, which negatively affects their growth rate after the parental period. The young of the parents who do not dig much would have poorer food resources and should have higher feeding and exploratory activity. Such fry would be characterized by a lower initial growth rate, but much better individual experiences. Ultimately, the differences in growth between the offspring of parents employing various food provisioning styles disappeared. Thus, this confirms the coexistence of alternative tactics with similar levels of inclusive fitness (Gross, 1996).

#### PRECOCIOUS AND COMPENSATORY BEHAVIOR IN CICHLID PARENTAL CARE

The differences in parental brood provisioning are not the only example of insufficiently studied separation of parental roles, characteristic of cichlids. As it has already been noted above, the digging intensity in females of the studied species begins to grow not precisely after the larvae transition to exogenous feeding, but somewhat earlier, at the prolarvae stage. Preliminary observations of *A. octofasciatum* females had indicated that they increase activity and reduce parental care. This requires a further analysis of such oscillatory patterns of female parental strategy, as well as an analysis of the conjoint behavior of males. It also seemed very productive to compare these patterns with the seemingly precocious increase in the digging frequency in females when they care for endogenously feeding prolarvae.

The results obtained (Zworykin, 1995; Zworykin *et al.*, 1998) confirmed that the locomotor activity in females is, on the whole, higher than in males. Males were characterized by a continuous growth of this measure with the brood age. In contrast, females displayed a sharp rise of activity just after the hatching of prolarva, which did not change subsequently. Beginning from this moment, the behavior of females was characteristic of the interactions between the parents and their free swimming offspring, even though the prolarvae at this developmental stage could not yet respond to such activity. As a result of this precocious activity of females, they spent significantly less time with their offspring. In addition, there was a sharp increase of this measure in males. In other words, the male, which has previously been driven out of the eggs, now became almost exclusively responsible for the parental care, collecting the chaotically moving prolarvae, removing dead individuals and fanning the nest, thereby compensating for the insufficient care on the part of the female. This phenomenon has been designated as male compensatory behavior.

After the onset of free swimming, the larva immediately begin to interact with their parents, which has been well documented in the literature (see, for exam-

ple, Baerends and Baerends van Roon, 1950). This causes an increase in the time which the female spends with its brood. No significant changes of this behavioral measure, nor any other differences between the partners, were observed during the subsequent period of parental care. Thus, the increase of the digging intensity by females at the prolarval developmental stage occurs simultaneously with a sharp growth of their locomotor activity and alteration of the whole behavioral repertoire—reorientation to freely swimming fry. Most probably, the transition to prolarval stage, especially different interaction patterns between immobile eggs and highly mobile larvae and fry, triggers the behavior of the female.

Using cluster analysis, we also distinguished two groups of males, which significantly differed in the intensity of the compensatory behavior. Males from cluster 1 were characterized by very close adjustment to the reduction of the parental care on the part of the female, occurring as a consequence of the precocious activity. These males tended to spend almost the same time in proximity of the brood as the female did at the previous as well as subsequent brood stages. Other males, cluster 2, exhibited a significantly lower level of this compensating behavior. These males were also characterized by greatly reduced locomotor activity, associated with alternative tactics of territory defense (patrolling or immobile hanging above the nest). Thus, these two groups would reflect two alternative tactics, differing in level and style of parental investment. There were no differences in the intensity of fin digging between these two groups.

We cannot exclude that these tactics are associated with similar total reproductive effort. They could also differ in the levels of parental effort per brood (Winkler, 1987). In this case, the low-adjustment males could compensate for their possibly reduced short-term reproductive success by, for example, a reduced pair bond and a higher frequency of mating. Additionally, a reasonable possibility is that the low-adjustment tactic is a weak form of parental desertion.

#### EFFECT OF INDIVIDUAL BEHAVIORAL DIFFERENCES (TEMPERAMENT) ON THE REALIZATION OF PARENTAL CARE

This part of the study is devoted to the relationships between individual behavioral differences (temperament) in the cichlids and the styles of their parental care, in particular, brood provisioning (Budaev *et al.*, 1999). Because parental care is an extremely important component of the overall reproductive strategy, individual differences in its realization have important evolutionary implications (Clutton-Brock, 1991), and their relationship with temperament may in part explain the high diversity of alternative reproductive strategies in fish (Gross, 1996; Henson and Warner, 1997; Taborsky, 1997; Wisenden, 1999). No such investigations have ever been conducted on cichlid fishes.

For the measurement of temperament traits, all adult individuals were tested in a battery of three tests: novel environment and a strange fish, test with mirror (response to a conspecific), as well as an open field test. We recorded common behavioral measures, such as the time spent freezing, moving, novel object inspection, aggressive displays, bites and various latency measures.

The resulting data were subjected to factor analysis, which enabled us to extract three main axes of temperament. The interpretation of these axes was based on concepts commonly utilized in the existing literature on animal temperament, such as aggressiveness, fear, boldness, shyness, etc. (Nebylitsyn, 1976; Boissy, 1995). For example, the very important concept of the shyness–boldness continuum is defined as the propensity to take risks (Wilson *et al.*, 1994). Thus, these factors were designated as “Shyness–Activity,” “Inspection–Shyness,” and the second-order factor of “General Boldness.”

Our analysis revealed a high consistency of individual differences in the intensity of parental brood provisioning (fin digging) over all brood stages. There was also a significant relationship between temperament and parental style, the exact nature of which, however, turned out to depend on the parent’s sex. The intensity of parental brood provisioning significantly correlated with all three factors, when the overall sample was used, combining males and females. In addition, bold, active and exploratory males of the convict cichlid had a tendency to higher intensity of brood provisioning, and were less aggressive. In females, the intensity of provisioning did not depend on temperament (Table 2).

The positive correlation between boldness and the value of parental investment, in particular, brood provisioning, agrees with the data obtained in other species, e.g., mammals (Benus and Røndigs, 1996). On the other hand, because the alternative temperaments are not eliminated by selection, they cannot be considered less adaptive. If shy or fearful parents cannot successfully defend the territory of the family group, they could reduce or transform their behavioral strategy. For example, instead of territory defense, such fish could switch to a straying tactic, exploiting borderline regions of others territories or free areas in search of good food patches, but avoid direct aggressive encounters with the territory owners. Such “farming out” of a brood has indeed been documented in some cichlid fishes (Perone, 1978; Kuwamura, 1986).

These considerations, considering the relationships between boldness and brood provisioning within the context of the parents’ ability to defend territories agrees with the fact that the correlation between boldness and the frequency of fin digging was found only in males. In the convict cichlid, as well as in other biparental cichlid species, it is the males who are mostly responsible for the defense of the nest and the adjacent territory (Keenleyside, 1991). In addition, the balance

**Table 2.** Relationships between the intensity of parental brood provisioning and the parents' temperament in the convict cichlid

| Temperament factor   | Both sexes combined |       | Males |       | Females |       |
|----------------------|---------------------|-------|-------|-------|---------|-------|
|                      | $R_S$               | $p$   | $R_S$ | $p$   | $R_S$   | $p$   |
| "Shyness–Activity"   | –0.43               | 0.030 | –0.45 | 0.118 | –0.21   | 0.481 |
| "Inspection–Shyness" | 0.47                | 0.015 | 0.38  | 0.200 | 0.13    | 0.667 |
| "General Boldness"   | 0.58                | 0.002 | 0.56  | 0.048 | 0.18    | 0.547 |

of costs and benefits of parental care is much more easily changed in males, so that they more often reduce their investment in offspring (Wisenden, 1994).

### ASSORTATIVE MATING IN THE CONVICT CICHLID

Boldness is obviously a characteristic indicating the potential quality of the parental care, including the intensity of parental brood provisioning. Therefore, mutual mate preference with respect to this trait should be expected. We have tested this hypothesis (Budaev *et al.*, 1999). Even though there exists only very scant literature on the effect of temperament on mate choice, it is known that individual behavioral differences may determine reproductive success in intrasexual competition, as well as success in offspring defense (Barlow *et al.*, 1986). Moreover, certain studies have revealed assortative mating with respect to individual behavioral characteristics in some teleost fish (Rogers and Barlow, 1991; Godin and Dugatkin, 1996).

It is also well known that, during the mutual mate choice, convict cichlids exhibit a pronounced size selectivity of potential partners, which is associated with the quality of parental care (Wisenden, 1995). As a rule, the degree of assortativeness is assessed in already mated fish, which are already caring for the offspring, i.e., ultimate assortativeness. However, our observations indicated that, first, size assortativeness is less conspicuous during the primary pair formation, and, second, some fish initially form pairs which break up during the preparation for spawning. This poses two important questions. First, at what stage of the reproduction do the partner relationships become finally

**Table 3.** Correlations in body length and temperament factors between the male and female in spawning and non-spawning pairs of the convict cichlid

| Measure              | Spawning pairs |       | Non-spawning pairs |       |
|----------------------|----------------|-------|--------------------|-------|
|                      | $R_S$          | $p$   | $R_S$              | $p$   |
| Standard length      | 0.91           | 0.000 | 0.03               | 0.470 |
| "Shyness–Activity"   | 0.57           | 0.029 | 0.03               | 0.473 |
| "Inspection–Shyness" | 0.06           | 0.436 | –0.02              | 0.486 |
| "General Boldness"   | 0.49           | 0.055 | –0.31              | 0.193 |

established? Second, what are the relationships between the primary selectivity and the final assortativeness in pairs?

Each pair was designated as spawning or non-spawning, depending on whether it resulted in spawning during one month after its natural formation. As in the previous parts of the study, all fish were tested in temperament tests, and factor analysis revealed two primary factors and one second-order factor. The interpretation of these axes was the same as in the previous investigations ("Shyness–Activity," "Inspection–Shyness," and the second-order factor of "General Boldness").

The results revealed a significant degree of size assortativeness in the spawning fish (Table 3). Large males preferred to form pairs and spawn with large females. In addition, there were significant positive correlations in the spawning fish in several characteristics of their temperament, associated, first of all, with boldness. There is, thus, a significant degree of assortative mating with respect to the body size and temperament traits. The observed assortment of breeding fish according to their behavioral profiles cannot be considered as a simple by-product of the strong size-assortativeness, because the "Shyness–Activity" factor, on which such assortment was obvious, did not correlate with standard length of the fish. Furthermore, partial Spearman correlations, adjusted for relationships with the standard length, were also very high. The results were completely different in the "nonspawning" group of fish, which initially formed pairs, but did not spawn subsequently. In this case, there was no assortativeness in body size or behavioral traits.

Thus, it has been shown that in successfully spawning pairs, the partners have similar levels of boldness. The results described in the previous section indicate that the parents' boldness is associated with the style and quality of their parental care. Furthermore, the animals, exhibiting mating selectivity with respect to some trait, prefer the most attractive, and therefore better partners, which increases the fitness of their offspring (Burley, 1983; Møller and Thornhill, 1998). Thus, we conclude that the convict cichlid prefer to mate with bold individuals, which exhibit better parental care and a higher level of parental brood provisioning.

However, the pairs are formed on the basis of mutual selectivity of partners, and the individual,

selecting an inappropriately high quality partner may be rejected by it. This would drive less attractive partners to mate with similarly lower quality fish, having comparable body size and temperament characteristics. Even though parental effort per brood in such pairs was relatively low, it could be compensated by alternative reproductive tactics. In any case, reproductive success can be associated with evolutionarily stable combinations of mutually complimentary strategies of males and females (Maynard Smith, 1984), depending on their temperament.

Finally, it is worth noting that the fish which did not exhibit any selectivity with respect to the body size or temperament also formed pairs. Such pairs were unstable and tended to break up without spawning. Most probably, complete mutual assessment of potential partners requires a relatively long time and occurs not only during the short prespawning period, but also at a later time, immediately prior to spawning.

#### POSSIBLE FACTORS, ASSOCIATED WITH THE EVOLUTION OF PARENTAL FIN DIGGING

The reconstruction of behavioral evolution almost always occurs on the basis of indirect evidence and in most cases remains relatively speculative and hypothetical (Gittleman and Decker, 1994). The situation with parental fin digging is even more difficult because of the scarcity of the available data. Nonetheless, we believe that it could be possible to formulate a reasonable and verifiable hypothesis of the evolution of fin digging (Zworykin, 1998, in press). One of the most widespread approaches to behavioral phylogeny is based on the classical work by Lorenz (1939), and involves comparative analysis of the behavioral trait in question in similar taxa with known phylogenetic relationships. Following this strategy, it seems appropriate to consider various patterns of parental digging and other similar forms of behavior in the monophyletic family Cichlidae, as well as to compare these patterns with close families of the wrassess (Labroidae) suborder (Kaufman and Liem, 1982; Stiassny and Jensen, 1987; Stiassny, 1991).

It is known that various forms of digging behavior occur in many teleost fishes, including various wrassess. We cannot exclude that this behavior independently evolved multiple times in various groups of fishes, and in any case it seems an evolutionarily old trait. Furthermore, no one behavioral unit, used by cichlids for stirring up the loose bottom material, is completely unique. However, this trait is better represented in the cichlid family than in other related taxa. In particular, only cichlids are known to use digging for parental brood provisioning.

The form of digging, analyzed in this paper, remains relatively uncommon even in cichlid, and has been documented only in 8 out of 1400 species. These fishes

represent a compact group of related species, and include only the two most evolutionarily young tribes of the *Cichlastomatinae* subfamily (Kullander, 1998). This strongly suggests that fin digging has only a relatively short evolutionary history, possibly even shorter than the separation of distal lineages from the monophyletic group of *Cichlidae*. The data obtained in this paper, indicating that parental fin digging is one of the few facultative components in the highly specialized parental strategy of cichlid fishes, agree with this.

The fact that fin digging is used both for parental foraging and offspring provisioning poses two important questions. First, are the two functions independent, and if not, is it more appropriate to consider them separately? Second, if the foraging and parental functions are associated, what was the original function?

The hypothesis of the complete independence of parental fin digging for the adults' own foraging and parental provisioning looks extremely implausible, because these two types of activity are completely identical in their functions—disclosing small benthos organisms out of the bottom substrate. The difference is only in the intensity of this behavior (frequency per unit time), intensity of feeding of the uncovered items, and the structuring of this behavioral pattern within the overall strategy of parental care. Furthermore, the evidence, obtained in this work revealed a close relationship between both functions: the fish satiation state was the proximate regulating factor in both cases.

It seems more plausible that parental fin digging evolved by means of an extension and change of function (Schmalhausen, 1983; Lorenz, 1966). We believe that fin digging behavior has originally evolved as a means of the adults' own foraging, but become also beneficial for increasing the availability of food for the offspring. As a result, a functional transformation of this behavior could occur. Because in modern cichlids parental fin digging plays a much more important role as a form of parental brood provisioning rather than adults' foraging, the evolutionary process may be conceived as a function shift in the bifunctional behavioral system.

Foraging and feeding obviously have much longer evolutionary function than parental care. In addition, it is foraging behavior, which has shown maximum plasticity in cichlids, being one of the most important "raw stuff" of natural selection (Kornfield *et al.*, 1982; Meyer, 1990; Greenwood, 1991).

Another important argument for the above hypothesis is the fact that in many animal species, including some cichlids, feeding on the same food by both adults and the young provides the basis for the evolution of parental brood provisioning (Yanagisawa and Sato, 1990; Yanagisawa and Ochi, 1991). Such a process is possible when the parents feed during the parental care and the young could take some of their food. It is obvious that coincidence of food spectra and absence of significant ontogenetic ration shift are the major condi-

tions for this mechanism to act. Cichlid fishes characterized by substrate digging could be subjected to such a mechanism because a considerable share of the food, both in adults and the fry, is represented by benthos and drift. In addition, in spite of the differences in food composition, both adults and the young obtain most of their food from the bottom substrate.

An important evidence for the primary role of the adult feeding origin of parental fin digging is that there exist certain species which use substrate digging only for adult feeding and species using it for both adult feeding and offspring provisioning, but no known species uses fin digging only for parental brood provisioning. Furthermore, substrate digging for adult feeding caused other interesting adaptations in cichlids, for example, various forms of commensalism (Mochek, 1987; Konings, 1991).

It is also worth noting that parental fin digging is observed predominantly in Central American cichlids. In this respect, analysis of ectomorphological divergence revealed a significantly higher rate of evolutionary diversification in Central American than in African or South American cichlids (Winemiller *et al.*, 1995).

A possible problem with the hypothesis, however, is that parental fin digging appears to be a less natural and efficient means of foraging than, for example, mouth digging. It has never been documented in any family of *Labroidei*, except cichlids. Even in cichlids, this behavior plays a disproportionately more important role for brood provisioning. Of course, it can be supposed that ecological conditions have changed in the past, and the real efficiency of such a strategy fell, but there exists no real ground for such an assumption. On the other hand, there could be a change in the feeding spectra of the fish. Because the rate of evolutionary change in these species is quite high, this seems plausible. Thus, the fact that fin digging currently plays a more important role for provisioning may be associated with function specialization (Ugolev, 1987).

As an alternative hypothesis, it is reasonable to suppose that the process of evolutionary change of this behavior was just the reverse. As many other fish species, cichlids fan the nest with their fins. The transition of the young to free swimming was associated with the growth of the parents' activity. Thus, parental fin digging could arise in this context as a form of displacement activity. The increase of the offspring fitness by means of food provisioning could therefore place fin digging within the framework of the overall parental care strategy. Further, such behavior could extend to the non-reproductive period. In species with wide food spectra, fin digging would be more efficient for foraging and therefore more strongly maintained by selection.

It should be noted, however, that the only advantage of the latter alternative hypothesis is that the potential efficiency of foraging by adult fish with fin digging need not be validated. We believe that more evidence,

though only indirect, exist for the first hypothesis. However, we cannot exclude that various forms of fin digging could arise independently by different mechanisms in various groups of cichlid fishes. This is corroborated by some information about a behavior similar to fin digging in some Asian and African cichlids (Myrberg, 1965; Barlow, 1974). These species are very far from Cichlasomatinae, both taxonomically and geographically. Further studies are clearly needed to verify the above hypotheses.

## CONCLUSIONS

1. Parental fin digging really increases the food availability for the young and their growth rate, and therefore has the brood provisioning function.

2. Higher intensity of digging provides better conditions for offspring feeding, but reduces their possibility to gain individual experiences of searching and hunting for food. The alternative parental strategy provides lower intensity of the offspring provisioning, but extends their individual foraging experience.

3. The intensity of fin digging intensity is regulated by the parents' satiation state. In this case, the intensity of digging increases with the offspring age, which is adaptive for growing and developing fry.

4. Females in cichlids are characterized by higher levels of provisioning than males. This is associated with separation of the parental roles. The so called "male compensatory behavior" is an important example of the parental coordination. This behavior compensates for the lack of care on the part of the female, occurring as a consequence of their precocious activity. Males may exhibit various degrees of this compensatory behavior, associated with other aspects of their parental behavior and reflecting alternative tactics.

5. Cichlid fish show highly consistent individual differences in patterns of fin digging over all brood stages. The parental styles of males are associated with their temperament traits. The most important temperament characteristics, associated with the intensity of parental brood provisioning, are individual boldness, general activity, propensity to exploratory behavior, and low aggressiveness.

6. Cichlid fish prefer to mate with bold individuals, which are characterized by higher intensity of parental care and parental brood provisioning. Only pairs characterized by assortativeness with respect to their body size and temperament traits last to spawning. Otherwise, they are unstable and, as a rule, break up without spawning.

7. The most probable mechanism of evolution of parental fin digging is extension and change of function from adult foraging to parental brood provisioning.



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