

Cichlids of the Americas - Mouthbrooders

Examining the whys and wherefores of mouthbrooding.

By Wayne Leibel

In past installments of Goin' South, we have focused our attention on the South American eartheaters, members of the genus *Geophagus* — broadly defined. One of the more interesting aspects of their natural history is the extent to which the reproductive strategy of mouthbrooding, or tending eggs and fry in the throat (buccal) cavity, has developed in this group.

Nearly three-quarters of the species commonly placed in the geophagine group practice either delayed or immediate mouthbrooding, and it seems as if mouthbrooding has evolved — independently — several times within the geophagine lineage. Moreover, given its parallel evolution in the mouthbrooding acaras of the genus *Bujurquina* and in two species of the "true" acaras, it is clear that mouthbrooding must be a useful reproductive strategy for these fish. I would like to use this installment on South American geophagines to further explore some aspects of mouthbrooding.

Why Parental Care?

It's a hard world out there, particularly if you are a newly hatched fish wriggler. Whereas many species play the numbers game and broadcast thousands of eggs (with no thought to parental care) in the hope that some small percentage — a very small number — will actually survive to adulthood, members of the family Cichlidae invest considerable energy in rearing their youngsters. Rather than expend energy and resources in the form of huge numbers of eggs, these fish spawn relatively few offspring but offer them protection until such time that they are fully functional.

To be sure, once the parents abandon their progeny, life is indeed tough. However, because they are functionally more mature — larger, somewhat more experienced and faster swimmers — they have a better chance of survival. Most likely the numbers surviving to adulthood are not significantly greater than those of the prodigious egg scatterers. However, the demands of the particular environments most cichlids find themselves in seem to lend themselves better to a parental-care strategy. And that, of course, is the charm of cichlids as aquarium fish!

For most non-mouthbrooding cichlids, and that is most neotropical cichlids, more or less stable pairs are formed and maintained through pair-bonding behaviors. Such behaviors as jaw locking, gill flaring (frontal displays) and beating/circling (lateral displays) function to allow inspection and "testing" of potential mates. This behavior will continue, following establishment of a pair bond, as a ritualistic recognition or greeting behavior reaffirming that bond.

In substrate-spawning cichlids, the pair bond is often of an extended duration (the early books were fond of stating that cichlids mated "for life"). However, this is often a consequence of the captive aquarium situation. Many substrate-spawning cichlids are, in fact, opportunistic harem spawners in the wild.

Nevertheless, the intent of that bonding is clear: to enable the successful hatching and rearing of offspring. In substrate-spawning cichlids, the parental roles are usually well defined. The female spends most of her time fanning the eggs with her fins, ensuring a constant turnover of clean, well-oxygenated water over them. The male, for his part, is responsible for perimeter defense: it is his job to attack and chase off any marauders that might snatch the eggs. Often, the partners will "spell" each other, particularly when eating is on the agenda, but the division of labor seems more or less fixed.

Care continues beyond hatching. Upon hatching, parents may move their wriggling fry from pit to freshly dug pit daily, gently transporting them in their mouths. Or, they may hang the fry in the plants where they attach via the cement glands (temporary secretory organs) on their heads. Finally, when free swimming, after the yolk sac is resorbed and the fry are ready to feed, the parents will continue to offer care for several weeks; in the case of pike cichlids of the genus *Crenicichla*, for several months.

This care is primarily for defense and usually involves a particular brood-care coloration that functions to attract the schooling fry to their parents. For instance, in female dwarf cichlids of the genus *Apistogramma*, the edges of the ventral fins blacken, as does the mid-lateral spot and the vertical eye bar. These markings against the bright lemon-yellow body coloration make the female visible to the fry and allow her to signal them when danger approaches: a quick flicking of her paired ventral fins will send the fry scurrying for cover. They quite literally "hit the dirt," and drop motionless to the substrate below her while dad does his best to threaten the intruder.

Parental care may even extend to an initial feeding of the youngsters. Newly hatched fry of several cichlid species, such as discus (*Symphysodon aequifasciata*), uaru (*Uaru amphiacanthoides*) and the Sri Lankan orange chromide (*Eetroplus maculatus*), feed on body secretions produced by glands located just under the "skin" of the parents. The fry literally rip the mucus off their parents in a behavior known as "contact" feeding.

Obviously, these behaviors are quite entertaining to observe in the aquarium, and, if you haven't done so, I suggest that you do! If you are a novice at the fish breeding game, let me recommend the convict cichlid ("*Cichlasoma*" *nigrofasciatum*), the mother-of-pearl eartheater ("*Geophagus*" *brasiliensis*) or the golden-eye dwarf acara (*Nanacara anomala*), as good candidates for a "first" cichlid spawning.

Such meticulous care does have its limitations. For some species, fry are literally abandoned after three to four weeks. In the wild, the parents simply swim off. In the aquarium, as the female ripens again and prepares to spawn, the youngsters may be unceremoniously eaten. If this is the case, why leave the fry with mom and dad?

Aesthetically, it's great to see cichlids do what cichlids are so good at! In practical terms, fry left with their parents seem to grow much faster than fry raised away from them. The trick is recognizing when to remove them. Usually the parents will tell you — they begin to look "uncomfortable" and seem to "avoid" their fry. This translates behaviorally, to strange body contortions that seem to say "get away from me." Evidence of courtship behavior or the appearance of spawning tubes should also be taken as a warning of imminent abandonment and/or infanticide.

Demands of Parental Care in the Wild

Spawning and rearing a clutch of young in an aquarium, where the biggest threat might be a school of tetras flitting overhead, is one thing. Rearing that same batch of fry in the wild is quite another.

Imagine this scenario: You are a young pair of *Apistogramma cacatuoides* (a dwarf cichlid all of 2 inches in length) in a Peruvian cocha (lake), thinking "family." The waters are filled with terror — larger chocolate cichlids and oscars, huge *Leporinus* characoids and marauding pairs of *Boulengerella*, a pike-like tetra, not to mention ravenous pimelodid catfish. Staying alive is, itself, a challenge, let alone raising a family. What would you do?

For starters, you might try hanging out in shallower water near some cover. Indeed, on a recent collecting trip to Peru we netted dwarf cichlids near the shore of the lake in thick leaf litter near submerged wood. If danger comes, you simply dart back into the leaves. In fact, dwarf cichlids have three-dimensional territories including the vertical axis down into the litter. Where would you hang your eggs? Well, you'd hide them, probably.

On that same trip, AFI columnist Chuck Davis pulled up a rolled-up leaf that poured

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Timms, A. M. and M. H. A. Keenleyside. 1975. The reproductive behavior of *Aequidens paraguayensis* (Pisces, Cichlidae). Zeit Tierpsychologie 39:8-23. out its contents: a brooding female *Apistogramma* and fry! While cichlids will accept almost any egg-bearing receptacle in the aquarium, even the bare bottom of a tank, in the wild many of them hide their eggs. The diminutive convict cichlid "*Cichlasoma*" *nigrofasciatum*, and even the predatory giant "*C.*" *dovii*, a piscivore that reaches lengths of nearly two feet, both preferentially select holes and crevices in Lake Jiloa, Nicaragua (McKaye 1977), as spawning sites, as does the Mexican firemouth, "*C.*" *meeki* (Neil 1984). But, in the aquarium, they'll spawn on anything.

So, hiding your spawn is one approach. Or, if not hiding, then at least hanging the eggs in a cavity so as to limit the direction danger might threaten from. Several species play this game, but the ultimate is, of course, *Acarichthys heckelii*. This fish is a tunnel excavator that lays its eggs under the substrate in a chamber dug for that purpose and then uses the series of tunnels and burrows as part of fry defense. If danger threatens, signaling from the parents prompts a rapid escape into the burrow (Cichocki 1976). So, choosing your site carefully is one way to improve the defensibility of your brood.

Another way is to abandon the immobility of your spawn and, in fact, render them transportable. We have already met some cichlids that have apparently developed a preference for movable egg platforms — in particular, leaves. These include several of the "port" acaras, at least one "blue" acara, "*Aequidens*" *coeruleopunctatus*, the mouthbrooding Bujurquina, *B. vittatus*, *Krobia guianensis* and the eartheater *Satanoperca leucosticta*. And, these are just the species that have been observed in the wild to use movable platforms (Barlow 1974, Timms and Keenleyside 1975, Cichocki 1976, Keenleyside and Bietz 1981).

Many of these species live in habitats known for the rapid, erratic and extreme changeability of water level. For example, in the Rupununi River of Guyana, home of *Krobia guianensis*, where the spawning activity of many fish is triggered by the seasonal rains and concomitant flooding, the rainy season may have several false torrential starts leaving eggs spawned in the shallows literally "high and dry" (see Lowe-McConnell 1964).

The choice of a movable leaf as an egg receptacle allows the parents to move the spawn to water of appropriate depth and speed (see Barlow 1974, Keenleyside 1979). Moreover, a movable platform serves an effective anti-predation role: egg-guarding pairs can simply pull the spawn-bearing leaf back under the stream bank or to shallow water to avoid any threatening predators (see Barlow 1974).

The most compelling observational anecdote is that of Cichocki (1976), who described the brood-care behaviors of several pairs of *Satanoperca leucosticta* he serendipitously encountered in Grani Pond, Guyana. Two pairs were initially found in no more than 6 inches of water near the shore of the pond. One pair had spawned on a "sponge" shoe sole and the second on a waterlogged block of wood. After observing each of the pairs for a short period of time, the parents dragged their clutches into deeper water by tugging the platforms with their mouths, while swimming backwards.

Interestingly, in both cases the eggs had been covered with a fine layer of silica sand much as they do to eggs deposited on hard, immovable substrates in aquariums. A third pair was observed in a tidal creek tugging a mangrove leaf covered with eggs into a tangle of roots in shallower water as the tide began to rise. There are many more such anecdotal observations and I direct you to an earlier review of this information (Leibel 1985) if you are interested.

While the above adaptational argument suggests that the fish are making a "choice" of leaves versus other receptacle options, it is also true that for many cichlids, rocks or driftwood are not available and leaves are the only game in town. Nevertheless, my own experiences with *Cichlasoma portalegrense* and *Bujurquina vittatus* in aquariums suggests that when blessed with several receptacle options, these fish will invariably choose leaves.

This impression is bolstered by more careful experiments done by Keenleyside and Prince (1976) in which multiple pairs of *B. vittatus* were offered alternative egg receptacles. In all cases, any movable site was preferred over any immovable site. Moreover, in the wild, *K. guianensis* was never observed spawning in areas lacking leaf litter, although these were only unevenly distributed throughout the habitat (Keenleyside and Bietz, 1981).

Why Mouthbrooding?

It should be remembered that movable-platform spawning is not the perfect solution to the problem of egg defense. The fact that most neotropical cichlids do not practice this strategy suggests that this is only one workable solution to the problem.

For starters, the leaf or platform may be snatched by marauders, as was my experience in the aquarium. Furthermore, once the eggs hatch, the parents still must defend and rear their fry — sans leaf! If you've been paying attention, you will realize that many of these movable platform spawners are also mouthbrooders — delayed mouthbrooders, to be exact. What does mouthbrooding buy for these species?

As Keenleyside (1979) pointed out, a more effective means of moving eggs is to carry them directly in or on the parent's body. In short, adults are no longer restricted to the immediate vicinity of their mass of immobile eggs or offspring, where they are quite vulnerable to a wide range of predators who may be after more than just the caviar! By carrying their young, they no longer have to make a choice between their own survival and that of their offspring.

The trade off is simply that by carrying their eggs buccally (i.e., in their throat cavities), they are limited physically in the number of youngsters they can actually accommodate and eventually raise. This is especially true of immediate mouthbrooders, like the red hump eartheaters, in which the females alone carry the eggs.

Biparental mouthbrooders, like *Satanoperca leucosticta*, benefit from the participation of both parents in uptaking the eggs — they can simply accommodate more eggs between them. Even so, a significant number of eggs are left to die on the substrate (see Reid and Atz 1958, Cichocki 1976).

There is also some advantage in providing two targets, rather than one, to prospective predators. However, most immediate mouthbrooders, in which only the females carry the eggs, are also harem polygynists so their genes are spread among several brooding females (apparent believers in the old adage concerned with putting all your eggs in one basket).

All of these arguments are, of course, somewhat specious since all forms of reproductive strategy are to be found in the neotropical cichlidae and none is particularly better than the other out of the context of the particular ecology of a species. Most neotropical cichlids, regardless of how they raise their youngsters, are successful at what they do.

From a growing fry's point of view, one obvious benefit of the mouthbrooding strategy is the continued buccal shelter provided by the parents for several weeks following release. Many aquarists are familiar with this behavior from direct experience. The foraging fry, when startled by anything, immediately swarm to their parents — often the female — who, in a series of gulps, accommodates all several hundred terrified fry in her throat. The sight is reminiscent of a stream of army ants from some cheap science fiction movie converging hurriedly, in tight formation, on her gaping mouth.

For her part, the sheltering parent, often the female, behaves in a stereotyped and predictable manner that triggers the swarming behavior of her fry. This display usually involves rapid and alternate flicking of the pelvic fins (which usually means "Hit the dirt!" in substrate spawners) and a head-down posture some 20 to 30 degrees from the horizontal, close to the substrate, while alternately gaping and gulping. The cloud of fry, attracted by the fin flicking, swims toward the moving fins and then swarms and dives deep into the open mouth. It's almost as if they are vacuumed up!

Once the threat — real or imagined — has passed, the fry are either spat out or gently blown through the gills, and they resume foraging. If you haven't seen this for yourself, I urge you to make room in your collection for some red hump eartheaters, "Geophagus" *steindachneri*, or some Egyptian mouthbrooders, *Pseudocrenilabrus multicolor*. It's just magical!

Buccal Escape Behavior: Innate or Learned?

Clearly the parental display is involved in eliciting the swarming escape response in the fry. Some of the more obvious behaviors have been described above. In addition, parents often assume a distinctive brood-care coloration (described earlier for *Apistogramma* females). Do the swarming fry use this distinctive brood dress to recognize their parent? And, if so, to what signal in particular do the fry react?

The classical approach to questions of this sort involves the use of models. I once attempted the creation of "mom" for fry

of the delayed mouthbrooder *Gymnogeophagus balzanii* by fashioning a life-sized model from styrofoam, complete with flexible plastic fins and the appropriate brood-care markings rendered in black ink. The open mouth was simulated with a black plastic vial cap, about 1 centimeter in diameter and 0.5 centimeters deep, which was sunk into the styrofoam model at the "mouth" end. The model was controlled by attaching it to a long clear plastic rod.

When first offered the somewhat bizarre model, two-week-old fry that had exhibited normal escape swarming with their biological mother as recently as 30 minutes before, at first fled in understandable terror of this ugly white whale, but calmed down (after becoming habituated to the model) in a manner of minutes. Knocking on the tank glass caused them to scatter in all directions if the model remained stationary. On the other hand, if the model was angled head-down and bobbed up and down slowly, the threatened fry swarmed and knocked themselves senseless attempting to enter the black plastic "mouth." Amazing! Believe me, I am no Michelangelo: the model was pretty crude.

To what signal, in particular, were the fry reacting? What property of the model was eliciting their swarming behavior? The answer became clear by systematically removing "brooding signals" from the styrofoam model with a razor blade.

Unbelievable as it may seem, "mom" could be reduced simply to a "moving black spot." When the black plastic vial cap was attached to the rod and bobbed slowly, it drew them like a magnet! Was it the shape of the cap (cave-like), or the color, that released the swarming behavior? Replacing the black cap with a gray or white cap failed to elicit swarming even in the complete model, but a black, two-dimensional circle worked just fine.

Actually, upon finer analysis, it is the moving black/white edges that the fry respond to (Leibel 1983), but you get the point: the simplest of releasing stimuli is sufficient to elicit this complex escape behavior. Why the brood-care coloration? It simply provides a highly visible orientation for the fry, which are attracted by movement of any kind.

I tried the same experiments with a variety of other eartheaters. Similar swarming behavior could be elicited from young of *Satanoperca leucosticta*, *Geophagus megasema* and "*Geophagus*" *steindachneri*. However, young of the substrate-spawning eartheaters ("*Geophagus*" *brasiliensis* and *Gymnogeophagus rhabdotus* species), in which buccal shelter is not a normal part of broodcare, failed to respond.

This suggested that there was certainly a difference, either learned or innate, in their reaction or lack thereof, between mouthbrooding and substrate-spawning eartheaters. Was the escape response genetically programmed — hard wired into the brains of mouthbrooding cichlid fry — or was it learned?

The delayed mouthbrooding strategy of *Gymnogeophagus balzanii* permitted an unambiguous answer. Because these fish lay their eggs first on a substrate and then some 48 hours later pick them up (actually the hatching larvae) for further buccal incubation, it would be theoretically possible to steal newly laid eggs and to rear them in isolation and then test the fry for their response to the moving black spot (also known as "mom"). The catch, of course, was rearing the eggs. That is, duplicating the intrabuccal conditions artificially.

While the eggs of African cichlid mouthbrooders are routinely stripped and artificially incubated in bubbler-type hatchers, the fact that neotropical mouthbrooder eggs actually hatch out of their shells at the time they are uptaken means they are incredibly delicate. My approach was to use a modified sponge-filter hatcher with an egg chamber, which enabled a steady stream of clean, oxygenated water to pass over the eggs without buffeting them with bubbles. I was successful in taking nearly 70 percent of the eggs I placed in it to free-swimming stages.

The experiment was simple: I stole a clutch of eggs from a female *Gg. balzanii* soon after they were laid and carefully scraped half of the 300-plus eggs off the slate with a razor blade. I placed these into my hatcher and returned the 150-plus eggs still on the slate to the female who readily accepted them back and continued fanning them, eventually buccally incubating them to the free-swimming stage.

I reared the fry artificially in isolation from their mother, and when they were free swimming, they responded to the moving black-spot model with the same stereotypical swarming escape behavior as their sibs, even though they had no previous experience with their biological mother! Moreover, when swapped for the parental female's "naturally" reared half flock, she readily accepted them and they responded to threats as any normal flock of *Gg. balzanii* might: they formed a tight swarm and dove deep into her gulping throat!

Apparently, both recognition of the appropriate releasing stimulus (moving black spot) and the complex swarming behavior itself are innate and not learned. This is just what you would want if you, yourself, were designing the system. The escape response, by necessity, should work perfectly first time, every time.

I had the opportunity several years ago (Leibel 1984) to try a few more tricks on eartheater moms that are both interesting and informative. Because of the number of different species I was keeping at the time, many of the spawnings were synchronous or near synchronous, allowing me to try some interspecific fry swapping.

Brooding *Gg. balzani* females will readily accept red hump ("*G.*" *steindachneri*) fry of similar age, and both will behave as expected, exhibiting the usual swarming behavior when elicited by their "adoptive" mothers. The same is also true when the mother and fry species are reversed.

Brooding *Gg. balzani* females will also adopt and rear "*G.*" *brasiliensis* fry despite markedly different appearance and behavior. Recall that "*G.*" *brasiliensis* is a non-mouthbrooding substrate spawner whose youngsters do not respond to flicking pelvic fins by dropping to the bottom and becoming immobile.

When mixed shoals of fry were threatened, the *Gg. balzani* swarmed as expected, but the "*G.*" *brasiliensis* became immobilized. After accommodating her own fry, the foster mother would gently scoop up the *brasiliensis* fry in her mouth. They were never eaten and were released with the rest of the *balzani* fry after danger passed. For their part, the "*G.*" *brasiliensis* fry never "learned" to swarm.

The complementary pairing, *Gg. balzani* fry with "*G.*" *brasiliensis* foster mother was not nearly so successful. Although she initially accepted her foster brood, when threatened the fry behaved as programmed: they swarmed and beat themselves senseless on the surprised "*G.*" *brasiliensis* female's pursed lips. But not for long. The puzzled and perhaps angered (pardon my unabashed anthropomorphism) female unceremoniously ate the foster fry.

However, when this same female — now quite full, thank you — was given jewelfish fry (the African *Hemichromis guttatus*) of similar age, these were accepted readily and not harmed even though they were conspicuously very different in shape and coloration than her own fry. Jewelfish are typical non-mouthbrooding substrate spawners. These are only a few of many informal fry-swapping experiments I tried (Leibel 1984), but the message is clear: mouthbrooding is not a learned behavior.

Conclusions

I hope you will pardon my digression in this installment of Goin' South, but the subject of parental care is central to an understanding of why cichlids have been so successful in their evolutionary radiations throughout the tropics. As a reproductive strategy, parental care of various sorts has assured continuing generations of cichlids.

The eartheaters, in particular, have experimented and continue to experiment with a form of parental care that has arisen several times independently in the cichlidae, most notably in African cichlids of Lakes Malawi, Tanganyika and Victoria. The details of that behavior are interesting indeed, as I hope this digression has demonstrated.