Are fishes good parents?

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Parental care is not the rule in fishes. Most species are quite content to abandon their offspring to the vagaries of a world populated by organisms that are fond of eating nutritious little snacks such as eggs and fry. These non-parental fishes may show discrimination as to where the eggs are deposited (covered by gravel in salmon, in thick mats of weeds for some minnows, in open water downstream from the reef in some wrasses) but I would classify this as careful spawning, not parental care.

Though they may form a minority, parental species are nevertheless very diverse.[1] They belong to many different families, marine as well as freshwater. About 80% of these families are represented by species that care only for eggs. These fishes prepare or build nests, sometimes nothing more than a cleaned rock, sometimes an amalgamation of vegetal matter, empty shells, pebbles, sand, or even air bubbles. At this site the eggs are vigorously defended against potential predators. (Some yellow-spotted triggerfish, *Pseudobalistes fuscus,* have sent divers to the hospital with serious bites to the legs [2]). Parents also tirelessly fan the eggs – moving water over the brood with their fins – to provide them with a good supply of oxygen (eggs consume oxygen like most other living things, and if water was stagnant the layer next to the eggs would soon become depleted and no more oxygen would be available). In addition, the parents clean their eggs by brushing them with their fins. With their mouth they remove dead or diseased eggs. Some also transfer onto their eggs mucus that has anti-microbial properties.[3] If the nest is in the intertidal zone, parents cover the egg batch with algae just before low tide, preventing desiccation. One species of characin even jumps onto a low-lying leaf above the water, lays and fertilises eggs that stick to the leaf, and then the male periodically splashes water from below onto the eggs to keep them moist. The young drop into the water when they hatch.

Many species carry eggs with them so that if a predator makes an entry onto the scene, the parents can flee and bring the brood with them. The eggs are carried outside or inside the body. Examples of outside-carriers include medakas (eggs stuck to the female's vent for a few hours), bagrid and banjo catfishes (eggs embedded on the surface of the belly) and suckermouth armoured catfishes (eggs attached to the male's lower lip). Inside-carriers include the numerous species of mouth-brooding cichlids, sea catfishes, lumpfishes, cardinalfishes, and gouramis (eggs carried inside the mouth, and regularly churned in there for proper cleaning and oxygenation), many seahorses and pipefishes (eggs developing inside a special ventral pouch on the male), and finally, all livebearers as well as many sharks and rays, where young develop inside the reproductive system of the female, sometimes nourished by special connections to a placenta-like structure. (In pipefishes too there are placenta-like connections between parent –always the father– and embryos, and nutrients pass up from father to embryos, but it can be a two-way street: if the father is malnourished, he can actually use his “placenta” to suck his embryos dry, a case of filial cannibalism.)[4] In some sharks like the porbeagle and the salmon shark, embryos inside the female feed on additional eggs that are produced by the ovaries for their sole benefit.[5]

It is estimated that only 20% of parental fishes care not only for their eggs but also for the fry that hatch out of them. These species include most cichlids, which are well known because of their popularity in the pet trade business.

Cichlids that lay eggs on a substrate (as opposed to those that carry eggs inside their mouth) are biparental. Both the male and the female care for the eggs and young. Outside of the cichlid family, such gender equality is rarely seen in parental fishes. In cichlids it is generally assumed that both parents are needed to defend the mobile fry against predators. Cichlids breed in areas that are rich in predators, usually other cichlids of the same species. The predation pressure is so high that one guardian alone could not fully protect the brood.

Miles Keenleyside demonstrated the necessity for biparental care in cichlids by forcefully removing one member from a number of parental pairs and then measuring offspring survival in the presence and absence of potential predators. The parental species he studied was the rainbow cichlid *Herotilapia multispinosa*. The predators, introduced soon after the parents spawned, were either two adult male convict cichlids, two or four juvenile Managua cichlids, or two juvenile rainbow cichlids. Fry survival was measured as the ratio of young still present 15 days after spawning relative to the number of eggs laid – the nest had been raised out of the water and the eggs had been photographed and later counted on an enlarged print. In the absence of predators (the control treatment), fry survival was around 50% in parental pairs as well as lone parents (survival was not 100% because many young commonly die owing to developmental abnormalities and within-brood competition). In the presence of predators, fry survival decreased to 30% even when both parents were present, showing that the chosen predators were not incompetents. The clincher here is that fry fared even worse when one of the parents was removed: survival was 15% when only the mother was there, and 10% when only the father remained. Obviously, biparental care afforded a much better protection to the young rainbows than the uniparental alternatives.[6]

Helpers at the nest

At least one cichlid species takes the concept of co-operative young-raising to extremes. In *Lamprologus brichardi* (=*Neolamprologus pulcher*), a substrate-brooder of Lake Tanganyika in Africa, offspring from previous broods stay with their parents and help them raise new broods. On average, 7-8 of these helpers can be found within the boundaries of the same natal territory, sharing all parental duties such as repelling territory intruders, removing debris, and fanning the eggs, all for the benefit of their younger brothers and sisters.[7] As they grow older and bigger, helpers have the option of moving out to initiate their own breeding venture (often a dicey proposition because safe spots are few and far in between in their natural habitat). Some on the other hand prefer to stay a while longer in the hope of inheriting their parents' territory should one of these parents disappear. Beyond a certain body size however, helpers are often expelled by the breeding pair. Helpers try to resist eviction by adopting submissive postures, but most parents are not easily dissuaded by such pleas.

Michael Taborsky, working at the Max-Planck-Institut für Verhaltensphysiologie in Germany, conducted a number of interesting experiments with this system, both in the lab and in the field. In the lab, he observed that parents who had expelled large helpers welcomed them back into the fold when potential territory usurpers were introduced into the tank. This shows that parents value the defensive contribution of their largest (and most aggressive) helpers. Taborsky also observed that natal territories in dense tanks – where competition for space was intense – held larger helpers, which suggests that parents delayed eviction of their largest helpers when this suited their needs.[8]

In the field, Taborsky showed that helpers pay a price for their good deeds: they grow more slowly than care-free non-helpers. On the other hand, they enjoy a lower mortality rate thanks to the fact that they reside inside a territory with good shelter. Taborsky also confirmed that natal territory inheritance takes place. In 40% of cases where he experimentally removed one member of a breeding pair, the replacement was drawn from the pool of on-site helpers. Often the replacement was the helper most similar in size to the missing parent.[9] Taborsky and his co-workers also observed that large male helpers sometimes steal fertilizations from their bosses.[10]

Male versus female care

Not all cichlids are biparental or co-operative breeders. In most mouthbrooders (those species that carry eggs and fry within their mouth), only one parent provides care. Only one parent is needed because the brood is mobile. When danger lurks, the parent can flee and take the brood with him or her. In most mouthbrooding cichlids, it so happens that the mother is the usual caregiver (there are very few instances of biparental and male-only mouthbrooders [11]). This preponderance of female-only care in mouthbrooders is a mystery. When all bony fishes are considered as a group, female-only care is the rarest form of parental involvement.

The most common form is male-only care. This is not very well exemplified by cichlids. For better examples we must turn to sticklebacks, sunfishes, blennies, cottids, and pomacentrids, to name but a few. In such species, males aggressively stake out territories, prepare a spawning site, and court passing females. Females who accept to spawn with a male do not linger afterwards. While the males are busy releasing milt over the eggs, the females promptly take off, leaving the males to keep on defending his territory along with the eggs he has just fertilized. The males usually tend to the eggs only, although in a few cases some attention may be granted to newly-hatched fry for a day or two.

Costs and benefits of parental care

Be they male or female, alone or part of a team, most parents seem to incur tangible costs because of their dedication. Substantial weight loss during the parental phase has been documented for many species. At least one of these studies even found a correlation between the size of the brood and the extent of weight loss, large broods being more detrimental.[12] Weight loss is probably an inescapable consequence of all the predator-chasing the parents do, as well as a lack of foraging time (or, in the case of mouthbrooders, a plain and simple inability to take in food; mouthbrooders cannot eat with their mouth full!) Demanding parental duties may so deplete energy reserves in parents that they cannot breed again for quite a while.[13]

Parents can also be stressed (what a surprise!), and sometimes it doesn't take much. Take sticklebacks for example, a species where roving gangs of females can attack the nests of parental males with the intent of eating all the eggs inside. In Gerry FitzGerald's lab, Michelle de Fraipont kept individual male sticklebacks in aquaria where they could collect the necessary material to build a nest, and where they had periodical access to gravid females for spawning. However, the living space of all of these males was limited to only half of the aquarium. The other half was barred by a transparent partition pierced with small holes. On the other side of this partition there lived, depending on the experimental condition, a solitary female, a solitary male, a solitary female from another stickleback species, or no other fish. De Fraipont observed that only one of these experimental treatments made any difference for the physical condition of the parental male. When the male could see and smell a conspecific female three-spined stickleback on the other side of the partition, he lost twice as much weight over the study period (80 days), he could not pack in as many reproductive cycles into this period, and in some cases he did not live as long. De Fraipont and her co-workers called this the "femme fatale effect": the stress imposed by a known egg predator, a female conspecific in this case, was said to be detrimental to the male's state of health.[14]

So there are hardships associated with parental care, but parents do get their just reward. This reward is paid in the main currency recognised by natural selection: a sizeable number of viable offspring. Parental species often breed in difficult habitats that impose a need for special care if any reproductive success is to be achieved. We saw an example above with the necessity for biparental care against predators in cichlids. Other factors such as harsh environmental conditions may also make parental attention mandatory. One lab study with sticklebacks witnessed the progressive demise of egg clutches following the removal of their parental caretaker. Spread of disease, accumulation of debris, and lack of oxygenation were to blame for the eggs' death.[15] Even a mere reduction in fanning levels, such as when an overabundance of territorial rivals diverts a father's attention, can have a measurable negative effect: eggs take longer to hatch, which means they remain vulnerable to predators for a longer period of time.[16]

Egg care: moving the eggs

Some substrate-brooding New World cichlids from the genus *Aequidens* lay their eggs on a submerged loose leaf. When disturbed, they move the leaf away by grabbing it with their mouth and swimming backwards with it. Miles Keenleyside and Cameron Prince conducted some interesting experiments with *Aequidens paraguayensis* (=*Bujurquina vittata*). They offered spawning pairs a choice between various artificial leaves made of black polyethylene. The leaves could be small or large (19 vs. 79 cm^2), and light or heavy (0.9 vs. 8.1 g, depending on the presence or absence of a piece of lead attached to one side). Almost all pairs preferred to spawn on small and light leaves. With a hydraulic flume, Keenleyside and Cameron proved that such leaves produce less drag. These results are consistent with the idea that the parents choose leaves that can be moved easily.

Next, Keenleyside and Cameron let a number of *A. paraguayensis* pairs spawn on leaves within aquaria with an uneven gravel surface. Some areas within the tank were under 15 cm of water while others were under 30 cm. Some areas offered good cover (many plastic plants) while other sections were bare. The researchers measured how often the parents moved the leaf, and where the leaf ended up lying most of the time, in the presence and absence of a crude predator model (a minnow-shaped Rapala fishing lure, painted to look like the predatory two-spot pike cichlid). When the predator was visible, the parents moved the leaf three times as much as usual. Most of the time, the leaf was pulled to a deep area with cover. Keenleyside and Cameron thus supported the notion that leaf-brooding and leaf-moving are an adaptation to minimise predator attacks on the eggs.[17]

Egg care: a "broken wing" display

As mentioned above, nest-raiding is an annoying habit of female three-spined sticklebacks. Shoals of females roam and sometimes fall upon the nest of a parental male, eating all the eggs inside and thoroughly devastating it.[18] Males take a dim view of this and they have worked out a defensive ruse. When a parental male sees a menacing shoal of hungry-looking females coming his way, he often swims a short distance away from his nest and starts poking his snout into the ground. This is the same action a female would perform while raiding a nest. This display commonly fools the females into believing that a nest has been discovered. They rush to the site and start digging there too. Meanwhile, the male leaves this writhing mass of females and returns to his territory, hoping (consciously or not) that the cloud of sediments lifted by the "feeding" frenzy will conceal his own real nest. This striking behaviour is similar to the "broken wing" display used by ground-nesting birds to lure predators away from their nest.[19]

Another similar behaviour has been reported for the bowfin *Amia calva*. Fry follow their male parent for a while after they hatch. Apparently, when a fry predator shows up, the male sometimes moves away and thrashes about in the water as if injured, thus drawing the attraction of the predator onto himself and away from the fry.[20]

"Cuckoos" that parasitize the parental efforts of other fishes

One way to guarantee egg care without risking weight loss is simply to let other fish do the work for you.[21] Sneaky copulations (see page on the sex lives of fishes) are one way to achieve this. Another way is "egg dumping" (also called "brood parasitism"), a behaviour whereby females deposit eggs inside the nest of other parents and let *them* take care of the brood. In fishes, egg dumping usually takes place between species. For example, many species of minnows are known to spawn in the nest of various sunfishes. While fussing over his own clutch – preventing silting over the eggs, fanning, chasing predators – the parental male sunfish unwittingly provides care for the minnow eggs hidden within the nest.[22] There are even some reports of a species of minnow, the golden shiner *Notemigonus crysoleucas*, dropping eggs into the nest of two of its predators, the bowfin and the largemouth bass. While doing their dirty deed, the minnows wisely stay near the tail of the bowfins, avoiding the dangerous mouth area.[23]

This system superficially resembles the nest parasitism practised by cuckoos, cowbirds, and other bird species. There are, however, important differences. The minnows usually do not depend on the presence of host nests to breed successfully. They can spawn on their own if no sunfish nest is available (the minnows just lay their eggs in weeds and leave them to their fate without any form of care, and this seems to work well enough). Moreover, contrary to bird hosts, which have evolved numerous countertactics to foil parasitic attempts, sunfishes seldom try to stop minnows from spawning in their nests. In most cases the sunfish host does not suffer from the presence of minnow eggs within the nest.[24] Sometimes they may even benefit. Experiments where different combinations of sunfish, minnows, and/or egg predators were mixed together and allowed to spawn showed that sunfish egg survived better when minnow eggs were also in residence, probably because of a dilution effect. When predators succeeded in piercing the sunfish's defense, the odds that they picked up sunfish eggs were reduced because of the simultaneous presence of minnow eggs.[25]

There is one fish analogy to the true brood parasitism found in birds. In Lake Tanganyika, the catfish *Synodontis multipunctatus* attends the spawning ritual of various mouthbrooding cichlids and lays eggs at the same time, in the same spot. The female cichlid, as is her normal habit, picks up all the eggs present and commences incubating them inside her mouth. Unbeknownst to her, some of those eggs are catfish. These alien eggs hatch earlier than cichlid eggs. While still in the mouth of the female cichlid, the catfish fry finish absorbing their yolk sac. Meanwhile the cichlid eggs hatch, but only just in time to be devoured by the baby catfish! So, all that the poor female cichlid has to show for her parental effort at the end of her reproductive cycle is a few fat young that are not even her own species.[26] One can almost picture the female catfish laughing depravedly on the sidelines.

Above I wrote that egg-dumping usually takes place between species. There is one example of egg-dumping within the same species. In the peacock wrasse *Symphodus tinca*, some large males circumvent the costs of egg care by temporarily usurping the successful nests of smaller males of the same species, spawning in these nests with various females for a day or so, and then abandoning the site. The original owners, whose eggs are still present among those of the usurper, may not want to let their part of the nest contents be wasted and so they often come back and resume guarding the nest, protecting the foreign eggs as well as their own. This tactic on the part of the big males is called piracy.[27]

Voluntarily caring for somebody else's eggs, and even stealing eggs to take care of them!

In some species, females prefer to spawn in nests that already contain eggs. This preference does not leave males indifferent. In fathead minnows for example, big newly reproductive males sometimes evict the owner of an already established nest rather than occupy a similar but empty site. Such usurpers do not destroy the previous owner's eggs but instead care for them (permanently, not temporarily like the peacock wrasse above). Why do these males care for eggs that are not their own? The behavior in fact makes sense when we learn that female fatheads, like other species, prefer to mate with males who are already caring for eggs. This preference may very well have led to the evolution of nest take-overs and adoption of eggs.[28]

In three-spined sticklebacks, territorial males have sometimes been observed dashing over to the nest of a neighbour and *stealing* eggs from him. They surreptitiously enter the nest, take a mouthful of eggs, swim back to their domain (often with the angry parent in hot pursuit) and deposit the kidnapped eggs into their own nest.[29] This behavior can only be explained in the light of females' preference for nests that already contain eggs. The thieving males are trying to make their nest more attractive.[30]

The Magellan plunder fish *Harpagifer bispinis* is found in shallow rubble coves along the Antarctic Peninsula. The female prepares a nest site by cleaning a patch of ground. After her eggs are laid and fertilized, she remains on the nest, cleaning the eggs and chasing predators until hatching occurs 4 to 5 months later. This is the longest brooding period reported of any fish (everything takes longer in cold water!) Interestingly, if the female is experimentally removed, a second guardian, usually a male, takes her place. If that male is removed, a third fish, again usually male, moves in and cares for the brood. There is as yet no explanation for these altruistic acts of replacement. The new guardians may be genetically related to the original parent or to the young, but this is not supported by the fact that captive plunder fish will often accept to guard broods from other populations experimentally given to them. It must be said however that the new guardians are less diligent in their duties than the original parent, and their feeding and growth rates stay on a par with those of non-guardians, so it seems there is little cost to this type of substitute care.[31]

Fry care: feeding one's young

As mentioned above, parental care can sometimes extend beyond the egg stage, into the fry stage. In addition to cichlids, fry care can be seen in marine catfishes (family Ariidae), freshwater catfishes (Ictaluridae), in the bowfin (don't golden shiners know it), and in the damselfish *Acanthochromis polyacanthus*. Care consists mainly of protecting the fry against predators, though a few peculiarities have been documented in some species.

Unlike birds, fishes generally do not feed their offspring. We can hardly expect them to feed hundreds of fry directly, nor to be able to collect and carry the micro-organisms on which the fry normally feed. But there are a few particular cases. (I'm talking about feeding already hatched young here; see the introduction for the mention of species that feed their young inside their reproductive tract or brooding pouch.)

In the Kampoyo catfish *Bagrus meridionalis*, which lives in Lake Malawi, females do not lay a full complement of eggs. Some eggs are unfertilised and held back within the ovaries. When the fry are old enough (more than 15 days old), mothers gradually force out these extra eggs and the young consume them. Every day, mostly in the morning, a mother hovers 1 m above the bottom and spreads her fins slightly downwards, at which point her young raise from the nest, line up at her vent, and grab the small eggs she exudes. Kenneth McKaye has observed this behaviour and has analysed the stomach content of wild-caught young, concluding that many of these young subsist mostly on these so-called "trophic" eggs. McKaye and colleagues also reported that the father, not to be outdone, commonly ploughs into the ground near the nest to stir up debris on which the young appear to feed. The father can also scoop up a mouthful of sediments in his mouth, churn it, and release it near the nest. The young can be seen gathering around the gills of the male as he opens and closes his opercula. They get small invertebrates that way.[32]

(Trophic eggs also exist in the cardinalfish *Apogon lineatus*, but here their role is to feed the parental male who cares for big egg broods inside his mouth, and who would be sorely tempted to eat the whole brood if he was not sustained by the trophic eggs [33] – see filial cannibalism below. The male temporarily spits out his brood to eat the trophic eggs.)

Several cichlids from the genus *Cichlasoma*, when they are accompanied by fry, are known to "fin-dig"; like the male catfish above they stir up gravel by vigorously rubbing their belly and fins against it. They also turn leaves over. Several lines of evidence suggest that this is a way for the parent to turn up food for their young, at least in the case of fin-digging. First, parents fin-dig more than non-parents. Second, parents with larger broods fin-dig more. Third, fin-digging rate increases as the brood gets older and hungrier. And fourth, young gather up near the fin-digging parent and appear to feed actively on the stirred-up material.

Of course, the possibility exists that fin-digging is not a means to provide food for the young but rather a way to obtain food for the adult itself (after all, parents, especially those that have been raising large broods for a long time, are more likely to be hungry themselves). However, Brian Wisenden and Tanya Lanfranconi-Izawa, working in the field in Costa Rica as well as in Miles Keenleyside's lab in Ontario, did not find any correlation between the frequency of fin-digging and the number of feeding bites taken by parental convict cichlids, suggesting that fin-digging was not necessarily for the benefit of the parent.[34] On the other hand, Dmitry Zworykin, from the Russian Academy of Sciences, found that *Cichlasoma octofasciatum* parents fin-dug more when they were kept on low-food rations. Reconciling this result with the notion of fry care, he suggested that parents use their own level of hunger to estimate the need of their young.[35]

One final way for parents to feed their young also involves cichlids. In many cichlids such as discus, Midas cichlid, angelfish, orange chromide, and others, fry can feed off the skin mucus produced by their parents. The number of visible mucus-producing glands in the parents' skin increases during the fry stage, and the young nip at the body surface of both the mother and the father. The fry do more nibbling when they are deprived of other sources of food, which shows that mucus is indeed a dietary supplement (in discus, it is in fact more than just a supplement: mucus-feeding appears to be essential for fry survival, even in the wild).[36]

Fry care: signalling danger to one's young

In most parental fishes, fry care includes the signalling of danger to the young. In Siamese fighting fish for example, the parental male can communicate danger to his young through surface waves. In their first few days of independence from the air-bubble nest, young fighting fish stay in contact with the surface – like most anabantids, they need to breathe some air. The parental male stays nearby and if he senses danger he shakes his pectoral fins close to the surface. The surface wavelets thus generated are perceived by the young at a distance of up to 40 cm (about a foot and a half). The young then swim in the direction of the source, and this action brings them close to the male who can then suck them up into his buccal cavity and carry them back to the nest.

In cichlids, various visual displays seem to warn young in a similar fashion. A mad dashing-about by parents induces the young to settle quickly to the bottom and remain still. Brief jerks of the head or twitches of the whole body induce the fry to swarm near the parent. In mouthbrooding species, an alarmed mother can pitch slightly head-down and swim slowly backwards, upon which the fry quickly dash into her open mouth for safety.

Some cichlids, when alarmed, signal their young by flickering their pelvic fins up and down. At Illinois State University, James Cole and Jack Ward used parent models to study this signalling behaviour in orange chromides. Their models featured a pelvic fin that could be made to bob up and down by pulling on a string attached to it. They offered fry a choice between two models, one that flickered versus one that did not. By and large, the fry preferred to gather near the model that flickered. More observations by Cole and Ward, this time on intact broods with their parents, showed that parents flicker more when a small red ball is swung near their aquarium, and that fry in response form a more compact swarm.[37]

In another study on convict cichlids, Michael Shennan, Joe Waas, and Robert Lavery demonstrated that parents also flick more when they see other parents flickering. The researchers built balsa wood models of convict cichlids. They mounted these models on a cardboard background that concealed the experimenter, whose role was to manually pivot a fake pelvic fin from behind. They placed models next to the tanks of parental convict parents and either moved the pelvic fin (one flick/second for 30 seconds) or let the fin hang down. Parents reacted by themselves flickering at a high rate in the presence of the moving model; in contrast, while viewing the motionless model they flickered very little.[38]

Fry care: retrieving the young

Many cichlids retrieve their fry when danger lurks. The parents suck 2-3 young at a time into their mouth and bring them back to the old nesting site or to a safe place where they spit them out. The fry then dart or sink towards the bottom, where they stay relatively immobile. My convict cichlids do this regularly at the end of the day. This ensures that by the time darkness comes, the young are all gathered in one place over which the parents can stand guard all night long. Dimming the light at the end of the day promotes the expression of this behaviour, but mid-day dimming does not. However, complete darkness imposed at midday does trigger retrieving, the parents somehow being able to find their young and their way back to the gathering place in the dark – as I could witness using infrared lighting and infrared goggles.[39]

Here is an old anecdote reported by Konrad Lorenz, one of the founders of ethology, in his 1952 book “King Solomon’s Ring”.[40] Late one day, Lorenz came to feed a pair of jewel cichlids he was keeping in his laboratory. That pair had just finished retrieving their young for the night. The female was keeping watch over the pit full of fry, while the male was dashing back and forth, looking for stragglers. Lorenz dropped a piece of earthworm into the water. The female did not flinch from her guarding post but the male rushed to the worm, seized it and started chewing. Then he saw a stray fry swimming by itself away from the pit. Bent on retrieving it, he took it in his already full mouth... and then paused. What to do? To eat or not to eat? To retrieve or not to retrieve? Part of the mouth content had to go to the nest, the other to the stomach. After a few moments, the father found a solution: he spat out both the worm piece and the young. Both sank to the bottom (as I mentioned earlier, heading down is an innate response of cichlid fry being retrieved, and as for the meat, well, that was only gravity). Then the father ate the worm, taking his time and watching the nearby fry. When he was done, he took the fry in his mouth once again and brought it back to its waiting mother.

Nearby students watching the scene spontaneously broke out into applause.

Fry care: brood mixing

It has been observed, both in the lab and the field, that cichlid parents sometimes guard swarms of fry that are made up of several sub-groups of different body size. It seems that such parents have accepted within their brood the young from other parents (the terms “brood adoption” and “brood mixing” are sometimes used interchangeably). Indeed, it is relatively easy to experimentally integrate foreign fry into the broods of cichlids kept in aquaria. The parents accept these new fry readily, provided that the newcomers are the same size or only slightly smaller than their own young.

One of the most thorough studies of this phenomenon has been carried out by Brian Wisenden during his graduate studies in Miles Keenleyside’s lab.[41] Laudably, Wisenden worked on convict cichlids in the field (very unusual given that convicts are so easy to keep and breed in the lab). Within stretches of small streams in Northwestern Costa Rica, Wisenden captured and marked all parental convict cichlids he could find, and at regular intervals he measured the size of their broods. He observed that some broods suddenly increased in numbers while others nearby suddenly decreased, and that smaller fry seemed to have been incorporated into the new inflated broods, confirming the existence of brood-mixing and brood adoption in this population. By hand, Wisenden also transferred some fry from one brood to another. Nine times he released fry that were bigger than those from the host parents, and every time the parents *ate up* these new fry. Sixteen times he released smaller fry, and every time the parents *accepted* the newcomers. Wisenden therefore showed that adoption is not a blind process, that parents have some say in the matter, showing a tolerance only for smaller refugees.

Why should parents accept small fry but not big ones? Indeed, why should they accept any fry at all? Maybe under some circumstances they cannot tell fry apart. And then again maybe there are specific advantages to adoption. Wisenden picked up an idea that had been floating around for a long time: the host parents’ young might benefit from a dilution effect when the brood is attacked by a predator. If a brood under attack was made up entirely of a parent’s own young, then any success by the predator would guarantee a lower reproductive success for the parent. If on the other hand the brood was twice as big but only half of it belonged to the parent, then statistically the chances for the parent’s young to be selected for attack would only be

50%. Better still, if the foreign young were smaller and predators had an easier time capturing smaller and less mobile fry, then the predator could specifically target the foreign young and leave the host fry alone. Big pay-off for the foster parents!

To test this, Wisenden moved to the lab. He unleashed natural predators (three juvenile convicts or one juvenile Guapote, *Parachromis dovii*) onto broods of 20 fry, the body size of which varied within the same broods. Looking at the survivors after 15 minutes, Wisenden saw that the smallest fry had indeed fallen prey to the predators more often than the largest ones.[42]

In view of this, why would any convict parents wish to "farm out" their young, to promote adoption of their young into a neighbouring brood? Wisenden proposed that if one of the two parents disappeared, the remaining parent might have too much trouble raising a brood on its own and might prefer to entrust the fry's fate to intact pairs nearby. Sure, the small young might suffer differential predation in their new foster family, but better that than sure death because of insufficient protection by a lone parent. Back in the field, Wisenden removed male parents from 21 pairs halfway through the fry stage (males were removed instead of females because male convicts are known to sometimes prematurely desert their family, especially if single and ready-to-breed females are abundant in the vicinity). Of the 21 uniparental broods, in 8 cases the mother steered the fry close to neighbouring groups and the fry were eventually integrated within these groups. Of the 13 mothers who decided to raise the brood on their own, only 5 saw their young survive. The other 8 disappeared, presumably at the hands of predators. [43]

Longer fry care in the presence of predators

The duration of parental care at the fry stage is often dictated by the age of the young, which after a while simply become too mobile for the parent(s) to watch over. However, in mouthbrooding species, the parents have a more direct say on when to end their duties. They can simply expel the young from their mouth and refuse to take them back in. One such species has given evidence that it can extend the duration of the incubation period if it perceives that risk of predation on the fry would be high. In a laboratory experiment, females of the mouthbrooding cichlid *Ctenochromis horei* kept young in their mouth about 4 days longer (beyond a normal incubation period of 15-23 days) when they swam in the presence of another predatory cichlid (*Lamprologus callipterus*). These species are both found in Lake Tanganyika. This extra effort took a toll on the females: they could not feed during those additional 4 days, and it took them longer to breed again, as compared to females that were not exposed to the predators and that ended incubation sooner.[44]

Filial cannibalism

Parents who face the spectre of weight loss through the reproductive phase can counteract this effect with a rather uncaring behaviour: filial cannibalism (eating one's own eggs or fry). Eggs represent very nutritious little packages for a hungry fish. That is why egg predators are so common. Of course, parents must see their own eggs in a different light; for reproduction to make sense, hungry parents must resist the temptation to eat their own brood. Most of them succeed in doing this. But in many families (cyprinodonts, gasterosteids, centrarchids, hexagrammids, cottids, cichlids, pomacentrids, tripterygiids, blennids, belontiids), parents sometimes eat a small part of their brood, and we are not talking about diseased eggs here. Many of the consumed eggs appear perfectly viable.[45]

To test the idea that filial cannibalism is an adaptation to counter the debilitating physical effects of parental care, an experimenter needs only give supplemental food to hard-working parents. If parents eat their eggs to avoid starvation, then cannibalism rates should decrease under conditions of plenty. Evidence of this kind has been obtained in studies on Cortez damselfish (a field study where some parents were fed eggs from other nests), a common goby (a lab study where the supplemental food was mussel meat) and the scissortail sergeant (a field study using crabmeat and eggs from other nests).[46] Annoyingly however, even the best-fed individuals still ate a few of their own eggs in these studies. Moreover, in two other studies (one on three-spined sticklebacks fed freeze-dried shrimp and one on fantail darters fed earthworms) supplemental rations did not affect the probability nor the extent of cannibalism.[47] Here we could object that the food supplements may have lacked some essential nutrients that could only be obtained from eggs. So, overall, supplemental food experiments leave us with a rather muddy picture about the adaptiveness of filial cannibalism.

Better evidence may be gleaned from another direction: several fish observers have noted a correlation between the physical condition of the parent and its tendency to cannibalise. In painted greenlings, river bullheads, bluegill sunfish, and the cardinal fish *Apogon doederleini*, the more emaciated a parental male is, the more of the eggs under his care he consumes.[48] However, this does not explain why even males who are in very good condition still eat up a few eggs. A word of wisdom on this subject: there may be an adaptive side to the behaviour of filial cannibalism, as suggested by some of the results above, but we must also recognise the possibility, the one that was favoured by earlier fish observers even though it was non-adaptive, that cannibalising one's own eggs is a pathological breakdown in the normal egg-eating inhibition shown by good parents. (The current fashion in animal behaviour research is to favour adaptive explanation of behaviour over non-adaptive ones, but still the latter should not be overlooked.)

Parental care adjustment as a function of brood value

In the late 1980s and early 1990s, the scientific literature saw a burst of publications on the topic of brood value. This was the idea that parents should be careful in how they award parental effort toward their progeny. In particular, because the business of looking after young is so costly in terms of energy, there was a risk for a parent to devote too much care to a current brood at the expense of its potential for future reproduction. If a parent was stuck with a small brood, it might consider limiting the energy invested into the care of such a low-yield evolutionary prospect, and instead save itself for better attempts in the future. All of these ideas came under the banner of "parental investment theory". Many of the published articles supported the notion that parents could adjust their level of care as a function of the value of their brood.

We saw earlier that parents sometimes eat part of their brood as an insurance against starvation. In some cases however, it is the whole brood that is devoured. This seems a bit extreme just to fend off starvation! Ethologists now consider that *total* brood cannibalism is a manifestation of parental investment theory. The parents eliminate a poor brood (which represents a low return on their parental investment) so as to be able to start a new and improved breeding attempt as soon as possible. Confirming this view, observations in many species have revealed that only *small* broods are the victim of total cannibalism. Large (and therefore more valuable) broods are left intact or only partially cannibalised.[49]

With a more experimental touch, Robert Lavery removed eggs from the nest of various pairs of convict cichlids he was keeping in Miles Keenleyside's lab. The diminished broods were 33%, 66% or 100% (untouched control) of their former size. More pairs (6-8 out of 10) consumed what was left of their brood in the 33% and 66% treatment than in the control 100% situation (only 2 pairs out of 10). And those parents who resigned themselves to the care of reduced broods did so only half-heartedly: as compared to the controls, they performed fewer parental acts, and the ovary weight of the females turned out to be higher at the end of the experiment, indicating that they had been secretly preparing for a future reproductive attempt rather than taking good care of the current, low-yield brood.[50]

Lavery conducted another experiment on convicts. He halved or doubled some broods by transferring wrigglers or fry from one brood to another, taking advantage of the fact that parental cichlid readily accept foreign fry if those fry are of the same size as their own. He measured parental behaviour such as the percentage of time spent near the brood, the frequency of retrieving young, and the intensity of attack on a predator model (which was moved in the water through an attachment to a toy car running on a portable track resting on top of the aquaria). Lavery observed that parental behaviours were more pronounced in the brood-augmented condition than in the brood-reduced one, lending credence to the theory of parental investment.[51]

Lavery was at it again a few years later, still with convicts but this time in Patrick Colgan's lab at Queen's University in Kingston, Ontario. He measured parental response to a predator model for various broods of similar size but at different stages of development: eggs, wrigglers, and fry. He found that parents gave more and more protection to their brood as the young grew from egg to wriggler to fry. This showed that parents view younger broods as less valuable. The rationale here is that younger broods are less valuable because there is still time in the reproductive season to initiate a new attempt, and energy reserves are still high at that time. With older broods, parents may be too weak, and the season may be too advanced to start anew. The old brood may therefore represent the only chance the parents will have, for a while anyway, to propagate their genes in the next generation, and the value of this old brood is therefore raised.[52]

Here is another variation to show that parental investment theory is a rich field for study. We are back with Brian Wisenden, still with convict cichlids. In the lab, Wisenden required his convicts to lay eggs in either a secure spawning "cave" (an overturned flowerpot with only one small triangular opening at the rim) or a risky one (an overturned flower pot again, but with two large openings). The risk stemmed from an inability to defend both openings simultaneously against egg predators. Wisenden counted the number of eggs laid in each type of cave by various females, and he found that fewer eggs were entrusted to the protection of risky caves. It was as if the females knew that the nest was less secure, sensed that the eggs ran a higher risk of perishing, and did not dare invest too many eggs in this risky venture, preferring perhaps to keep some energy in reserve (eggs can be reabsorbed) for a future attempt in a hopefully more secure site the next time around.[53]

Ron Coleman is also a long-time student of parental investment theory in fishes, having conducted several tests with bluegill sunfish.[54] Switching to convict cichlids, he and Alison Galvani went back to the idea that smaller broods hold less value in the eyes of their parents, and asked: well, what kind of parents? Would size of the parents matter? Would a small brood have the same value for a small parent as it does for a larger parent? For a small female that cannot lay more than 200 eggs at the best of time, a brood reduced to 100 can still have a fair amount of residual value, as compared to a large female who can lay as many as 500 eggs. Galvani and Coleman uniformly reduced the egg batches of small and large female convict cichlids down to 100 by scraping eggs off the flowerpot on which they had been laid. This represented a relatively more extensive reduction for the larger females. Six days later, at the fry stage, the model of a tiger tilapia was moved through the tank, and the number of bites directed at it by the female was recorded. As compared to their larger counterparts, smaller females were fiercer and bit the predator model more, even though the predator probably appeared larger to them. So, brood value is a relative thing; it is in the eye of the beholder. Female convict cichlids of different sizes do not value the same brood number equally. For a small female, investing in a small brood is not such a bad thing after all.[55]

In species where cuckolder males are present in the population (see page on the sex lives of fishes), there is a chance that some of the young under a male's care might not be his. In such a case, what may matter most for parental adjustment is not brood size, but rather "effective" brood size, that is, the percentage of the brood made up of the male's own progeny. One may therefore predict that males would give less care to their brood if they can perceive that they have been cuckolded. Bluegill sunfish can provide a test of this idea. Males of this species fan and defend their eggs until they hatch (2-3 days) and protect the fry from predators until they leave the nest (5-7 days). Care is costly: the parental males do not feed and they lose about 10 % of their body weight. Unfortunately for them, other small males are cuckolders and steal fertilizations. Parents can estimate the risk of cuckoldry from simply seeing small males in the vicinity of their nest on spawning day, and they can also estimate how much of their brood at the fry stage is made up of illegitimate offspring from their different smell.[56] Research by Brian Neff has shown that parents can indeed adjust their level of care according to their perceived paternity.[57]

Working in the field, Neff selected the nests of males that were about to spawn, and he surrounded those nests with 4 bottles that each contained a small male. This simulated a risk of being cuckolded. Control nests were surrounded by empty bottles. The bottles were removed at the end of the spawning day, and the next day the nest owners' parental fervour was tested by pushing towards them a bottle containing an egg and fry predator (a pumpkinseed sunfish). Neff observed that the males which had been exposed to potential cuckolders directed fewer displays and delivered fewer bites to the predator as compared to the controls, in line with what the theory predicted. He repeated the predator presentation at the fry stage, and now the treatment males defended their brood just as much as the controls, presumably because the parents could now see (well, smell) that they had not in fact been cuckolded and that the whole brood was theirs.

In another part of the bluegill colonies, Neff swapped eggs (about a third of each brood) between nests. He predicted that the level of parental care would remain the same at the egg stage (since bluegill cannot distinguish between own and foreign eggs) but that the artificially cuckolded males would be less parental at the fry stage, now that they could recognize the foreign young from their different odour. This is indeed what he observed, once again based on the response of males to a predator presentation.

Something similar happens in *Telmatherina sarasinorum*, a small fish found in Lake Matano in Indonesia. Increased risk of cuckoldry leads to increased rates of brood cannibalism by the father. It must be said, however, that this species is not parental. The eggs, when eaten, meet that fate soon after mating takes place. [58]

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