Aggression in fishes

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2008

Competition is a fact of life. It can take many forms, but biologists usually recognize two broad categories. In the first one, called exploitative or scramble competition, the contests are like races. The most food goes to the animal that eats the fastest, the best shelter is occupied by whoever reaches it first, and the largest share of eggs are fertilized by those males which produce the most sperm. There is usually little aggression displayed in such cases. However, in the second category, which is called interference or defense competition, animals fight among themselves for the right to monopolize food, to occupy alone a shelter or a territory, or to secure exclusive access to a mate. Following are some concepts and examples dealing with interference competition in fishes.

Dominance hierarchies

Aggression allows some social fishes to sort out their relative ranks within a dominance hierarchy. Thus, when a few individuals from a social yet slightly aggressive species are placed together for the first time into a tank, a lot of nipping and chasing commonly occurs. After a while however, this aggression subsides. A pecking order has developed, every individual having figured out its place in the hierarchy. Researchers can determine the ranking of each fish by carefully observing the outcome of the initial skirmishes. The more bites an individual delivers, the more chases it initiates, and the more adversaries it wins against, then the more dominant it is. Often a linear hierarchy emerges, going from the so-called “alpha” fish at the top, to “beta” and “gamma” just below, and so on down the Greek alphabet until we reach poor “omega” at the bottom of the heap. Such a phenomenon can be observed in many salmonids, poeciliids, and centrarchids. Alternatively, the hierarchy can be despotic rather than linear. In such a case a single individual, the despot, is dominant over the other fish, who are all equally miserable. Captive eels and catfishes sometimes show this pattern.

Development of a stable and peaceful dominance hierarchy benefits everyone because fighting is energetically costly, potentially injurious, and therefore not to be done on a regular basis. However, it goes without saying that the low-ranking subordinates are not necessarily living the happiest existence. Typically their access to food is limited, as suggested by the fact that their growth rate is slower than that of dominants. For the experimenter, the challenge here resides in showing that poor growth is indeed caused directly by interference from bossy dominants, rather than poor growth and subordinate status both being caused by a third factor, such as inefficient physiology.

One way to obtain such a proof is to directly observe dominants chasing subordinates away from the best food sources, as has been done with cichlids, salmon, medaka, and brown bullhead.[1]

One can also compare the growth rate of fish raised alone and raised in groups. The usual result here is that fish raised alone show a very consistent growth rate (little variation from one lone individual to another, indicating that their physiology is uniformly fine) whereas groups yield some fish that grow well and others that do not. The slow growers usually turn out to be those that were subordinate during behavioural interactions. Moreover – and this is the clinching experimental demonstration – the growth rate of these subordinates speeds up after dominants and other competitors are either removed from the tank or isolated behind a partition. Such a sudden improvement in growth rate would not happen if weak physiology was the original cause of slow growth.[2]

Another sore point in the life of subordinate fish is that they seem to be more stressed. Stress probably develops because of the fear of being chased and chastised by bullies, and from having to worry more about where the next meal is going to come from. Stress reactions are often characterised by a rise in the production of certain hormones and metabolic products, and indeed the blood of subordinate fish often contains higher amounts of these substances.[3]

The impact of stress on the life of a fish can be substantial. In some cases, it could account for at least part of the slow growth rate of subordinates. In an experiment conducted with Larry Dill at Simon Fraser University in Vancouver, Jeremy Abbott kept pairs of rainbow trout in tanks, each pair being made up of one dominant and one subordinate individual. These fish were of very similar size but this similarity did not prevent the dominant trout from nipping and charging at the subordinate. Now, at dinner time each day, Abbott separated the fish and fed them the same number of individual brine shrimp, fruit fly, or onion fly, which were all eaten by each fish. Despite the fact that food intake was the same for both dominant and subordinate, the subordinate ended up becoming smaller than the dominant in 10 out of 12 pairs. Abbott and Dill proposed that stress, along with the necessary investment in energy to repair fin damage, was the best way to explain why subordinates grew less than dominants despite their equal food intake.[4]

Subordinates may also be forcefully relegated to less suitable habitat. In stream species such as the mottled sculpin *Cottus bairdii* and the longnose dace *Rhinichthys cataractae*, adults often can be found in deep pools while juveniles loiter in the shallows. It is tempting to conclude that the adults expel the less competitive juveniles from their preferred habitat and force them to eke out a dangerous living in the shallows, at risk from bird predation. However, we must first disprove the alternative hypothesis that juveniles stay in the shallows of their own volition, perhaps because their food requirement is different from the adults' and can best be met by foraging around weeds. Experimenters can tackle this problem by building enclosures encompassing both types of habitat within a stream, by placing adults in some of these enclosures but not in others, and finally by releasing juveniles in all enclosures. If juveniles like the shallows, they should live there irrespective of the adults' presence or absence in the pools. The results, however, are that in the absence of adults the juveniles set up shop in the deep pools. With the adults present, the juveniles end up in the shallows. So there does seem to be competitive exclusion by the more dominant adults.[5]

And now for the ultimate evolutionary slight: the sex life of subordinates also suffers. In groups of guppies and swordtails for example, some alpha males have been reported to monopolise the area of the aquarium where females hang out, and to account for more than 80% of all copulations with them.[6] This must leave the subordinate males fairly frustrated. Fortunately, at least in the case of guppies, subordinates can achieve some mating success by other means. They can become suave rather than strong. If they happen to have brighter body colours than dominants, or if they display more, they can garner their fair share of the mating market in spite of the dominants' attempts to suppress their sexual activity.[7]

If subordinates remain within groups despite all of the inconveniences they must put up with, then probably the general advantages of social living – mutual defence against predators, discovery of food in greater amount than can be monopolised by a single alpha fish – outweigh the disadvantages of a limited existence next to bossy dominants. In fact, the necessity for harmonious group living may set a ceiling to the levels of aggression expressed by some fishes. A study by Anne Magurran and Benoni Seghers supports this idea. In the streams of Trinidad, some guppy populations are exposed to predators and therefore show strong shoaling behaviour, while others see few predators and shoal only loosely. When Magurran and Seghers brought these fish into the lab and placed them next to a small food patch, the strong shoalers showed little aggression among themselves while eating, whereas the loose shoalers fought with one another for better position over the food patch.[8] Cohesive shoaling and high aggression don't seem to go hand in hand very well.

How stable are dominance relationships? The answer is: it depends on the species. Rainbow trout, for example, seem to remember their place in a hierarchy for a long time. Consider the following experiment by Jeremy Abbott and his co-workers. Rainbow trouts were paired up and left to establish a dominance relationship between themselves. If one fish was 5 % larger than the other, it always won. Then, the researchers separated the two fish of each pair and fed the subordinate in excess, so much so that it eventually became at least 15% bigger than the dominant. The two fish were reunited, and surprisingly the subordinate still cowered in front of the dominant in spite of its newly acquired size advantage. Abbott and his colleagues concluded that the risk of injury during fighting is so pronounced that trout prefer to use memory rather than renewed combat to settle contests between themselves.[9]

On the other hand, catfish may constantly monitor the well-being of their competitors, looking for sudden weaknesses and chances to climb up the social ladder. In one experiment, John Todd, his graduate advisor John Bardach, and neurologist Jelle Atema, all at the University of Michigan in Ann Arbor, forced two yellow bullheads *Ameiurus natalis* to share a 190-liter aquarium. One of the two fish was clearly dominant over the other, forcing it to flee at every encounter. When this dominant was removed, kept in a separate aquarium overnight, and then returned, the submissive recognized it right away and fled from it again. However, if during its overnight leave of absence the dominant bullhead was exposed to, and beaten by, an even more dominant catfish, then upon its return to the home tank the submissive individual *attacked* it. The defeat during the overnight contest altered something in the former dominant (its smell, perhaps, or its bravado – see loser effect below) and this change was immediately perceived by the former submissive, who seemed to take advantage of this weakness to stage a coup.[10]

In the cichlid *Astatotilapia (Haplochromis) burtoni*, only dominant males get to occupy breeding territories. They are surrounded by younger subordinate males who often try to take over the dominants' territories. At night, all males are pale, but at first light in the morning, dominant males brighten their blue and yellow colours, and a black stripe appears near their eyes. The subordinates stay pale. However, if a dominant disappears overnight (dip-netted by an experimenter, as it happens), then within 1 h past first light a subordinate will develop the livery of a dominant male and start courting nearby females. This shows that social hierarchies are very dynamic in this species and that social opportunities can be quickly seized upon. [11]

Territoriality

A territory can be defined as "any defended area". In fishes, territories are usually held by single individuals or by breeding pairs. The defended resource may be food, shelter, a sexual partner, spawning sites, or offspring. The defenders aimed their aggression mostly at conspecifics, although other species with similar ecological requirements (or a taste for eggs and young fish) can also be targeted.

Some territorial fishes are good at discriminating between full and partial competitors. They seem to realize the degree of overlap between their own requirements and those of other species. For example, in fishes that defend food territories on coral reefs, the more an intruding species shares the diet of the territory owner, the more often it will be attacked. Moreover, it will be challenged from a greater distance. In one typical experiment, individual fish from various species were placed in bottles. These bottles were pushed incrementally towards the shelter hole of a threespot damselfish, near the centre of its territory. The diver who pushed the bottle always retreated some distance and observed whether the bottle was attacked by the resident damsel. The results: bottled fish that were known to have a strong diet overlap with the damselfish were attacked at a distance of about 1 m from the shelter hole, whereas bottled fish that did not share the damsel's diet were either overlooked or only attacked when the bottle came within less than 0.5 m from the shelter hole. Species with intermediate levels of diet overlap were attacked at intermediate distances.[12]

Good discrimination can also be found in black-belt cichlids, *Cichlasoma maculicauda,* defending their breeding territory. When there are eggs in the territory, the parents will attack egg predators and non-egg predators, but they will tolerate closer approaches by the non-egg predators before launching an attack. Moreover, egg predators that hover and seem to ogle the nest are attacked more assiduously (from a greater distance) than egg predators that just pass by. Finally, when they have fry, parents chase predators only when these predators reach the distance from which they normally lunge at the fry. This distance varies from species to species and the parents seem to know this, for they adjust their attack distance accordingly.[13]

Territoriality is a viable strategy when two conditions are met: (1) the defended resource is sufficiently localised so that it is physically possible to defend it, and (2) there is some competition for this resource, but not too much. Let's illustrate both principles by using food as an example of defended resource.

First, the question of localised resource. Suppose a fish needs a certain daily amount of food to survive. If this amount can be found in a relatively small area, then this food clump is relatively easy to defend and territoriality becomes a suitable strategy. If the food is more spread out, territoriality can still take place but the territory will have to expand – and therefore become harder to defend. At the extreme, if food is very thinly distributed, the required territory size would have to be so large that it would be physically impossible to guard all of its boundaries. In such cases, territorial behaviour is absent.

These ideas lead to testable hypotheses. One is that territory size should increase as food becomes less abundant, but only up to a certain extent. Territory size can be estimated by linking, on a map, all of the outermost places where intruders are attacked by a given defender. It is then possible to measure the size of the area thus delimited. Food abundance, for its part, can be sampled by researchers within the territory itself (much to the dismay of the territorial fish who usually cannot defend against big human intruders – although some puny but pugnacious damselfishes have been known to try). In this way, salmon and trout have been shown to indeed occupy larger territories when food is less abundant.[14]

With a more experimental touch, Mark Hixon, of the University of California at Santa Barbara, found territorial male black surfperch *Embiotoca jacksoni*, a coral-dwelling species, and decreased the amount of food accessible to them. He did this by covering portions of the coral reef with swatches of nylon netting through which the fish could not pass. Unfazed, the surfperch reacted by increasing the size of their territories and appropriating neighbouring patches of untouched coral. However, when the reduction in food supply was very great, as occurred when overgrazing sea urchins invaded the area, the surfperch abandoned their territories rather than try to expand their boundaries.[15]

The disappearance of territorial behaviour when food becomes too thinly distributed has also been documented in controlled lab experiments. In most cases, automatic feeders were set up over a very large aquarium containing many fish. The feeders were programmed so that only one of them dispensed all the food, or each one of them gave a little bit of food. The prediction was that fish would become territorial in the first instance but not in the second, and this is indeed what happened. When only one feeder was activated, the dominant fish in a group soon started to defend the area around that feeder. When all the feeders were activated, it became impossible to defend all of them. The group therefore spread out and swam all over the tank. Very few individuals, if any at all, bothered to defend a given area. This was observed in studies with medaka, pygmy sunfish, salmon, and juvenile cichlids.[16]

In the wild, feeding territories are seldom observed in freshwater habitats, but they are fairly ubiquitous over coral reefs. One possible explanation for this state of affairs is that coral reefs offer a richer supply of food – their rate of production has been estimated to be 10 times as high as that of an average lake or stream. Therefore, over coral reefs, food can be concentrated in one area sufficiently small to be successfully defended. Conversely, the relative lack of territoriality in freshwater habitats could be linked to the greater dispersion of food sources. This is not to say that freshwater species are incapable of establishing territories when conditions are right, in other words when resources suddenly become clumped. The species mentioned in the preceding paragraph, where dominant individuals defended territories around single feeders in the lab, were all freshwater species.

Now, on to the question of competition level. If food is superabundant everywhere, so much so that everyone gets to eat to their heart's content and no competition exists, then obviously there is no point in establishing a territory. At the other extreme, if the number of competitors and intruders is so high that a single fish cannot defend even the smallest of territories against everyone, then obviously there is no point in territoriality. It is at intermediate levels of competition that territoriality becomes a viable prospect.

These ideas can also be tested in the lab. One can set up a great number of feeders over a tank, and switch from a situation where only a few feeders are giving food (territories will probably be defended around them) to an all-you-can-eat buffet where all the feeders are offering a lot of food. In such a tank of plenty, harmony should reign supreme and aggression should subside. In medaka, this is what happens. Interestingly, if some of the medaka get paranoiac and persist in their belligerent ways even though food is superabundant, they turn out to grow more slowly, probably because of all the energy they needlessly spend in chases and threats directed at others.[17]

Intruder pressure, for its part, can be experimentally intensified simply by adding fish to a tank. A number of species have thus been shown to have a harder time maintaining a territory when competitor density is very high.[18] One of the first reactions of territory owners when intruders become too numerous is to decrease the size of their territory to make it easier to defend against this onslaught of trespassers. Later, if competitors (or alternately, territory neighbours) are experimentally removed, the remaining residents expand their domain back to what they see as an ideal size.[19]

Note that topography can also influence territory size. In habitats that are structurally complex, with lots of rocks or plants (some of which may have been added by curious experimenters), territorial defense is more difficult because boundaries cannot be visually monitored all at once. This results in smaller territories, and in more fish cohabitating next to one another.[20] Topography may also provide natural landmarks that act as bastions for territorial defence, and if such landmarks are abundant, the tendency to use them as borders may lead to smaller territories.[21]

What makes a good fighter?

If a fight erupts between two fish, can we predict which one will be the winner? The answer is yes if there is a big size difference between the contestants. As one might expect, big fish have the upper hand. One example of this comes from Indiana University, where William Rowland kept a large number of three-spined sticklebacks in stock tanks. These fish were somewhat crowded in a bare environment and could not establish territories. Rowland dipnetted various males from the stock tanks and weighed them. To put these males in a fighting mood, he placed them into individual aquaria and let them establish breeding territories. Then he picked two of these territorial males at random and moved them together to yet another aquarium, one that was unfamiliar to both of them, although it still looked like their own. The two males soon faced each other and initiated a fight. After much spine-erecting, head-to-tail chasing, and biting, the loser declared itself by breaking off the fight and cowering in a corner. Rowland staged 31 such encounters in which a clear winner emerged, and he found that the heaviest male was victorious in 22, or 71%, of them. Statistical methods revealed that the greater the weight difference was between contestants, the greater the chances that the heavier fish would end up winning. A weight difference of 15% practically guaranteed victory for the heavies.[22]

In the experiment above, it was important to stage the contest in a neutral arena unfamiliar to both fish. If the contest had taken place in the home tank of one of the two sticklebacks, the territory owner would have held a much greater probability of winning than might be inferred simply from its body size. Being in one’s own territory seems to confer more confidence, or perhaps a greater realisation of what is at stake for the owner. Sports fans call this the home turf advantage. Ethologists prefer to speak of a “prior residency effect”. Within certain limits, the prior residency effect is enough to prevent large intruders from usurping the territory of smaller residents.[23]

The duration of prior residency may also have an influence: in brown trout *Salmo trutta*, longer-term residents (4 days) outperform shorter-term residents (2 days) in the defense of their territory.[24]

Another factor that may influence the outcome of a fight between two closely-matched fish is a prior experience of submissiveness. A fish that has just lost a contest is more likely to give up during the next fight as well, even when this second fight is against a new adversary. It is as if the first setback created a general losing state of mind. In sticklebacks, this lingering "loser effect" can last up to 6 h.

As an example, we can look at the work of Theo Bakker and his colleagues at the University of Leiden in the Netherlands. These researchers kept a great number of territorial male sticklebacks in individual tanks. They chose a few individuals at random and subjected them to a losing experience by dropping them into the tank of another male: this other male beat them up, taking advantage of the prior residency effect since he was in his home territory. Other males were also chosen at random and they experienced a win by having another male dropped into their own tank (for them, the prior residency effect worked in their favour). Three or six hours later, these respective losers and winners each met an inexperienced male within the confines of a neutral arena unfamiliar to all of them. If it was not for their previous experience, we would expect the previous losers as well as the previous winners to dominate this new encounter on only half of all tests since all of these fish were chosen at random. Previous winners indeed won only half of the time, indicating that their previous winning experience did not make them stronger. But a different picture emerged in the case of the previous losers: none of them won a single fight when this fight was held 3 h past their first debacle. Even after 6 h, the previous losers won on only 20% of all tests.[25]

Similar results have been obtained with blue gourami, paradise fish, green swordtail, and pumpkinseed sunfish.[26] In the case of the blue gourami and the pumpkinseed sunfish, it seems that a previous *winning* experience can instill confidence and help a combatant win its next encounter. This winner effect does not last very long in the sunfish – no more than 1 h – but it does persist for at least 3 days in the gourami.[27] There is also the Mangrove rivulus *Rivulus marmoratus*, where both a winner and a loser effect exist for about 2 days.[28] Maybe prior experience fine-tunes the information a fish has about its own fighting ability. Or maybe the fight alters hormone production differently in winners and losers, with an impact on their willingness to fight again. (This hormonal hypothesis has been invoked to explain another short-term winner-loser effect: in the Mozambique tilapia *Oreochromis mossambicus*, 15 minutes after a fight, winners court females more readily, for a longer time, and with more courtship sounds than losers, even when each male is alone with the female.[29])

Fighters are more successful when they can first impress their opponents with signs of their good health and good growth. Sometimes, these signs are the same ones that are used to woo females. In swordtails for example, males possess an elongated lower tail section that resembles a sword. Females prefer to mate with males who have longer tails; interestingly, males with longer tails also win more fights, even when matched with opponents of similar body size. It is possible to attach plastic extensions to the tail of a given male, and all of a sudden this male starts to win more fights than he used to do, probably because his big sword incites his adversaries to back down.[30] In the same vein, male sticklebacks with brighter red throats attract more females, and also win more fights against other males. Intimidation is probably involved rather than actual fighting ability, because when fights are staged under blue light (which makes the throat appear black instead of red), males with brighter red throats do not win more fights any more.[31]

Intimidation is behind all of the ritualized displays that are performed by both contestants at the beginning of a fight. In fishes, such displays include booming sounds, water-displacing tail beats, fin erection, gill cover spreads, head shakes, body twists, lateral displays that reveal the full size of the body, colour changes, exposure of brightly coloured body parts, and intricate swimming manoeuvres. These actions are meant to signal fighting ability and to encourage opponents to give up.

Other determinants of dominance during fights include stamina and motivation. Escalated fights may last for a long time (a half-hour is not uncommon in some species) and stamina would prove an asset in such a situation. Consider the work of Francis Neat and co-workers on the redbelly tilapia *Tilapia zillii*. These researchers found that losers of territorial fights harboured more lactate within their muscle than winners did immediately following the fight. Lactate is a metabolic by-product that can cause fatigue. So the vanquished fish may have lost because they were the first ones to get tired out.[32]

Motivation, or “fighting spirit”, could also characterise good combatants. In another study on redbelly tilapia by Neat, small males sometimes won over larger ones. These smaller winners were more aggressive during the fights and inflicted more bites. They also had larger gonads, indicating that they were more ready to spawn, and therefore perhaps more inclined to defend their breeding territory.[33] Being closer to spawning may also explain why breeding pairs of convict cichlids that have been together for a longer rime (96 h versus 48 h) fight more successfully for breeding sites.[34]

In some species, motivation to fight may also be influenced by a “priming” effect. If a male fighting fish who has just witnessed a combat between two other males is allowed to interact with a male who has just seen two other fish not fighting, the former usually behaves more aggressively than the latter. It’s as if viewing a fight put the male in a fighting mood. In the same vein, three-spot gouramis who have learned to associate the appearance of a red light with the imminent arrival of an opponent win more fights when they are forewarned by the red light.[35]

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