No effect of anthropogenic food provisioning and population density on the aggressive behavior of a territorial Cichlid: a case study

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Resumo

Efeito nulo do provisionamento antropogênico de alimento e da densidade populacional no comportamento agressivo de um ciclídeo territorial: um estudo de caso. A oferta de alimentos para peixes é uma atividade de lazer muito comum, especialmente em atrações turísticas, causando impactos que ainda são pouco compreendidos. Existem muitas espécies de peixes territoriais para as quais a disponibilidade de energia pode limitar a agressividade e o crescimento populacional. Nosso estudo de caso avaliou se o provisionamento de alimentos e o adensamento populacional resultante modificam o comportamento agressivo em um ciclídeo territorial, a tilápia do Congo (*Tilapia rendalli*). Comparamos a agressividade entre uma população que recebe grandes quantidades de alimento e tem alta densidade e uma não alimentada e de baixa densidade. A agressividade foi igual entre grupos provisionados e não provisionados, exceto quando oferecemos alimentos, o que estimulava a agressão na área não provisionada. A oferta de alimento por humanos e a densidade reduziram a área dos ninhos, mas não aumentaram a agressividade, sugerindo uma possível habituação à presença de conspecíficos e uma redução da agressividade competitiva.

Palavras-chave: Agonismo; Competição; Comportamento animal; *Tilapia rendalli*; Turismo

Abstract

Food provisioning for fish is a very common leisure activity, especially in tourist attractions, causing impacts that are still poorly understood. There are many species of territorial fish to whom energy availability can limit aggressiveness and population growth. Our case study evaluated whether food provisioning and the resulting population density modify aggressive behavior in a territorial cichlid, the Congo tilapia (*Tilapia rendalli*). We compared the aggressiveness between a population that receives large amounts of food and has high density and an unfed and low-density population. Aggressiveness was the same between provisioned and non-provisioned treatments, except when we offered food, which stimulated aggression in the unprovisioned area. Food provisioning by humans and density reduced nest area, but did not increase aggressiveness, suggesting a possible habituation to the presence of conspecifics and a reduction in competitive aggression.

Key words: Agonism; Animal behavior; Competition; *Tilapia rendalli*; Tourism

Introduction

Feeding fish as a tourism and leisure attraction affects the natural behavior of many species (BESSA; GONÇALVES-DE-FREITAS, 2014). Although there are some situations, for example environments with food shortages or with a lot of competition, in which habitat change reduces food availability and conservation could benefit from food provisioning (EWEN et al., 2015), this is becoming an urgent issue with the growing presence of humans in preserved locations, and the impacts this human-wildlife interaction brings (BLUMSTEIN et al., 2017), including to the aquatic environment. One way sought by people to interact with fish is provisioning them with food, which is often excessive and inadequate (BESSA et al., 2017). The bad quality and large quantity of the food offered by visitors often cause health problems to these fish (LAROCHE et al., 2007). Food provisioning negatively affects fish by reducing health (BROOKHOUSE et al., 2013), altering habitat use (FITZPATRICK et al., 2011; ALBUQUERQUE et al., 2014) and changing population structure (MILAZZO et al., 2005; ILARRI et al., 2008; FEITOSA et al., 2012). It is also possible that food provisioning accelerates fish habituation to humans (GEFFROY et al., 2015), reducing escape reactions and increasing predation risk (MILAZZO et al., 2006). Many populations, including fish, tend to grow in response to food availability (STENBERGER; GILBERT, 1985; PETRIK et al., 2019), and this bottom-up population control has been shown to be more effective than top-down control by predators in fish (KOKKONEN et al., 2018). Therefore, food offered by humans has a large array of effects on fish, reaching aspects of fish biology still understudied.

Territoriality is the defense of a limited area, within which there is some valuable resource with concentrated distribution, against intra- or interspecific competitors (MAHER; LOTT, 2000). Aggressiveness, either indirect (sequential behavior that uses visual, acoustic and chemical cues to threat without direct contact) or direct (physical aggressiveness, which causes damage to the body), is often applied to territorial defense (ROS et al., 2006). Aggressiveness is a time-consuming and costly activity in terms of energy expenses (GILL; WOLF, 1975), predation risk (MAGNHAGEN, 1995; CANDOLIN; VOIGT, 2001) and increase in parasite load (CAVALHEIRO; BESSA, 2016). Therefore, territory size and territorial aggression should be limited by food and energy availability, especially if the territory does not provide, or even limits, access to food.

Cichlids are freshwater fishes (FELDBERG et al., 2003) who defend reproductive territories with strong aggression (KULLANDER, 1998). They are mostly diurnal with intense and complex parental care (KEENLEYSIDE, 1991). Such characteristics make the Cichlids good models to study the effects of feeding on aggressiveness. The Congo tilapia (*Tilapia rendalli*) is a generalist and invasive Cichlid, which adapts easily to different environments (LAZZARO, 1991). Such species also has some similarities with reef species targeted by tourism and fish feeding, with phylogenetic relatedness and ecological similarities, such as many damselfishes (WESTNEAT; ALFARO, 2005), allowing us to make parallels between freshwater and reef ecosystems where divers or snorkelers feed fish.

Since fish will have more energy to invest in displays (indirect aggression) and fights (direct aggression), food provisioning could increase territorial aggression, especially if the territory does not include a food resource. Thus, the provision of supplemental food would increase fish aggression, as fish would have more access to food and, therefore, more energy available to invest in defending the territory. How population density and energy availability interact is poorly understood thus far and few studies have investigated how food provisioning affect fish behavior (BROOKHOUSE et al., 2013). Here we aim to identify if supplementary food and population density affect territory size and aggressiveness in Congo tilapia populations. This case study was carried out in an artificial environment, which has two lakes with natural substrate, one holding more tilapias that continuously received large amounts of food, and another with fewer tilapias in which the fish could only rely on natural sources of food, such as insects, algae, microcrustaceans, and roots and leaves of *Typhonodorum lindleyanum*. Our initial prediction was that supplementary feeding and population density would increase aggression in two complementary

ways, i) by increasing territory and nest size, and ii) by providing more energy for territorial disputes.

Material and Methods

Model species and study area

The Congo tilapia (*Tilapia rendalli*) we used reach as much as 45 cm in standard length and 2.5 kg (BOULENGER, 1897), inhabiting warm lenthic water bodies (CAULTON, 1977). Adults reach sexual maturity after six months, when males dig bowl nests on clay, sand or gravel substrate (BOULENGER, 1897), spawning in them (RIBBINK et al., 1981). Adult tilapias protect first the eggs and then the fry for as long as one month after hatching (BALSHINE; BUSTUN, 2008) with fry as large as 4 cm (RIBBINK et al., 1981). The males aggressively defend their nests and territories (RIPLEY; LOBEL, 2005), while the females choose their mate, evaluating territory and nest characteristics (KEENLEYSIDE, 1991). Adults' territories are only reproductive and provide no food, but they tend to stay close to their territories to feed (HERT, 1992).

Our case study was performed in two nearby artificial ponds with around 50 m², similar in depth (66 cm), pH (7 according to MACHEREY-NAGEL pH Indicator Test Sticks) volume (33000 L), bottom profile (flat, mostly concrete), turbidity (between 5.6 and 8.5 NTU according to an ISO 2100P Portable Turbidimeter) and temperature (21º-24º C, fully exposed to the sun), located in Brasília, Brazil (Lat. 15º45'50"S, Long. 47º51 '57 "W). Both ponds have a concrete bottom, but contain three submerged gardens each, with *Typhonodorum lindleyanum* and *Nymphaea sp.* plants. The areas of the gardens are similar (2.70 m²) filled with silt, in which introduced tilapias defend territories and build nests.

Congo tilapia's populations were already present in both ponds for more than a decade. Original introduced populations were of similar densities, but later diverged possibly due to the food offering. The Congo tilapias we observed were larger than 15 cm in total length to avoid sampling juveniles and held nests measuring between 10 and 20 cm in diameter (see results for more data). Measures were taken with a ruler attached to a rod.

One of the ponds (food provisioned/high-density treatment) is located near a restaurant and receives large amounts of food daily (we estimate it around 1,5 kg/day provided negligibly by customers throughout the day and abundantly by restaurant staff directly from the kitchen) and sustained a population of 7.8 ± 1.6 ind. m^{-2} (mean $\pm$ SD). Although the other pond is only 23 m away from the first, we only observed food provisioning there twice during our study, and in a much smaller scale. It also held about one-fourth the population density of the provisioned pond, with 2.1 ± 1.5 ind. m^{-2}. The ponds differed in population density (t test, $t = 9.67$, $p < 0.0001$). This unfed and low-density pond constituted our control condition.

Sampling and data analysis

We calculated the area (A) of each nest considering it as a circle, measuring its diameter (ø) and dividing it by two to have the radius (r) and then using the $A = \Pi.r^2$ formula. Each nest was considered a sample unit.

Behavioral data were collected between March and May, 2019, adding up to a total of 30 observed days. First, we used direct *in situ* observations with continuous sampling, to get familiarized with aggressive behaviors and to quantify the frequency of behaviors, and second scan sampling, to evaluate the frequency of aggressive behaviors per session (MARTIN; BATESON, 2007). Each session occurred between 8 h and 16 h and lasted for 2 h for each pond (control and treatment). We quantified the frequency of direct (with contact between individuals) and indirect (no contact) aggressive behaviors in territory-holders based on the behavioral categories described to the Cichlids *Cichlasoma dimerus* (ALONSO et al., 2011) and *Oreochromis niloticus* (CARVALHO; GONÇALVES-DE-FREITAS, 2008). A list of the behaviors applied here and their description can be found in the supplementary material (Appendix 1). In accordance with these authors, we considered bites, jaw-locking, attacks from the side, front or back of the contestant as direct aggressions;

while we considered chasing, frontal and lateral threats as indirect aggression.

After the initial observations based on food offering by the restaurant costumers were finished, we also sporadically offered 500 g of food (a mixture of seeds, chopped vegetables and Ora-pro-nobis leaves, strawberry and mango) around 14 h, the same period as the typical provisioning by the restaurant. Food was sporadically offered to both the provisioned/high-density and to the control ponds in 16 different days interspaced by at least four days. After that we performed the same 30 repetitions of the 2-h sessions, recording the frequency of aggressive behaviors as described in the previous paragraph. This allowed us to evaluate the effect of occasional feeding on aggressive behavior.

We compared the nest size between the control and treatment ponds using a t test (N = 58 nests). Then, we used a Generalized Linear Model to compare the frequency of aggressive behaviors per observation session (sample unit) in relation to three independent variables: type of aggression (direct or indirect), fish density/usual feeding (provisioned or unprovisioned) and sporadic feeding (with or without feeding by the researchers). Although our residuals were normally distributed according to QQ-Plot, overdispersion of the variance data prevented us from using Poisson's distribution. Thus, we fitted our model to a Quasi-Poisson's distribution. We applied a critical significance level of α = 0.05. Descriptive statistics values represent mean ± standard deviation. All analyses were performed using R version 4.1.0 (R DEVELOPMENT CORE TEAM, 2013) with the function glm in package stats.

Results

Nest size and fish aggressiveness compared between provisioned/high-density and control ponds

The unprovisioned pond with lower population density (control) presented larger nests (366.2 ± 9.07 cm²) than the provisioned pond with higher fish density (88.2 ± 1.13 cm², t test, N = 58, t = 3.53, p = 0.0009).

We completed 38 h of observations. Congo tilapias showed aggressive behavior against conspecifics. Nonetheless, indirect aggression was more frequent than direct aggression (F = 82.861; p < 0.001; Table 1). The most frequent aggressive behavior summing both treatment and control ponds was chasing (Figure 1).

Usual anthropogenic food provisioning did not alter the occurrence of aggressive behaviors in tilapias (F = 1.674; p = 0.198; Table 1) neither in indirect (Figure 2a) nor in direct aggression (Figure 2b). When we offered the fish sporadic food in both the regularly provisioned/high-density and control ponds, indirect aggression became more frequent in fish from the control pond (Figure 2c), while direct aggression remained the same (F = 194.545; p < 0.001; Table 1; Figure 2d).

TABLE 1: Results of the Generalized Linear Model on the frequency of aggressive behavior. DF = degrees of freedom; F = statistical result of the test; p = probability of type I error.

	DF	Deviance residue	F	p
Aggression type	1	454.78	82.861	1.197e-15
Usual provisioning/fish density	1	9.19	1.674	0.198
Sporadic provisioning	1	1067.74	194.545	2.2e-16

FIGURE 1: Total number of occurrences of each aggressive behaviors in *Tilapia rendalli* in both control and treatment ponds (sum). Black bars represent indirect aggression and grey bars direct aggression.
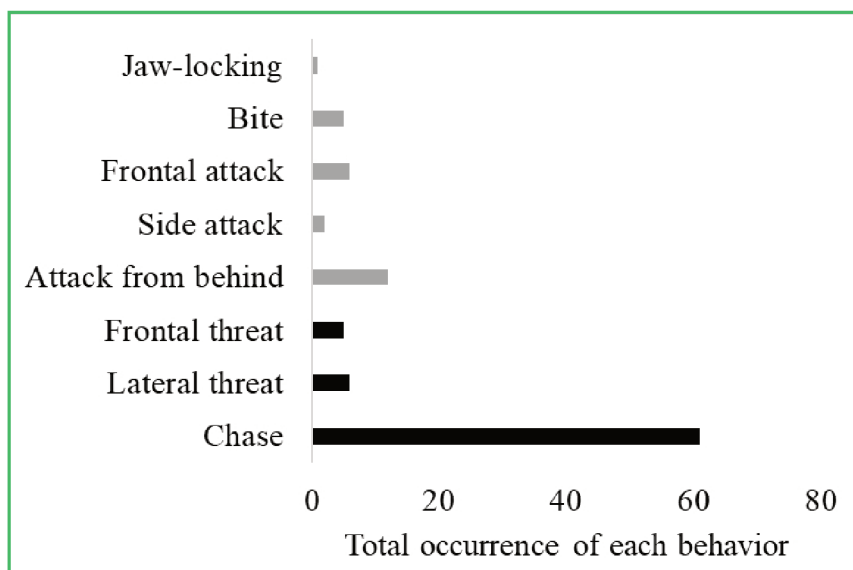

FIGURE 2: Effect of usual food provisioning on (a) indirect aggression, and (b) direct aggression; and effect of sporadic food provisioning by the researchers on (c) indirect and (d) direct aggression in both the treatment (provisioned, high-density) and control (unprovisioned, low-density) ponds. The only difference occurred in indirect aggression when food was sporadically offered. Bars represent means, while whiskers represent standard deviation; * indicates significant difference between control and treatment.
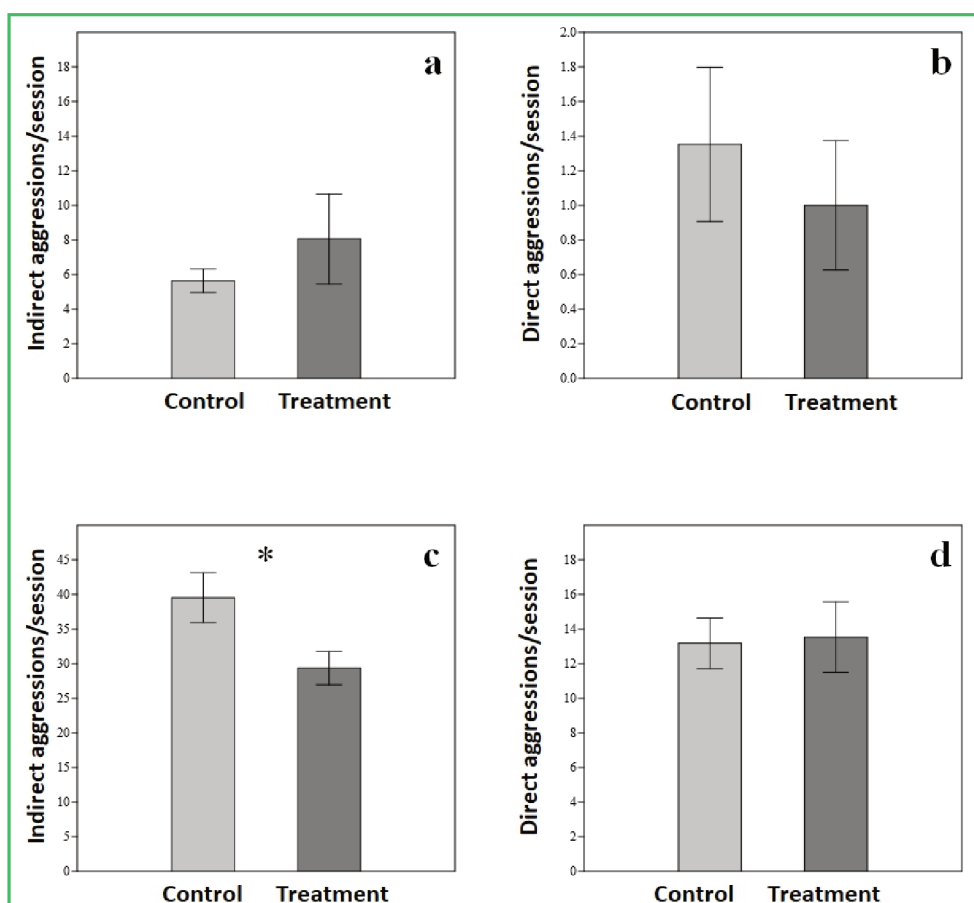
Discussion

Our study case showed that nest size in Congo tilapia, an admittedly aggressive fish, was lower in the pond with food provisioning and higher population. However, food abundance and fish density did not make these fish more aggressive. On the contrary, the food competition made these animals display more indirect aggression when sporadic food, in this case, a limiting resource, was experimentally delivered by the researchers.

We observed larger nests in the unprovisioned/ lower density control pond. Nests with 20 cm in diameter, such as we observed, are described for another much smaller Brazilian cichlid, *Cichlasoma dimerus* (ALONSO et al., 2011). Our results point to a difference in nest size in response to food provisioning and/or population density. The territory and maintenance of nests are part of the reproductive behavior of cichlids, as females select partners with larger territories and better nests (KEENLEYSIDE, 1991). It is noteworthy that, in Congo tilapias, the guarded areas provide males with nest, not food. According to Grant (1997), optimal territorial size is reduced with the presence of numerous competitors, so this could result in proportionally smaller nests. Population density probably constrains nest area in the Congo tilapia.

Tilapias perform around three times more indirect aggressive displays than direct aggression. This is explained by the much higher costs of direct aggressiveness, expected with an escalation of the conflict (O'CONNOR et al., 2015). Game theory based on the hawk-dove game (PARKER, 1984) proposes that, if fight injuries are more costly than the gains from feeding, it is more advantageous to ritualize disputes. In the Midas cichlid (*Amphilophus citrinellum*) food disputes were often solved by threat displays (BARLOW et al., 1975). Social hierarchy is well known in cichlids and reduces aggression (GONÇALVES-DE-FREITAS et al., 2019), especially if the group is stable and status cues are available (GONÇALVES-DE-FREITAS et al., 2008) such as in our study area. In regularly provisioned environments, animals can wait for future feeding opportunities instead of fighting for food momentarily available (GRAND; GRANT, 1994). Moreover, increased food availability by provisioning may reduce food competition and lower agonistic competition in general.

Aggressiveness did not increase with usual food provisioning and population density in our study. A positive correlation between aggression and both food availability and fish density was expected because of energy availability and the probability of encounters between two individuals (GONÇALVES-DE-FREITAS et al., 2019) and because population density destabilizes social hierarchy in cichlids (LAMBERT; DUTIL, 2001). Other researchers observed reduced aggression in highly dense aquaculture tanks, but this occurred in a less aggressive and non-territorial group, the salmonids, and aggression did increase with food availability (ELLIS et al., 2005; ADAMS et al., 2007). Nevertheless, results consistent with ours were observed previously in Congo tilapia (BHUJEL, 2000). This author reported that, packed in high densities, Congo tilapia reduces aggressiveness counterbalancing density. These data also agree with Schwedler and Johnson (2000), which propose that low population densities stimulate territorial aggression among tilapia. Food availability could also have reduced agonism by affecting competitive aggressiveness, but only if population density did not increase in parallel to food availability and if competition for food was stronger than that over reproductive territories. Grant et al. (2002) reported that food abundance and aggression resulted in a Gaussian graph, with aggressiveness returning to the original levels when food was abundant due to reduced competitive aggression, but this occurred between juveniles with no reproductive territoriality. Our findings that food provisioning and high fish density does not increase aggression contradict our original hypothesis and are somewhat surprising, although some previous studies have anticipated similar results.

Direct and indirect aggressiveness increased more than six times when food was offered sporadically, in the unprovisioned/lower-density control population. Thus, competition for food, not abundant feeding, stimulated indirect aggressiveness. Aggressive competition can

explain the increase in aggression when sporadic food was delivered to the unprovisioned control pond, but it cannot be accounted for in the provisioned pond if fish population there is proportionally large or if competition over reproductive territories is stronger than that over food. Competitive aggression over food was observed in the Midas cichlids, in which gold juveniles were rarely aggressed when food was abundant (BARLOW et al., 1975) but became harassed by larger juveniles after food deprivation (BARLOW; MCKAYE, 1982). There are other costs to territoriality that could deter aggressiveness besides the energetic ones, such as the risk of predation (CANDOLIN; VOIGT, 2001), and exposure to threats such as divers (BESSA; GONÇALVES-DE-FREITAS, 2014). It may also be that the cost-benefit trade-off of territoriality (HINSCH; KOMDEUR, 2010) in terms of reproductive success is achieved by benefits other than territorial dominance in a food-saturated environment, such as increased female fecundity and nutrient deposition in yolk. A shift in the cost-benefit trade-off in territoriality and reduced competition over food may hinder tilapia aggressiveness in the provisioned and high-density pond.

In our study, feeding did not increase aggression, but excessive food is known to cause water quality loss by pH and dissolved oxygen reduction and increased ammonia (DE CASTRO et al., 2014). Although feeding is generally described as an impact (BESSA et al., 2017), in scenarios where natural food is being depleted feeding may be considered a conservation strategy (SERESS et al., 2020), as long as it follows quality and quantity guidelines (EWEN et al., 2015). Tilapia are omnivorous and generalist animals (CHERVINSKI, 1982), the trophic level most affected by food provisioning (MEDEIROS et al., 2007; ILARRI et al., 2008). The appropriate level for ingestion of provisioned food is still unknown to many species (DA SILVA et al., 2020).

Some limitations of this research are that the provisioned pond and the denser pond were the same, so it is more difficult to specify which factor influenced our results. While this is true, fish densities were similar when the ponds were first colonized. That suggests that provisioning resulted in higher population densities,

allowing us to attribute our main findings to fish feeding, even when it is more related to higher density, because population growth probably results from feeding. During our observations we saw tilapia fingerlings and more nests in the provisioned pond, indicating that population in the provisioned pond was probably still increasing by the time of the experiment. We also evaluated a single pond as control and treatment, although this could result in the lack of study site replications, making ours a study case, we considered as sampling unit each nest (nest diameter) or each observation session (aggressiveness). Generalizations made from this case study to other situations should be made with great caution, due to lack of replication.

Tilapias are not often considered a target species for tourism, but some parallels with tourism sites in which tourists feed fish as a leisure activity can be drawn. There are many destinations where tourists contribute to local economies (GARROD; WILSON, 2004) but offer large amounts of food to the fish (BESSA et al., 2017). Several species in such environments are closely related to tilapias and resemble them ecologically, being highly territorial with demersal habits, omnivorous diet and nesting, such as many pomacentrids (HOSTIM-SILVA et al., 2006) and other cichlids (BESSA; GONÇALVES-DE-FREITAS, 2014). Such species may respond to feeding in the same manner as tilapias, with increase in density, smaller nests and altered territorial aggressiveness.

We conclude that anthropogenic food provisioning and high fish density, which is probably a result of the food provisioning, may act by three pathways on the aggressiveness of territorial fish. First, high population density reduces aggression possibly due to habituation to conspecifics. Second, excessive feeding reduces competitive aggression if it overcomes population growth. Third, more food increases aggression by reducing the energetic cost of aggressiveness, while high density increases the chance of aggressive encounters. These opposing effects of food provisioning and density on aggression could cancel one another, avoiding changes in aggression frequency. Future studies should concentrate on untangling energy intake and population density in laboratory conditions to test the

aforementioned scenario. It would also be important to have more population replicates analyzed to confirm the food provisioning effects we got on population density. Finally, our study did not show evidence that feeding increases aggression, nevertheless, excessive food may result in other problems, such as water-quality loss (DE CASTRO et al., 2014). Thus, we hope our study will increase public awareness, and regulation of fish feeding as a leisure practice.

Acknowledgments

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Appendix 1

Supplementary Table 1: Aggressive behavior categories observed in the Congo Tilapia and their descriptions.

Category	Description
Bites	A fish approaches its opponent and touches its body with its mouth, biting.
Jaw-locking	Two fish approach one another and simultaneously bite their jaws. They may swim in a circle while keeping their mouth attached.
Frontal Attack	It was characterized by head-to-head bumps between two individuals.
Attack from behind	In this behavior the aggressor fish hits the tail of the attacked fish, sometimes nipping on the fin.
Side attack	A fish bumps its head on the sides of the attacked individual.
Lateral threat	A fish swims parallel in proximity with the opponent, bristles its fins and opens the operculum.
Frontal threat	Two fish stand face to face without opening the opercula, each one with its mouth open, its body inclined and head up. There is no physical contact.
Chasing	A fish swims towards another, following its trajectory, without physic contact, while the chased animal moved in escape.