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Agonistic behaviour and feed efficiency in juvenile Nile tilapia *Oreochromis niloticus*

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ABSTRACT

Given the strong effects of behavioural hierarchies on growth in many cultured species and the key role of feed efficiency in aquaculture economics, understanding the nature of the interaction of these variables is important for the sustainability of aquaculture. The relationship between agonistic behaviour, growth and feed efficiency in Nile tilapia, *Oreochromis niloticus*, was studied by rearing 120 fish in eight aquaria. Fish were video-recorded to estimate the occurrence of agonistic behaviour during a fasting and a refeeding period. Growth, feed intake and feed conversion efficiency (FCE - calculated as the inverse of feed conversion ratio (FCR)) were subsequently measured individually for each fish. Fish showed 58% less agonistic traits during the fasting period compared to the feeding period, but generally, an aggressive fish during the fasting period was also aggressive during the refeeding period. The nature of agonistic behaviours between individuals was used to assess the presence of hierarchical relationships between fish. There were dominance hierarchies established in each experimental aquarium that despite minor shifts were maintained throughout the experiment. Agonistic behaviours were strongly correlated with each other, the aggression Index (AI) and with hierarchy rank. PCA analysis of the agonistic behaviours summarising the behavioural information showed little or no correlation between agonistic behaviour, fish growth or FCE. FCE was correlated with body weight gain (BWG). These results suggest that agonistic interactions in juvenile Nile tilapia do not have a large impact on growth and feed conversion efficiency.

Keywords: agonistic behaviour, feed efficiency, Nile tilapia, performances, correlation

Introduction

Social behaviour and resulting hierarchies have been shown to have a high impact on performance and survival in **terrestrial** animals and in their performance in production systems (Bruno et al., 2018; Burrow, 1997; Hayne and Gonyou, 2006) and a growing body of information from aquatic species (Jobling, 1983; Martins et al., 2008; Montero et al., 2009). In fish, limiting resources may lead to the emergence of competitive behaviour, which may take the form of dominance rank-based hierarchies (Jobling, 1983). This kind of hierarchy is generally established after agonistic encounters between two or more individuals, and the rank within the hierarchy depends on their ability to fight (Andrew et al., 2004).

Previous studies have shown **that** growth traits are related to the social rank of the fish within the group, with dominant fish being bigger than subordinates (Abbott and Dill, 1989; Alanärä et al., 1998; Carline and Hall, 1973; Fernandes and Volpato, 1993). Dominant fish have been shown to increase their feed intake while subordinates have reduced or even suppressed growth, due to a reduction in access to feed or greater consumption of their energetic reserves due to stress (Fernandes and Volpato, 1993). Bigger fish (and higher ranked in the hierarchy) will fight lower ranked fish for the feed area lowering the feed consumption of subordinates (Alanärä et al., 2001; Cutts et al., 1998), with dominant fish occupying more of the tank space and monopolizing the feeding area. Furthermore, a number of studies on salmonids and cichlids have highlighted that subordinates generally suppress their agonistic behaviour, reduce feed consumption and reduce physical activity (Abbott and Dill, 1989; Jobling, 1983; McCarthy et al., 1992; Winberg et al., 1992). The main hypothesis linked with all these results is that higher individual growth would be a consequence of higher position in the hierarchy, associated with greater feed intake that is highly correlated with agonistic behaviours (Cutts et al., 2001; Montero et al., 2009).

However, dominant fish can have high energy expenditure resulting from their increased swimming activity to keep the best position in the tank, close to the feeding area and in fighting off other fish (Le François et al., 2005; Montero et al., 2009). Dominant and subordinate fish may therefore have different strategies: dominant fish will consume a lot of feed but will expend a lot of energy to maintain their dominance, whereas subordinate fish will avoid conflicts, reduce their activity and consume less feed (Metcalf et al., 1989; Sloman et al., 2000). The extent to which a fish is an efficient consumer of energy and would demonstrate an improved feed conversion efficiency (FCE) is not therefore necessarily related to their position in a hierarchy. In addition, other studies have shown that when the hierarchy is fixed or if the dominant fish is much bigger than the rest of the fish, there is a reduction of agonistic behaviour overall and removal of the large fish induces an increase in aggression (Adams et al., 2000, 1998). According to these authors, the growth rates of all the fish in a tank were much higher when a bigger fish (dominant) was present in the tank than when all the fish had homogeneous size, suggesting a more complex relationship between fish behaviours and the growth performance of fish in a given production system.

In aquaculture, the main trait selected for is growth (Gjedrem et al., 2012), although FCE (or its inverse, feed conversion ratio - FCR) is a trait with increased interest due to its major impact on sustainability, at the economic, social and environmental levels (Besson et al., 2016; Omasaki et al., 2017). As both growth and FCE can be affected by social hierarchy, understanding their interrelationships is necessary to develop efficient breeding programs and better predict the evolution of populations over time. Nile tilapia *Oreochromis niloticus* presents agonistic and territorial behaviour, showing a social hierarchy linked with fish body size (Boscolo et al., 2011; Domingues Alvarenga and Volpato, 1995; Giaquinto and Volpato, 1997; Gonçalves-de-Freitas et al., 2008; Volpato et al., 1989; Volpato and Fernandes, 1994).

As discussed above, there is an overall positive correlation between fish body weight and rank in the hierarchy in studies reported to date. However, at the energetic level, it can be as expensive to be subordinate as dominant and the impact of the hierarchy on feed intake and growth rate is not straightforward. Growth and FCE may be affected differently according to the hierarchy of the fish. In addition, the measurement of hierarchy in tilapia has normally been done between isolated pairs of fish rather than in groups and so may not accurately reflect aquaculture production environments (see de Verdal et al., 2017a). Growth and FCE have been accurately measured only rarely in Nile tilapia at an individual level (de Verdal et al., 2017b), let alone in conjunction with measurements of agonistic behaviour.

The main hypothesis of the present study was that an aggressive and dominant fish would eat more feed and would be more efficient. To test this hypothesis, estimations of the relationships between agonistic behaviour, growth and feed efficiency in Nile tilapia were calculated to attempt a clearer understanding of their effects on each other, and whether Nile tilapia displaying particular behaviours could be identified as growing faster, and if so whether they did so more efficiently or not.

Materials and Methods

Fish and rearing conditions

The study was carried out on Nile tilapia produced by natural spawning in December 2014 by WorldFish at the Jitra Research station, Malaysia. The fish used in the present study were also used for the genetic estimation of feed efficiency, published by de Verdal et al (2018).

The fish used in the present study were from the 15th generation of the GIFT strain, genetically improved for growth (Ponzoni et al., 2011). After transfer to the Penang WorldFish station, fish were reared until the fry reached approximately 10 g of body weight. After a one-week quarantine in tanks, fish were sorted to reduce the body weight variability (from 27.8 to 17.0% of body weight CV) and moved to eight aquaria in a recirculating water

system, with 15 fish per 100 L indoor tank (120 cm length, 35 cm width and 24 cm depth), providing 120 individual fish at the beginning of the experiment. The average temperature was $28 \pm 1^\circ\text{C}$ and the photoperiod 12L:12D. Two coloured T-bar tags (Avery Dennison tags, 25mm) were inserted in each fish (using an Avery Dennison Mark III pistol Grip tool) in the dorsal muscle after the fish had been anaesthetized with clove oil. A different colour combination was used for every fish within an aquarium so that each fish could be visually identified. Fish were fed on a commercially available tilapia feed (34% crude proteins, 5% crude fat, 5% crude fibre and 12% moisture) at a daily rate calculated according to Mélard, et al. (1997) as follows:

$$\text{DFR} = 14.23 * \text{Mean body weight}^{-0.322}$$

where DFR is the daily food ration, expressed in % of body weight per day, and mean body weight was the average body weight of the fish within each aquarium. Daily feed ration, ranged between the optimal and the maximal feeding ration.

Mortality was recorded daily and the feed ration changed accordingly. During the experiment, six fish died, three of them before the beginning of the video recording and the other three during the records. These last three were at the bottom of the hierarchy and this did not change the hierarchy ranks of the other fish in the aquariums. Fish were fed the daily feed ration, and not to apparent satiation, because the latter method varies considerably with the observer, thus reducing repeatability of the experiment and increasing the aquarium effect.

Fish experimental protocol and measured traits

The experimental protocol was previously described in detail by de Verdal et al. (2017b). At the beginning, the experiment was mainly developed to accurately measure individual feed intake and estimate individual feed efficiency. The choice to add behaviour analyses was

taken later, as it was particularly interesting to understand the relations between feed efficiency, performances and agonistic behaviours between fish. This had consequences on different aspects of the experiment protocol, such as the sorting step at the beginning of the experiment. Briefly, fish were reared for four different periods. The first period was an adaptation period where groups of fish were reared in aquaria for two weeks. After these two weeks, the second period was a fasting period, where fish were not fed for 10 days. Fish were weighed at the beginning (BW1) and at the end (BW2) of the period and the loss of weight (BWG.fasting) was calculated. The third period was a period of 17 days of growth compensation where fish were fed using the calculated ration. Fish were weighed at the beginning (BW2) and at the end (BW3) of this period and the weight gain (BWG.refeed) was calculated. Finally, the last period was a 10 day period where feed intake (FI) was recorded individually for each fish by counting for the number of pellets eaten by each fish in a group using video analyses of the meals (Hugues de Verdal et al., 2017b). Fish were weighed at the beginning (BW3) and at the end (BW4) of the period from which growth (BWG) was calculated. Feed conversion efficiency ($FCE = BWG.FI^{-1}$) was calculated as an indicator of the individual feed efficiency of each fish.

To monitor the behaviour of the fish, each tank was video-recorded eight days in total, four days during the fasting period, and four days during the refeeding period. Each day, the video-recordings were carried out twice, once in the morning (between 8 and 9am) and once in the afternoon (between 1 and 2pm) for 20 minutes each. Video-recordings were carried out one hour after the end of the meal during the refeeding period to be sure that the meal did not bias the behaviour of the fish, and the experimenter was not in the aquarium room during the video-recordings. For the whole experiment, the behaviour of each fish was observed and quantified over a total of 5h and 20 minutes. Nile tilapia individual behaviour was assessed by the frequency per individual of agonistic behaviour activities in view of an ethogram for *O.*

niloticus depicted in Falter (1983) and Alvarenga and Volpato (1995). The initiator of an assault was distinguished by watching who drew closer to the opponent and began the assault; the defeated fish was the one who left the site of the assault. An aggressive act was defined as one of the six following: chasing, circling, flight, mouth fight, lateral fight and nipping. The characteristics of each behaviour is described in Table 1. The aggression index (AI) described by Bailey et al. (2000) was calculated as $AI = Aggr^+ / (Aggr^+ + Aggr^-)$, where $Aggr^+$ and $Aggr^-$ correspond to the aggressive acts given and received by an individual.

Hierarchy assessment

The Bradley Terry Model (Bradley and Terry, 1952) was used to establish an overall hierarchy rank of the fish in each aquarium and periodical hierarchy ranks of these fish across different times based on the combined observations of chasing and nipping. This test uses all pairwise interactions to establish the rank based on linearly independent pairwise comparisons. Since each tank contained 15 fish a matrix of 225 possible combinations (15x15) and of 105 unique pairwise combinations $((225-15)/2 = 105)$ was possible. Given the total data set of observed interactions was 7172, or around 900 per tank, that implies around 7 observations per cell in the Bradley Terry calculations per tank $((1000 \times 0.85)/105 = 7.3)$, but less than one for the other behaviours. Cells with missing data prevent accurate hierarchy calculation. We therefore restricted the calculation of hierarchies to chase and nipping as these were the only behaviours sufficiently common to allow a reasonable chance of getting observations in all the possible pairwise comparisons of the fish, required to formulate a reliable hierarchy.

Statistical analyses

Descriptive statistics, including the number of observations, means and their standard deviations were used to summarize the behaviour and performance traits of each fish in each aquarium. The Shapiro-Wilks test was used to check the normality of variables using the LambertW package in R (Goerg, 2016, 2011). Logarithm or square root transformations failed to normalize the behavioural data, and so non-parametric tests were used to analyse these traits. Spearman correlations were calculated using the cor procedure of R software (R Development Core Team, 2018) between 1) behaviour traits within each period (fasting and refeeding), 2) behaviour traits between periods and 3) behaviour and performance traits for each period separated. Principal component analysis was done using the FactoMineR package of R (Lê et al., 2008). The factoextra package (Kassambara, 2017) was used to perform the cluster analysis. All statistical analyses were performed using R software (R Development Core Team, 2018). To understand each component of the PCA, we calculated the correlations between the data and each principal component. To interpret each principal component of the PCA, we examined the sign and direction of the coefficients for the measured traits. The larger the absolute value of the coefficient, the more important the corresponding variable was in calculating the component. Furthermore, when two traits have a strong positive correlation, they will be located close to each other in the PCA diagrams. These two traits will be opposite if they have a negative strong correlation, and they will be orthogonal if there is no correlation.

Results

Basic statistics

The total number of agonistic interactions was 2783 during fasting and 4389 during the refeeding period (Table 2). Fish were generally more aggressive during the refeeding period: chasing and nipping, the most frequent behaviours, were 74.3 and 72.5% more frequent,

respectively, during the refeeding period than during the fasting period. However, the occurrence of circling and lateral fights did not change significantly and the number of mouth fight was 39.4% less frequent during the refeeding period.

The high coefficients of variation (CVs) of the occurrence of agonistic interactions illustrated the high degree of variation in the level of agonistic behaviours between individual fish, with CVs ranging from 58.3 to 221.6 % during the fasting period and from 55.3 to 260.5 % during the refeeding period (Table 2). The effect of sex of the fish and aquarium were not significant for any of the behavioural traits (Kruskal Wallis Test, P ranging from 0.3-0.9 for both sex and aquarium).

During the 10 day fasting period, fish lost on average 1.5 ± 0.4 g of body weight (BW), while they gained 17.7 ± 4.3 g of BW during the 17 days of refeeding (Table 3). Coefficients of variation for body weight and growth ranged from 21.6 to 24.3 %. Feed intake during the FI measurement period ranged from 5.0 to 15.4 g, with an average of 10.4 ± 2.5 g. Feed conversion efficiency was in the same range of variability (CV=21.0 %) as growth, and with a mean of 1.21 ± 0.3 .

Hierarchy

The Bradley Terry Model analysis demonstrated hierarchies in each of the aquaria. Although the change of ranking over the four different weeks of measurement was not significant (P=0.763), the dominance hierarchies did not remain stable in detail throughout the observation period. Indeed, hierarchies alternated with the dominant positions of rank 1, 2 and 3 being occupied by different fish at different time periods, but rarely with fish of lower rank. In essence there were two groups of fish in each aquarium: the dominant group, with one or more generally two fish, and the subordinate group, with the rest of the fish. In one case the

death of a top ranking fish led to a restructuring of the hierarchical rank order. The death of a lower order fish (e.g. rank no 15, 14) appeared to have little effect on top ranked fish. Rank was also not significantly related to sex (Pearson Chi-square test 15.3, d.f. =14, $P = 0.36$).

In nearly all of the groups observed, the majority of top hierarchical positions were held by fish who committed high levels of agonistic behaviours throughout the experimental period. Correlations of hierarchy rank and the AI in both feeding and fasting periods were 0.9. In contrast there was no strong relationship of hierarchy rank with body weight measures (ranging from 0.18-0.28).

Agonistic behaviours

Agonistic behaviours were related to each other to varying degrees as illustrated by the PCA results (Table 4 and Fig 1). Cluster analyses identified four groups of behaviours showing similar relationships, two composed of measurements from the fasting period (groups 1 and 4), and two composed of measurements from the feeding period (groups 2 and 3) one of which (group 2) included one behaviour from the fasting group (FAST_flight.given) (Table 4). Groups 1 and 2 were composed largely of agonistic behaviours received - noting here that flight given is also equivalent a less aggressive response **as opposed to the other agonistic behaviour given**. Groups 1 and 2 had major correlations on dimension 2 and contrasting negative correlations for group 1 and positive correlations for group 2 on dimension 3.

In contrast, groups 3 and 4 reflected agonistic behaviours given, with flight received, with high correlations of both groups of dimension 1, but differentiated on dimension 2 with generally positive correlations of group 4 and negative correlations of group 3, which were reversed on dimension 3. The high correlations of the AIs on dimension 1 and their association with groups 3 and 4 are consistent with these groups being associated with greater

agonistic behaviour. The occurrence of mouth fight, both given and received, in groups 3 and 4 may suggest interactions of more evenly matched fish and the less divergent outcomes of this behaviour. In total the first three dimensions explained more than 50% of the variation in the data set (Table 4).

Given the strong associations of the agonistic behaviours with each other, irrespective of whether they were measured in the fasting or feeding periods, and their strong correlation with the AIs (and of the correlation of the AIs with Hierarchy rank), the AIs were used to represent the behaviours on a joint analysis of behaviour, growth and feed conversion efficiency (Table 5 and Fig 2). The results show a close association of the measures of fish weight and growth together with feed intake, all of which show high correlations on dimension 1, with the BWG during the fasting period showing a strong negative correlation as there was weight loss during fasting (Table 5). There is a clear separation of these variables from the AIs which all correlate strongly on dimension 2, and with FCE which shows a high correlation only with dimension 3, on which there is also a strong correlation with BWG. The extent to which these three sets of variables (growth related measures, agonistic behaviour measures and the feed conversion efficiency) are largely uncorrelated, in an analysis that explains almost 80% of the variation in the data set is demonstrated clearly in their orthogonal relationships shown in Fig 2.

Discussion

In both fasting and refeeding periods, some fish were not at all aggressive while others were very aggressive. Dominance hierarchies were present throughout the study. Although no significant change of global rank position (dominant vs. subordinate) was observed over the

four weeks of measurement, this may be as a result of a dramatic change of position in only a few individuals out of a total of 120, although there were many minor shifts in rank. This is in accordance with results from McCarthy et al. (1999) on another cichlid species, *Tilapia rendalli*, where groups of eight fish were reared for at least three weeks, showing stable individual dominance hierarchies. However, the dominance hierarchy was not stable for *Oreochromis mossambicus* reared in groups of six fish and measured during eight consecutive weeks (Oliveira and Almada, 1996). This last experiment was done at the onset of sexual maturity, whereas the present study and the *T. rendalli* experiment were performed on juvenile and immature fish, which may explain the differences in hierarchy stability and this lack of sex effect, as described by Pinho-Neto et al. (2014).

It is generally accepted that body size is a good indicator of the social status of the fish, with larger fish becoming dominant compared to smaller fish (Abbott et al., 1985; Bailey et al., 2000; de Oliveira Fernandes and Volpato, 1993; Turner and Huntingford, 1986; Volpato et al., 1989). A proposed explanation for this difference in growth was that subordinates showed a higher basal metabolism compared to dominant fish, and that the energy used for this higher metabolism of the subordinate fish was not available for growth (de Oliveira Fernandes and Volpato, 1993). In the present study, the fact that fish were sorted at the beginning to reduce the size variability could be the cause of the low correlations between body weight and the occurrence of agonistic behaviours, and between weight and hierarchy rank. Furthermore, according to Volpato et al. (1989), the hierarchy rank in Nile tilapia exists even when animals are of the same size, suggesting that fish size is not the only factor explaining hierarchy in the group. In the Volpato et al. (1989) experiment, one or two fish were easily observed as dominant, fighting with all the other fish and defending as much space as they could in the aquarium. For the rest of the fish, it was particularly difficult to distinguish a real hierarchy, as

these subordinate fish generally did not fight each other, and stayed grouped in a small area. Similar results were observed in the present study at each measurement day, with two groups of fish in each aquarium: the dominant group, with one or more generally two fish, and the subordinate group, with the rest of the fish group. However, from one day to another one, hierarchy changed, with the dominant positions occupied by different fish at different time periods.

It was previously shown in Atlantic salmon that subordinates fed less than dominant fish (Huntingford et al., 1993) because dominant fish kept the feeding area for themselves and consequently, had more access to feed. The low correlation between FI and agonistic behaviours in Nile tilapia in the present study are not in accordance with this assumption. This could be due to a number of reasons. Firstly, the period of behaviour measurement was not concomitant with the period of FI measurement, they were consecutive periods. This could have an impact, even with a stable hierarchy from one period to another one. Secondly, during the feeding period, feed was dispersed on the top of the aquarium, and not given in a small specific area. According to McCarthy et al (1999), a spatial fixed localization of feed distribution increases the possibility of a fish to defend this specific area, and allows more agonistic behaviours, with a dominant fish intimidating the other ones, defending the feed distribution area and monopolizing the feed resource. On the other hand, a dispersion of the feed supply would reduce the agonistic behaviours and would increase the uniformity of feeding opportunity. Interestingly, from our observations, during the meals, every fish spent time for feeding rather than controlling its area. Dominants and subordinates came to the surface to feed on the floating pellets. The non-significant correlation between aggression index, agonistic behaviours and feed intake confirms this observation. The present rearing conditions can be compared with the low interaction environment used in Ruzzante and Doyle (1991) where the floating pellets were spread over the tank surface, allowing a good access to

feed by all the fish. In these specific conditions, social behaviours were not a major component of growth variations, explaining the low interactions between growth and the occurrence of agonistic behaviours. Thirdly, the calculated feed ration was close to the the maximal, so fish did not need to fight for feed, which reduces the occurrence of agonistic behaviours.

According to McCarthy et al. (1999), feeding rank could be a good estimator of the social status of each fish in a group only if the pattern of feed delivery allows a high competition and consequently, a possibility for a fish to monopolize the feed resource. In Arctic char *Salvelinus alpinus*, Adams et al. (1995) identified a positive relationship between the social status of the fish measured as the frequency of initial attacks, and the feeding rank, measured as the share of the group meal. With the same species, Bailey et al. (2000) estimated a significant correlation between AI and FI (0.43, $p < 0.05$). The correlations between aggressiveness and feed intake was not seen- in the present study. A possible explanation of these different results could be linked with the fact that agonistic interactions were measured in several consecutive days in the present study and not on a single day (Adams et al., 1995) or on three inconsecutive days (Bailey et al., 2000).

In any case, in our rearing conditions, agonistic behaviours and hierarchy in Nile tilapia were not good estimators of FI and FCE. This low or non-significant relationship between hierarchy and FI was also observed by Alanärä et al. (1998) showing that subordinates in Arctic char were as successful as dominant fish to catch feed, without having a high frequency of agonistic behaviours.

Since FI and growth were not correlated with agonistic behaviour in our study, the non-significant correlation between FCE and the agonistic behaviour frequency is not surprising. Similarly, Martins et al. (2008) showed that body weight, growth rate and FI did not differ between more and less aggressive African catfish *Clarias gariepinus*. Furthermore, they

showed that residual feed intake, another trait estimating feed efficiency, was not correlated with any of the agonistic behaviours measured at the individual level. These results are also in accordance with those of Silverstein (2006) on rainbow trout *Oncorhynchus mykiss* showing that feed efficiency measured on individually reared fish correlated well ($r = 0.66$, $p = 0.03$) with the same trait expressed in social groups. One of the main conclusions of the present work, in accordance with the studies just cited, is that aggressiveness and hierarchy are not good indicators of the feed efficiency in juvenile Nile tilapia under our rearing conditions. If this is the case, this raises the question of how dominant and subordinate fish use their energy intake to reach a similar feed efficiency. What is the best strategy for a fish: being a dominant or a subordinate? In terms of metabolism and energy, some studies had opposite results. Volpato et al. (1989) estimated that submissive conditions increased the metabolism in the Nile tilapia, explaining the lower growth of these fish. In contrast, it was previously shown on different fish species that dominant fish invested a lot of energy to keep this status (Boujard et al., 2006; Nelissen, 1985). Corrêa et al. (2003) measured cortisol level of dominant and subordinate fish stressed by an acute stress, showing that the level of cortisol was not different between the fish. These authors suggested that the social interactions during the hierarchy establishment were an important source of stress for Nile tilapia, but cause similar increase in the cortisol level in both dominant and subordinate fish.

In conclusion, social behaviour in fish can have a direct effect on aquaculture production efficiency. Mortality or heterogeneous growth due to reduced feed access or low feed conversion efficiency can reduce productivity and profit. However, it appears from the present results that agonistic interactions in juvenile Nile tilapia do not have a large impact on growth and feed conversion efficiency. This could be explained by a low occurrence of agonistic behaviours in the present study or, more probably, by the fact that fish received enough feed using a dispersed feed supply.

Conflict of interest

The authors declare that they have no conflict of interest.

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Tables

Table 1 – Description of the characteristics of each measured agonistic behavioural trait. The fish initiating the behaviour was scored as giving the behaviour, the fish to which the behaviour was directed is scored as receiving the behaviour.

Behaviour	Description
Chasing	One fish follows the opponent who swims in an opposite direction.
Circling	Two fish with erected dorsal fin swim following each other, describing a circle, like a slow chasing.
Flight	The assaulted or pursued fish avoids the challenge place.
Mouth fight	Both fish approach frontally one another with their mouths opened and bite the rival's mouth. Their mouths are kept firmly together while one fish displaces the opponent backward.
Lateral fight	The fish stay close to one another facing the same or opposite direction and beat their tails sideways.
Nipping	The aggressor swims towards the opponent and bites its body.

Table 2 – Basic statistics: number of **total** occurrences during (N), mean \pm standard deviation **per fish** (SD), minimum, maximum and coefficient of variation (CV) of behavioural agonistic traits during the fasting and the refeeding periods.

Trait	Fasting period					Refeeding period				
	N	Mean \pm SD	Min	Max	CV (%)	N	Mean \pm SD	Min	Max	CV (%)
Chasing given	1598	13.3 \pm 11.9	0	61	89.2	2785	23.2 \pm 27.1	0	153	116.7
Chasing received		13.3 \pm 7.8	0	33	58.3		23.2 \pm 12.8	0	54	55.3
Circling given	140	1.2 \pm 1.9	0	12	164.2	143	1.2 \pm 2.6	0	16	216.3
Circling received		1.2 \pm 1.4	0	6	118.3		1.2 \pm 1.4	0	6	115.3
Flight given	31	0.3 \pm 0.5	0	3	209.9	100	0.8 \pm 1.2	0	7	142.0
Flight received		0.3 \pm 0.6	0	3	221.6		0.8 \pm 2.2	0	17	260.5
Mouth Fight given	302	2.5 \pm 2.6	0	15	103.9	183	1.5 \pm 1.7	0	7	114.4
Mouth Fight received		2.5 \pm 2.3	0	10	92.7		1.5 \pm 1.7	0	9	111.5
Lateral Fight given	82	0.7 \pm 1.1	0	5	164.3	91	0.8 \pm 1.3	0	5	173.5
Lateral Fight received		0.7 \pm 0.9	0	4	130.0		0.8 \pm 1.1	0	6	146.1
Nipping given	630	5.3 \pm 4.4	0	23	83.2	1087	9.1 \pm 9.7	0	44	107.2
Nipping received		5.3 \pm 3.7	0	18	70.3		9.1 \pm 6.4	0	30	70.5
Aggression Index		0.5 \pm 0.2	0	1	41.8		0.4 \pm 0.2	0	0.87	50.1

Table 3 – Basic statistics (N, Mean \pm Standard deviation SD, minimum, maximum and coefficient of variation) of growth performances, feed intake and feed efficiency for all the rearing fish.

¹BW1: body weight at the beginning of the fasting period (in g); BW2: body weight at the end of the fasting period and at the beginning of the refeeding period (in g); BW3: body weight at the end of the refeeding period (in g); BWG.fasting: loss of weight during the fasting period (in g); BWG.refeed: gain of weight during the refeeding period (in g); BWG: body weight gain during the period of feed intake measurement (in g); FI: feed intake (in g); FCE: feed conversion efficiency ($FCE = BWG.FI^{-1}$).

Trait1	N	Mean \pm SD	Min	Max	CV (%)
BW1	118	10.6 \pm 2.3	6.3	15.7	21.6
BW2	115	9.10 \pm 2.1	5.3	13.7	22.6
BW3	110	26.9 \pm 6.0	13.4	40.2	22.4
BWG.fasting	115	-1.5 \pm 0.4	-2.6	-0.3	23.9
BWG.refeed	110	17.7 \pm 4.3	6.9	28.1	24.3
BWG	94	12.9 \pm 2.9	4.9	18.3	22.1
FI	83	10.4 \pm 2.5	5.0	15.4	23.7
FCE	83	1.21 \pm 0.3	0.7	1.79	21.0

Table 4 – The correlations between the agonistic behaviours and the first four PCA dimensions (Dim 1-4). The individual behaviours are organized in the four groups identified by cluster analysis (coded 1-40). The codes used in figure 1 for the individual variables are given in the second column. The eigenvalues of the PCA analysis, percent variance (and cumulative percent variance) explained by each PCA dimension are given at the bottom of the table. Strong associations with a PCA dimension are in bold, with positive associations highlighted in dark grey and negative associations in light grey.

Variable	Variable code	Cluster Code	Dim.1	Dim.2	Dim.3	Dim.4
FAST_Chase.Received	V2	1	-0.06	0.73	0.11	0.29
FAST_Circling.Received	V4	1	-0.12	0.34	-0.49	0.26
FAST_Mouth.Fight.Received	V8	1	0.26	0.52	-0.26	0.42
FAST_Lateral.Fight.Received	V10	1	0.27	0.24	-0.51	0.26
FAST_Nipping.Received	V12	1	0.04	0.68	0.1	0.39
FAST_Flight.Given	V5	2	-0.04	0.35	0.18	-0.42
FEED_Chase.Received	V14	2	0.19	0.68	0.43	-0.17
FEED_Circling.Received	V16	2	0.25	0.17	0.38	-0.07
FEED_Flight.Given	V17	2	-0.08	0.31	0.41	0.02
FEED_Lateral.Fight.Received	V22	2	0.2	0.34	0.46	-0.1
FEED_Nipping.Received	V24	2	0.24	0.50	0.56	-0.17
FAST_Chase.Given	V1	4	0.79	0.34	-0.19	-0.13
FAST_Circling.Given	V3	4	0.61	0.16	-0.42	-0.16
FAST_Flight.Received	V6	4	0.56	0.21	0.02	-0.32
FAST_Mouth.Fight.Given	V7	4	0.42	0.45	-0.42	-0.08
FAST_Lateral.Fight.Given	V9	4	0.27	0.26	-0.49	-0.22
FAST_Nipping.Given	V11	4	0.74	0.40	-0.25	-0.13
FAST_AI	V25	4	0.76	-0.02	-0.22	-0.37
FEED_Chase.Given	V13	3	0.87	-0.28	0.1	0.09
FEED_Circling.Given	V15	3	0.79	-0.25	0.13	-0.04
FEED_Flight.Received	V18	3	0.75	-0.32	0.03	-0.05
FEED_Mouth.Fight.Given	V19	3	0.61	-0.12	0.31	0.26
FEED_Mouth.Fight.Received	V20	3	0.49	0.02	0.24	0.40
FEED_Lateral.Fight.Given	V21	3	0.60	-0.18	0.34	0.2
FEED_Nipping.Given	V23	3	0.79	-0.17	0.3	0.11
FEED_AI	V26	3	0.73	-0.36	-0.02	0.25
AI	V27	3	0.85	-0.28	-0.13	0.04

Eigenvalues	7.8	3.7	2.8	1.5
% variance explained	29	13.6	10.3	5.6
Cumul. % variance expl.	29	42.6	52.9	58.4

Table 5 – The correlations between growth and efficiency measurements and agonistic behaviours represented by the AIs for the total data set and each experimental period and the first three PCA dimensions (Dim 1-3). The eigenvalues of the PCA analysis, percent variance and cumulative percent variance explained by each PCA dimension are given at the bottom of the table. Strong positive associations with a PCA dimension are given in bold and strong negative associations in italics.

	Dim.1	Dim.2	Dim.3
BW1	0.90	-0.14	-0.29
BW2	0.89	-0.11	-0.25
BW3	0.95	-0.09	0.10
BW.fasting	<i>-0.55</i>	0.26	0.41
BW.refeed	0.89	-0.08	0.27
BWG	0.49	<i>-0.31</i>	0.76
FI	0.72	<i>-0.29</i>	0.16
FCE	<i>-0.27</i>	-0.11	0.80
FAST_AI	0.30	0.72	0.12
FEED_AI	0.36	0.81	0.10
AI	0.38	0.90	0.08
Eigenvalues	4.8	2.3	1.7
% variance explained	43.6	20.9	15.2
Cumul. % variance expl.	43.6	64.5	79.7

Figures

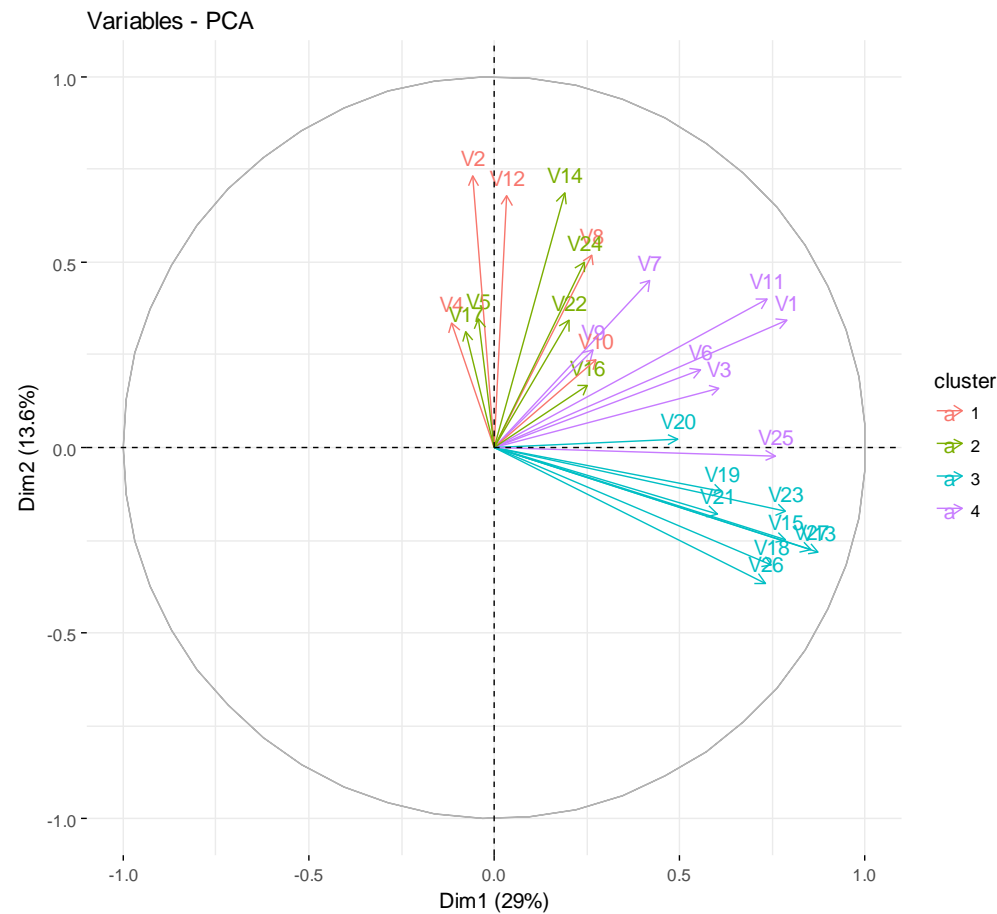


Figure 1 – The relationships among the 27 agonistic behaviours with four groups identified from cluster analysis shown in different colours under the heading cluster 1 (green), 2 (red), 3 (purple), 4 (blue). Details of the characters are given in Table 4.

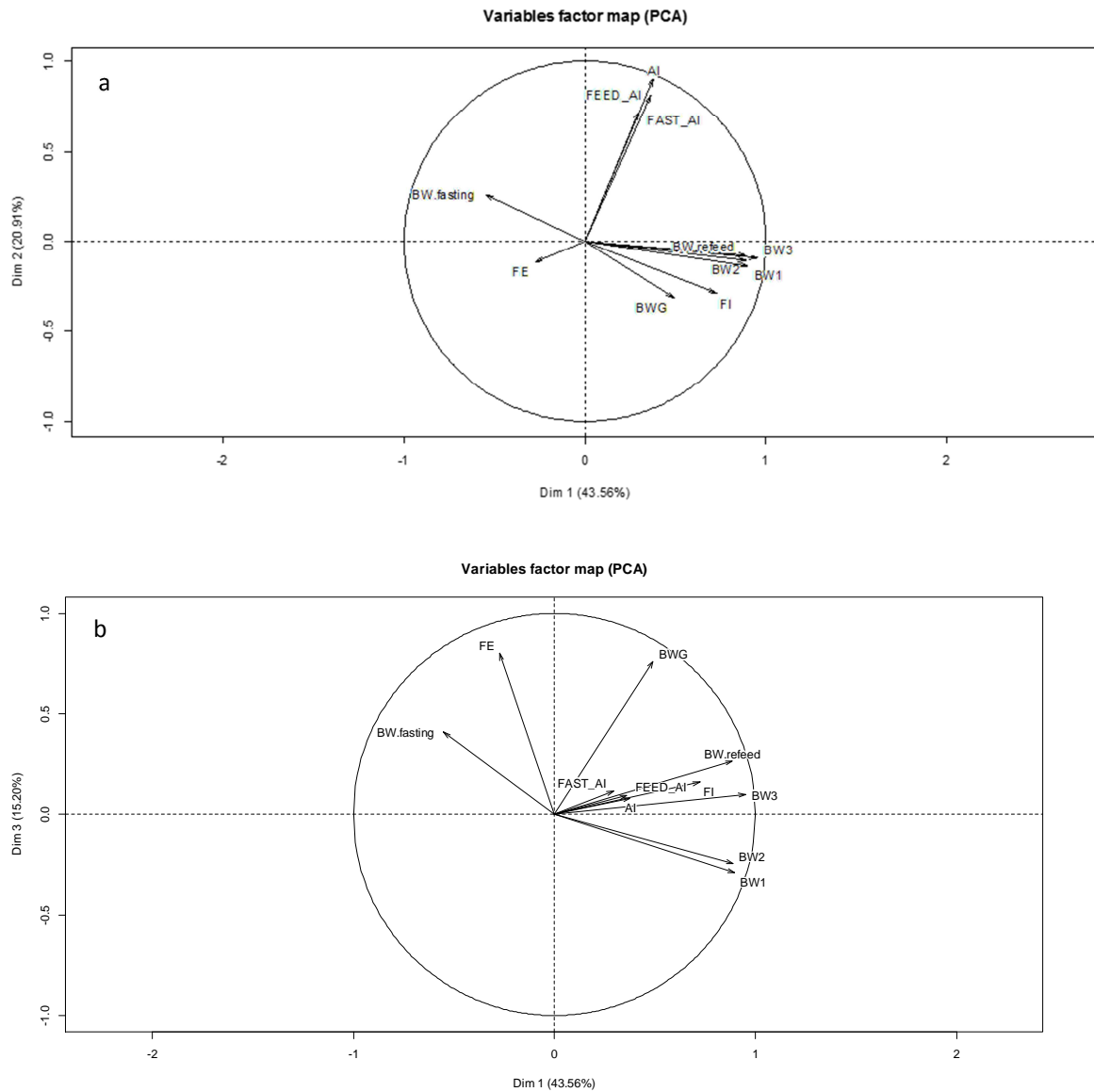


Figure 2 – The relationships among the growth and feed efficiency measurements and the agonistic behaviours represented by the aggressive indices for the total data set and for each of the fasting and feeding periods: **a)** axes represented dimensions 1 and 2 (total of 64.47 % of variance explained) and **b)** axes represent dimensions 1 and 3 (total of 58.76 % of variance explained).