

Research article

Aquarium cichlid fish *Tropheus moorii* flexibly adjust hierarchy when tank fish species composition changes: A pilot study

Elisabetta Palagi¹, Roberto Barbuti¹ and Ivan Norscia^{1,2}

¹Natural History Museum, University of Pisa, Via Roma 79, Calci, Pisa 56011, Italy.

²Department of Life Sciences and System Biology, University of Torino, Via dell'Accademia Albertina, 13, Turin 10123, Italy.

Correspondence: Elisabetta Palagi, elisabetta.palagi@unipi.it

Keywords: dyadic aggression; fish composition management; hierarchical adjustment; socio-environmental perturbation; winner–loser matrix;

Article history:

Received: 30 Apr 2018

Accepted: 27 Nov 2019

Published online: 30 Apr 2020

Abstract

An important aspect in the assessment of an individual's life quality is the impact of such changes on dominance hierarchy, which in turn affects physiology, food access and reproductive success. This study measured the effect of changes in tank fish composition on the hierarchy of a stock of 10 individuals of the cichlid fish (*Tropheus moorii*) hosted in the aquarium of the Natural History Museum of the University of Pisa. During data collection, to ensure animal welfare in the management process, 10 individuals of *Neolamprologus multifasciatus* were introduced and one individual of *Simochromis babaulti* removed (perturbation event). For the first time in a fish species, measures of linearity (corrected Landau's h' index based on binary dyadic dominance relationships), steepness (based on Normalised David's Scores), and triangle transitivity (based on the transitivity of dominance relationships within triads) were combined. A total of 932 agonistic encounters were collected across three observation periods: Periods 1, 2 and 3 (25 hours of observations/period). Hierarchical relationships were assessed using aggressor/aggressee socio-matrices. Aggression rates plummeted from Period 1 (prior to the perturbing event) to Period 2 (immediately following the event) probably due to novel-event related behavioural inhibition. Linearity and steepness levels decreased with an increase in unknown relationships, but the frequency of one-way relationships increased possibly because high ranking individuals targeted subordinates to avoid rank reversal. In Period 3, steepness, linearity and aggression levels increased to initial levels (Period 1). Only the alpha male remained unchanged across the three periods. Thus, dominance relationships remained linear, but the initial hierarchy was not fully restored following the perturbing event. In conclusion, to ensure welfare it is suggested that aquarium stocks of *Tropheus moorii* be monitored following tank composition changes, because although they may flexibly adapt to them this does not necessarily occur in the short term.

Introduction

A common environmental perturbation to which aquarium fish are exposed is the change in composition of species and/or number of subjects in the tank. In group-living vertebrates, from fish to mammals, a crucial variable that affects life quality is dominance hierarchy, as this can impact on health, access to food and reproductive potential (Clutton-Brock 1982; Cordonni and Palagi 2015; Gilmour et al. 2005; Jobling 1993; Krebs and Davies 1987; Sapolsky 2005; von Holst et al. 2002). In fish, the social status of individuals resulting from dominance relationships can affect organism physiology and stress responses (e.g. in different cichlid species; Fox et al. 1997; Maruska 2014; Rodgers et al. 2007; Sloman et al. 2000),

with possible repercussions on reproductive success (Maruska 2014; Paull et al. 2010) and group stability (Nelissen 1985). On the other hand, environmental changes can influence the stability of dominance hierarchy by modifying competitive abilities of individuals within a social group (McNicol and Noakes 1984; Sneddon et al. 2006). In captivity, this aspect is particularly important for animal welfare, because during aggressive encounters, individuals cannot flee as they would in the wild and mismanagement can lead to increased mortality (Huntingford et al. 2016).

Different methods and analytical tools have been elaborated to measure the dominance hierarchy of social groups, starting from winner–loser matrices of dyadic aggression (Landau 1951; Shizuka and McDonald 2012; de Vries et al. 2006). However, no

single method can fully define the dominance relationships and in order to ensure a proper assessment for management purposes, different methods must be combined for a reliable profile of social dominance (Balasubramaniam et al. 2012; Norscia and Palagi 2015, 2016).

One basic measure of hierarchy properties is linearity, which depends on the binary dominance relationships existing within the social group, the proportion of known versus unknown relationships, and their transitivity (Appleby 1983; Kendall 1962; Landau 1951; de Vries 1995). The level of linearity can be quantified via the corrected Landau's index (h' ; Landau 1951). Nevertheless, some scholars have observed that hierarchies with comparable linearity values (h') can differ in the degree of inter-individual power asymmetry (Flack and de Waal 2004). Therefore, linearity alone is not sufficient to describe hierarchy (Balasubramaniam et al. 2012; Norscia and Palagi 2015). Following this observation, another property of dominance hierarchy has been elaborated, known as steepness (de Vries et al. 2006). This measure is related to the size of the absolute differences between adjacently ranked individuals in their success in winning agonistic encounters. In sum, linearity results from the direction of power asymmetry, whereas steepness also considers the extent of power asymmetry (Flack and de Waal 2004; de Vries et al. 2006).

The steepness measure also has its limitations, because it is negatively influenced by the proportion of zero dyads in the matrix corresponding to the pairs of individuals with no interactions (Klass and Cords 2011; de Vries et al. 2006). To overcome this possible problem, Shizuka and McDonald (2012, 2014) elaborated a further hierarchy measure, known as triangle transitivity (t_{tri}), which is based on the transitivity of dominance relationships among sets of three individuals all interacting with each other. This measure is less sensitive to zero dyads, thus being more reliable in case of unknown relationships. Since the triangle transitivity index refers to the whole group, it is suitable for inter-group comparisons, but it does not allow calculating inter-individual dominance differences within groups.

Given the advantages and drawbacks of each hierarchy measure, this work combines the three approaches described above to define hierarchy properties, and this is done for the first time in a fish species. This study investigates hierarchy changes in a captive stock of cichlid fish (*Tropheus moorii*) known for possessing directional dominance relationships both within and between morphs (Kohda 1991). To this purpose, the following predictions were formulated.

Prediction 1 – Hierarchy linearity

The literature provides direct and indirect evidence that in different cichlid species individuals can be arranged within their groups according to a linear ranking order (Alonso et al. 2012; Nelissen 1985; Olivera and Almada 1995). Chase et al. (2002) described linear hierarchy for the cichlid fish *Metriaclicma zebra* and linearity was re-established and maintained when individuals and subgroups were isolated and then reunited. Dey et al. (2013) found that dominance hierarchy of the cooperatively breeding cichlid *Neolamprologus pulcher* was highly linear and that interactions within dyads were directionally consistent. Additionally, Kohda (1991) observed that in wild *Tropheus moorii* the majority of aggressive encounters were directional, which suggests hierarchy linearity. Based on these elements, a linear dominance hierarchy is expected in captive *Tropheus moorii*, characterised by a high level of transitive relationships.

Prediction 2 – Hierarchy maintenance

The scarce literature available indicates that different types of perturbing events (e.g. habitat changes or presence of sexually active individuals) can change the structure of intra-group

dominance relationships in fish (Sloman et al. 2000; Sneddon et al. 2006) and other animals (e.g. house sparrows, *Passer domesticus*: Kubitz et al. 2015; wolves, *Canis lupus*: Cordoni and Palagi 2015; primates: Pruett and Isbell 2000; Sclafani et al. 2012). Fish hierarchies can become unstable after environmental perturbations (McNicol and Noakes 1984; Sneddon et al. 2006). Moreover, hierarchy linearity alone does not necessarily inform the stability of the dominance structure (e.g. in *Oreochromis mossambicus*: Olivera and Almada 1996). Based on this framework, this study expected the properties of the dominance relationships—degree of linearity, steepness and transitivity—in the study stock of *Tropheus moorii* to change after an event perturbing the homeostasis of the tank environment.

Materials and methods

Ethics statement

This research complied with current laws of Italy and the European Community. This investigation was purely observational and opportunistic. No animal was moved or manipulated for this specific study. Observations were carried out during the routine management procedures that are performed, in compliance with the law, to ensure animal welfare. Hence, the ethical committee of the University of Pisa waived the need for a permit.

Study species and group, and captive conditions

The cichlid fish *Tropheus moorii* is endemic to Lake Tanganyika. The species is sexually monomorphic and territorial. *Tropheus moorii* inhabit rocky shores where they feed on hypolithic algae. Males and females actively defend their territory (Egger et al. 2006; Sturmbauer and Dallinger 1994; Sturmbauer et al. 2008; Yanagisawa and Nishida 1991; Yanagisawa and Sato 1990). More than 100 different colour morphs can be distinguished in *Tropheus moorii* (Herler et al. 2010; Maderbacher et al. 2008). Each morph inhabits a specific rocky area separated from the others by sandy gaps. Because the species is confined to rocky environments, the mixing of different morphs is highly improbable. Different morphs exhibit assortative mating among populations (Egger et al. 2008; Hermann et al. 2015; Salzburger et al. 2006; Sefc et al. 2015).

The study group comprised 10 immature individuals of the regional morph “black Bemba”, hosted in a tank with multiple fish species. The individuals of this morph can be easily recognised by the orange spots on their body. The group was composed of six males (labelled: V, LI, FA, S, P, TR) and four females (labelled: CI, CH, DO, TO). Individuals had been together in the tank for six months before the beginning of the study.

Sex identification was carried out by examining the genital papilla. In females, the size of the genital papilla is twice that of males (Sturmbauer et al. 2010). Individual identification was based on the different colouration of individuals; in particular, the orange spots covering the middle third of the body. The chemical–physical conditions and group composition were not changed during the observation period. The study group was kept in a tank of 110×100×75 cm with a capacity of 650 l, constant temperature (24°C), pH=7.5, and with 12 hours light (constant illumination) and 12 hours dark. For the tank, tap water of the public supply was used. A quantity of water corresponding to 10% of the tank capacity was changed on a daily basis. The tank substrate was composed by gravel and small rocks. The fish were fed every morning with a vegetable-based fish food (Tetra-Phyll; TETRA Werke, Melle, Germany).

Study period, data collection and perturbing event

At the beginning of the study, the same tank hosted seven individuals of *Tropheus brichardi*, seven individuals of *Tropheus polli*, and one individual of *Simochromis babaulti*. After a 10-hour

Table 1. Winner–loser socio-matrices based on aggressive events that occurred between the individuals of the study stock (10 individuals of *Tropheus moorii*) during the three observation periods: Period 1 (top), Period 2 (middle) and Period 3 (bottom). Grey cells indicate females and white cells males.

Period 1											
	CI	V	LI	FA	CH	S	TR	DO	TO	P	
CI	0	5	1	4	4	8	0	11	0	4	
V	1	0	4	5	0	2	0	3	0	0	
LO	0	1	0	0	1	2	0	0	0	0	
FA	2	11	16	0	3	14	3	13	3	12	
CH	1	6	10	5	0	1	0	2	1	2	
S	1	2	4	2	3	0	0	1	0	0	
TR	3	2	15	4	3	21	0	12	21	17	
DO	4	34	6	11	5	16	1	0	5	8	
TO	16	9	0	9	7	17	2	17	0	5	
P	2	1	1	0	5	4	2	0	0	0	
Period 2											
	CI	V	LI	FA	CH	S	TR	DO	TO	P	
CI	0	4	1	1	1	2	0	6	0	0	
V	0	0	0	0	0	1	0	0	0	1	
LO	0	0	0	0	0	1	0	0	0	1	
FA	2	1	2	0	4	5	0	1	0	2	
CH	0	2	4	2	0	1	0	2	1	2	
S	0	1	0	0	0	0	0	1	0	0	
TR	1	0	0	2	0	2	0	3	3	4	
DO	0	3	0	1	0	0	0	0	1	1	
TO	1	0	0	0	0	1	1	4	0	2	
P	1	1	0	0	0	0	0	0	0	0	
Period 3											
	CI	V	LI	FA	CH	S	TR	DO	TO	P	
CI	0	12	7	10	4	7	2	34	0	3	
V	0	0	1	2	0	2	0	0	0	3	
LO	0	2	0	0	0	5	0	0	0	1	
FA	2	2	13	0	4	8	0	1	2	12	
CH	0	5	4	4	0	10	0	5	1	12	
S	0	2	3	1	1	0	0	0	1	1	
TR	5	4	2	11	4	7	0	5	32	7	
DO	3	19	3	11	6	13	1	0	5	3	
TO	2	7	3	1	1	17	0	5	0	0	
P	0	10	0	0	10	4	0	0	2	0	

training period, individuals of *Tropheus moorii* were observed over four non-consecutive days for about 25 hours, from 24 to 30 January 2013.

In the period 1 to 4 February 2013, observations were suspended because, for management purposes, 10 individuals of *Neolamprologus multifasciatus* were introduced in the tank and the individual *S. babaulti* removed due to its aggressive behaviour

toward the newly introduced individuals. Two individuals of *T. brichardi* were eventually removed and the final arrangement of the tank was reached. Figure 1 provides an overview of the changes that occurred in the tank.

Observations resumed after this perturbing event, on 5 February 2013. The animals were observed during the period 5 to 26 February 2013 (on non-consecutive days) during two blocks of data collection (25 hours each). Observations always took place between 1000 and 1500.

The whole observation period was divided into three blocks of the same duration: Period 1 (25 observation hours prior to the perturbing event), Period 3 (the last 25 hours of observations) and Period 2 (25 hours of observation in between Periods 1 and 3).

During the observation period, the dyadic agonistic encounters (one-sided attack and chase; Kohda 1991) were recorded via all occurrence sampling (Altmann 1974). The opponents' identity was recorded. Data were used to fill in aggression socio-matrices, shown in Table 1.

Hierarchy linearity, steepness, triangle transitivity and statistical approach

Hierarchy linearity was measured using software Matman 1.0 (10.000 randomisations), which returned the value of the Landau's corrected linearity index h' and its statistical significance. The index takes into account the number of unknown relationships and ties (de Vries 1995, 1998; de Vries et al. 1993). The analysis was conducted on aggression socio-matrices (Table 1).

Using the same socio-matrices, the steepness was determined via Steepness 2.2 (Leiva and de Vries 2011). This measure indicates the absolute slope of the straight line fitted to the Normalised David's Scores (NDS) plotted against the subjects' ranks (de Vries et al. 2006). Normalised David's Scores were obtained using a dyadic dominance index (Dij) in which the observed proportion of wins (Pij) is corrected for the chance occurrence of the observed outcome. The chance occurrence of the observed outcome is calculated based on a binomial distribution with each animal having an equal chance of winning or losing every dominance encounter (de Vries et al. 2006). The correction is necessary when, as in the case of the present study group, the interaction numbers greatly differ between dyads. The NDS-based hierarchy was determined by ranking the individuals according to their NDSs.

The proportion of transitive triangles relative to all triangles (P_t) and the triangle transitivity metric (t_{tri}) were calculated using the codes provided in Shizuka and McDonald (2012; supplementary material; errata corrige: Shizuka and McDonald 2014). Such codes were applied to aggression socio-matrices, entered into csv files, using the package 'statnet' (Hancock et al. 2003) in the R programming environment (R Development Core Team 2011).

To account for possible data pseudo-replication, statistical randomisation procedures were employed for across-period comparisons (Resampling Procedures 1.3 by David C. Howell; 10,000 permutations). In particular, one-way Anova via randomisation was used to compare the aggression frequencies between periods at the individual level, and to compare the absolute differences of steepness values between adjacently ranked individuals across the three periods. The correlation test via randomisation was used to compare individuals' ranking positions across periods. To carry out the analyses, data were entered into text files saved with ".dat" extension.

Results

A total of 932 agonistic encounters were recorded (Period 1: 456; Period 2: 84; Period 3: 392; Table 1). The aggression frequencies were significantly different across periods (one-way Anova via randomisation: F=6.159, n=10, P=0.006). Pairwise comparisons

Table 2. Table showing, for the three study periods (Period 1: P1; Period 2: P2; Period 3: P3), the values related to binary dyadic relationships (I&SI), including Landau's corrected index (h'), unknown and one-way relationships (%), and the Directional Consistency Index (DC). It also shows the steepness values, with related probability, based on Normalised David's Scores, and triangle transitivity (P_t : proportion of transitive triangles over the total; t_{tri} : triangle transitivity metric). All results were obtained from aggression socio-matrices (see Figure 2).

	Linearity	h'	DC	Unknown relationships	One-way relationships	Steepness	P_t	t_{tri}
P1	yes	0.824 (P=0.0006)	0.733	2.22%	46.67%	0.795 (P=0.0001)	0.771	0.083
P2	yes	0.533 (P=0.0460)	0.810	20%	64.44%	0.527 (P=0.0019)	0.869	0.475
P3	yes	0.776 (P=0.0005)	0.745	0%	55.56%	0.786 (P=0.0001)	0.863	0.450

revealed that aggression frequencies significantly decreased from Period 1 to Period 2 (paired-sample via randomisation: $t=-3.525$, $n=10$, $P=0.0001$; Figure 2) and significantly increased from Period 2 to Period 3 (paired-sample via randomisation: $t=3.776$, $n=10$, $P=0.0023$; Figure 2). Instead, no significant difference was found between Periods 1 and 3 (paired-sample via randomisation: $t=-2.416$, $n=10$, $P=0.070$; Figure 2), which indicates that the initial aggression levels (Period 1), which plummeted in the transitional period (2), were restored in the final period (3).

Table 2 shows the results of the analyses conducted on aggression socio-matrices, to calculate hierarchy linearity, steepness and triangle transitivity. Hierarchy remained linear across periods even though the percentage of unknown relationships was highest and the degree of linearity (measured via Landau's corrected index), the steepness and the level of triangle transitivity, were lowest during Period 2. Figure 3 shows the different steepness of hierarchy in the three periods. However, during Period 2, the frequency of one-way relationships was highest, as indicated by the highest

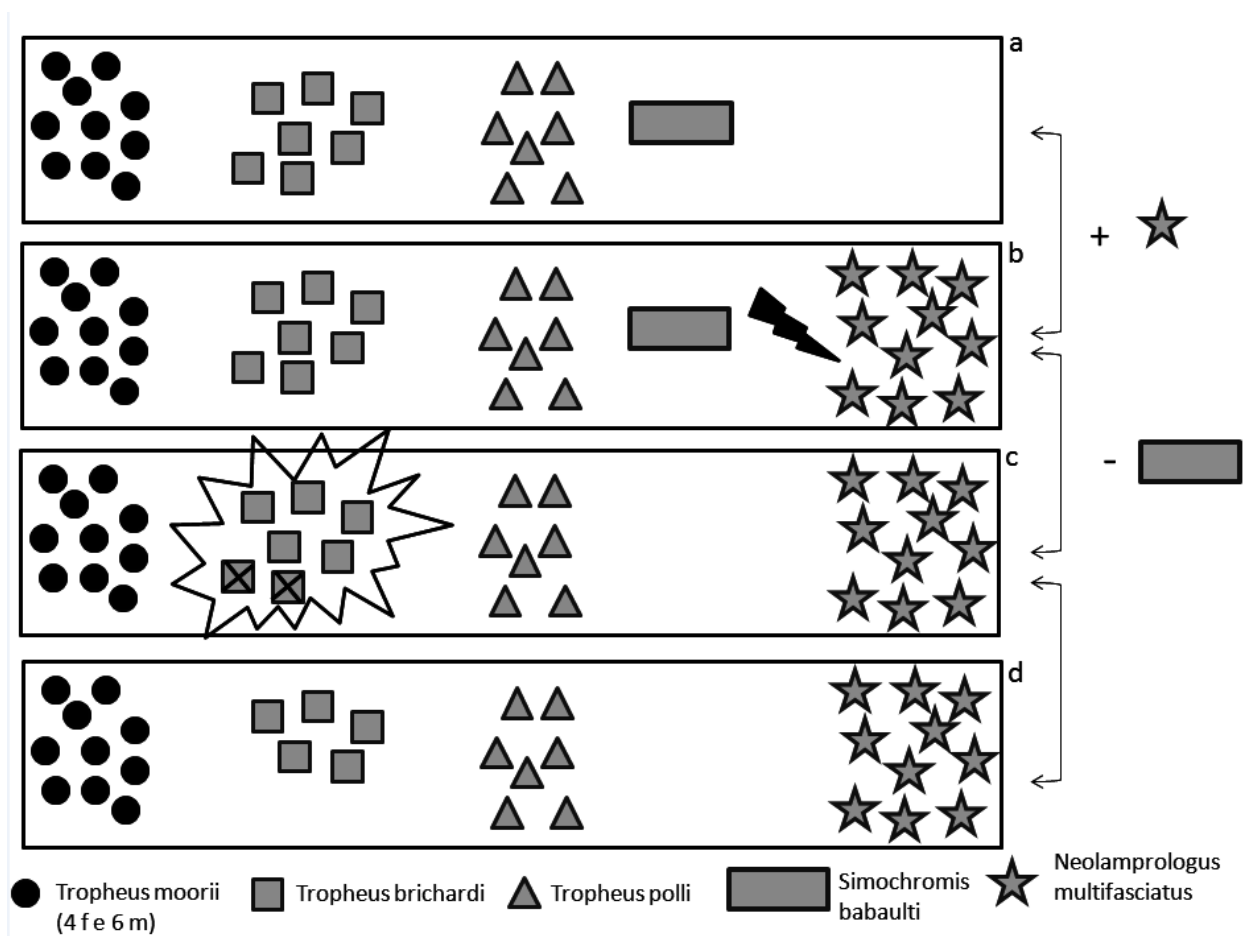


Figure 1. The arrangement of the tank changed over time: (a) initially (24 January 2013), the tank hosted the study stock of 10 individuals of *Tropheus moorii* (regional morph Black Bemba), seven individuals of *Tropheus brichardi*, seven individuals of *Tropheus polli* and one individual of *Simochromis babaulti*; (b) in the period 1 to 4 February 2013, 10 individuals of *Neolamprologus multifasciatus* were introduced into the tank and the individual *S. babaulti* removed; (c) due to an increase in aggression, two individuals of *T. brichardi* were then removed, which led to the final arrangement of the tank (d).

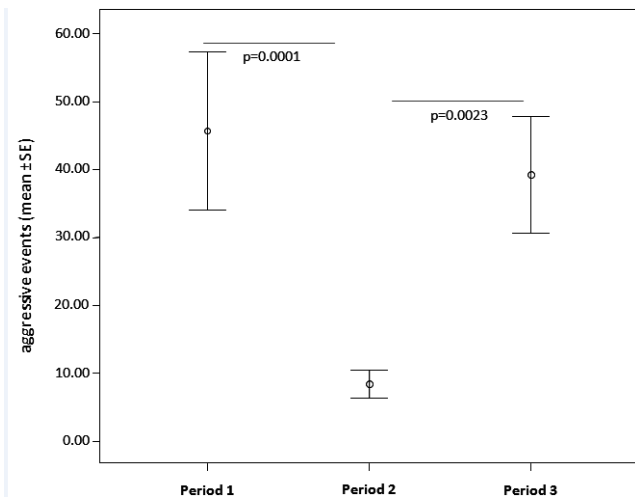


Figure 2. Number of aggressive events (mean \pm SD; Y axis) that occurred between the individuals of *Tropheus moorii* during the three study periods (X axis: Period 1, left; Period 2, centre; Period 3: right). Aggression frequencies significantly decreased from Period 1 to Period 2 (paired-sample via randomisation: $t=-3.525$, $n=10$, $P=0.0001$) and significantly increased from Period 2 to Period 3 (paired-sample via randomisation: $t=3.776$, $n=10$, $P=0.0023$). No significant difference was found between Periods 1 and 3 (paired-sample via randomisation: $t=-2.416$, $n=10$, $P=0.070$). Only significant results are reported in the figure.

value of the directional consistency index (Table 2). Moreover, the ranking order did not remain the same across periods (Figure 3). The dominant male (TR) was the only individual maintaining the same exact hierarchical position in all periods.

When the individuals were ordered, within each period, according to the Normalised David's Scores (NDS, Figure 3), the resulting hierarchies were strongly correlated in all periods (correlation via randomisation; Period 1 vs Period 2: $r=0.976$, $P<0.0001$; Period 2 vs Period 3: $r=0.952$, $P<0.0001$; Period 1 vs Period 3: $r=0.952$, $P<0.0001$). However, the ranking order of individuals was not exactly the same (Figure 3).

Discussion

The results show that in the study stock of *Tropheus moorii*, the hierarchy is linear (Prediction 1 confirmed) and that although linearity is maintained over time, the structure of the dominance relationships changes after environmental perturbation (Prediction 2 confirmed). A correct assessment of the dominance relationships is important in captive management because adding and/or removing fish can disrupt hierarchies and potentially cause injury and or death. This study provides a tool to reliably measure variation in aggression dynamics following perturbation caused by management, a factor that should be explicitly considered by aquarium keepers to ensure animal welfare.

The linear hierarchy found in the present study stock is in line with Kohda (1991)'s observation that more than 90% of aggressive events between individuals of *Tropheus moorii* were one sided, thus clearly unidirectional. The possibility that individuals

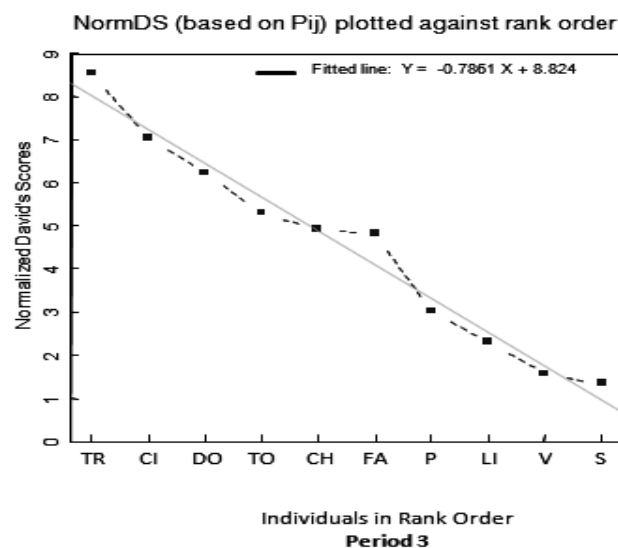
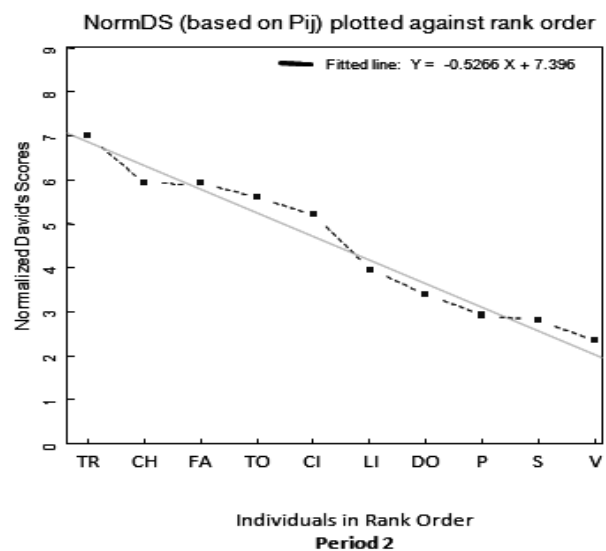
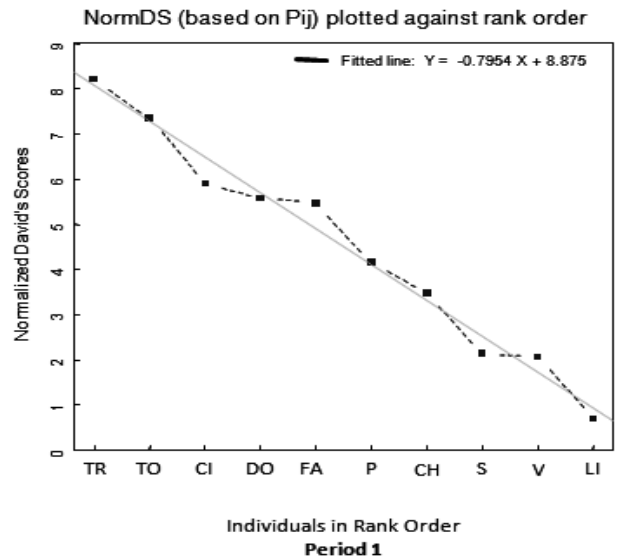


Figure 3. The graph—output of Steepness 2.2—shows Normalised David's Scores (corrected for chance; Y axis) plotted against ordinal rank order (dashed black line), and the fitted line (black, solid line) for the study stock (10 individuals of *Tropheus moorii*) in the three observation periods. The ranking order of individuals (X axis) shows that the dominant male (TR) remained the same in the three periods. Two other males, S and V, remained within the bottom three positions for the whole study period.

can be arranged according to a linear ranking order has also been suggested in other cichlid fish species via: i) removal/re-introduction of dominant individuals (*Cichlasoma dimerus*; Alonso et al. 2012); ii) the possibility to arrange individuals according to a linear ranking order (*Melanochromis auratus*; Nelissen 1985); iii) calculation of Landau's linearity index (*Oreochromis mossambicus*; Olivera and Almada 1995); and iv) calculation of triangle transitivity (*Neolamprologus pulcher*; Dey et al. 2013).

Linearity was maintained across the three study periods (Periods 1 to 3; Table 2), prior to and following the perturbing event (introduction in the tank of 10 individuals of *Neolamprologus multifasciatus* and removal of the individual *Simochromis babaulti*; Figure 1). Moreover, hierarchies were strongly correlated between periods, thus suggesting that dominance relationships of *Tropheus moorii* were, at least to a certain extent, stable. This is in line with the overall dominance network stability found in the cichlid *Neolamprologus pulcher* across different periods (Dey et al. 2015).

However, although hierarchy linearity was preserved over time in the present study stock, the ranking order of individuals did not remain the same after the perturbation event (Figure 3), which indicates that the original dominance relationships were not restored. In the cichlid species *Metriaclima zebra*, Chase et al. (2002) found that when the fish stocks were separated into subgroups and then reunited, the linearity of the structures persisted but the individual ranks changed. In the same species, transitive dominance relationships also changed depending on the social context (socially embedded pairs than in isolated pairs; Chase et al. 2003), which is consistent with the hypothesis that the hierarchy results from a dynamic network of aggressive interactions among group members that is updated with each successive act (Chase and Lindquist 2016). Consistently, Olivera and Almada (1996) found that in *Oreochromis mossambicus*, the hierarchical arrangements changed over the study period, even though linear structures tended to succeed to linear structures as time passed. Environmental modifications resulted in changes in the ranking order of individuals in other fish species, such as *Salvelinus fontinalis* (McNicol and Noakes 1984) and *Gasterosteus aculeatus* (Sneddon et al. 2006).

In the present study stock, the perturbing event was followed by a significant decrease of aggression (Period 2) whose initial levels (those of Period 1) were restored at a later stage (Period 3; Figure 2). The lower rates of attacks probably explain the highest percentage of unknown relationships that led to a lower degree of hierarchy linearity, steepness and triangle transitivity (Table 2; Figure 3) recorded in Period 2 compared to the other periods. After the perturbing event, the hierarchy was less linear (but still linear, as explained above) and shallower. The individuals of *Neolamprologus multifasciatus* introduced between Periods 1 and 2 are characterised by a very small size (reaching hardly more than 3 cm total length). They occupied empty shells on the floor, as is typical for this species (Schradin and Lamprecht 2002). Thus, the decrease in frequency of aggressive encounters observed in the study species in Period 2 was not due to general motor activity inhibition caused by crowding (elevator effect, sensu de Waal et al. 2000). Instead, the aggression reduction that followed the introduction of *Neolamprologus multifasciatus* may have been due to a form of behavioural withdrawal (or freezing effect) related to the novel situation. This strategy might be adaptive due to the potential risks associated with an unknown environment (Tang et al. 2012). Aggression reduction can be observed after perturbing events, as it occurs in aquaculture salmonid fish: hierarchy is artificially disrupted in aquaculture salmonid fish via environmental perturbation to lower the levels of aggression and allow uniform growth of all individuals (Adams et al. 1995; Cutts et al. 1998; Davis and Olla 1987; Huntingford and Leaniz 1997).

In the present study group, the decrease of aggression rates

was accompanied by an increase in the frequency of one-way relationships, as also indicated by the value of the directional consistency index, which peaked during Period 2 (Table 2). A plausible explanation is that when the number of aggressive events is reduced, so are the occasions that high-ranking individuals have to re-establish their dominance over others. Consequently, it is likely that high-ranking individuals strategically targeted subordinates leaving few, if no, possibilities for subordinates to attack back (bidirectional encounters) and attempt rank reversal. This aspect is important for animal welfare and should be considered in aquarium management, with future work also extending the analysis to changes in aggression intensity. Intensity is currently not taken into account as a variable in the hierarchy calculation from aggression socio-matrices.

Indeed, it has been demonstrated in the cichlid *Astatotilapia burtoni* that males are aware of their social environment and are able to modulate their aggressive behaviours for reproductive and social advantage (Desjardins et al. 2012). Consistently, it was found that the dominant individual (TR) remained the same across the three periods and that the subordinate individuals occupying the lowest three positions were the same in the initial and final periods (S, V and LI) with two of them (S and V) remaining in the last three positions in all periods. This situation is consistent with previous findings by Sneddon et al. (2006) in the three spined stickleback (*Gasterosteus aculeatus*). After examining how social interactions changed following environmental perturbations, the authors concluded that it would benefit an individual to be either dominant, because it can have access to food through high aggression levels, or highly submissive, in the lowest ranks of the hierarchy, so as to avoid aggressive interactions and sneakily obtain access to food.

In conclusion, the use of different quantitative methods to highlight the hierarchy properties in *Tropheus moorii* has revealed, for the first time in this species, that dominance relationships can be adjusted and partially restored after a perturbing event, in the short period. This multifaceted methodology can shed light on the behavioural mechanisms that may be used by these cichlids to cope with environmental perturbations in a confined space. If properly replicated and confirmed, these findings can enhance the management of *Tropheus moorii* in aquaria, frequently involving changes in the composition of species and/or number of subjects in the tank to ensure animal welfare.

Acknowledgements

The authors would like to thank Claudia Lucchesi for her assistance in data collection, David Leiva for guidance on the use of the steepness add-in for Excel and Paolo Rosa-Clot for his help with the R codes for triangle transitivity. We also thank Centine Banfi for useful suggestions. We do not have any conflict of interest to declare.

References

- Adams C.E., Huntingford F.A., Krpal J., Jobling M., Burnett S.J. (1995) Exercise, agonistic behaviour and food acquisition in Arctic charr, *Salvelinus alpinus*. *Environmental Biology of Fishes* 43: 213–218.
- Alonso F., Honji R.M., Moreira R.G., Pandolfi M. (2012) Dominance hierarchies and social status ascent opportunity: anticipatory behavioral and physiological adjustments in a Neotropical cichlid fish. *Physiological Behaviour* 106: 612–618.
- Altmann J. (1974) Observational study of behaviour sampling methods. *Behaviour* 49: 227–265.
- Appleby M.C. (1983) The probability of linearity in hierarchies. *Animal Behaviour* 31: 600–608.
- Balasubramaniam K.N., Dittmar K., Berman C.M., Butovskaya M., Cooper M.A., Majolo B., Ogawa H., Schino G., Thierry B., de Waal F.B.M. (2012) Hierarchical steepness, counter aggression, and macaque social style scale. *American Journal of Primatology* 74: 915–925.

- Chase I.D., Tovey C., Spangler-Martin D., Manfredonia M. (2002) Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences USA* 99: 5744–5749.
- Chase I.D., Tovey C., Murch P. (2003) Two's company, three's a crowd: differences in dominance relationships in isolated versus socially embedded pairs of fish. *Behaviour* 140: 1193–1217.
- Chase I.D., Lindquist W.B. (2016) The fragility of individual-based explanations of social hierarchies: a test using animal pecking orders. *PLoS ONE* 11(7): e0158900.
- Clutton-Brock T.H. (1982) *Red deer. Behaviour and ecology of two sexes*. Edinburgh University Press, Edinburgh, UK.
- Cordoni G., Palagi E. (2015) Aggression and hierarchical steepness inhibit social play in adult wolves. *Behaviour* 153: 749–766.
- Cutts C.J., Betcalfe N.B., Caylor A.C. (1998) Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology* 52: 1026–1037.
- Davis M.W., Olla B.L. (1987) Aggression and variation in growth of chum salmon (*Oncorhynchus keta*) juveniles in seawater: effects of limited ration. *Canadian Journal of Fish and Aquatic Science* 44: 192–197.
- Desjardins J.K., Hofmann H.A., Fernald R.D. (2012) Social context influences aggressive and courtship behavior in a cichlid fish. *PLoS ONE* 7: e32781.
- Dey C.J., Reddon A.R., O'Connor C.M., Balshine S. (2013) Network structure is related to social conflict in a cooperatively breeding fish. *Animal Behaviour* 85: 395–402.
- Dey C.J., Tan Q.J., O'Connor C.M., Reddon A.R., Caldwell J.R. (2015) Dominance network structure across reproductive contexts in the cooperatively breeding cichlid fish *Neolamprologus pulcher*. *Current Zoology* 61: 45–54.
- de Waal F.B., Aureli F., Judge P.G. (2000) Coping with crowding. *Scientific American* 282: 76–81.
- de Vries H. (1995) An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour* 50: 1375–1389.
- de Vries H. (1998) Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. *Animal Behaviour* 55: 827–843.
- de Vries H., Netto W.J., Hanegraaf P.L.H. (1993) MatMan: a program for the analysis of sociometric matrices and behavioural transition matrices. *Behaviour* 125: 157–175.
- de Vries H., Stevens J.M.G., Vervaecke H. (2006). Measuring and testing steepness of dominance hierarchies. *Animal Behaviour* 71: 585–592.
- Egger B., Obermüller B., Sturmbauer C., Phiri H., Sefc K.M. (2006) Monogamy in the maternally mouthbrooding Lake Tanganyika cichlid fish *Tropheus moorii*. *Proceedings of the Royal Society of Biology* 273: 1797–1803.
- Egger B., Obermüller B., Eigner E., Sturmbauer C., Sefc K.M. (2008) Assortative mating preferences between colour morphs of the endemic Lake Tanganyika cichlid genus *Tropheus*. *Hydrobiologia* 615: 37–48.
- Flack J., de Waal F.B.M. (2004) *Dominance style, social power, and conflict*. In: Thierry B., Singh M., Kaumanns W. (eds.). *Macaque societies: a model for the study of social organization*. Cambridge University Press, Cambridge, UK, pp. 157–185.
- Fox H.E., White S.A., Kao M.H., Fernald R.D. (1997) Stress and dominance in a social fish. *Journal of Neuroscience* 17: 6463–6469.
- Gilmour K.M., Di Battista J.D., Thomas J.B. (2005) Physiological causes and consequences of social status in salmonid fish. *Integrative and Comparative Biology* 45: 263–273.
- Hancock M., Hunter D., Butts C., Goodreau S., Morris M. (2003) Statnet: software tools for the statistical modelling of network data. Available at <http://statnetproject.org>.
- Herler J., Kerschbaumer M., Mitteroecker P., Postl L., Sturmbauer C. (2010) Sexual dimorphism and population divergence in the Lake Tanganyika cichlid fish genus *Tropheus*. *Frontiers in Zoology* 7: 1–10.
- Hermann C.M., Bruderer V., Zimmermann H., Vollmann J., Sefc K.M. (2015) Female preferences for male traits and territory characteristics in the cichlid fish *Tropheus moorii*. *Hydrobiologia* 748: 61–74.
- von Holst D., Hutzelmeyer H., Kaetzke P., Khachei M., Rodel H.G., Schrutka H. (2002) Social rank, fecundity and lifetime reproductive success in wild European rabbits (*Oryctolagus cuniculus*). *Behavioural and Ecological Sociobiology* 51: 245–254.
- Huntingford F.A., Leanin C.G. (1997) Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. *Journal of Fish Biology* 51: 1009–1014.
- Huntingford F.A., Adams C., Braithwaite V.A., Kadri S., Pottinger T.G., Sandøe P., Turnbull J.F. (2006) Current issues in fish welfare. *Journal of Fish Biology* 68: 332–372.
- Jobling M. (1993) *Bioenergetics: feed intake and energy partitioning*. In: Rankin J.C., Jensen F.B. (eds.). *Fish ecophysiology*. Springer, Netherlands, pp. 1–44.
- Klass K., Cords M. (2011) Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: simulation studies based on data from wild monkeys. *Behavioural Proceedings* 88: 168–176.
- Krebs J.R., Davies N.B. (1987) *An introduction to behavioural ecology*. Blackwell, Boston, pp. 340.
- Kohda M. (1991) Intra- and interspecific social organization among three herbivorous cichlid fishes in Lake Tanganyika, Japan. *Journal of Ichthyology* 38: 147–163.
- Kubitzka R.J., Suhonen J., Vuorisalo T. (2015) Effects of experimental perturbation of group structure on hierarchy formation and behaviour in House Sparrows. *Ornis Fennica* 92: 157–171.
- Landau H.G. (1951) On dominance relations and the structure of animal societies: I. Effect of inherent characteristics. *Bulletin of Mathematical Biophysics* 13: 1–19.
- Maderbacher M., Bauer C., Herler J., Postl L., Makasa L., Sturmbauer C. (2008) Assessment of traditional versus geometric morphometrics for discriminating populations of the *Tropheus moorii* species complex (Teleostei: Cichlidae), a Lake Tanganyika model for allopatric speciation. *Journal of Zoological Systematics and Evolutionary Research* 46: 153–161.
- Maruska K.P. (2014) Social regulation of reproduction in male cichlid fishes. *General and Comparative Endocrinology* 207: 2–12.
- McNicol R.E., Noakes D.L. (1984) Environmental influences on territoriality of juvenile brook charr, *Salvelinus fontinalis*, in a stream environment. *Environmental Biology of Fishes* 10: 29–42.
- Nelissen M.H.J. (1985) Structure of the dominance hierarchy and dominance determining “group factors” in *Melanochromis auratus* (Pisces, Cichlidae). *Behaviour* 94: 85–107.
- Norscia I., Palagi E. (2015) The socio-matrix reloaded: from hierarchy to dominance profile in wild lemurs. *PeerJ* 3: e729. DOI:10.7717/peerj.729.
- Norscia I., Palagi E. (2016) *The missing lemur link: an ancestral step in human evolution*. Cambridge University Press, UK, pp. 289.
- Oliveira R.F., Almada V.C. (1996) On the (in)stability of dominance hierarchies in the cichlid fish *Oreochromis mossambicus*. *Aggressive Behaviour* 22: 37–45.
- Paul G.C., Filby A.L., Giddins H.G., Coe T.S., Hamilton P.B., Tyler C.R. (2010) Dominance hierarchies in zebrafish (*Danio rerio*) and their relationship with reproductive success. *Zebrafish* 7: 109–117.
- Pruett J.D., Isbell L.A. (2000) Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioural Ecology and Sociobiology* 49: 38–47.
- Rodgers E.W., Earley R.L., Grober M.S. (2007) Social status determines sexual phenotype in the bi-directional sex changing bluebanded goby *Lythrypnus dalli*. *Journal of Fish Biology* 70: 1660–1668.
- Salzburger W., Niederstätter H., Brandstätter A., Berger B., Parson W., Snoeks J., Sturmbauer C. (2006) Colour-assortative mating among populations of *Tropheus moorii*, a cichlid fish from Lake Tanganyika, East Africa. *Proceedings of the Royal Society of London [Biology]* 273: 257–266.
- Sapolsky R.M. (2005) The influence of social hierarchy on primate health. *Science* 308: 648–652.
- Schradin C., Lamprecht J. (2002) Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. *Ethology* 108: 237–248.
- Sclafani V., Norscia I., Antonacci D., Palagi E. (2012) Scratching around mating: factors affecting anxiety in wild *Lemur catta*. *Primates* 53: 247–254.
- Sefc K.M., Hermann C.M., Steinwender B., Brindl H., Zimmermann H., Mattersdorfer K., Postl L., Makasa L., Sturmbauer C., Koblmüller S. (2015) Asymmetric dominance and asymmetric mate choice oppose premating isolation after allopatric divergence. *Ecology and Evolution* 5: 1549–1562.
- Shizuka D., McDonald D.B. (2012) A social network perspective on measurements of dominance hierarchies. *Animal Behaviour* 83: 925–934.
- Shizuka D., McDonald D.B. (2014) Errata corrige to (Shizuka, D. and McDonald, D. B. (2012) A social network perspective on measurements of dominance hierarchies. *Animal Behaviour* 83: 925–934). *Animal Behaviour* 87: 243.

- Slovan K.A., Gilmour K.M., Taylor A.C., Metcalfe N.B. (2000) Physiological effects of dominance hierarchies within groups of brown trout, *Salmo trutta*, held under simulated natural conditions. *Fish Physiology and Biochemistry* 22: 11–20.
- Sneddon L.U., Hawkesworth S., Braithwaite V.A., Yerbury J. (2006) Impact of environmental disturbance on the stability and benefits of individual status within dominance hierarchies. *Ethology* 112: 437–447.
- Sturmbauer C., Dallinger R. (1994) Diurnal variation of spacing and foraging behaviour in *Tropheus moorii* (Cichlidae) in Lake Tanganyika, Eastern Africa. *Netherlands Journal of Zoology* 45: 386–401.
- Sturmbauer C., Fuchs C., Harb G., Damm E., Duftner N., Maderbacher M., Koch M., Koblmüller S. (2008) Abundance, distribution, and territory areas of rock-dwelling Lake Tanganyika cichlid fish species. *Hydrobiologia* 615: 57–68.
- Sturmbauer C., Salzburger W., Duftner N., Schelly R., Koblmüller S. (2010) Evolutionary history of the Lake Tanganyika cichlid tribe Lamprologini (Teleostei: Perciformes) derived from mitochondrial and nuclear DNA data. *Molecular Phylogenetics and Evolution* 57: 266–284.
- Tang A.C., Reeb-Sutherland B.C., Romeo R.D., McEwen B.S. (2012) Reducing behavioral inhibition to novelty via systematic neonatal novelty exposure: the influence of maternal hypothalamic-pituitary-adrenal regulation. *Biological Psychiatry* 72: 150–156.
- Yanagisawa Y., Sato T. (1990) Active browsing by mouthbrooding females of *Tropheus duboisi* and *Tropheus moorii* (Cichlidae) to feed the young and/or themselves. *Environmental Biology of Fishes* 27: 43–50.
- Yanagisawa Y., Nishida M. (1991) The social and mating system of the maternal mouthbrooder *Tropheus moorii* (Cichlidae) in Lake Tanganyika. *Japanese Journal of Ichthyology* 38: 271–282.