The interplay between winner—loser effects and social rank in cooperatively breeding vertebrates

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Winner and loser effects are widespread among animal taxa and are known to influence hierarchy formation, although it is unclear how rank influences such effects in species organized in social hierarchies. We investigated the existence of winner and loser effects and the effect of social rank on such effects in Neolamprologus pulcher, a cooperatively breeding cichlid fish. Social groups of these fish are organized in strict linear, size-based hierarchies. We successively assigned a dominant or subordinate rank to each of 18 focal individuals in balanced order, followed by an assigned winning or losing experience, respectively, resulting in a two-by-two factorial design. For each of the four treatment combinations, we recorded the performance of the focal fish in contests over a resource with similar-sized, naïve opponents. Assigned winners won subsequent contests more often than losers, were more likely to escalate the contest and showed more overt aggression during a contest. Moreover, individuals with assigned subordinate rank showed more restrained aggression. However, winner and loser effects were not modulated by rank. This study shows that winner—loser effects exist in a highly social fish with linear social hierarchy. Moreover, fighting experience and rank may play complementary roles in conflict resolution.

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Winner and loser effects arise from social experiences and influence the outcome of animal conflicts as evidenced by experiments (Hsu & Wolf, 1999; Oliveira, Silva, & Canario, 2009) and theoretical modelling (Dugatkin, 1997; Van Doorn, Hengeveld, & Weissing, 2003a,b). Winner and loser effects are defined as a higher probability of a winner winning a subsequent encounter and a loser losing a subsequent encounter, respectively, regardless of the identity of the opponent (Dugatkin, 1997; Hsu & Wolf, 1999; Oliveira et al., 2009). A previous loser shows an increased probability of retreating from conflicts, whereas a previous winner should be more aggressive and thus be more likely to escalate subsequent conflicts (Hsu & Wolf, 2001; Van Doorn et al., 2003a,b; Oliveira, 2009; Fawcett & Johnstone, 2010). Generally, loser effects are stronger and longer lasting than winner effects (reviewed in Hsu, Earley, & Wolf, 2006; Oliveira et al., 2009), although there are exceptions (Hsu & Wolf, 1999). A meta-analysis revealed that losers have, on average, a more than five times lower chance of winning a subsequent contest, whereas for winners, the chances nearly doubled (Rutte, Taborsky, & Brinkhof, 2006). Aggressive behaviour has energetic and injury costs, and bears opportunity costs such as distraction from being vigilant (Hess, Fischer, & Taborsky, 2016). Winner and loser effects are therefore likely to be adaptive, as they can aid in the faster and more efficient resolution of conflicts at lower energetic costs (Lehner and Taborsky 2011; Rutte et al., 2006; Taborsky & Oliveira, 2012).

Several theoretical models have suggested that linear hierarchies arise from series of pairwise interactions involving winner and loser effects (reviewed in Lindquist & Chase, 2009). For instance, models of self-organization showed how feedback from previous wins and losses can lead to linear hierarchies (Bonabeau, Theraulaz, & Deneubourg, 1999; Hemelrijk, 2000). The analysis of a large data set of domestic chickens, Gallus gallus domesticus, suggests a low fit between model assumptions and data (Lindquist & Chase, 2009). Chickens seemed to use more sophisticated behavioural mechanisms of hierarchy formation than assumed in the models, and integrated information about many other group members (Lindquist & Chase, 2009). However, some experiments also support the predicted influence of winner—loser effects on hierarchy formation. In some group-living species, losing outside their social group may lead to a lowering of rank within their group (e.g. in chickens, Ratner, 1961). Further, in the Amazon molly,
Poecilia formosa, winner—loser effects experienced during early development influenced the hierarchy position achieved as adults (Laskowski, Wolf, & Bierbach, 2016). Theoretical models showed that winner—loser effects can influence the hierarchy established in a newly merged group, even when differences in fighting abilities exist (e.g., Bonabeau, Theraulaz, & Deneubourg, 1996; Beaugrand, 1997; Dugatin, 1997), a finding that has received experimental support in green swordtails, Xiphophorus hellerii (Dugatin & Druen, 2004).

While a large body of work has focused on the effect of winning and losing experiences on hierarchy formation, studies on the reverse effect of rank on winner—loser effects are surprisingly missing. Given the assumed importance of winner—loser effects in hierarchy formation, this lack is remarkable. Because achieving a dominance rank in a hierarchy typically involves antagonistic social interactions, one should expect that the current rank in a hierarchy would influence contest outcomes and the expressed behaviours during contests, and thereby also modulate winner—loser effects. If dominant individuals achieved their rank due to physical strength or better fighting ability, they should be expected to be more likely to win. As dominance is usually accompanied by improved reproductive prospects and thus potentially losing a dominant position is costly, dominants should have stronger winner and loser effects than subordinates. For the same reason, one should expect dominants to escalate faster and to show more aggressive behaviour than subordinates. The reverse should be true for subordinates.

The cooperatively breeding cichlid Neolamprologus pulcher lives in social groups with stable linear size-based hierarchies (Dey, Reddon, O’Connor, & Balshine, 2013). As fish have indeterminate growth, smaller fish are also usually younger. In natural social groups the youngest group members join the lowest end of the hierarchy once they become independent of direct brood care. By growing larger, they gradually increase their rank in the hierarchy (Taborsky, 2016). Immigration into groups is rare (Jungwirth et al., n.d.) and joining group members find their place in the hierarchy quickly according to their body size (Fischer, Bessert-Nettlebeck, Kotrschal, & Taborsky, 2015). Therefore, in this species the existence of winner—loser effects does not seem necessary to promote or maintain the structure of social groups. Winner—loser effects might still exist in N. pulcher, as in natural territories similar-sized group members compete aggressively over access and ownership of shelters, which are defended as private space within the territories of social groups (Werner, Balshine, Leach, & Lotem, 2003).

This study had three aims: to test (1) whether winner—loser effects exist in N. pulcher, (2) if they do, how they affect behavioural displays and escalation probability and (3) whether the social rank of an individual affects the strength of winner—loser effects. The latter is expected mainly for three reasons. (1) Winner and loser experiences can promote linear hierarchies as outlined above so effects in the opposite direction of causality (rank influencing winner—loser effects) should be expected as well. (2) In N. pulcher, the same sensory channels, namely vision and olfaction, are used to detect the rank of conspecifics (Taborsky et al., n.d.) or their aggressive motivation during encounters (Balzarini, Taborsky, Villa, & Frommen, 2016; Bayani, Taborsky, & Frommen, 2017). (3) Potential costs of conflicts, including opportunity costs, injury and energy costs (e.g. sustained aggression in N. pulcher increases the metabolism by almost fivefold, Granter & Taborsky, 1998) could be reduced by efficiently resolving aggressive encounters (Taborsky & Oliveira, 2012), using information on rank and previous winning and losing experience. This should be especially important in highly social species as social encounters and thus possibilities for conflict are frequent.

If winner—loser effects exist, we predicted that winners would win more often, start a contest more readily and be more aggressive, while losers would lose more often and be less aggressive. We further predicted that both winner and loser effects would be stronger at the top of the hierarchy in N. pulcher. This is because the value of winning and the costs of losing increase the higher an individual’s position is in the hierarchy (Dey et al., 2013). Moreover, loser effects might be smaller among low-ranked individuals due to habituation, as they are regularly exposed to aggression from more dominant group members.

To investigate whether winner and loser effects in N. pulcher exist, and how they are influenced by rank, adult focal fish were first assigned a rank (dominant or subordinate), and then given a winning or losing experience, respectively, in a two-by-two factorial experiment. In a second contest against a same-sized, naive opponent, expressed social behaviours and contest outcomes were analysed.

**METHODS**

**Study Species**

*Neolamprologus pulcher* is a cooperatively breeding cichlid endemic to the Lake Tanganyika. Groups consist of a dominant pair of breeders and up to 20 adult and juvenile subordinates of both sexes ranging widely in size. Groups are structured by linear, size-dependent hierarchies (Dey et al., 2013; Taborsky, 2016). Subordinates delay dispersal and help by engaging in alloparental care, territory defence and maintenance to be allowed to stay in the protection of the natal territory (Taborsky & Limberger, 1981; Balshine et al., 2001; Heg & Taborsky, 2010; Bruintjes & Taborsky, 2011).

**Animal Husbandry and Study Subjects**

The experiments were conducted at the Ethologische Station Hasli of the Institute of Ecology and Evolution, University of Bern, Switzerland, under license BE 74/15 of the Veterinary Office of Kanton Bern. All stock tanks and experimental tanks were equipped with shelters (e.g. stones and clay flowerpots at the bottom, semitransparent plastic bottles mounted near the water surface), one to two biological filters and a 2 cm sand layer. In the experimental tanks, clay flowerpot halves of 8 cm diameter were used as shelters. Water temperature was kept at 27 ± 1 °C. The light conditions matched those at Lake Tanganyika, with a light:dark cycle of 13:11 h and a 10 min dimmed light period in between. Fish were fed ad libitum with commercial flake food TetraMin 5 days a week and frozen zooplankton 1 day a week.

For the experimental trials, we used *N. pulcher* from six stock tanks, in which fish are kept in large aggregations. The sex of the experimental fish was determined by visual inspection of the genital papillae. All fish were measured to the nearest 0.5 mm and weighed to the nearest 0.01 g with an electronic balance. Most fish taken from the stock tanks were already individually marked with visual implant elastomer (VIE) tags (Northwest Marine Technologies, Anacortes, WA, U.S.A.); any unmarked fish were given a fresh VIE tag at the onset of the experiment. VIE tags are small (ca 0.3 × 2 mm) coloured silicon tags, which have become standard in marking of small fish, because fish can be identified without the necessity to catch them, and they do not impair behaviour or survival (Jungwirth et al., 2019). In *N. pulcher* VIE tags are recognizable for up to 2 years, both in the aquarium and in field studies (Jungwirth et al., 2019). Handling was performed without anaesthesia in accordance with our aquarium guidelines, as *N. pulcher* suffer substantial stress before and after anaesthesia. Anaesthetized fish may develop signs of stress and show abnormal behaviour for extended periods of up to 30 min after anaesthesia.
aesthetized fish that are briefly and carefully handled do not show signs of stress and resume normal behaviour immediately after release back to their home tank. To keep stress at a minimum during handling, the fish’s surface and gills are kept well covered with water during measuring, weighing and marking. Before, between and after each handling procedure, which each takes only a few seconds, fish are allowed a recovery phase swimming freely in a large, dark holding container for about 5 min. There was no mortality in this study, either after handling or during or after the experimental trials.

All fish encountering each other during this experiment were of the same sex. Half of the trials were done with males and half with females. Further, we ensured that all opponents in contests were unfamiliar to each other before the trial started. The 18 focal fish and their same-sized (standard length difference <1 mm) test phase opponents ranged between 33 and 40 mm in size. For the social rank assignment, fish differing approximately 30% in size were used. Individuals used to induce a subordinate rank ranged between 42 and 53 mm, whereas those used to induce a dominant rank ranged between 22 and 28 mm (Taborsky et al., n.d.). For the experience phase, an opponent differing 2–3 mm in size was used; their sizes ranged between 30 and 42 mm.

**Experimental Procedures**

**Experimental design**

Each of the 18 focal individuals was tested after being assigned a dominant and a subordinate rank and after experiencing winning and losing. Thus, each fish was tested in four conditions (dominant winner, dominant loser, subordinate winner, subordinate loser), the order of which was fully balanced. This repeated-measures design allowed us to control for individual differences. For each of the successive trials, each focal fish stayed for 1.5 days in the ‘social rank assignment’ set-up (one evening/night and the entire following day and night). The next morning, focal fish were then first exposed to the experience phase and, after a 1 h break (see below), to the test phase.

If two successive trials of a focal fish happened to have the same rank, we ensured that there was a gap of at least 7 days between runs, whereas runs with the opposite rank were at least 12 days apart.

Although we do not know how long possible winner and loser effects persist, we assume that they vanished until individuals were retested. This is reasonable as social interactions in *N. pulcher* are frequent and thus information about the competitive ability of Opponents were returned to their original home stock tank after their last trial.

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losing in the focal fish were returned to their home tanks after being used in an experience trial and were not used further in this study.

**Test phase**

After the 1 h separation of opponents following the contest experience, focal fish entered the test phase (i.e. the experience phase and test phase were on the same day). The test phase followed a similar procedure as the experience phase, but here the focal fish was confronted with a same-sized, naïve opponent (Fig. A2). Both fish were placed in a new 20-litre tank supplied with one shelter per compartment, separated by an opaque divider. After 1 h acclimation time both shelters were removed for 5 min. This should increase the need for a shelter, i.e. the value of the contested resource should rise, usually leading to a more persistent fighting strategy (see Enquist & Leimar, 1987 for theoretical support). Then, the divider was removed, and a new shelter was placed in the middle of the tank (Fig. A2). The contest start was determined as in the experience phase. The test phase was recorded by video (Sony DCR-SR200) and later analysed with the behavioural software Boris, version 6.3.5 (Friard and Gamba, 2016). While analysing the videos, the observer (D.L.) was blind to the treatment of the fish. The identity of the first fish crossing the centre line, all social behaviours of both opponents (restrained aggression, overt aggression and submission; see Table A1 for a detailed ethogram), whether the fish were in- or outside the shelter, the activity level every 30 s (active, inactive or in the shelter) and the time of the end of the contest were recorded. The contest was considered terminated when there was a clear winner and loser, i.e. one of the fish clearly owned the shelter (the winner kept the loser away from the shelter; see Nyman, Fischer, Aubin-Horth, & Taborsky, 2017) and/or was clearly dominating the loser (the loser showed submission in response to aggressive displays by the winner; see Nyman et al., 2017). All contests were terminated within 20 min, and none of the fish was injured during contest trials (see below).

**Statistical Analyses**

The statistical analyses were performed in R, version 3.4.2 (R Core Team, 2017). We tested for correlation of corresponding behaviours between the focal fish and their opponents by calculating Spearman rho using the package ‘devtools’ (Wickham, Hester, & Chang, 2018). If a correlation was significant, the behaviour of the opponent was included as a covariate in the respective initial model (Table A2). This applied to models of restrained aggression (rho = 0.41, P = 0.002), overt aggression (rho = −0.3, P = 0.028) and latency to first overt aggression (rho = 0.64, P < 0.0001).

Behaviours were combined into three behavioural classes, restrained aggression, overt aggression and submission (Table A1). Submissive behaviours were not analysed because of their low occurrence in most fish. Contest duration was included as offset in all models of behaviours.

Models for the following response variables were fitted using the package ‘lme4’ (Bates et al., 2015) and ‘glmmTMB’ (Brooks et al., 2017): contest outcome, contest duration, restrained aggression, overt aggression, latency to contest start, which fish started the contest (the focal fish or the opponent) and which fish escalated first (focal fish or opponent). All statistical models included experimentally assigned rank (dominant or subordinate) and experience (winner or loser) as fixed effects. Moreover, we included focal fish identity as random factor in all initial models to account for repeated testing of individuals. If the random factor explained zero variance, we simplified the model and fitted a linear model (LM) or generalized linear model (GLM) without it (see comment by D. Bates at https://stat.ethz.ch/pipermail/r-sig-mixed-models/2014q3/022509.html for the treatment of zero-variance random factors). All initial models also contained the interaction term ‘rank*experience’, focal standard length (SL, log transformed) and the ratio of focal fish/opponent weight (Table A2). To find the model making the best predictions, backward selection of fixed factors was used, while always retaining the experimental treatments ‘rank’ and ‘experience’ in the model. Model comparisons were done using the likelihood ratio test from the package ‘lmtest’ (Zeileis & Hothorn, 2002) for normally distributed residuals. Otherwise, model selection was based on Akaike information criterion (AIC) comparison; only variables decreasing the AIC by at least 2 were kept. Final models were checked to satisfy all assumptions of the chosen distribution. Significance testing was based on deviance when removing respective terms from the model using likelihood ratio tests for generalized linear mixed models (GLMMs) and the Satterthwaite’s degrees of freedom for linear mixed models (LMMs). Moreover, for each model, we provide marginal $R^2$ (variability explained by the fixed effects) and conditional $R^2$ (variability explained by the entire model, including both fixed and random effects), calculated with the R package ‘MuMln’ (Barton, 2020).

When the error term of a model was normally distributed, data were analysed by LMMs. Normality of residuals was tested by visually inspecting their distribution, Tukey—Anscombe plots and quantile—quantile (Q—Q) plots. Further, a Shapiro—Wilk test and a Kolmogorov—Smirnov test with Lilliefors correction from the package ‘nortest’ (Gross & Lligges, 2015) were performed. Otherwise, a GLMM assuming a gamma distribution or a Poisson distribution was fitted. GLMMs with Poisson distribution were checked for overdispersion; if overdispersion occurred, a GLMM assuming negative binomial distribution was fitted. If the data contained zeros, we checked for zero inflation. We compared the AICs of the final model with the same model but assuming zero inflation, using the package ‘glmmTMB’ (Brooks et al., 2017); zero inflation only occurred in the model for overt aggression. All initial and final models are listed in Table A2.

To detect winner and loser effects separately, one-tailed exact binomial tests were performed comparing the observed winning probability of winners and losers, respectively, with the expected winning probability of 0.5 in the test phase.

**RESULTS**

**Contest Outcome and Duration**

Prior experience but not rank affected the outcome of the contest (Tables 1, 2). Fish with previous winning experience won more often than losers (Fig. 1a): 66.7% (confidence interval, CI: 47.9

| Contest in test phase | Won | Lost |
|-----------------------|-----|------|
| Dominant winner       | 8   | 4    |
| Subordinate winner    | 8   | 4    |
| Dominant loser        | 4   | 9    |
| Subordinate loser     | 7   | 10   |

Table 1

Outcome of contests in the test phase, sorted by preassigned rank and prior experience.
to 100%) of focal subjects with a winner experience won, i.e. their odds for winning were 2.0, and 63.3% (CI: 46.7 to 100%) of focal subjects with loser experience lost (odds of experienced losers to winners were 2.0, and 63.3% (CI: 46.7 to 100%) of focal subjects with a winner experience won, i.e. their latency to start a contest (Table 2). Rank and prior experience did not affect which of the fish started a contest. Smaller focal fish started the contest more often (Table 2). Prior winners were more likely to escalate the contest (i.e. they showed the first overt aggression in a contest) than prior losers, whereas rank did not influence this parameter (Table 2, Fig. 3); furthermore, larger focal fish were more likely to escalate first (Table 2).

**DISCUSSION**

Here we showed that prior winners win more often than prior losers. Thus winner–loser effects exist in *N. pulcher*, although winner effects and loser effects could not be demonstrated separately. Furthermore, overt aggressive behaviour occurred significantly more often in previous winners than in previous losers, and winners escalated contests more frequently. Fish with assigned subordinate rank showed more restrained aggression. We found no evidence that preassigned rank modulates contest outcome or any of the behavioural parameters, as none of the two-way interactions between rank and prior contest experience were significant.

**Winner and Loser Effects**

Effects of prior experience became manifest by preassigned winners winning more often in the test trials than losers, and winners tending to win more often than expected by chance. Further, winners showed more overt aggression than losers, they
were more likely to escalate contests and contests tended to be shorter when the focal fish was a preassigned winner. This indicates that (1) either winners had an increased motivation for engaging in aggression or losers tried to avoid becoming involved in a consecutive contest and (2) winners might be more efficient in solving escalated conflicts over resources. (1) An increased motivation to engage in aggression after winning a contest has been demonstrated in several other species including the killifish, Rivulus marmoratus (Hsu & Wolf, 2001), Norway rats, Rattus norvegicus (Lehner, Rutte, & Taborsky, 2011) and mice, Mus musculus (Martinez, Salvador, & Simón, 1994). It has been suggested that the increased fighting motivation of previous winners is important in the development of a winner effect (Oliveira et al., 2009; Oyegbile & Marler, 2005). (2) There is also evidence that winners benefit from being more efficient in subsequent contests. For instance, in Norway rats, previous winners attacked more readily, but then won fights after a shorter time and by reducing aggression sooner (Lehner et al., 2011). Moreover, winner effects in mice of the genus Peromyscus reduced their own losing behaviour, but induced stronger losing behaviour in their opponents, increasing the efficiency of winners at resolving contests (Fuxjager, Montgomery, & Marler, 2011). Finally, winner effects may also qualitatively change territorial behaviour: in red-bellied woodpeckers, Melanerpes carolinus, winner effects not only reduced aggressive response latency and intensity, but also caused more switches between different types of territorial displays (Miles & Fuxjager, 2019). To investigate whether winners, losers or both changed their

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**Figure 1.** Effect of assigned rank and prior experience on (a) the probability of winning a contest in the test phase and (b) the duration of contests in the test phase (residuals of the final model are shown after accounting for effects of focal identity). Medians and interquartile ranges are shown. Dom: dominant; sub: subordinate.

**Figure 2.** The effect of rank and prior experience on aggressive behaviours of the focal fish during the contest. (a) Amount of restrained aggression: residuals of the final model after accounting for contest duration (offset) and focal identity. (b) Amount of overt aggression: residuals of the final model after accounting for amount of overt aggression by opponent, contest duration (offset) and focal identity. Medians and interquartile ranges are shown. Dom: dominant; sub: subordinate.

**Figure 3.** The effect of rank and prior experience on the likelihood of escalating a contest (i.e. to show first overt aggression). Dom: dominant; sub: subordinate.
The effect sizes for winner and loser effects were of approximately equal magnitude (odds for winning as experienced winner = 2.0; odds for losing as experienced loser = 1.72). The odds for winning in *N. pulcher* are in line with the results of a meta-analysis across several taxa (average odds for winning = 1.87, Rutte et al., 2006), whereas the odds of losers for losing in *N. pulcher* are smaller than the reported values of 5.56 in the meta-analysis. The suggested equality of effect sizes of winner and loser effects in our study can be explained by theoretical predictions for linear hierarchies (as present in *N. pulcher*): if the loser effect is much stronger than the winner effect, theory predicts that only one individual becomes dominant while all others will end up at the bottom of the hierarchy (Bonabeau et al., 1996). Both effect sizes were rather small as predicted for highly social species engaging in frequent, but short and rather ‘cheap’ aggressive encounters in terms of energy expenditure and risk of injury (Hick, Reddon, O’Connor, & Balshine, 2014). Effects of contest experience might play a smaller role in species living in stable social groups like *N. pulcher* compared to species with a more solitary lifestyle. For instance, in the cichlid *Pseudotropheus trophops*, individuals showed a stronger loser effect in isolated dyads than in dyads embedded in a social group (Chase, Tovey, & Murch, 2003).

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### Appendix

#### Table A1

| Behaviour                  | Description                                                                 | Category          |
|----------------------------|-----------------------------------------------------------------------------|-------------------|
| Ramming*                   | Very fast linear approach towards another fish ending with physical contact (ramming) | Overt aggression  |
| Biting*                    | Biting another fish or attempting to do so (with physical contact)          | Overt aggression  |
| Mouthfight*                | Grasping an opponent on the jaw and intensive pulling or pushing            | Overt aggression  |
| Fin spread**               | All fins, particularly the unpaired fins, are maximally spread, body kept in a stiff posture | Attention         |
| Opercula spread*           | Spreading of opercula and lowering the branchiostegal membrane              | Restrained aggression |
| Frontal approach*          | Linear approach towards another fish that is abruptly stopped before physical contact | Restrained aggression |
| Head down display*         | Body tilted with head pointing downwards                                    | Restrained aggression |
| S-bend*                    | Body kept in an S-shaped posture                                            | Submission        |
| Tail quiver*               | Caudal peduncle, tail fin and back end of dorsal fin are intensively vibrating while the unpaired fins are folded; body may be pressed on the ground | Submission        |
| Leading                    | A fish swims in front of another towards or into a shelter, usually while intensively quivering with the tail | Submission        |
| Zig-zag swimming           | Swimming in short bursts in a zig-zag pattern in front of a (usually dominant) fish | Submission        |
| Hook display               | Bow swimming towards another fish usually with light touch at the apex of the bow (no ramming) and subsequent pausing close to the other fish | Submission        |
| Head up posture*           | A fish takes up a head up position with folded fins | Submission        |

* Behaviours that occurred during the contests.

** This behaviour was recorded as duration and is not analysed here; all other behaviours were recorded as counts.
| Model                  | Factors                             | Interaction                  | Covariates                          | Random factor | Offset      | Model type | Distribution | Transformation |
|-----------------------|-------------------------------------|------------------------------|-------------------------------------|---------------|-------------|------------|--------------|----------------|
| **Contest outcome**   |                                     |                              |                                     |               |             | GLMM       | Binomial     |                |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      |             | GLMM       | Binomial     |                |
| Final model           | Rank                                |                              |                                     |               |             | GLMM       | Binomial     |                |
| **Contest duration**  |                                     |                              |                                     |               |             | GLMM       | Gamma        |                |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      |             | GLMM       | Gamma        |                |
| Final model           | Rank                                |                              |                                     |               |             | GLMM       | Gamma        |                |
| **Restrained aggression** |                                     |                              |                                     |               |             | GLMM       | Negative binomial |                |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      | Log (time) | GLMM       | Negative binomial |                |
| Final model           | Rank                                |                              |                                     |               |             | GLMM       | Neg. binomial |                |
| **Overt aggression**  |                                     |                              |                                     |               |             | GLMM       | Gaussian, Zero inflated | Log (x + 1) |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      | Log (time) | LMM        | Gaussian, Zero inflated | Log (x + 1) |
| Final model           | Rank                                |                              |                                     |               |             | LMM        | Gaussian, Zero inflated | Log (x + 1) |
| **Latency to contest start** |                                     |                              |                                     |               |             | LMM        | Gamma        | Log (x + 1) |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      |             | LMM        | Gamma        | Log (x + 1) |
| Final model           | Rank                                |                              |                                     |               |             | LM         | Gamma        | Log (x + 1) |
| **Fish starting the contest** |                                     |                              |                                     |               |             | GLMM       | Binomial     |                |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      |             | GLMM       | Binomial     |                |
| Final model           | Rank                                |                              |                                     |               |             | GLM        | Binomial     |                |
| **Fish escalating first** |                                     |                              |                                     |               |             | GLMM       | Binomial     |                |
| Initial model         | Rank                                | Rank * Experience            | Log (SL)                            | Focal ID      |             | GLMM       | Binomial     |                |
| Final model           | Rank                                |                              |                                     |               |             | GLM        | Binomial     |                |

Focal ID was included as random factor to account for repeated testing of individuals. SL: standard length; WR: weight ratio – weight of focal/weight of opponent. Variables in the column ‘offset’ are assumed to have a coefficient of 1.
Focal and stimulus fish separated by an opaque wall, both supplied with a shelter. Both shelters are removed 5 min before the fight. The separation wall is removed and a new neutral shelter is put in the middle. 

**Figure A1.** Experimental set-up in the experience phase. In this example the left-hand fish is the focal fish and is given a loser experience by pairing it with a slightly bigger opponent. After the trial, the opponent is moved back to its home tank and not used further, whereas the focal fish enters the test phase.

Focal fish  Opponent

Predetermined winner and loser both with a shelter, separated by an opaque wall.

The shelter of the winner is removed 5 min before the fight.

The separation wall is removed and the shelter of the loser is put in the middle.

**Figure A2.** Experimental set-up in the test phase.