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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.

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,

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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; Dugatkin, 1997), a finding that has received experimental support in green swordtails, *Xiphophorus hellerii* (Dugatkin & 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, Grantner & 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, naïve 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. Nonanaesthetized 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 while 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 other group members should be updated continually (Schuett, 1997; Hsu & Wolf, 1999). A longer time interval between tests with opposite ranks was chosen as the rank effect might persist longer than winner–loser effects. Between trials, the fish were kept in their home stock tanks, in which aggregations of larger, smaller and same-sized conspecifics of both sexes were present. All fish were returned to their original home stock tank after their last trial.

Opponents

For each of the focal fish, opponents were caught 1 day before the contest (in total 27 experience phase opponents and 23 test phase opponents). These opponents were placed in a 20-litre tank containing a shelter.

Social rank assignment of focal fish

Fish differing by approximately 30% from the focal subject's body size (standard length) were caught. Assigned dominants faced a 30% smaller stimulus fish, while assigned subordinates experienced a 30% larger stimulus fish. After size measurements, the larger fish was immediately released in a 20-litre tank containing one shelter, while the smaller fish was placed in a small mesh cage therein for 15 min before being released. Both the size difference and the time delay of releasing the smaller fish ensured that the two fish did not engage in escalated aggression resulting in a winner–loser effect but formed a hierarchy without showing much social behaviour. The two fish stayed in this 20-litre tank for 1.5 days. The method of how to assign ranks to experimental fish has been developed in a previous study, in which an even shorter duration of 1 day proved to be long enough to establish a stable hierarchy and assign a rank to a fish (Taborsky et al., n.d.). In this earlier study we showed that after 1 day of rank assignment to a 'stimulus fish', focal *N. pulcher* were able to distinguish between matching and nonmatching visual and olfactory cues of rank (dominant or subordinate) of these stimulus fish, which otherwise did not differ in body size, sex or any other detectable trait.

Experience phase

After the 1.5 days of rank assignment, the focal fish was provided with a contest experience, which was predetermined by the experimenter (D.L.), either an assigned winning or an assigned losing experience. To achieve this, we paired the 18 focal individuals with opponents differing slightly (2–3 mm) in size. Assigned winners faced a slightly smaller fish and assigned losers a slightly larger fish. During the study, all 18 fish received each combination of rank and experience in fully balanced order, as explained above, unless the experience phase was not successful (see below). The focal fish and its opponent were placed in a 20-litre tank divided by an opaque divider and both compartments were supplied with a shelter (Fig. A1). Fish were left for 1 h to acclimatize to the new tank. After the acclimatization period the shelter of the assigned winner was removed 5 min prior to the beginning of the experience phase, whereas the assigned loser kept its shelter right until the onset of the experience phase. This should (1) ensure the fish is motivated to engage in a contest over the shelter, because a smaller individual might be more likely to fight a bigger one if it has to defend a resource; and (2) increase the experience effect during the subsequent staged contest (i.e. if the loser loses its shelter during the contest and the winner wins the opponent's shelter). Afterwards, the video recording was started (Sony DCR-SR200), the separation wall was removed, and the shelter of the predetermined loser was placed exactly in the middle of the tank (Fig. A1). We defined the start of the contest as when one fish entered the other's territory by crossing the 'centre line' (i.e. the virtual division between the left and right half of a tank). The latency to start the contest was measured using a stopwatch. Recordings were continued for 20 min after the contest had started. To determine whether the fish received the assigned winner or loser experiences, the end of the video recordings were analysed. None of the fish was injured after the experience phase. In 18/72 trials involving 11 individuals, the fish received the opposite experience than assigned by us. We expected this to happen in some cases, as the size difference between opponents was intended to be very small (2–3 mm). While this is usually sufficient to give a larger fish an advantage in a contest, a highly aggressive or motivated smaller fish may overcome this size difference and win even against a slightly larger fish. We could not simply choose a bigger size difference, as then most likely the two fish would have formed a rank hierarchy without a contest. In these cases, where the focal fish received the opposite experience than intended, it was excluded from the following test phase, leaving 54 test phase trials. After the experience phase, the fish were separated for 1 h, during which winners were left with the shelter, while losers stayed without a shelter. Leaving the winner with the competed for resource, and the loser without it, should help to consolidate the winner–loser effect. The opponent fish used to induce winning or 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 analysing the behaviour focal fish (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 (variance explained by the fixed effects) and conditional R^2 (variance explained by the entire model, including both fixed and random effects), calculated with the R package 'MuMIn' (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 & Ligges, 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.

Table 1
Outcome of contests in the test phase, sorted by preassigned rank and prior experience

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

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

Table 2
Effects of rank and prior experience on behaviour

	Estimate	SE	χ^2/F[a]	P	$R^2_{Marginal}$	$R^2_{Conditional}$
Contest outcome					0.097	0.23
Intercept	−0.711	0.572				
Rank	0.204	0.619	0.108	0.74		
Experience	1.282	0.627	4.280	**0.039**		
Contest duration					0.066	0.30
Intercept	1.746	0.031				
Rank	−0.043	0.025	2.75	*0.097*		
Experience	−0.045	0.027	2.76	*0.097*		
Restrained aggression					0.55	0.97
Intercept	−5.715	0.394				
Rank	0.794	0.376	4.60	**0.032**		
Experience	0.675	0.380	3.12	*0.077*		
Overt aggression					NA	NA
Intercept	−4.560	0.293				
Rank	0.167	0.294	0.32[a]	0.57		
Experience	1.124	0.307	11.75[a]	**0.0006**		
Opponent overt aggression	−0.094	0.041	4.62[a]	**0.032**		
Latency to contest start					NA	NA
Intercept	0.833	0.118				
Rank	−0.222	0.127	3.23	*0.072*		
Experience	0.047	0.120	0.15	0.70		
Fish starting the contest					0.26	(no RF)
Intercept	45.245	15.934				
Rank	0.514	0.631	0.67	0.41		
Experience	1.051	0.660	2.71	*0.10*		
Log (size)	−12.727	4.473	9.24	**0.002**		
Fish escalating first					0.35	(no RF)
Intercept	−47.297	22.382				
Rank	−0.015	0.810	0.0003	0.99		
Experience	1.637	0.836	4.23	**0.040**		
Log (size)	13.120	6.260	5.32	**0.021**		

Contest outcome: GLMM, binomial; contest duration: GLMM, gamma; restrained aggression: GLMM, negative binomial; overt aggression: GLMM, negative binomial; latency to start the contest: GLMM, gamma; individual starting the contest: GLMM, binomial; and individual escalating the contest (i.e. showing the first overt aggression: GLMM, binomial. All $N = 54$ trials except in 'Fish escalating first' , where $N = 34$, because in 20 trials the stimulus fish escalated first. For the interpretation of the estimates, dominants are the reference category for 'Rank' and losers are the reference category for 'Experience'. Significant P values are in bold and $P < 0.1$ in italics. Marginal and conditional R^2 are given, except for the zero-inflated model in 'Overt aggression and the gamma model in 'Latency to contest start', for which these values could not be calculated (i.e. are not available, NA). RF = random factor.

[a] These are F values; all other figures in this column are chi-square values.

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 lose were 1.72). However, the probability of winning and losing, respectively, did not deviate significantly from the expected equal distribution, although there was a trend in winners (one-tailed exact binomial test: winners: $P = 0.076$; losers: $P = 0.1$). Contest duration was highly variable (mean = 299.9, SD = 248.0, range 65.2−1307.4) , but it did not significantly affect outcome (duration was dropped during stepwise backwards selection, see 'Statistical analyses'). Contests in which the focal fish was a prior winner were shorter while contests involving dominant focal fish tended to be longer (Table 2, Fig. 1b).

Aggression

Subordinate focal fish showed more restrained aggression than dominants (Table 2, Fig. 2a), whereas previous experience did not affect restrained aggression. Conversely, overt aggression was not affected by rank, but focal fish with prior winning experience showed more overt aggression than prior losers (Table 2, Fig. 2b). Moreover, the focal subject's overt aggression decreased with increasing received overt aggression (Table 2).

Latencies to Start and Escalate a Contest

Contests tended to start earlier when the focal subject was a subordinate fish, whereas prior contest experience did not affect the 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

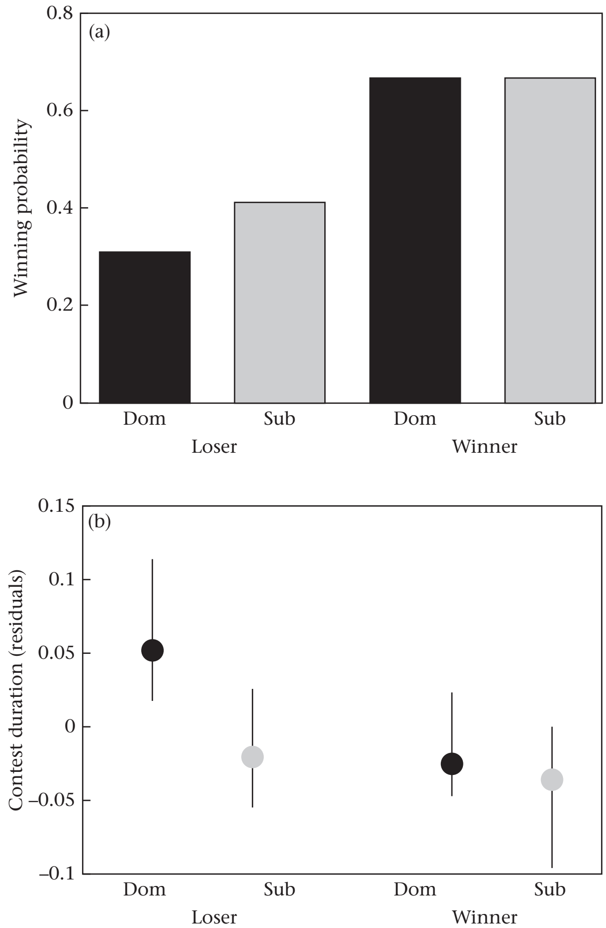

Figure 1. Effect of assigned rank and prior experience on (a) the probability of winning a contest in the test phase and (b) the duration of contests in the test phase (residuals of the final model are shown after accounting for effects of focal identity). Medians and interquartile ranges are shown.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

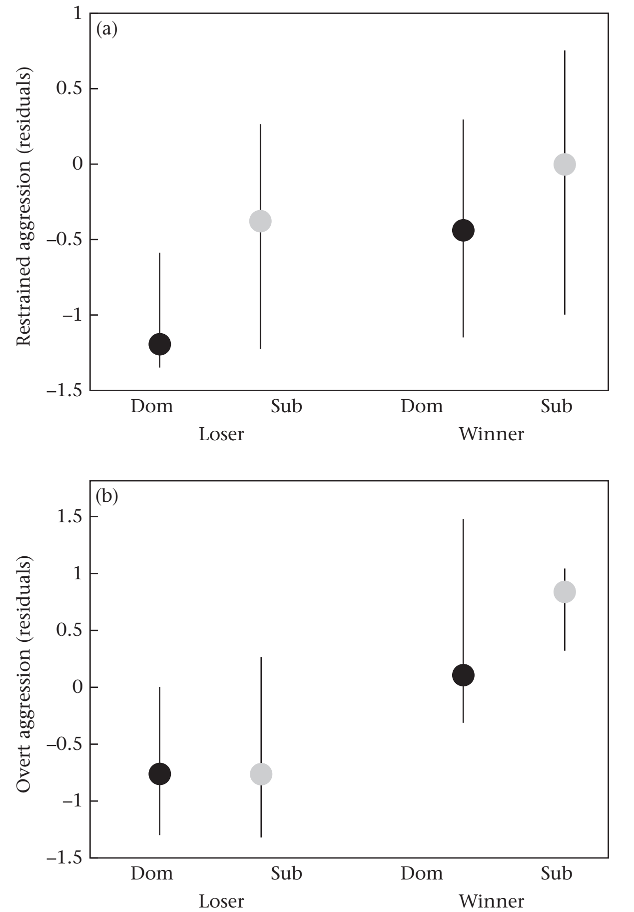

Figure 2. The effect of rank and prior experience on aggressive behaviours of the focal fish during the contest. (a) Amount of restrained aggression: residuals of the final model after accounting for contest duration (offset) and focal identity. (b) Amount of overt aggression: residuals of the final 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.

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

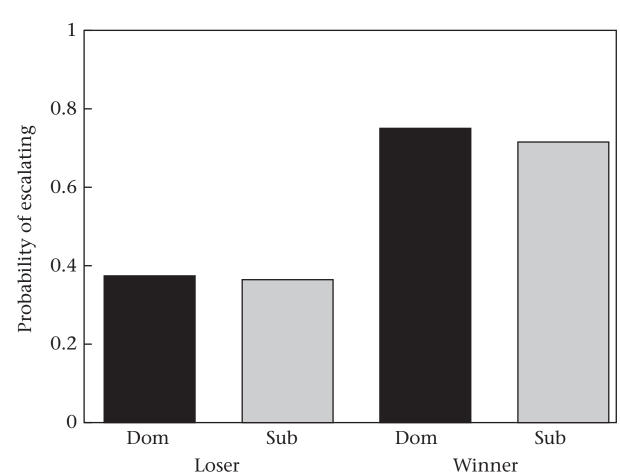

Figure 3. The effect of rank and prior experience on the likelihood of escalating a contest (i.e. to show first overt aggression). Dom: dominant; sub: subordinate.

behaviour, one would have to compare the results of our test phase trials to the behaviours in a contest between two naïve individuals (Bevan, Daves, & Levy, 1960; Martinez et al., 1994).

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 tropheops*, individuals showed a stronger loser effect in isolated dyads than in dyads embedded in a social group (Chase, Tovey, & Murch, 2003).

Rank Effects

Interestingly, preassigned rank only influenced restrained aggression significantly, whereas contest outcome was not affected by rank. Subordinates showed more restrained aggression, a set of behaviours serving to threaten an opponent (Table A1), which subordinates might possibly have shown in an attempt to prevent an escalated contest. Also, winner–loser experiments in the cichlid *Pelvicachromis taeniatus* revealed that cues received long before a contest modulated aggressive displays, but not contest outcome (Meuthen, Bakker, & Thünken, 2019; *P. taeniatus* had been exposed to early life predation cues versus control cues). Contests involving dominant focal *N. pulcher* tended to start later than when subordinates were involved, but rank did not influence which fish started the contests. Furthermore, contest duration tended to be longer when the focal fish was dominant, which was mainly caused by long contest durations of dominant losers (see Fig. 1b), which might have been less inclined to accept their loser state than subordinates.

The fact that rank affected threat behaviour but not contest outcome suggests that prior rank and prior contest experience play complementary roles for the hierarchy formation in this species. When size differences are large, hierarchies form quickly and involve little aggression (Fischer et al., 2015, 2017; Taborsky, Arnold, Junker, & Tschopp, 2012), which we also observed during the rank assignment phase of this study. Contests with a lot of mutual aggression and a clear winner and loser might only be important among individuals of similar size and rank (Taborsky et al., 2012). In *N. pulcher*, each group member defends its own shelter within the larger territory of a social group, mainly against similarly sized peers (Werner et al. 2013), in which case winner–loser effects might be relevant. Alternatively, it might be that the rank assignment phase was too short to have strong and lasting effects. However, in a previous experiment, an even shorter rank assignment phase proved to induce a stable subordinate or dominant rank over several days of experimental testing (Taborsky et al., n.d.), which is why we believe the rank assignment was successful.

Size Effects

Interestingly, smaller focal fish more readily started the contest by moving into the territory of same-sized opponents. Possibly, contests are less costly among smaller fish, as bites and ramming in small fish have lower impact, and thus they might more readily engage in a contest. Alternatively, or in addition, smaller fish may be more explorative and/or risk prone, as shown in other cichlids (Segers et al., 2011), and may therefore have entered the tank compartment of the opponent more readily. However, larger fish escalated contests more often, a result frequently observed among fish species (Fischer et al., 2015; Meekan, von Kuerthy, McCormick, & Radford, 2010; Poulos & McCormick, 2014).

Conclusions

Although winner–loser effects are widespread and have been described in many species across the animal kingdom (Rutte et al., 2006), their connection to social hierarchies is not well understood. While there is theoretical support (reviewed in Lindquist & Chase, 2009) and experimental evidence (e.g. Laskowski et al., 2016; Ratner, 1961) for their role in hierarchy formation, it is still unknown whether, in reverse, winner–loser effects are modulated by social rank. The position of an individual within a social hierarchy has a substantial influence on its performance in social interactions, be it cooperative (Tebbich, Taborsky, & Winkler, 1996) or competitive (Dey et al., 2013). For instance, there is increased social conflict among higher-ranked individuals in *N. pulcher* (Dey et al., 2013) and rank influences contest outcome among similar-sized individuals in the damselfish *Pomacentrus amboinensis* (Poulos & McCormick, 2014).

Presumably, hierarchy might influence winner–loser effects as well, possibly even increasing self-reinforcement of the existing rank order through experience effects. Our study provides a first step to investigate this subject, suggesting that rank and experience play complementary roles in conflict resolution in *N. pulcher*. However, more work on this question is required. Shedding more light on the interaction between rank and winner–loser experience would greatly further our understanding of animal conflict resolution and the function and maintenance of social hierarchies. In particular, (1) the interaction between rank and winner–loser experience should be studied in individuals that have held a certain rank for a longer time than in our study. (2) Furthermore, the relative importance of multiple prior fighting experiences, time- or event-driven decay of the experience effect (Devenport & Devenport, 1994) and variation in contest intensity and/or duration during fighting experience should be considered, which may all influence the effect sizes of winner–loser effects.

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Appendix

Table A1
Ethogram for aggressive and submissive behaviours in *N. pulcher*

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*, [D]	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	Restrained aggression
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.
[D] This behaviour was recorded as duration and is not analysed here; all other behaviours were recorded as counts.

Table A2
Terms of initial and final models

Model	Factors	Interaction	Covariates	Random factor	Offset	Model type	Distribution	Transformation
Contest outcome								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Log (WR)	Focal ID		GLMM	Binomial	
Final model	Rank Experience			Focal ID		GLMM	Binomial	
Contest duration								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Log (WR)	Focal ID		GLMM	Gamma	
Final model	Rank Experience			Focal ID		GLMM	Gamma	
Restrained aggression								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Log (WR) Opponent restrained aggression	Focal ID	Log (time)	GLMM	Negative binomial	
Final model	Rank Experience		Focal ID Log (WR)	Log (time)	GLMM	Neg. binomial		
Overt aggression								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Opponent overt aggression	Focal ID	Log (time)	LMM	Gaussian, Zero inflated	Log (x+1)
Final model	Rank Experience		Opponent overt aggression	Focal ID	Log (time)	LMM	Gaussian, Zero inflated	Log (x+1)
Latency to contest start								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Log (WR)	Focal ID		LMM	Gamma	Log (x +1)
Final model	Rank Experience					LM	Gamma	Log (x +1)
Fish starting the contest								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Log (WR)	Focal ID		GLMM	Binomial	
Final model	Rank Experience		Log (SL)			GLM	Binomial	
Fish escalating first								
Initial model	Rank Experience	Rank * Experience	Log (SL) Sex Log (WR)	Focal ID		GLMM	Binomial	
Final model	Rank Experience		Log (SL)			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.

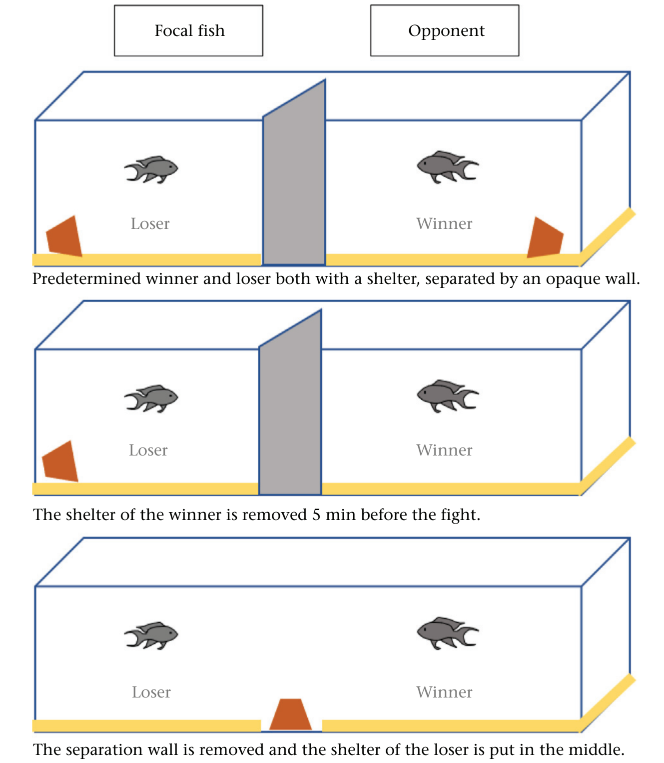

Figure A1. Experimental set-up in the experience phase. In this example the left-hand fish is the focal fish and is given a loser experience by pairing it with a slightly bigger opponent. After the trial, the opponent is moved back to its home tank and not used further, whereas the focal fish enters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

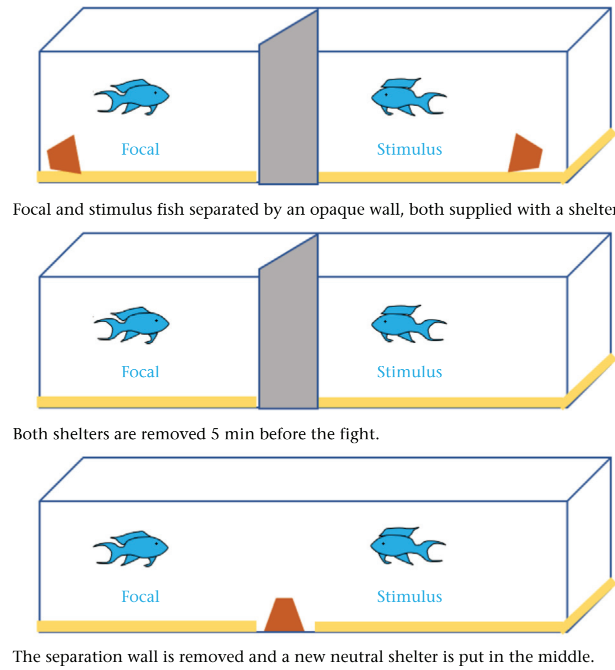

Figure A2. Experimental set-up in the test phase.