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# Prior contest information: mechanisms underlying winner and loser effects

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**Abstract** Animals' contest performance is influenced by their recent contest experiences. This influence could either be exerted by individuals re-estimating their own fighting ability (self-assessment) or by their opponents responding to status-related cues (social-cue mechanism) or both. Individuals of *Kryptolebias marmoratus*, a hermaphroditic killifish, were given different contest experiences to examine how two opponents' prior experiences combined to determine their contest interaction and to test both of these mechanisms as potential causes of the observed experience effect. Our data showed that losers' decisions to retreat at different stages of a contest were influenced by their own but not by the winners' contest experience—a result consistent with self-assessment but not with the social-cue mechanism. An association between the fish initiating and winning contests thus probably arose because both were correlated with an individual's assessment of its fighting ability, but not because initiating contests made opponents more inclined to retreat.

**Keywords** Winner–loser effect · Animal contest · Self-assessment · Social-cue · Killifish, *Kryptolebias marmoratus*

## Introduction

Animals' performance in contests is often influenced by the outcomes of previous contests: A recent victory increases and a recent defeat reduces the probability of an individual winning again (winner and loser effects; see Hsu et al. 2006 for a review). Winner and loser effects are probably not merely by-products of hormonal mechanisms that regulate agonistic behaviour, because similar winner/loser effects exist in vertebrates and invertebrates which have significantly different physiological mechanisms to regulate agonistic behaviour; the duration of the effects also appears not to coincide with the persistence of changed hormone levels after a fight (see Rutte et al. 2006 for a discussion). An adaptive explanation is that recent contest experiences shape future contests by providing information on contestants' fighting ability (or resource holding power; Parker 1974). Two non-mutually exclusive mechanisms for this have been proposed (Rutte et al. 2006): Individuals could re-estimate their fighting abilities (self-assessment mechanism) or produce status-related cues useful for opponents to assess their fighting ability (social-cue mechanism). According to the self-assessment hypothesis, winning experience raises but losing experience lowers an individual's estimate of its own fighting ability. This affects its expected cost of engaging in a fight and thus influences its decisions and its probability of winning (e.g. Otronen 1990; Whitehouse 1997). That contestants change contest behaviour after a recent win or loss has been observed in many studies. The number of attacks delivered in standard tests (e.g. Kahn 1951; Huhman et al. 2003) and the likelihood of initiating a new conflict (e.g. McDonald et al. 1968; Bergman et al. 2003) often increase after a recent victory and decrease after a recent defeat. These differences in contest behaviour between prior winners and losers are similar to those between larger and smaller contestants: Larger individuals deliver more attacks in standard tests (Earley, unpublished data), are more likely to initiate confrontation (Dugatkin and Ohlsen 1990; Earley and Hsu

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2008) and have a higher probability of winning a contest (Hsu et al. 2006) than smaller individuals. Because body size is a good surrogate index for fighting ability in many species of animals (Hsu et al. 2006), the results that individuals with a recent winning or losing experience behave as if they were respectively larger or smaller than their size-matched opponents provide reasonable support for the self-assessment hypothesis.

According to the social-cue hypothesis, an individual uses status-related cues to assess its opponent's contest history and fighting ability and adjusts its contest strategy as a result. There is empirical evidence that individuals modify their contest strategy when information on opponents' past contest interaction is available. A bystander, for instance, would alter its fighting strategy against an opponent whose performance it observed in a contest with a third party (McGregor 1993; Earley and Dugatkin 2002; Brown and Laland 2003). However, because unfamiliar rivals display winner and loser effects, they would have to rely on indirect (behavioural, morphological, physiological etc.) cues to evaluate each other's contest history. Aggressiveness and readiness to initiate a fight, for example, could serve as status-related behavioural cues. Dominant and subordinate individuals also release different chemicals. Dominant crayfish (Bergman et al. 2005) and tilapia (Barata et al. 2007) release more urine than subordinates; dominant tilapia urine has greater olfactory potency than subordinates' (Barata et al. 2007). In addition, dominant individuals in many species have more elevated testosterone (e.g. Oliveira et al. 2002; Wingfield 2005; Parikh et al. 2006) and glucocorticoids levels which are less elevated or return to baseline more quickly (e.g. Schuett et al. 1996; Summers et al. 2003). Despite this abundance of status-related information available for contestants' use, the impact of an individual's prior experience on its opponent's contest strategy has rarely been examined, so direct evidence of the social-cue hypothesis between unfamiliar opponents is limited. In snapping shrimp, losers behaved less aggressively towards both familiar and unfamiliar winners than towards naïve opponents (Obermeier and Schmitz 2003). However, because the study adopted self-selection procedures for experience training (see Chase et al. 1994 for a discussion), it is difficult to ascertain whether losers were responding to winner's status-related cues or to superior intrinsic fighting ability unrelated to their status as winners. In another study (Bergman and Moore 2005), crayfish were exposed for five consecutive days to odours from randomly selected naïve crayfish, forced winners and forced losers. Individuals exposed to winners' odours were less likely to initiate or win fights than those exposed to naïves' odours, whilst those exposed to losers' odours were more likely to win, suggesting that contestants adjusted their behaviour in response to odours from different sources. These results provide strong evidence for the social-cue mechanism although focal crayfish did not fight directly with individuals with different contest histories.

To the best of our knowledge, no study has evaluated the relative contributions of the self-assessment and social-cue mechanisms to winner and loser effects. This study attempted to do so by examining how the prior experiences of two contestants combine to influence their contest interaction, using *Kryptolebias marmoratus*, a hermaphroditic killifish, as the study organism. Contest behaviour and outcome of *K. marmoratus* are positively and negatively influenced by recent winning and losing experiences, respectively (Hsu and Wolf 1999, 2001). Although eventual losers and winners did not differ significantly in the post-fight levels of water-borne cortisol, testosterone or 11-ketotestosterone, losers that escalated with winners had higher post-fight levels of all three hormones than losers that retreated without escalation (Earley and Hsu 2008). Besides, winners that attacked losers at higher frequency had higher levels of post-fight cortisol. Together, higher levels of post-fight cortisol, testosterone or 11-ketotestosterone could signal aggressive losers or winners. Moreover, contests between *K. marmoratus* of variable sizes showed that contest duration and intensity correlated positively with the size of the smaller/weaker opponent but negatively with the size of the larger/stronger opponent, consistent with the hypothesis that the fish assess each other's fighting ability at early stages of a contest (Hsu et al. 2008). Because the fish exhibit both winner and loser effects, adopt different contest strategies after winning or losing a fight, respond differently in post-fight hormones between aggressive and non-aggressive fighters and assess their opponents' fighting ability, this species is ideal for exploring what information is extracted from past contest to influence the outcomes of new contests.

## Materials and methods

### Study organism

The mangrove killifish, *K. marmoratus*, is an internally self-fertilising hermaphroditic fish (Taylor et al. 2001). Their standard length (SL; from the tip of the snout to caudal peduncle) can be less than 1.5 cm when first matured but reaches 4 cm in the laboratory (personal observation). The species produces fertilised eggs all year round with no obvious oviposition cycles (Harrington 1963). Most natural populations are isogenic homozygous strains, although outcrossing heterozygous populations were discovered in Twin Cays, Belize (Taylor et al. 2001). This study used five strains of fish from various areas (DAN2K: Dangria, Belize; HON9: Utila, Honduras; RHL: San Salvador, Bahamas; SLC8E: St. Lucie County, FL, USA; VOL: Volusia County, Florida, USA) being F2 to F6 generations of fish originally collected by Dr. D. Scott Taylor. A week after hatching, fish were isolated in a 10×10×10-cm translucent polypropylene container filled with 400–500 ml 25 ppt synthetic sea water (Instant Ocean™ powder) and labelled with unique identification codes. Containers were cleaned and water replaced every 2 weeks. Fish were kept at 25±2°C on a 14:10-h photoperiod and fed newly hatched brine shrimp (*Artemia*) nauplii daily.

### Experimental design

Individuals of *K. marmoratus* were given a win (W), a loss (L) or no fighting experience (N). Contests were staged between individuals with six experience combinations: L–L (L individual fighting against L individual), L–N, L–W, N–N, N–W and W–W, allowing the impact of an individual's and its opponent's recent experience on its contest performance to be evaluated simultaneously. We analysed (1) whether display and attack initiators were more likely to win contests than their opponents, (2) how two opponents' recent contest experiences influenced the likelihood of their initiating displays and attacks and winning contests and (3) how two opponents' recent contest experiences combined to determine contest intensity. Questions 1 and 2 together explored whether initiation behaviours could serve as useful cues for fish to judge their opponents' contest history. For instance, if display and/or attack initiators were more likely to win and individuals with different contest experience differ in their likelihood to initiate displays and/or attacks, these behaviours could be useful for an individual to evaluate its opponent's recent contest history and fighting ability (social-cue mechanism). In addition, question 2 also clarified the presence of winner and loser effects in the contest behaviour of the fish, which was essential to our main objective of testing the two mechanisms which might cause these effects. Question 3 directly examined the relative contribution of the self-assessment and social-cue mechanisms to the winner and loser effects. If self-assessment is important, a loser's decision to retreat at different stages of a contest should depend on its own experience (its recent loss/win causing earlier/later retreats, respectively). If, however, the social-cue mechanism is important, its opponent's recent win/loss should make it retreat earlier/later, respectively.

### Procedures

All fish used in this study had been re-isolated for at least a month after use in previous studies and contest pairs were matched for their last contest outcome (i.e. previous winners with previous winners and previous losers with previous losers). The experiences that these test individuals gained from previous studies (last contest outcome) were results of 'self-selection' procedures (see Hsu et al. 2006 for a discussion), which confound winner/loser effects with intrinsic fighting ability. Because unpublished results indicate that winner/loser effects in the fish disappear in 7 days (i.e. after this time, the probability of winning and the likelihood of escalation no longer differed between individuals with a winning and a losing experience fighting against a naïve opponent), any differences that might be found in later analyses between contest pairs that had won or lost a month previously would more likely to result from differences in intrinsic aggressiveness than from so-called winner/loser effects. Contest pairs were also matched for their strain and body size (SL difference<1 mm). Fifty pairs of fish (ten/strain) were used for each contest type (total $N$=300 pairs). Each fish was used only once in the experiment. The pair SL ranged between 20.72 and 26.60 mm (mean ± SD=23.18±1.17).

On day 1, the fish were identified by breaking the non-vascularised thin membrane between two soft-rays in either the upper or lower margins of a contestant's caudal fin (randomly assigned). The procedure did not cause bleeding or observable adverse effects upon the fishes' health or behaviour.

On day 2, fish received a pre-designated randomly assigned experience (W, L or N). To ensure that the focal individuals lost or won, we fought them against much larger/smaller (difference >2 mm) standard winners/losers that had won/lost several fights with similar-sized opponents. For experience training, a fish was placed in each of two equal-sized symmetrical compartments (randomly selected) of a standard aquarium (12×8×20 cm, containing water 16 cm deep and 2 cm of gravel) divided by an opaque partition. After 15-min acclimatisation, the partition was removed to allow them to interact. Experiment individuals acquired their pre-designated experiences quickly due to the large size differences and were allowed to continue to interact with their trainers for 1 h. No dominance reversion was observed. Fish assigned to receive no (N) experience were treated exactly as above, except with no opponent in the standard aquarium.

After experience training, the fish were replaced in their maintenance containers and fed newly hatched brine shrimp. One hour later, the pre-designated opponents were each placed in one of the two compartments (randomly assigned) of a standard aquarium separated by an opaque partition to acclimatise. After 20 h acclimatisation (day 3), the partition was lifted and the contest began; the fishes' interactions were then videotaped for up to 1 h as explained in the next section.

### Contest behaviours

The fighting behaviour of *K. marmoratus* is described in Hsu et al. (2008). At the start of the contest, the fish usually moved towards each other, often with gill covers erected. The fish that first oriented and moved towards its opponent was the display initiator. After a few bouts of mutual displays, one fish sometimes retreated and the contest was considered resolved in favour of the other. If not, one fish launched a first attack by swimming rapidly towards and pushing against or biting its opponent and was defined as the attack initiator. If the fish receiving the first attack retreated, the contest was consider resolved as before. Contests that resolved with mutual displays or one attack were classified as non-escalated contests. If the fish being attacked retaliated with attacks, the contest was classified as escalated. Escalation duration was measured as the time between the first attack and the loser's first retreat. Losers persistently avoided the winners by swimming away when the winners approached. The fish that first chased and/or attacked its opponent for 5 min without retaliation was the contest winner. Once this criterion was met, we re-inserted the opaque partition to separate the two contestants and terminate the contest. Contests resulting in clear winners/losers were 'resolved'. If neither opponent initiated attacks and no obvious winner/loser were observed in 1 h, the contest was terminated and classified as 'unresolved'. All fish were returned to their maintenance containers after the experiments.

### Statistical analysis

We used goodness-of-fit likelihood ratio $G$ statistics to analyse whether display/attack initiators were more likely to win contests than their opponents (question 1). Because initiating displays and initiating attacks were probably correlated, we adjusted $\alpha$ for these tests with Bonferroni procedures to 0.025 (= 0.05/2). To examine the influence of contestants' prior experience on each other's propensity to initiate displays and attacks and to win contests (question 2), we randomly designated the two individuals as 'focal' and 'opponent' and modelled the probabilities for the focal individuals with multiple logistic regression. If a recent contest experience influences how an individual perceives its fighting ability (self-assessment mechanism) or how its opponent responds to it (social-cue mechanism), then the one with the better experience will probably be the first to display and attack and will probably win. The likelihood of a focal individual displaying/attacking before its opponent and its likelihood of winning should therefore depend on how positive its experience was relative to that of its opponent (influenced positively by its own experience but negatively by its opponent's experience). These trends are thus only useful in evaluating whether winner and loser effects are important to the fish's contest behaviour but not in evaluating the relative contribution of the self-assessment and the social-cue mechanisms to these effects. In addition to the focal individual's and the opponent's experiences, we included their interactions in the regression models to detect the interdependence of two individuals' contest experiences in influencing each other's contest behaviour, which could lend support to the social-cue mechanism for the experience effects. Because initiating displays, initiating attacks and winning were probably correlated, we adjusted $\alpha$ for these tests with Bonferroni procedures to 0.017 (= 0.05/3). Because recent winning and losing experiences have stronger influence on the outcome of non-escalated than escalated contests (Hsu and Wolf 1999; Hsu et al. 2006), we analysed these two types of contests separately.

The contribution of the self-assessment and social-cue mechanisms were directly evaluated by examining how the loser's and the winner's recent contest experience influenced the loser's decision to retreat at different stages of a contest (question 3). When two individuals meet in a contest, the eventual loser's persistence determines when a contest ends. If a recent contest experience influences how an individual evaluates its own fighting ability (self-assessment mechanism), a loser's persistence should be influenced by its own contest experience. If a loser detects some experience-mediated cues from the winner and modifies its contest decision based on these cues (social-cue mechanism), then its persistence should be influenced by the winner's contest experience. Thus, the eventual loser's decision to retreat or persist at different stages of a contest should depend on its own experience if the self-assessment mechanism is important, depend on the winner's experience if the social-cue mechanism is important and depend on both loser's and winner's experiences if both mechanisms are important. We examined losers' decisions to retreat at three different contest stages: after mutual displays, after one attack and after some period of mutual attacks (escalation). We adjusted $\alpha$ for these tests with Bonferroni procedures to 0.017 (= 0.05/3). We used multiple logistic regression to examine how losers' and winners' recent contest experiences combined to determine the likelihood of losers retreating after mutual displays and one attack. The influences of losers' and winners' contest experiences on escalation duration were analysed with multiple linear regression, where escalation duration was ln-transformed for the residuals of the regression model to fit the normal distribution (Shapiro–Wilk $W$ test, $p=0.193$). We included the interactions of loser's and winner's experiences in the regression models to detect any possible interdependence of the two individuals' contest experiences on the loser's decision to retreat.

We included size, last contest outcome and strain type in all regression models. Two-tailed tests were employed throughout. JMP (v. 5.0.1 SAS Institute Inc., Cary, NC, USA), a commercial statistical package, was used for the statistical analyses.

## Results

### Relationship between initiation behaviours and winning

Two hundred and ninety out of the 300 contests resolved in 1 h, a proportion which was independent of the contest type ($G_5$=1.99, $p$=0.851). Contestants that initiated either displays (183/290=63%, $G_1$=20.15, $p$<0.001) or attacks (232/290=80%, $G_1$=111.79, $p$<0.001) won significantly more of the resolved contests than their opponents. When examined separately, the trend existed in all six contest types but reached significance in only two (L–L, N–N) for display initiators (adjusted $\alpha$=0.025; Fig. 1). The result was significant in all six types of contests for attack initiators (each $p\leq$0.002, adjusted $\alpha$=0.025; Fig. 2). Not surprisingly, initiating attacks was a stronger indicator for winning than initiating displays ($G_1$=20.57, $p$<0.001).

### Effect of contestants' recent contest experiences on initiation behaviour and probability of winning

The overall influence of recent contest experience (the pooled effect of a winning and a losing experience) on the probability of initiating displays was not significant (Table 1; Fig. 3; focal individuals' experience: $p$=0.079; opponents' experience: $p$=0.057; adjusted $\alpha$=0.017). When examining the effect of winning and losing experiences separately, however, the focal individual's winning experience increased (though not significantly, $p$=0.035) whilst its opponent's winning experience decreased (though not significantly, $p$=0.070) the likelihood of the focal individual displaying first. Losing experience, on the other hand, did not appear to have any influence on the behaviour (focal individual's: $p$=0.699; opponent's: $p$=0.614).

The probability of initiating attacks (Table 1; Fig. 3) was significantly affected by recent contest experience (the pooled effect of a winning and a losing experience; focal individuals' experience: $p$=0.006; opponents' experience: $p$=0.017; adjusted $\alpha$=0.017). When examining the effect of winning and losing experiences separately, the effects came primarily from winning experiences: Focal individuals' winning experience increased (though not significantly, $p$=0.018) whilst opponents' winning experience decreased (though not significantly, $p$=0.041) the likelihood of focal individuals attacking first. Losing experience, whether the focal individual's ($p$=0.475) or the opponent's ($p$=0.440), did not have much impact on the behaviour.

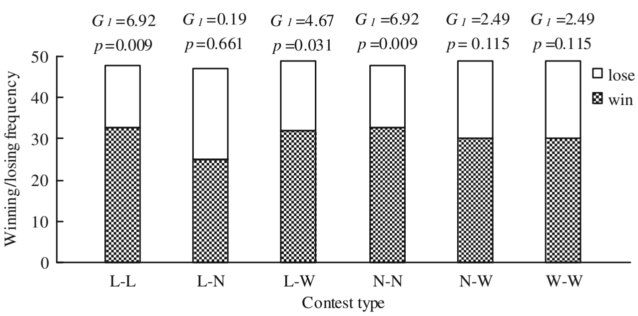


**Fig. 1** Number of resolved contests won or lost by the display initiator

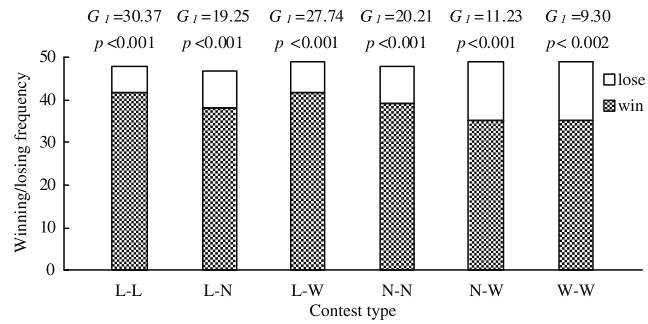


**Fig. 2** Number of resolved contests won or lost by the attack initiator

The probability of winning non-escalated contests (Table 1; Fig. 4) was also significantly influenced by recent contest experiences (the pooled effect of a winning and a losing experience; focal individuals' experience: $p$<0.001; opponents' experience: $p$<0.001; adjusted $\alpha$=0.017). When examining the effect of winning and losing experiences separately, the focal individual's recent winning experience increased (though not significantly, $p$=0.025) but losing experience decreased (though not significantly, $p$=0.038) its own likelihood of winning non-escalated contests, whilst its opponent's winning ($p$=0.070) and losing ($p$=0.028) experiences had the opposite effects (although also not significant). The overall effect of experience on the probability of winning escalated contests did not reach significance (Table 1; Fig. 4; focal individuals' experience: $p$=0.117; opponents' experience: $p$=0.029; adjusted $\alpha$=0.017). However, when examining the effect of winning and losing experiences effects separately, the focal individual had (though not significantly, $p$=0.021) a higher probability of winning escalated contest when fighting against an opponent with a recent losing experience.

Focal individuals' and opponents' recent contest experiences did not have significant interaction effects on any of the contest behaviours examined. Likewise, strain type, pair size and pair's last contest outcome (>1 month) did not have significant effects on any of these contest behaviours.

Overall, these results show that recent contest experiences had the most significant effects on the probability of winning non-escalated contest, followed by initiating

**Table 1** Logistic regression modelling the influence and the interaction effects of focal individuals' and opponents' recent contest experiences on the likelihood of the focal individuals (1) initiating displays, (2) initiating attacks and (3) winning non-escalated and escalated contests, with contest pairs' strain, size and last contest outcome included in the models

| | $b$±SE | $\chi^2$ | *df* | *p* |
|---|---|---|---|---|
| Initiating displays ($n$=300) | | | | |
| Focal individuals' experience | | 5.08 | 2 | 0.079 |
| Focal_W | 0.664±0.318 | 4.47 | 1 | 0.035 |
| Focal_L | 0.120±0.311 | 0.15 | 1 | 0.699 |
| Opponents' experience | | 5.72 | 2 | 0.057 |
| Opponent_W | −0.562±0.312 | 3.29 | 1 | 0.070 |
| Opponent_L | 0.156±0.311 | 0.25 | 1 | 0.614 |
| Focal experience × opponent experience | | 5.10 | 4 | 0.277 |
| Strain | | 3.80 | 4 | 0.434 |
| Pair size | −0.094±0.110 | 0.74 | 1 | 0.390 |
| Last outcome_W | 0.320±0.239 | 1.79 | 1 | 0.181 |
| Initiating attacks ($n$=287) | | | | |
| Focal individuals' experience | | 10.26 | 2 | 0.006[a] |
| Focal_W | 0.757±0.326 | 5.57 | 1 | 0.018 |
| Focal_L | −0.230±0.323 | 0.51 | 1 | 0.475 |
| Opponents' experience | | 8.12 | 2 | 0.017[a] |
| Opponent_W | −0.652±0.322 | 4.18 | 1 | 0.041 |
| Opponent_L | 0.249±0.324 | 0.60 | 1 | 0.440 |
| Focal experience × opponent experience | | 1.54 | 4 | 0.820 |
| Strain | | 6.87 | 4 | 0.143 |
| Pair size | −0.011±0.114 | 0.01 | 1 | 0.920 |
| Last outcome_W | 0.240±0.248 | 0.94 | 1 | 0.332 |
| Winning | | | | |
| Non-escalated contest ($n$=166) | | | | |
| Focal individuals' experience | | 17.03 | 2 | <0.001[a] |
| Focal_W | 1.298±0.620 | 5.05 | 1 | 0.025 |
| Focal_L | −0.903±0.4383 | 4.32 | 1 | 0.038 |
| Opponents' experience | | 19.10 | 2 | <0.001[a] |
| Opponent_W | −0.880±0.495 | 3.27 | 1 | 0.070 |
| Opponent_L | 1.034±0.483 | 4.85 | 1 | 0.028 |
| Focal experience × opponent experience | | 2.56 | 4 | 0.635 |
| Strain | | 4.44 | 4 | 0.350 |
| Pair size | 0.084±0.162 | 0.27 | 1 | 0.605 |
| Last outcome_W | 0.636±0.360 | 3.20 | 1 | 0.074 |
| Escalated contest ($n$=124) | | | | |
| Focal individuals' experience | | 4.29 | 2 | 0.117 |
| Focal_W | −0.648±0.483 | 1.89 | 1 | 0.169 |
| Focal_L | 0.357±0.661 | 0.29 | 1 | 0.590 |
| Opponents' experience | | 7.09 | 2 | 0.029 |
| Opponent_W | 0.004±0.458 | 0.00 | 1 | 0.993 |
| Opponent_L | 1.282±0.588 | 5.31 | 1 | 0.021 |
| Focal experience × opponent experience | | 3.36 | 4 | 0.500 |
| Strain | | 2.22 | 4 | 0.696 |
| Pair size | 0.304±0.191 | 2.64 | 1 | 0.104 |
| Last outcome_W | −0.123±0.393 | 0.10 | 1 | 0.754 |

Focal_W and Focal_L are indicator variables, where Focal_N (no experience) is the baseline. Opponent_W and Opponent_L are indicator variables, where Opponent_N (no experience) is the baseline

[a] Significant $p$ values after Bonferroni adjustment ($\alpha$=0.017)

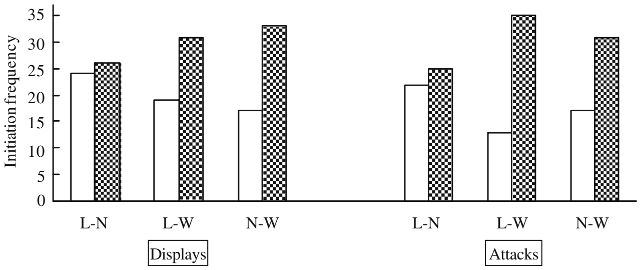


**Fig. 3** Number of displays and attacks initiated by individuals with different prior contest experiences; the *empty and shaded bars* represent the initiation frequency of the first (e.g. *L*) and the second (e.g. *N*) contestants of a contest type (e.g. *L–N*), respectively

attacks, whereas their influences on initiating displays and winning escalated contests did not reach significance levels. Both winner and loser effects contributed to the significant overall impact of experience on the outcome of non-escalated contests, whereas the significant overall effect of experience on initiating attacks resulted primarily from winning experiences. It should be noted that although these results showed the importance of prior contest experiences on an individual's strategy in a subsequent contest, as they were consistent with the predictions from both the self-assessment and the social-cue mechanisms, they could not be used to test between these two. This is dealt with in the next section.

Effect of winners' and losers' contest experience on losers' decision to retreat at different stages

Losers' but not winners' recent contest experience (Table 2) had significant effects on losers' decisions to retreat at all stages of a contest (the pooled effect of a winning and a losing experience; losers' experience: $p<0.001$ for retreating after mutual displays, retreating after one attack and escalation duration; winners' experience: $p\geq0.395$ for all; adjusted $\alpha=0.017$). More detailed patterns emerged when examining separately the effects of losers' winning and losing experiences on their own decisions to retreat. A recent losing experience made a loser more likely to retreat after mutual displays ($p<0.001$; Table 2). For contests that did not resolve with mutual displays, losers that had a recent winning experience were less likely to retreat after an attack ($p=0.002$; Table 2), i.e. they were more likely to escalate contests into physical fights. Once contests were escalated (Table 2), losers that had recently won persisted longer (though not significantly, $p=0.037$) than losers with no recent contest experience; the insignificance was probably a result of the small sample size ($n=124$), as less than 50% of contests were escalated.

Losers' and winners' recent contest experiences did not have significant interaction effects on losers' decision to retreat at any stage of the contest. Strain type and pair size also did not have significant effects on losers' decisions. However, the pair's last contest outcome had a significant effect on the loser's persistence in escalated contests: When both contestants had won their last fights before this study (more than a month before), the eventual losers persisted longer in escalated contests before retreating ($p=0.002$).

Overall, losers' decisions to retreat at various stages were influenced by their own contest experience but not by the winners'. Losers that had recently lost were likely to retreat before any attacks were launched whilst losers that had recently won were likely to escalate contests into physical fights. Once a contest was escalated, a loser's recent winning experience had a positive effect on its persistence.

## Discussion

Our study showed that in *K. marmoratus*, a loser's decision to retreat at different stages of a contest was influenced by its own but not winner's contest experience. These results are consistent with the self-assessment hypothesis for winner and loser effects but did not provide support for the social-cue hypothesis. Although these results indicate that the fish do not respond to each other's past contest history, they are not inconsistent with the fish assessing each other's fighting ability in other ways. A recent study (Hsu et al. 2008) on the fish's assessment strategy showed that opponents evaluated each other's size/strength; the likelihood of the weaker individual retreating at earlier stages of a contest related negatively with its own size but positively with its opponent's. Therefore, when evaluating an opponent, the fish appear to compare size/strength directly but not to put much weight, if any, on indirect cues.

It has been reported that bystanders of many species modify fighting tactics against winners and losers whose contests they have observed (see Bonnie and Earley 2007 for a brief review). Because the eavesdropping effect involves bystanders witnessing interactions and altering contest

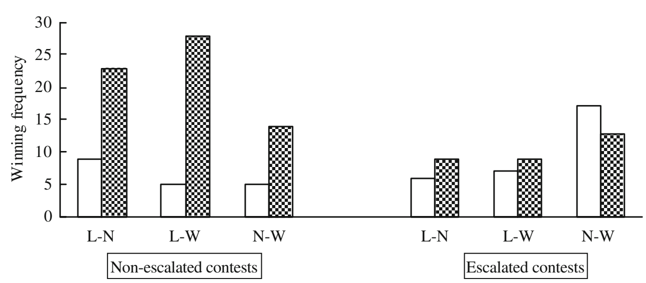


**Fig. 4** Number of non-escalated and escalated contest won by individuals with different prior contest experiences; the *empty and shaded bars* represent the winning frequency of the first (e.g. *L*) and the second (e.g. *N*) contestants of a contest type (e.g. *L–N*), respectively

**Table 2** Influence and interaction effects of losers' and winners' recent experience on (1) the likelihood of contests being resolved with mutual displays (multiple logistic regression), (2) the likelihood of contests being resolved with one attack (multiple logistic regression) and (3) the duration of escalation (multiple linear regression), with contest pairs' strain, size and last contest outcome included in the models

| | $b$±SE | Test statistic | *df* | *p* |
|---|---|---|---|---|
| Likelihood of contest resolved with mutual displays ($n$=290) | | | | |
| Losers' experience | | 26.69 | 2 | <0.001[a] |
| Loser_W | −0.194±0.574 | 0.12 | 1 | 0.734 |
| Loser_L | 1.579±0.422 | 17.59 | 1 | <0.001[a] |
| Winners' experience | | 1.86 | 2 | 0.395 |
| Winner_W | 0.405±0.435 | 0.93 | 1 | 0.336 |
| Winner_L | 0.674±0.532 | 1.50 | 1 | 0.221 |
| Loser experience × winner experience | | 5.59 | 4 | 0.232 |
| Strain | | 3.98 | 4 | 0.409 |
| Pair size | 0.119±0.136 | 0.77 | 1 | 0.379 |
| Last outcome_W | −0.023±0.300 | 0.01 | 1 | 0.938 |
| Likelihood of contests resolved with an initial attack ($n$=219) | | | | |
| Losers' experience | | 15.42 | 2 | <0.001[a] |
| Loser_W | −1.248±0.427 | 9.59 | 1 | 0.002[a] |
| Loser_L | 0.308±0.363 | 0.72 | 1 | 0.395 |
| Winners' experience | | 0.12 | 2 | 0.942 |
| Winner_W | 0.107±0.351 | 0.09 | 1 | 0.761 |
| Winner_L | 0.087±0.509 | 0.03 | 1 | 0.864 |
| Loser experience × winner experience | | 2.99 | 4 | 0.559 |
| Strain | | 1.45 | 4 | 0.835 |
| Pair size | −0.002±0.142 | 0.00 | 1 | 0.992 |
| Last outcome_W | −0.545±0.297 | 3.40 | 1 | 0.065 |
| Duration of escalation ($n$=124) | | | | |
| Losers' experience | | 8.23 | 2,109 | <0.001[a] |
| Loser_W | 0.613±0.290 | 4.46 | 1,109 | 0.037 |
| Loser_L | −0.494±0.342 | 2.09 | 1,109 | 0.150 |
| Winners' experience | | 0.71 | 2,109 | 0.496 |
| Winner_W | −0.398±0.2794 | 2.04 | 1,109 | 0.156 |
| Winner_L | 0.092±0.363 | 0.06 | 1,109 | 0.801 |
| Loser experience × winner experience | | 1.38 | 4,109 | 0.245 |
| Strain | | 0.32 | 4,109 | 0.864 |
| Pair size | −0.158±0.114 | 1.92 | 1,109 | 0.168 |
| Last outcome_W | 0.759±0.242 | 9.85 | 1,109 | 0.002[a] |

Test statistic: likelihood ratio $\chi^2$ test for likelihood of contest resolved with mutual displays and likelihood of contests resolved with an initial attack and $F$ test for duration of escalation. Loser_W and Loser_L are indicator variables, where Loser_N (no experience) is the baseline. Winner_W and Winner_L are indicator variables, where Winner_N (no experience) is the baseline

[a] Significant $p$ values after Bonferroni adjustment ($\alpha$=0.017)

strategy towards the observed (and thus familiar) winners and losers, it differs from winner and loser effects, which are commonly detected between unfamiliar contestants. Oliveira and colleagues (1998) have demonstrated in Siamese fighting fish (*Betta splendens*) that bystanders take longer to approach and display to observed winners than observed losers but do not show differential responses towards unseen winners and losers. Thus, the bystanders did not appear to detect or respond to the unseen winners' and losers' changes in behaviour. In a different study, individuals of Siamese fighting fish with recent winning experiences were observed to display more, behave more aggressively and win more contests when fighting against unfamiliar opponents with recent losing experiences (Wallen and Wojciechowski-Metzlar 1985), demonstrating winner/loser effects in the fish. Because individuals of Siamese fighting fish changed contest strategies after winning and losing experiences (self-assessment mechanism) but bystanders did not respond to the behavioural changes (social cues) of the unseen winners and losers, winner/loser effects in this fish might also operate through the self-assessment but not the social-cue mechanism. It should be noted that chemical exchanges between focal individuals and the winners/losers of unobserved contests were not permitted in the study by Oliveira et al. (1998) and thus, it is not clear whether the fish would use chemical cues to assess opponents. The results, nonetheless, show that behavioural status-related cues alone are not sufficient to elicit differential responses in competitor Siamese fighting fish, as in our fish.

Initiation behaviours in *K. marmoratus*, especially initiating attacks, correlated significantly with winning contests and thus should be reasonable predictors for contestants' relative fighting abilities. Because the relationship between initiation and winning contest was similar across different contest types in the present study and the relationship has been reported in many other species (e.g. opisthobranch molluscs *Hermissenda crassicornis*, Zack 1975; sticklebacks *Gasterosteus aculeatus*, Bakker et al. 1989; juncos *Junco hyemalis oreganus*, Jackson 1991; hens *Gallus domesticus* Martin et al. 1997; green swordtails *Xiphophorus helleri*, Earley and Dugatkin 2002), it is probably a common characteristic of animal contest. Because an individual's contest strategy was not influenced by its opponent's contest experience, it was probably also not influenced by its opponent's experience-mediated initiation behaviours. These results indicate that the correlations between initiating behaviours and winning contest in the fish arise because both are correlated with an individual's assessment of its own fighting ability, itself influenced by prior contest experience, but not because initiating a contest makes the opponent more inclined to retreat. An individual that evaluates itself to have good fighting ability tends to behave aggressively and actively initiates and intensifies confrontations. It also persists longer and ends up with a higher probability of winning. In the present study, display or attack initiators that won contests also delivered more post-retreat attacks per minute on losers than the non-initiators, which supports this interpretation (display: ln-transformed mean ± SE—0.82± 0.05 vs. 0.60±0.07; $t_{288}$=2.46, $p$=0.014; attack [escalated contests only as attack initiators could only lose in escalated contests, hence smaller sample size]—1.03±0.09 vs. 0.79± 0.09; $t_{122}$=2.00, $p$=0.048). These positive relationships between initiation behaviour, winning contests and post-retreat attacks in *K. marmoratus* have physiological bases as they all correlate positively with testosterone level and negatively with cortisol level (Earley and Hsu 2008). Individuals that have higher testosterone and lower cortisol levels behave more aggressively, have a higher tendency to initiate displays and attacks, to win contests and to deliver more post-retreat attacks on losers. As behavioural tendencies are modulated by recent contest experience, testosterone and cortisol levels might also be. Earley and Hsu (2008), however, found that self-selection winning and losing experiences did not cause differential changes in fishes' testosterone or cortisol levels. Random-selection studies of winning and losing experiences are needed to improve our understanding of whether and how these hormones are involved in the winner and loser effects' physiological mechanisms.

Despite the strong correlation between fish initiating attacks and winning contests, it is interesting that the magnitude of the influences of winning and losing experiences on an individual's chance of winning a non-escalated contest were similar ($p$=0.025 and 0.070 for winning experiences; $p$=0.038, 0.028 for losing experiences; Table 1) but losing experiences appeared to have less effect than winning experiences on the likelihood of initiating attacks ($p$=0.018 and 0.041 for winning experiences; $p$=0.475, 0.440 for losing experiences; Table 1). Since, as discussed above, initiating an attack does not change a fish's chances of winning by altering its opponent's tendency to retreat, it could simply be that losing experiences act through reducing a fish's persistence in the contest, or perhaps they also make the fish generally less aggressive, in which case a larger sample size might make the existing tendency for fish with losing experience to initiate fewer attacks easier to detect. In a different (unpublished) experiment, we staged 150 contests between fish with a recent losing experience and individuals with no recent contest experience. Here, a losing experience significantly reduced the likelihood of both initiating attacks and winning contests, consistent with the notion that a recent losing experience makes the fish less aggressive and less persistent in contests.

Like many previous studies (see Hsu et al. 2006 for a review), we used small standard losers and large standard winners for training. Despite previous observation that the fish adopt different contest strategies against different-sized opponents (Hsu et al. 2008), a learning experience gained from a much bigger or smaller opponent still significantly affects the fish's later performance against a same-sized opponent. These results have two implications. Firstly, visual inspection of each other's size might not contribute much to the fishes' contest decisions, even though size has a deterministic impact on contest outcome. When difference in body length exceeds 2 mm, the chance of the larger opponent winning reaches 93% (77/83; data from Hsu et al. 2008). Nevertheless, very few smaller opponents (6/83) retreated as soon as challenged by a much larger opponent. Most retreated after some period of mutual display or physical interaction. The fish thus seem to strive for confirmation of each other's fighting ability in the presence of reliable morphological cues rather than retreating immediately. Since body size is probably a good surrogate for strength, the observation of Hsu et al. (2008) that the fish adopt different contest strategies against different-sized opponents may be a consequence of them adopting different contest strategies against opponents of different strength. Secondly, experience effects may not be strongly influenced by the relative size or strength of the experience provider. This is consistent with the proposition that individuals use recent contests to evaluate their own fighting ability relative to the population of fighting abilities (Whitehouse 1997) but not that individuals use experience to associate cues (e.g. size) with their opponents' fighting ability (Whitehouse 1997). If a contest experience simply provides sampling information about the population of fighting abilities, a win should lead an individual to raise its assessment of its relative fighting ability and thus the expected chance of winning over the next competitor, whether its opponent was large or small. An easy win, however, could potentially 'inform' the individual that it was much better than its opponent and raise its assessment more than a difficult win. This effect of 'experience quality' remains to be tested.

The major benefit of using small and submissive standard losers and large and aggressive standard winners for experience training is to ensure that the individuals receive their pre-designated experiences (random selection procedure; Hsu et al. 2006). This avoids confounding experience effects with intrinsic fighting ability. Nonetheless, because individuals receive winning and losing experience from different 'types' (size, behaviour etc.) of trainers, we cannot know whether the observed winner and loser effects resulted from individuals experiencing different contest outcomes (winning or losing), interacting with different type of individuals or simply viewing different types of opponents. As mentioned earlier, smaller opponents do not usually retreat immediately on being challenged by a much larger opponent; they mostly retreat after some period of mutual display or physical interaction. These results suggest that some interaction with the trainer is likely to be required for an individual to exhibit a winner or loser effect in a subsequent contest. Nonetheless, further study would be needed to understand what number, length or type of interactions with an opponent is required before an individual changes its contest strategy in a subsequent contest.

Dominant and subordinate fish have been observed to release different chemicals or different quantities of the same chemicals (Oliveira et al. 1996; Barata et al. 2007, 2008). Although it is not clear whether these status-related chemical cues would elicit differential responses from their competitors in a contest, they have been shown to facilitate inter-sexual communication (Barata et al. 2007, 2008). In the Mozambique tilapia (*Oreochromis mossambicus*), for instance, in the presence of females that are ready to spawn, dominant males urinate more frequently than subordinates, produce more urine and their urine has greater olfactory potency (Barata et al. 2007, 2008). Furthermore, female tilapia's olfactory system is more sensitive to dominants' urine, which led the authors to conclude that dominant tilapia males use the urinary odorant to signal dominance to the females (Barata et al. 2008). Clearly, fish are capable of detecting and responding to chemical cues released by conspecifics. However, we are not aware of studies demonstrating that chemicals from dominant and subordinate fish elicit submissive and dominating behaviour, respectively, from their competitors. Our study fish, *K marmoratus*, did not respond to their opponents' contest history and thus, the fish either do not release status-related chemical cues or those cues, like the behavioural cues, do not elicit differential responses in the competitors.

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