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The winner and loser effect: what fighting behaviours are influenced?

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We examined the effect of prior winning and losing experiences on the initiating and responding strategies of contestants in contests between individuals of *Rivulus marmoratus* (Cyprinodontidae). Each contestant was given a penultimate and a recent fighting experience approximately 48 and 24 h prior to the dyadic contests, respectively, through randomly selected procedures. Winning and losing experience appeared to influence different types of fighting behaviours. Losing experiences decreased the probability of an individual initiating a confrontation and thus increased its tendency to retreat immediately when challenged. Winning experiences did not affect the probability of initiation, but significantly increased the likelihood of an individual initiating with attacks that effectively deterred its opponents. A substantial proportion (59/153) of individuals retreated immediately when challenged and reduced the number of fights available for examining experience effects on responding strategies at later stages of a contest. None the less, winning experiences consistently increased the likelihood of an individual retaliating by attacking its opponent at various stages of a contest, and eventually increased its probability of escalating a confrontation into physical fights. However, the effects of losing experiences on these responding strategies were undetectable. Recent experiences significantly affected all fighting behaviours examined, but penultimate experiences significantly affected only the tendency to initiate a confrontation with attacks and the likelihood of escalation. These results indicated that prior experiences had the longest lasting effect on the potentially most costly fighting behaviour. Prior experiences influenced the outcome of nonescalated contests as well as the probability of escalation, but did not significantly affect the outcome of escalated contests. These results are consistent with the hypothesis that prior experiences modify the information that an individual has about its fighting ability but do not alter its actual fighting ability and that actual fighting ability becomes the more important influence on outcomes of escalated contests.

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Prior fighting experience affects an individual's probability of winning a later contest (see Hsu & Wolf 1999). A prior losing experience often decreases the likelihood of an individual winning a subsequent contest (but see Thorpe et al. 1995). Nevertheless, the effect of a winning experience varies among studies; some detected an increase, while others observed no significant difference in the probability of winning a subsequent contest after a winning experience (but see Hsu & Wolf 1999; also see Chase et al. 1994 for discussion).

The majority of previous studies has focused on the outcome of subsequent contests. A few studies have also examined experience effects on the likelihood of initiating future agonistic interactions (e.g. McDonald et al. 1968; Franck & Ribowski 1987; Schuett 1997). The general result of these studies is that when previous fighting experience significantly affects an individual's probability of winning its next contest, it also affects the individual's likelihood of initiating the contest. Nevertheless, a contest is more than just initiating a confrontation. It is a series of interactions between the contestants, with each having the option of terminating or continuing the contest at any time. To influence the outcome of a contest, prior fighting experience also should affect how individuals interact with each other during a contest.

The effect of prior experience on the fighting behaviours of contestants after initiating a contest is much less reported. One possible reason for this information to be scarce is that, after one losing experience, the individuals of some species always retreat when challenged again

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(Schuett 1997), leaving little subsequent fighting behaviour to study. Furthermore, the effect of a winning experience is not as significant as the effect of a losing experience in many species, which makes it even harder to examine the influence of winning experience on sequential fighting behaviours.

In a recent study of *Rivulus marmoratus* (Hsu & Wolf 1999), a cyprinodont fish, individuals were given different combinations of two fighting experiences to investigate how a recent experience (given 24 h prior to the contest) and a penultimate experience (given 48 h prior to the contest) were integrated to influence the outcome of a subsequent contest. The study showed: (1) winning and losing experiences had opposite but equal effects on the fighting outcomes of subsequent contests and (2) both winning and losing effects lasted for at least 48 h. These results indicate that *R. marmoratus* can be used to explore how winning and losing experiences influence behaviour during a contest to affect the fighting outcome, which is the first objective of this study.

Fighting can be costly to animals. Potential costs include: the time and energy (Haller & Wittenberger 1988; Haller 1991; Thorpe et al. 1995) required for fighting, the likelihood of injury (Neat et al. 1998), and the increased risk of predation (Jakobsson et al. 1995; Brick 1999). We thus expect animals to adjust their investment in a contest based on the benefits and costs associated with the contest (Maynard Smith & Price 1973; Maynard Smith 1974; Maynard Smith & Parker 1976). Empirical studies that manipulated payoffs and/or fighting costs for contestants often successfully altered the fighting behaviour of these contestants as predicted (e.g. Austad 1983; Dugatkin & Ohlsen 1990; Lindström 1992). In these studies, the payoff for a contest was often varied by offering the contestants food or mates of different quantity/quality, while the fighting costs were controlled by presenting a contestant with opponents of different sizes (e.g. body weight, body length, weapon size).

In previous studies of the effect of fighting experience, prior winning or losing experiences did not seem likely to change how the contestants evaluated their benefits to cause the observed difference in the probability of winning. Therefore, experiences were usually hypothesized to influence how the contestants assessed their fighting ability and thus their fighting costs in subsequent contests (e.g. Beaugrand et al. 1991; Miklósi et al. 1997; Hsu & Wolf 1999). However, interpretations disagreed about how prior fighting experiences influenced an individual's assessment of its fighting ability. Some authors (e.g. Beacham 1988; Beaugrand et al. 1991) suggested that prior winning and losing experience changed an individual's actual fighting ability, while others (Miklósi et al. 1997; Whitehouse 1997; Hsu & Wolf 1999) hypothesized that prior fights added to the information that an individual had for evaluating its relative fighting ability, but did not alter its actual fighting ability. Both hypotheses predict that prior fighting experiences would influence an individual's assessment of its fighting cost and thus its probability of winning a subsequent contest. Thus, it is difficult to test between the two hypotheses by examining the effect of prior fighting experiences on the outcomes of later contests.

The two hypotheses differ in the importance of prior experience as contests progress according to the sequential assessment model. This model views a contest as a series of interactions during which contestants gradually assess each other's true fighting ability (Enquist & Leimar 1983; Enquist et al. 1985, 1990); as the contest progresses to later stages with more costly physical interactions, more reliable information would have been accumulated. Thus, if prior experiences merely influence how an individual assesses its relative fighting ability but do not change its actual fighting ability, prior experiences should have a significant impact on its fighting behaviour before physical interactions occur. Once a contest escalates into costly physical interactions, the importance of experience effects should decline and the outcome will be determined by the contestants' true fighting abilities. On the other hand, if prior experiences alter an individual's fighting ability, prior fighting experiences should influence the outcomes of escalated contests as well. The second objective of this study was to examine the effect of prior fighting experiences on the outcomes of contests settled with and without physical fights to test whether prior fighting experiences influence fighting outcomes by altering the actual fighting ability for an individual.

METHODS

The data in the study were acquired from videotapes of the contests staged in the experiments described in Hsu & Wolf (1999). Readers should refer to that paper for details of the Study Species, Study Design, Procedures, Providing a Losing/Winning Experience and Staging Contests.

The Study Species

Rivulus marmoratus is an internally self-fertilizing hermaphroditic fish (Harrington 1961) that is aggressive in both the field and laboratory (Kristensen 1970; Huehner et al. 1985; Taylor 1990). Two individuals confined in a small aquarium usually establish a dominant–subordinate relationship within 1 h (Hsu 1997). Genetic studies suggest that the fish exist in nature as isogenic, homozygous strains (Vrijenhoek 1985; Turner et al. 1990). We used individuals from two strains for this study. Strain NA (Florida, U.S.A.) had been kept in captivity for more than 15 generations. Strain B was the first generation from Belize. Both strains were maintained and bred at Syracuse University successfully for 3 years (two generations).

Study Design

We presented individual *R. marmoratus* with different combinations of wins (W), losses (L), or no fighting experience (N) (one experience per day for 2 consecutive days; each experience lasted for 1 h as explained below): WL (winning on day 1, losing on day 2), WW, LW, LL, LN and NN. On the third day, we staged contests between

individuals with different prior fighting experiences as follows: (1) WW–LW (WW individuals against LW individuals); (2) LL–WL; (3) LW–WL; (4) LN–WL; and (5) NN–LW. Hereafter, the experiences received on day 1 and day 2 will be referred as penultimate and recent experiences, respectively.

Both WW–LW and LL–WL contests test the effect of a penultimate experience because the opponents in these two types of contests had the same recent experiences, but different penultimate experiences. LW–WL contests test for the relative importance of the recent and the penultimate experiences because the opponents had opposite penultimate and recent experiences. To test for the effect of recent winning and losing experiences separately, we compared the outcome of LN–WL contests to that of LL–WL and LW–WL contests because in these three sets of contests, LL, LW and LN individuals all fought against WL individuals but differed in their recent experiences. We examined the effect of two consecutive winning experiences by comparing the outcome of NN–LW contests to that of the WW–LW contests. The effect of a penultimate winning experience was deduced by comparing the effect of two consecutive winning experiences with the effect of a recent winning experience. The effect of a penultimate losing experience can then be deduced by comparing the effect of a penultimate winning experience with the effect of a penultimate winning experience combined with the effect of a penultimate losing experience (measured from the WW–LW or the LL–WL contests earlier).

Each individual was used only once in one type of contest and was isolated for at least 3 months before it was used for a different type of contest (see Hsu & Wolf 1999 for details).

Procedures

To stage the five types of contests, we divided reproductively mature individuals of *R. marmoratus* into pairs so that the difference in total body length was less than 1 mm (<3.5% of the body length of the smaller fish) and the difference in age was less than 7 days to equalize their intrinsic fighting ability. We randomly assigned two individuals in a pair to receive one of the two opposing sets of prior fighting experiences. Fish were always paired with individuals of the same strain for all contests. Clonal type had no significant effect on any contest behaviours examined or on contest outcomes (Hsu 1997) and data from the two strains used were pooled for the analyses of experience effects.

For individual identification, we clipped the non-vascularized, outer margins of caudal fins of the fish, without removing any tissue, 24 h prior to their first experience. The cut healed in 3–4 days and no sign of infection was ever observed.

Providing a Losing/Winning Experience and Staging Contests

For these experiments, we used 'standard' winners/losers to give the test fish losing/winning experiences, respectively (see Hsu & Wolf 1999 for details). The contest occurred on day 3 when the opaque partition separating the fish for 24 h after the second experience was removed. All contests and experience training took place in standard aquaria ($12 \times 8 \times 20$ cm^3) containing 2 cm of gravel and water 16 cm deep. No geographic landmark except the sides of the aquarium was available for the fish to defend. A Plexiglas sheet was placed over the top of the aquarium to prevent the fish from jumping out. All contests between individuals with different prior experiences were videotaped from directly in front of the aquarium approximately 1 m away. To reduce possible disturbance from the movement of people, we left the room and closed the door after the partition was lifted. We returned 1 h later to separate the contestants. All contests resulted in clear winners and losers (see below) in 1 h.

Definitions/Descriptions of the Fighting Behaviour Measured

We quantified the fighting behaviour of *R. marmoratus* by watching the videotapes at slow speeds (1:1 to 1:30). The fighting behaviour of *R. marmoratus* is similar to that of other fish (e.g. the cichlid, *Nannocara anomala*, Enquist et al. 1990) and is described in detail in Hsu (1997).

When the partition was lifted, the two contestants would rapidly swim towards the bottom of the aquarium and stay still on or close to the gravel. All test fish resumed activities in 16 min in this experiment. One could argue that the fish were recovering from the disturbance of lifting the partition. However, once a fish resumed activities, it often (1) swam directly towards its opponent, or (2) it maintained its position but oriented its head towards its opponent and paused at this posture. Therefore, the fish appeared to have assessed visually the standard aquarium, including their opponents, while they remained still. As soon as one fish started moving, the other fish also usually would start to move. A 'display' initiator started the confrontation by performing circling, lateral displays, frontal displays, head-to-head displays, or following behaviours with its opponent. An 'attack' initiator started a contest by swimming rapidly towards, and pushing or biting, its opponent.

A contest ends when one contestant retreats. All contests resulted in clear winners and losers in 1 h. The most frequently observed behaviour after an individual retreats is chasing, with one individual (the winner) swimming quickly towards its opponent (the loser) and the opponent swimming away. A winner usually also attacks (bites) a loser. Winners and losers often show different pigmentation patterns after a contest ends. A winner develops dark pigmentation on its back but its sides remain pale. The dark ocelli on its posterior become more conspicuous against its pale body. In contrast, a loser has a pale back and develops dark spots on its sides. Its ocelli become greyish and less apparent against its dark-pigmented body. The winner usually swims freely in the aquarium but the loser stays close to the gravel and remains still. The loser sometimes flips out of the water and sticks on the side wall of the aquarium. This

Table 1. The number of contests initiated and the initiation strategies used by individuals with different prior fighting experiences

	Contest type									
	WW–LW		LL–WL		LN–WL		LW–WL		NN–LW	
Number of contests initiated	11	16	12	19	16	9	26	12	17	15
Initiation strategy										
Display	7	14	11	14	12	4	15	11	13	11
Attack	4	2	1	5	4	5	11	1	4	4

'emersion' behaviour of losers has been described by Taylor (1990). The fish has a unique epidermal capillary bed that facilitates aerial respiration (Grizzle & Thiyagarajah 1987; Davis et al. 1990; Taylor 1990). Therefore, flipping out of water did not harm the loser but enabled it to avoid further attacks from the winner.

A nonescalated contest included only display behaviours until the winner chased/attacked its opponent. An escalated contest was resolved after some period of mutual attacks between the two contestants.

We studied the influence of prior fighting experiences on the fighting strategies of contestants at two stages of a contest, the initiation stage and the response stage. For the initiation stage, we examined the effect of prior experience on whether and how an individual initiated a confrontation. For the response stage, we examined the effect of prior experience on whether an individual retreated or retaliated after being challenged with different types of agonistic acts. We then examined the effect of prior experience on the outcome of the contests that were resolved with and without escalated fights.

Ethical Note

The research presented here was described in Animal Research Protocol No. 95-102, approved on 15 September 1995 by the Institutional Animal Care and Use Committee of Syracuse University. All contests lasted 1 h. During the 1-h interaction, losers were able to avoid attacks by flipping out of the water. None of the fish appeared to suffer from observable physical damage during the contests.

Statistical Tests

G statistics (log-likelihood ratio) were employed to test the goodness of fit of the subclasses within one factor and the independence between two or three factors (log-linear models), except for 2×2 designs where Fisher's exact tests were used. The null hypothesis for the goodness-of-fit tests was that all subclasses occurred at equal frequency. The null hypotheses for the independence tests was that there were no two-way and three-way interactions between the two and three factors examined, respectively. The power of tests was calculated for nonsignificant results with small sample sizes (Milligan 1980; Cohen 1988).

RESULTS

The Effect of Prior Experience on Initiation Strategies

Whether to initiate aggressive interactions

The frequencies of initiating interactions by the contestants in the five types of contests are summarized in Table 1.

The contestants with different penultimate experiences in both WW–LW and LL–WL contests did not differ significantly in their probability of initiating aggressive interactions (goodness of fit: WW–LW: $G_1=0.931$, $P=0.335$; LL–WL: $G_1=1.594$, $P=0.207$). These results indicated that penultimate experiences did not have significant effects on the likelihood of initiating confrontations.

In LW–WL contests, LW individuals initiated significantly more confrontations than WL individuals (goodness of fit: $G_1=5.281$, $P=0.022$). This result indicated that, even with opposite penultimate experience, individuals with a recent winning experience still initiated significantly more aggressive interactions than individuals with a recent losing experience. Therefore, a recent experience had more influence on this behavioural measure than a penultimate experience.

The overall difference in the probability of initiating aggressive interactions when LW, LN and LL individuals fought WL individuals was significant (log-linear model, $G_2=6.769$, $P=0.034$). Nevertheless, pairwise comparisons revealed that the difference was only significant between LL and LW individuals (Fisher's exact test: $P=0.013$) but not between LL and LN individuals (Fisher's exact test: $P=0.053$) or between LW and LN individuals (Fisher's exact test: $P=0.461$) after adjusting α values (0.017, 0.025 and 0.050 for the three subtests, respectively) with the sequential Bonferroni technique for simultaneous tests (Rice 1989).

These results indicated that a recent losing experience might have more effect on initiation than a recent winning experience. To test further the effect of a recent losing experience on this behaviour, we used additional information from WL and NN individuals fighting against LW opponents and LL and LN individuals fighting against WL opponents to form a $2 \times 2 \times 2$ table. For the difference in the probability of initiation between WL and NN individuals when fighting against LW

opponents, the effect from the penultimate winning experience of WL individuals should not be a concern because penultimate experiences had no significant effect on this behaviour. An influence of opponent's experience (LW, WL) on the effect of a recent loss was undetectable in this three-way table (log-linear model, three-way interaction: G_1=0.033, P=0.856). On the other hand, a recent losing experience significantly reduced the likelihood of initiating a future contest (log-linear model, two-way interaction: G_1=6.887, P=0.009).

The difference between WW and NN individuals in the probability of initiating aggressive interactions when fighting against LW individuals measured the effect of a recent winning experience plus the effect of a penultimate winning experience, which was not significant (Fisher's exact test: P=0.246). This result confirmed that recent winning experiences did not have much effect on the likelihood of initiating aggressive interactions.

Conclusion

We concluded that a recent losing experience significantly reduced the likelihood of an individual initiating a future contest, but winning experiences did not have an appreciable influence on the same behaviour. Furthermore, the experience effect on contest initiation became undetectable 48 h after the experience.

How to initiate aggressive interactions

The effect of prior experience on the likelihood of adopting display and attack initiation strategies is summarized in Table 1.

Contestants with different penultimate experiences in WW–LW and LL–WL contests did not differ significantly in their initiation behaviour (Fisher's exact test: P=0.160 and 0.226, respectively), which indicated that the penultimate experience did not have a significant effect on the type of initiation behaviour adopted. The difference in the recent experiences between the contestants in these two types of contests did not have a significant influence on the effect of penultimate experiences on initiation strategies (log-linear model, three-way interaction: G_1=0.000, P=0.991) and there was no significant interaction between recent experience and penultimate experience (log-linear model, two-way interaction: G_1=1.85, P=0.174), which justified combining the data from these two types of contests for a retest of the effect of penultimate experience (Collapsing Theorem, Fienberg 1980). With pooled data, although individuals with a penultimate winning experience (WW individuals in the WW–LW contests and WL individuals in the LL–WL contests) had a higher tendency to attack when initiating a confrontation compared with individuals having a penultimate losing experience, this tendency was not statistically significant (Fisher's exact test: P=0.067).

LW individuals in LW–WL contests had a higher probability of attacking when initiating a contest than WL individuals (Fisher's exact test: P=0.038). This result indicated that the effect of recent experiences on the initiating strategies was more significant than the effect of penultimate experience.

LL, LN and LW individuals differed significantly in their probability of initiating by attacks when fighting against WL individuals (log-linear model: G_2=9.056, P=0.011). Pairwise comparisons revealed that LW individuals were more likely to initiate by attacking than LN individuals (log-linear model: G_1=7.05, P=0.008) and LL individuals (log-linear model: G_1=6.022, P=0.014). However, LN and LL individuals did not differ significantly in their initiating strategies (log-linear model: G_1=0.001, P=0.975). Therefore, a recent winning experience significantly increased the likelihood of initiating by attacks, but the effect of a recent losing experience on this behaviour was not detectable.

WW individuals and NN individuals did not differ significantly in their fighting strategies when initiating a confrontation against LW individuals (log-linear model: G_1=1.520, P=0.220). Although this result is somewhat inconsistent with the earlier outcome that a recent winning experience alone was sufficient to cause a significant increase in the probability of initiating by attacks, the trend was in the predicted direction.

Conclusion

The results in this section indicated that a recent winning experience significantly increased the probability of an individual initiating a contest with attacks; however, the effect of a losing experience on this behaviour was negligible. The experience effect on this behaviour became marginally insignificant 48 h after the experience.

The Effect of Prior Experience on Responding Strategies

After dividing the initiator's behaviour into 'attacks' and 'displays', the sample size for most contest types became very small for differentiating the effect of recent versus penultimate experiences and the effect of winning versus losing on responding strategies. We thus pooled the data from different contest types to test first whether experience had any significant effect on the behavioural response following a display or an attack initiation. To do so, we classified the contestants in WW–LW, NN–LW, LW–WL and LL–WL contests into relative winners and losers. Relative winners were contestants that had more or more recent winning experience(s) than their opponents (i.e. WW individuals in WW–LW contests, LW individuals in NN–LW contests, LW individuals in LW–WL contests, and WL individuals in WL–LL contests). Relative losers had more or more recent losing experience(s) than their opponents and were the opponents of the relative winners. We examined the effects of prior experiences on the responding strategies by comparing the responses of the relative winners and relative losers when challenged. If a specific responding behaviour was significantly influenced by prior experiences, we then analysed the influence of recent and penultimate winning versus losing experience on this specific behaviour.

Table 2. The responses (retreat/persist) of the receivers with different prior fighting experiences when challenged with attacks and displays

	Initiation strategy			
	Attack		Display	
Receiver's experience type	Relative winner	Relative loser	Relative winner	Relative loser
Receiver's strategy				
Retreat	8	22	7	10
Persist	0	2	40	37

Response to attack

When an initiator attacked, 30 of the 32 receivers (93.75%) retreated immediately (Table 2). The prior experience of the receivers did not significantly affect the likelihood of retreating after attacked (Fisher's exact test: P=0.557).

Response to display: probability of retreating

The receivers retreated after the initiators displayed in only 17 out of the 96 contests (17.71%). The likelihood of retreating or persisting after being displayed at was independent of the prior experience of the receivers (Fisher's exact test: P=0.297; Table 2). In two of these 96 contests, the initiators (both relative losers) swam towards their opponents but retreated as soon as their opponents moved towards them. The frequency of these incidents was too low for further analyses to be performed.

Response to display: probability of attacking

Pooled data. Among individuals that persisted when challenged with display, relative winners were more likely to respond with an attack than relative losers (Fisher's exact test: P=0.008; Table 3).

Individual contest types. The effect of recent versus penultimate experience and the effect of winning versus losing experience on this responding strategy was less clear probably because of the small sample size for each individual contest type.

The contestants with different penultimate experiences in WW–LW and LL–WL contests did not differ significantly in the likelihood of attacking when challenged with displays (Fisher's exact test: P=0.437 and 0.500, respectively). The difference in contestant's recent experience between these two types of contests did not significantly influence the effect of their penultimate experiences (log-linear model, three-way interaction: G_1=0.008, P=0.928) and there was no significant interaction between recent and penultimate experiences (log-linear model, two-way interaction: G_1=0.706, P=0.401). Thus the data from these two types of contests were pooled (Collapsing Theorem). With pooled data, the effect of penultimate experiences on the likelihood of responding to a display with an attack remained nonsignificant (Fisher's exact test: P=0.456).

The difference in this behaviour between LW and WL individuals in LW–WL contests was significant (Fisher's exact test: P=0.052), indicating that recent experiences had more effect than penultimate experiences on the likelihood of responding to a display with an attack.

LL, LN and LW individuals, fighting against WL individuals, did not differ significantly in their likelihood of attacking after the initiator displayed (log-linear model: G_2=2.924, P=0.232). A difference in the effect of a recent winning or losing experience, therefore, could not be detected. However, this test had low power (N=53, df=2, 0.23<power<0.54) in detecting the difference in the probability of attacking among the three groups as manifested in the data (0.43:2.67:6.67).

Comparing the behaviour of WW and NN individuals fighting against LW individuals revealed that two consecutive winning experiences significantly increased the probability of initiating attacks when challenged with displays (log-linear model: G_1=4.231, P=0.040).

Conclusion

The analyses indicated that recent winning experience clearly increased the likelihood of attacking in response to display. Nevertheless, we did not detect any significant effect of losing experiences on this behaviour. The effect of prior experience on this behaviour could no longer be detected 48 h after an experience.

Table 3. The frequency of the receivers with different prior experiences attacking first/not attacking first after being challenged with displays and retreating/escalating after being attacked in these contests

	Contest type										Pooled count relative winner–loser	
	WW*–LW		LL–WL*		LN–WL		LW*–WL		NN–LW*			
After displayed												
Attack	6	2	6	7	2	3	6	3	1	6	25	12
Not attack	6	4	2	1	2	8	3	10	9	5	15	25
After attacked												
Retreat	1	6	8	4	5	6	4	13	11	3	12	38
Escalate	7	4	1	3	0	4	2	3	4	3	15	12

*These individuals contributed to the count for the relative winners in the pooled data. The opponents of these individuals contributed to the count for the relative losers in the pooled data.

Table 4. The number of contests won by individuals with different prior experiences in escalated and nonescalated contests

	Contest type										Pooled count relative winner–loser	
	WW*–LW		LL–WL*		LN–WL		LW*–WL		NN–LW*			
Escalated contests won												
Initiated with an attack	0	0	0	0	0	0	2	0	0	0		
Initiated with a display	7	4	2	2	2	2	1	4	3	4	14	13
Nonescalated contests won	12	4	8	19	11	10	24	7	10	15	72	29

*These individuals contributed to the count for the relative winners in the pooled data. The opponents of these individuals contributed to the count for the relative losers in the pooled data.

Response to display: probability of escalation

Pooled data. In contests initiated with displays, relative winners were more likely to attack in return and escalate the fights when attacked (Fisher's exact test: $P=0.006$; Table 3) than were relative losers.

Individual contest types. Contestants with different penultimate experiences in WW–LW contests differed marginally in the probability of escalating or retreating (Fisher's exact test: $P=0.057$) but not in LL–WL contests (Fisher's exact test: $P=0.192$). The difference in the recent experiences between contestants in these two types of contests did not have a significant influence on the effect of penultimate experiences on the behaviour (log-linear model: $G_1=0.096$, $P=0.757$) and there was no significant interaction between recent and penultimate experiences (log-linear model, two-way interaction: $G_1=0.963$, $P=0.327$), which justified pooling the data (Collapsing Theorem). With pooled data, individuals with a winning penultimate experience were significantly more likely to escalate after being attacked than individuals with a losing penultimate experience (Fisher's exact test: $P=0.022$).

The opponents in LW–WL contests did not differ in this behaviour measure (Fisher's exact test: $P=0.419$; 0.08<power<0.17 for H_0=1:1 against H_1=0.50:0.23 as exhibited in the data). The difference among LL, LN and LW individuals in this behaviour when each fought against WL individuals was not statistically significant (log-linear model: $G_2=4.740$, $P=0.093$). However, this test had low power ($N=53$, $df=2$, 0.46<power<0.54) in detecting the difference in the probability of escalating among the three groups as manifested in the data (0.17:0.00:2.17).

Two consecutive winning experiences significantly increased the probability of escalating when attacked as indicated by the comparison between the behaviour of WW and NN individuals when fighting against LW individuals (log-linear model: $G_1=4.960$, $P=0.026$). Although, the effect of a recent winning experience was not significant in the previous analysis, this result indicated that winning experiences had a weak but consistent positive effect on the likelihood of retaliating when attacked.

Conclusion

Prior winning experiences had a significant positive effect on the probability of escalating when attacked in contests that were initiated with displays. The influence of penultimate experiences was statistically significant in the pooled data. But, with our small sample sizes, the effect of recent experiences was not more pronounced than the effect of penultimate experiences, and no significant effect from prior losing experiences was detected.

Response to display: the outcome of escalation

When a contest that was initiated with a display was escalated, relative winners and losers did not differ significantly in the probability of winning (Table 4; goodness of fit: $G_1=0.037$, $P=0.847$). Including only the two contests that were escalated after being initiated with an attack did not change the conclusion. This result indicates that for prior experience to affect the outcome of a contest, it must have affected the outcome of nonescalated contests (Table 4; goodness of fit: $G_1=18.904$, $P<0.001$).

DISCUSSION

The outcome of a contest that was escalated to physical fights was not significantly influenced by the prior experience of the contestants. This indicates that prior fighting experiences significantly affected the probability of winning a subsequent contest for an individual by affecting the outcomes of nonescalated contests but not the outcomes of escalated contests. These results are consistent with the hypothesis that prior fighting experiences modify an individual's estimate of its fighting ability but do not change its actual fighting ability. An alternative explanation to this lack of experience effect on escalation outcome is that prior experiences did change the actual fighting ability of most individuals but only the few unstressed losers escalated. However, this hypothesis does not explain why prior winning experiences increased the probability of individuals to escalate but did not increase their probability of winning escalated contests against prior losers.

Winning and losing experiences led to different types of aggressive behaviour during the interactions of a

contest in *R. marmoratus*, even though they appeared to have equal, but opposite, effects on the probability of winning (Hsu & Wolf 1999). Losing experiences decreased the willingness of an individual to initiate a contest, but did not have significant effects on any other fighting behaviours examined. On the other hand, winning experiences did not have significant effect on the likelihood of initiating a contest but increased the readiness of an individual to attack and escalate the contest into physical fights. Therefore, by decreasing the likelihood to initiate, prior losing experiences increased the probability of an individual being the receiver that retreated immediately when challenged. On the other hand, prior winning experiences increased the probability of an individual winning a subsequent contest by increasing its tendency to initiate a contest with attacks that effectively deterred most opponents. Winning experience also consistently increased the likelihood of an individual attacking after being challenged with displays and, eventually, the likelihood of escalation. By increasing the willingness of a contestant to use more costly fighting, winning experiences further decreased the probability of retreating before obtaining more accurate information regarding actual fighting ability of both contestants.

An initiator that attacked won virtually all fights in our study because the receiver retreated without any retaliation. Thus, it seems beneficial for an individual to attack its opponent as soon as possible in a confrontation. However, only 59 of 153 contests staged in our study were initiated with attacks, and an individual's prior fighting experience influenced its likelihood of initiating by attacking. These results indicate that early in a contest individuals signalled honestly in relation to their prior experience. What could have stopped them from cheating (Enquist 1985; Számadó 2000)? In Siamese fighting fish (*Betta splendens*), the hyperaggressive cheaters lose the majority of fights by exhausting themselves (Halperin et al. 1998). This is not the case in *R. marmoratus* because the initiators that attacked won the contests. In serins (*Serinus serinus*), a subordinate is more likely to win a fight against a dominant if it initiates by attacking than by displaying (Senar et al. 1992). Nevertheless, a subordinate that initiates by attacking but loses suffers more from retaliation. Unfortunately, in our study, it is not clear whether the two contestants that initiated by attacking but lost suffered more cost from retaliation than the ones that initiated by displaying. Although it is a plausible explanation, further study will be necessary to test this hypothesis.

Previous studies have demonstrated that contestants with a higher relative fighting ability (e.g. larger body size) have a higher probability of initiating a contest with attacks (Dugatkin & Ohlsen 1990; Dugatkin & Biederman 1991; Jackson 1991; Senar et al. 1992; Olsson 1994) than their opponents. *Rivulus marmoratus* that had prior winning experiences were also more likely to initiate a contest with attacks. These results are consistent with the hypothesis that *R. marmoratus* that had more or more recent winning experiences behaved as if they had good fighting ability.

Experience effects on different fighting behaviours seemed to decay at different rates. Recent experiences received 24 h before dyadic contests significantly affected all the fighting behaviours examined. However, penultimate experiences received 48 h before had only a marginal effect on the tendency to initiate a confrontation with attacks and a significant effect on the likelihood of escalating after being attacked. Thus, experiences 48 h earlier still had detectable influence on an individual's willingness to engage in physical fights, which could impose higher costs of injury, energy and predation risk to the individual than threat displays (Jakobsson et al. 1995; Neat et al. 1998). The results that prior experiences had a longer lasting/stronger effect on more costly fighting behaviours is not surprising because individuals are expected to regulate more closely the behaviours that are more likely to have significant impact on fitness. However, it is worth noting that although experience effects on the overall fighting outcomes lasted longer than 48 h (Hsu & Wolf 1999), no experience effect was detectable on the outcomes of escalated contests 24 h after the experiences. The importance of experience effects greatly diminishes once a contest is escalated because the contestants obtain more accurate information regarding their relative fighting ability through direct physical interactions and quickly adjust their behaviour to this most recent and reliable information.

We do not know what physiological changes mediate the effects of experience on behaviour (e.g. modified synaptic transmission: Yeh et al. 1996, hormone levels: Hannes et al. 1984; Cardwell & Liley 1991), but they presumably involve the neuroendocrine system. The general effects of experience on subsequent types of behaviour, including decreased probability of initiating with losing experience and increased probability of attacking with winning experience, is consistent with the differential influences of hormones, especially androgens and glucocorticoids (e.g. Svare 1983). In many vertebrates, testosterone tends to increase following a win and increases aggression, while corticosterone increases with a loss and is associated with increased passivity. However, the situation is less clear from studies of temporal patterns of hormone titres following aggressive interactions in fish (e.g. Villars 1983). The role of memory in some aspects of modification of aggressive behaviour (e.g. Hollis et al. 1995; Jenkins & Rowland 1996; Hollis 1999) suggests the possibility of neural effects that last beyond the generally transitory changes in hormone titres (e.g. Blanchard et al. 1993; Yeh et al. 1996).

If hormones are critical in terms of modulating the behaviour of fish in relation to expected costs in subsequent fights, it is important to recognize that increasing titres also have potentially significant negative effects on numerous other physiological properties of vertebrates, such as immunocompetence (Barnard et al. 1998) and general stress responses in metabolism and activity levels (Wingfield 1994). Thus, we might expect close regulation of hormone titres and perhaps rapid return to baseline levels, but the rate of return could vary with the relative importance of the costs and benefits of high titres among individuals.

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