Persistence of Winner and Loser Effects Depends on the Behaviour Measured
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Introduction

Many animals’ contest decisions are influenced by their recent contest interactions. In general, winning and losing experiences, respectively, increase and decrease an individual’s aggressiveness and chances of winning future contests (see Hsu et al. 2006 for a review). These winner and loser effects have been reported for animals of all different taxa, including insects (e.g. Alexander 1961; Adamo & Hoy 1995), arachnids (e.g. Dodson & Schwaab 2001; Hoefler 2002), crustaceans (e.g. Bergman et al. 2003), fish (e.g. McDonald et al. 1968; Bakker et al. 1989; Chase et al. 1994), reptiles (Schuett 1997), birds (e.g. Martin et al. 1997; Drummond & Canales 1998) and mammals (e.g. Ginsburg & Allee 1942; Huhman et al. 2003). Winner/loser effects are often considered to result from changes in individuals’ perception of their fighting ability (Whitehouse 1997; Mesterton-Gibbons 1999) and consequently their estimation of the costs of taking part in later contests.

Abstract

Recent contest experience can influence an individual’s behaviour in subsequent contests. When the probability of winning a subsequent contest is used to quantify experience effects, a loser effect usually lasts longer than a winner effect. This conclusion, however, may be caused by this probability understating the persistence of the influence of a winning experience on contest decisions. Using Kryptolebias marmoratus, a mangrove killifish, as the study organism, we investigated whether different conclusions about the relative persistence of winning and losing experiences would be reached when different aspects of contest behaviour (probability of initiating attacks, probability of winning non-escalated and escalated contests, escalation rate and contest duration) were measured. The results indicated that the apparent persistence of the effect of winning or losing experiences varied with the behaviour studied. When the likelihood to initiate attacks was used, no winner effect was detected while the loser effect lasted for <1 d. When escalation rate was used, the winner effect lasted for 2–4 d, while the loser effect lasted for 1–2 d. When the probability of winning non-escalated contests was used, the winner effect was detectable for <1 d, while the loser effect lasted for 2–4 d. And, when contest duration was used, the winner effect was detectable for 2–4 d, but no loser effect was detectable. These results show that (1) the probability of winning a subsequent contest understated the persistence of the influence of a winning experience on the fish’s contest decisions, (2) the measures most effective at detecting winner effects are different from those most effective at detecting loser effects and (3) in K. marmoratus, both effects can be detected 2 d after the completion of experience training but both dissipate in 4 d.

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Received: August 26, 2010
Initial acceptance: October 3, 2010
Final acceptance: October 22, 2010
(J. Wright)
doi: 10.1111/j.1439-0310.2010.01856.x
Most studies of winner and/or loser effects tested the significance of the effect at a fixed time after the experience. Only a fraction of studies examined the effect at two or more time intervals to inspect its persistence; most used the probability of winning a subsequent contest to evaluate the effect. These studies show a trend for loser effects to be stronger and longer lasting than winner effects (Hsu et al. 2006). For instance, a winning experience persisted for <3 h, while a losing experience lasted for more than 6 h in the stickleback fish *Gasterosteus aculeatus* (Bakker et al. 1989). In copperhead snakes (*Agkistrodon contortrix*), a winning experience did not show any effect, while a losing experience persisted for more than 1 d (Schuett 1997).

Although the probability of winning might be the aspect most relevant to contestants’ fitness, it may not be the best measure of the influence of a prior contest experience on an individual’s contest decisions. Even when winning and losing experiences have opposite but symmetrical effects, respectively increasing and decreasing an individual’s aggressive tendency, loser effects may appear more pronounced because it is easier for a prior loser to lose a contest than for a prior winner to win (Mesterton-Gibbons 1999). Individuals with losing experiences can lose a subsequent contest by voluntarily retreating, but even if those with winning experiences become more aggressive and actively challenge their naïve opponents, they may not be able to win as the opponent may escalate the contest. In male copperheads, for instance, 24 h after experience training, none of the contests between prior losers and naïve opponents were escalated: all the prior losers retreated and lost when challenged so that a loser effect was detected (Schuett 1997). Eight of ten contests between prior winners and naïve opponents were escalated, however. Prior winners won six of the ten contests and no winner effect was detected. The outcome of an escalated contest probably depends on the true fighting ability of the two opponents (Enquist et al. 1990; Hsu & Wolf 1999). If a recent winning experience acts through an individual’s perceived fighting ability, a win may have little influence on the outcome of escalated contests. The probability of winning a subsequent contest is therefore not necessarily the best index for revealing the effect of a winning experience on an individual’s contest decisions.

If a recent winning or losing experience influences an individual’s behaviour by affecting how it evaluates its fighting ability, then the best indicator of its persistence would be the behaviour most associated with this perception and also the least influenced by the opponent’s contest behaviour. The sequential assessment model considers animal contests to be processes for contestants to evaluate their relative fighting ability and predicts contests to start with low cost behaviour and progress to high cost interactions (Enquist & Leimar 1983; Enquist et al. 1990). In this case, an individual would be more willing to use more costly behaviour and prolong a contest when it perceives its fighting ability to be good. The willingness to initiate costly interactions, contest intensity and contest duration are thus potential indicators of winner/loser effects. These behaviours are no doubt determined by not only the focal individual but also its opponent. They may, however, be less distorted indicators of an individual’s intention to persist than contest outcome, particularly when measuring the winner effect. A previous winner that perceived itself to have a good fighting ability could, for instance, elect to use costly behaviour and persist longer in a contest but still lose to its naïve opponent. These behaviours probably provide alternative but not necessarily better measures for a loser effect, because contest outcome is already sensitive to a loser’s decision to retreat (Schuett 1997; Mesterton-Gibbons 1999).

Evidence that the apparent significance of experience effects differs with the behaviours measured can be found in previous studies. For instance, one winning experience did not significantly increase winning probability but significantly shortened attack latency in the California mouse (*Peromyscus californicus*; Oyegbile & Marler 2005), which was consistent with the conclusion that contest outcome may not be the most appropriate way of measuring the winner effect. In *Kryptolebias marmoratus*, a winning experience significantly influenced the likelihood of both initiating attacks and winning subsequent contests, while a losing experience influenced only the likelihood of winning (Hsu et al. 2009). To understand whether an individual’s contest decisions are affected by a winning or losing experience and how the effects dissipate over time, aspects of contest interaction other than outcome should therefore be inspected. These more comprehensive measurements will also facilitate a more accurate assessment of the relative importance of information obtained from winning and losing experiences and how the importance of the effects may be influenced by intrinsic (e.g. growth rate, see Hsu et al. 2006 for discussion) and extrinsic (e.g. contest environment, Fuxjager & Marler 2010) factors.

*Kryptolebias marmoratus* is an ideal organism for investigating the influence of recent contest experience on contest decisions because both winning and losing experiences have been shown to influence...
contest behaviour and outcome (Hsu & Wolf 2001; Hsu et al. 2009) and the effects appear to decay with time but last for more than 2 d (Hsu & Wolf 1999). This study examined how long the influence of a winning and a losing experience lasted for different aspects of contest behaviour and whether different conclusions would be reached about the effects’ relative persistence if different aspects of contest behaviour were used to evaluate them.

Methods

Study Organism

Kryptolebias marmoratus is an internally self-fertilising hermaphroditic fish (Taylor et al. 2001), distributed from Belize, Central America to Florida (Harrington 1961). Natural populations mainly consist of isogenic homozygous hermaphrodites with very low incidence (<1%) of males, although an out-crossing heterozygous population with approximately 20% males has been discovered in Twin Cays, Belize (Mackiewicz et al. 2006). This study used five strains of K. marmoratus from various geographical areas (DAN2K: Dangría, Belize; HON9: Utila, Honduras; RHL: San Salvador, Bahamas; SLC8E: St Lucie County, FL, USA; VOL: Volusia County, FL, USA), which were F2 to F5 generations of fish originally collected from the field by Dr. D. Scott Taylor. Fish were isolated a week after hatching and kept alone in a 10 × 10 × 10 cm³ translucent polypropylene container filled with approximately 500 ml 25 ppt synthetic sea water (Instant Ocean® powder, United States Pet Group, Inc., Cincinnati, OH, USA) and labelled with unique identification codes. Fish were kept at 25 ± 2°C on a 14:10-h photoperiod in a laboratory at the National Taiwan Normal University and fed newly hatched brine shrimp (Artemia) nauplii daily. Containers were cleaned and water replaced every 2 wk. This fish begins laying eggs 3–6 mo after hatching in the laboratory (Harrington 1975). All fish used for this study were hermaphrodites, more than 8 mo old, with standard length (from the tip of the snout to the caudal peduncle) >20 mm (x = 23.4 mm).

Experiments were conducted in accordance with a protocol approved by the Animal Care and Use Committee of National Taiwan Normal University (permit #95010).

Experimental Design

The goal of this study was to investigate whether conclusions about the persistence of a winner and loser effect would change with the aspect of contest behaviour measured. On day 0, individuals of K. marmoratus were given a win (W individuals), a loss (L individuals) or no fighting experience (N individuals) using random selection procedures (described in detail below). This is because self-selection procedures (staging contests between size-matched opponents and treating contest winners/losers as having received a winning/losing experience) can confound experience effects with intrinsic fighting ability (Chase et al. 1994; Bégin et al. 1996). Contests were then staged between L and N individuals (L–N contests) and between W and N individuals (W–N contests) at each of three hours (0 d), one day (1 d), two days (2 d), four days (4 d) and seven days (7 d) after experience training, a total of ten treatments (two contest types × five time treatments). Fifty contests (distributed equally among the five strains of fish) were staged for each of the ten treatments, a total of five hundred contests (1000 fish). We analysed various aspects of contest behaviour and outcome, notably which fish initiated attacks, which fish won, whether contests were escalated to physical fights and the overall contest duration.

We chose 7 d as the last time point based primarily on the findings of Hsu & Wolf (1999). This study showed that 1 d after an experience, a recent win and loss increased and decreased, respectively, the fish’s winning probability by roughly 0.2 and that the effect decayed by 50% 2 d after the experience. We thus expected the influence on contest outcome to be too small to be detectable by the 4th day. But because (as explained in the Introduction) other contest behaviours might be more effective than contest outcome in detecting the influence of a recent win/loss on contest decisions, we used a longer decay time (7 d) as the last time point. Experience effects in other species of fish are also reported to disappear before 7 d (Francis 1983; Bakker et al. 1989; Chase et al. 1994; Miklosi et al. 1997).

Procedures

All the fish had been re-isolated for at least a month after use in previous experiments. Fish of the same strain were matched by size (SL difference <1 mm, average difference = 0.33 mm) and last contest outcome (more than a month previously), because both might indicate intrinsic fighting ability. Each pair of fish was then randomly assigned to form either a W–N or an L–N contest and to one of the five time treatments. Within each pair, one fish was randomly
chosen to be the focal (W or L) individual and the other its naïve opponent (N individual). Each fish was used only once in the experiment.

To ensure that focal (W or L) individuals received their pre-designated winning or losing experience on day 0, we fought them against much smaller/larger trainers (difference in SL >2 mm) that had lost/won several fights with fish of a similar size. For experience training, a focal individual and its trainer were placed in the two equal-sized, symmetrical compartments (one fish in a compartment, randomly assigned) of a standard aquarium (12 × 8 × 20 cm³, 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 the focal fish to interact with its trainer. Focal individuals acquired their pre-designated experiences quickly because of the large size difference and were allowed to continue to interact with their trainers for 1 h. No dominance reversion was observed. Fish assigned to receive no experience (N individuals) were treated as earlier, except with no trainer in the other compartment of the aquarium. After experience training, the fish were replaced in their maintenance containers and fed newly hatched brine shrimp.

We marked all the study fish (W, L and N individuals) by breaking the non-vascularised thin membrane between two soft-rays in either the upper or lower margins (randomly assigned) of the caudal fin. As the membrane usually grows back in 3 d, we marked the fish 2 d before their W–N or L–N contests. This meant that marking took place before experience training for the fish in the 0- and 1-d treatments and after for those in the 4- and 7-d treatments. Fish in the 2-d time treatment were marked roughly 6 h after the experience training was completed. Immediately after marking, fish were replaced in their maintenance containers and fed small amounts of newly hatched brine shrimp. All fish resumed regular feeding behaviour within 5 s. Marking did not cause bleeding or observable adverse effects upon the fishes’ health or behaviour.

Roughly 20 h before the pre-designated contests (except for the 0 d group), the opponents were placed for acclimatisation, one in each of two compartments (randomly assigned) of a standard aquarium separated by an opaque partition. Although this partition prevented the two opponents from interacting with each other visually or physically during the acclimation period, it could not stop water circulating between the two compartments. Chemical communication between the two contestants in this period could therefore not be eliminated. The opponents of the 0-d group were placed in the standard aquarium for acclimatisation 2 h before contests (i.e. 1 h after experience training). Contests began after the partition was lifted; the fishes’ interactions (as explained below) were video-taped.

Contest Behaviours

The fighting behaviour of *K. marmoratus* is described in Hsu et al. (2008). At the start of the contest, the fish usually move towards each other, often with gill covers erected. After a few bouts of mutual displays, one fish sometimes retreats and the contest is resolved in favour of the other. If not, one fish launches a first attack, swimming rapidly towards and pushing against or biting its opponent and is the attack initiator. If the fish receiving the first attack retreats, the contest is consider resolved as earlier. Contests that resolve with mutual displays or one attack are classified as non-escalated. If the fish being attacked retaliates with attacks, the contest is escalated. The fish that first chases or attacks its opponent for 5 min without retaliation is the winner. Losers persistently avoid the winners by swimming away when the winners approach. Contest duration is defined as the time between the first display and the loser’s first retreat.

Once the winning criterion was met, we reinserted the opaque partition to separate the two contestants and terminate the contest. All fish were returned to their maintenance containers after the contests.

Statistical Analysis

We used one-tailed binomial tests (Zar 1999) to determine whether W fish in each time treatment were more likely (and L fish less likely) to initiate attacks, win non-escalated contests and win escalated contests than their N opponents. One-tailed tests were used because a winner or loser effect would be established only if the W or L fish displayed the behaviours significantly more or less frequently, respectively, than their naïve opponents (N fish). We have never observed the opposite result (for winners to be significantly less or losers significantly more aggressive than naïve fish). Had we observed it here we would simply have drawn the same conclusion as when the focal individuals’ behaviour did not differ from that of the naïve fish (that no winner or loser effect existed for that time treatment) and not given it any other interpretation. Both the theory that winner/loser effects act through perceived fighting ability (Whitehouse...
1997; Hsu et al. 2006) and previous research on this fish (Hsu & Wolf 1999; Hsu et al. 2009) indicate that the effects should be more noticeable in non-escalated than in escalated fights. We used chi-square tests for both W–N and L–N contests to determine whether escalation rates differed significantly between the five time treatments and Fisher’s exact tests to test whether the escalation rate for each of the 0-, 1-, 2- and 4-d treatments was significantly higher (for the W–N contest) or lower (for the L–N contest) than that for the 7-d treatment. The 7-d time treatment was used as the baseline group because we expected the experience effect to disappear by the 7th day. We used single-factor analysis of variance (F tests) to examine whether the natural log of contest duration \( \ln (\text{duration (in seconds)} + 1) \) varied among the five time treatments and Dunnett’s method (Zar 1999) to test whether the duration of each of the first four time treatments for the W–N and L–N contests was significantly longer and shorter, respectively, than the 7-d baseline.

Data from different strains were pooled for analyses, because strain did not significantly influence the behaviours measured for either W–N contests (initiating attacks: \( \chi^2 = 1.66, p = 0.799 \); escalation rate: \( \chi^2 = 7.54, p = 0.110 \); winning non-escalated contests: \( \chi^2 = 4.67, p = 0.323 \); winning escalated contests: \( \chi^2 = 7.34, p = 0.119 \); contest duration: \( F_{4,245} = 1.38, p = 0.241 \)) or L–N contests (initiating attacks: \( \chi^2 = 0.553, p = 0.968 \); escalation rate: \( \chi^2 = 2.91, p = 0.573 \); winning non-escalated contests: \( \chi^2 = 5.50, p = 0.240 \); winning escalated contests: \( \chi^2 = 1.96, p = 0.744 \); contest duration: \( F_{4,245} = 2.30, p = 0.059 \)). JMP (v. 8.0.2 SAS Institute Inc., Cary, NC, USA), a commercial statistical package, was used for the statistical analyses.

### Results

#### Initiating Attacks

Fish with losing experiences were significantly less likely to initiate attacks than their naïve opponents (Fig. 1), but only for the 0-d (binomial test, \( p = 0.003 \)) and not for other (binomial test, 1 d: \( p = 0.556 \); 2 d: \( p = 0.161 \); 4 d: \( p = 0.161 \); 7 d: \( p = 0.760 \)) time treatments. Animals with winning experiences were not more likely to initiate attacks than their naïve opponents for any time treatment (binomial test, 0 d: \( p = 0.161 \); 1 d: \( p = 0.101 \); 2 d: \( p = 0.556 \); 4 d: \( p = 0.968 \); 7 d: \( p = 0.240 \)).

#### Escalating Contests

The escalation rates for the five time treatments differed significantly (Fig. 2) for both W–N (\( \chi^2 = 10.37, p = 0.035 \)) and L–N contests (\( \chi^2 = 16.46, p = 0.003 \)). For W–N contests, the escalation rate of the 0-d (Fisher’s exact test, \( p = 0.033 \)) and 2-d (Fisher’s exact test, \( p = 0.033 \)) but not the 1-d (Fisher’s exact test, \( p = 0.157 \)) or 4-d (Fisher’s exact test, \( p = 0.726 \)) treatments was significantly higher than that of the 7-d treatment. For the L–N contests, the escalation rate of the 0-d (Fisher’s exact test, \( p < 0.001 \)) and 1-d (Fisher’s exact test, \( p = 0.013 \)) but not the 2-d (Fisher’s exact test, \( p = 0.274 \)) or 4-d (Fisher’s exact test, \( p = 0.115 \)) treatments was significantly lower than that of the 7-d treatment.

Although the trend in escalation rate was not clear-cut for W–N contests (higher for 0 d and 2 d but dropping and levelling off 4 d after experience training), it was more clear-cut for the L–N contests (lowest for 0 d but gradually increasing and levelling off 2 d after the experience training).

**Fig. 1:** Proportion of attacks initiated by L individuals (hatched bar) in L–N contests, W individuals (black bar) in W–N contests and their N opponents (open bar) for each of the time treatments; \( N = 50 \) for each bar; ** indicates \( p < 0.01 \) significance (one-tailed binomial test) of deviation from a proportion of 0.5.
Winning Non-escalated and Escalated Contests

Individuals with a winning experience were more likely to win non-escalated contests than their naïve opponents only for the 0-d treatment (binomial test, p = 0.018) and not for other time treatments (binomial test, 1 d: p = 0.084, 2 d: p = 0.304, 4 d: p = 0.779; 7 d: p = 0.105; Fig. 3). Individuals with a losing experience, on the other hand, were less likely to win non-escalated contests for the 0-d (binomial test, p < 0.001), 1-d (binomial test, p = 0.005) and 2-d (binomial test, p = 0.015) treatments but not for the 4-d (binomial test, p = 0.229) and 7-d (binomial test, p = 0.808) treatments (Fig. 3). The influence of winning and losing experiences on winning non-escalated contests thus lasted for less than a day and 2–4 d, respectively.

In general, there was no significant effect from a winning (binomial test, 0 d: p = 0.750, 1 d: p = 0.925, 2 d: p = 0.250, 4 d: p = 0.046; 7 d: p = 0.351) or a losing (binomial test, 0 d: p = 0.179, 1 d: p = 0.402, 2 d: p = 0.320, 4 d: p = 0.668; 7 d: p = 0.645) experience on winning escalated contests (Fig. 4), although individuals with a winning experience appeared to have an advantage against their naïve opponents on the 4-d treatment.

Contest Duration

There were significant differences in the duration of W–N (F_{4,245} = 3.96, p = 0.004) but not in that of L–N contests (F_{4,245} = 0.66, p = 0.6224) for the five time treatments. For the W–N contests, Dunnett’s tests showed that contest duration of the 0-d (q_{245,5} = −3.02, p = 0.005), 1-d (q_{245,5} = −2.77, p = 0.011) and 2-d (q_{245,5} = −3.07, p = 0.004) treatments, but not the 4-d treatment (q_{245,5} = −0.93, p = 0.381), was significantly longer that of the 7-d treatment (Fig. 5). These analyses revealed that winning but not losing had a significant effect on contest duration and that the effect of a winning experience lasted for 2–4 d.

Discussion

We have demonstrated that measuring different aspects of behaviour can lead to different conclusions concerning the significance and persistence of the effect of winning or losing experiences on subsequent contest decisions. In the literature concerning experience effects (based on the outcome of a subsequent contest), loser effects are reported to be more pronounced and last longer than winner effects in most animal species (e.g. sticklebacks: Bakker et al.)
1989; copperheads: Schuett 1997; also see Hsu et al. 2006; Rutte et al. 2006 for reviews). The same conclusion would have been reached for this study if only contest outcome had been measured. By measuring multiple aspects of contest behaviour, however, we discovered that losing experience had a more profound influence on initiating attacks and winning non-escalated contests, but that winning experience had stronger and more persistent impact on contest duration and the tendency to escalate. Based on these results, we conclude that the influences of both winning and losing experiences on the fish’s contest decisions lasted for 2–4 d, with no asymmetry between them in persistence. This conclusion is similar to that of Hsu & Wolf (1999).

In this study, contest duration and intensity were found, as expected, to be better indicators of the winner effect than contest outcome. It was, however, unexpected that contest duration was not affected by a recent losing experience. Contest duration in many species (e.g. Austad 1983; Rosenberg & Enquist 1991; Taylor & Elwood 2003), including K. marmoratus (Hsu et al. 2008), has been shown to be sensitive to how an individual assesses its and/or its opponent’s fighting ability. Because a recent winning/losing experience is hypothesised to influence how an individual perceives its fighting ability (Whitehouse 1997; Mesterton-Gibbons 1999), it was reasonable to expect both recent winning and losing experiences to influence this contest behaviour. One possible explanation for contest duration to appear insensitive to a losing experience was that, although prior losers tended to retreat when challenged, their retreating behaviour was only observable after their naïve opponents displayed or attacked. How fast their naïve opponents displayed or attacked was independent of the decay time treatment as they had not received any recent contest experience. Thus, in this fish, contest duration is good for measuring the prior winners’ intention to prolong the contest, but not for quantifying for the prior losers’ intention to avoid a confrontation.

That winning and losing experiences do not affect all aspects of contest behaviour equally is not unique to K. marmoratus. In the California mouse (P. californicus; Oyegbile & Marler 2005), for instance, one winning experience was enough to significantly reduce attack latency, while two winning experiences were needed to reduce freeze latency significantly and three were required to increase winning probability significantly. In male crayfish (Orconectes rusticus), a winning experience had opposite effects (negative and positive, respectively) on initiating and winning fights 20 min after the experience (Bergman et al. 2003). Using re-match between

![Fig. 4](image-url) Proportion of escalated contests won by L individuals (hatched bar) in L–N contests, W individuals (black bar) in W–N contests and their N opponents (open bar) for each of the time treatments. The sample size for each bar is indicated by the number in parentheses. *indicates p < 0.05 significance (one-tailed binomial test) of deviation from a proportion of 0.5.

![Fig. 5](image-url) Contest duration (in seconds, ln transformed, x ± SE) for L–N (□) and W–N (■) contests in each time treatment. N = 50 for each of the treatments. Indication of significant deviation from the contest duration of the 7-d treatment (Dunnett’s test): **p < 0.01, *p < 0.05.
self-selected winners and losers in juvenile American lobsters (Homarus americanus; Rutishauser et al. 2004), contest experiences were found to have more persistent effects on contest duration (between 4 and 7 d) than on contest intensity (between 1 and 4 d). As a consequence, to understand whether and how long an individual’s contest decisions are influenced by a winning or losing experience, different aspects of contest interaction should be observed, and not just outcome. This more comprehensive investigative approach should provide an impartial overview of the importance of winning and losing experiences and an unbiased foundation for exploring their effects’ adaptive value (Hsu et al. 2006; Rutte et al. 2006).

Different studies in this fish have shown winning and losing experiences to increase and decrease, respectively, the tendency to escalate to physical fights and to win non-escalated contests (Hsu & Wolf 2001; Hsu et al. 2009). Conclusions about their impact on initiating strategies, however, appear to vary among studies. In the current study, a losing but not a winning experience significantly influenced the tendency to initiate attacks. Hsu & Wolf (2001) reached similar conclusions, but Hsu et al. (2009) concluded that winning but not losing experiences significantly affected the tendency to initiate displays or attacks. A few factors may contribute to the variation in the effect of recent wins/losses on initiation behaviours. Initiation behaviours occur in early stages of a contest and are more susceptible than later behaviours to influence by chance factors such as disturbance from removing the opaque partition, which is the opponents first spotted its opponent when the partition is removed, etc. In addition, initiating displays/attacks may not be very costly (in terms of energy and/or physical injury; Neat et al. 1998; Ros et al. 2006; see Briffa & Sneddon 2007 for a review) and thus not as good an indicator for fighting ability as escalating and persisting in a contest. Initiation strategy therefore does not appear to be a good behavioural trait for quantifying winner/loser effects in this fish. The tendencies to escalate a fight and to win non-escalated contests, on the other hand, are more stable traits. However, because W–N contests tend to escalate, more contests need to be staged to accumulate enough non-escalated contests for an accurate assessment of the winner effect. The tendency to escalate therefore seems to be the best index for quantifying winner/loser effects. It could perhaps be made better still by staging contests between two prior losers, two naïve opponents and two prior winners (instead of prior winner/loser vs. naïve). A potential shortcoming of such pairings is not being able to measure impact on winning probability.

The persistence of the effect from one winning or losing experience tends to be short when random selection methods (Chase et al. 1994; Bégin et al. 1996) are used to avoid confounding these effects with intrinsic fighting ability. Persistence ranges from less than an hour (e.g. crayfish, Bergman et al. 2003; Pumpkinseed sunfish, Chase et al. 1994) to a few days (e.g. >2 d in mangrove killifish, Hsu & Wolf 1999, 2001; <7 d in Copperhead snake, Schuett 1997) (also see review of Hsu et al. 2006; Rutte et al. 2006). Animals have, however, been shown to be capable of retaining information for much longer periods of time in other fields of study. Crayfish (O. rusticus), for instance, remember the association between two odours for 2–4 wk (Hazlett et al. 2002), and fathead minnow (Pimephales promelas) remember the association between a visual stimulus and alarm substance for more than 2 mo (Chivers & Smith 1994). It is therefore probably not an animal’s memory capacity that limits the persistence of winner/loser effects. Recent wins or losses may provide an individual with information about its fighting ability relative to those of the others in the population (Whitehouse 1997). The value of information should be positively influenced by signal reliability and environmental uncertainty (McLinn & Stephens 2006). The persistence of winner and loser effects may therefore reflect how long previous contest outcome remains a reliable index for fighting ability and the uncertainty of an individual’s ability relative to those of others in the population. It is also important to keep in mind that an individual could acquire information about its or its opponent’s ability from other sources. An individual can, for example, monitor its own physiological state, use morphological, behavioural or physiological cues to evaluate its opponent, remember the opponent’s identity and past performance, etc. Fighting ability–related information acquired from recent contests thus competes with information from other sources to influence contest decisions. In this study, for instance, the interaction between a prior winner/loser and its naïve opponent was probably influenced by factors other than their recent contest experience. The interaction could be influenced by each other’s morphological (including size), behavioural and/or physiological traits. Mutual evaluation of olfactory cues could have begun as soon as the two contestants were placed in the same fighting tank, while separated by an opaque partition. If winner
and loser effects are adaptive features of animal contests and provide information about relative fighting ability, these effects’ persistence will probably be shaped by the relative reliability of the information and the potential costs of acquiring information from different sources as well as the variability of the local population’s fighting ability, which is yet to be explored.

Acknowledgements

We thank Alan Watson for help with comments and on the manuscript and three anonymous reviewers for their helpful suggestions as to how the draft paper could be improved. This research was supported by Taiwan National Science Council (NSC 94WFA0300389).

Literature Cited


