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The winner and loser effect: integrating multiple experiences

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An important question in state-dependent behaviour is how multiple influences on state are integrated to determine current behaviour. Aggressive behaviour is known to be affected by a prior contest experience. Nevertheless, whether and how multiple prior fighting experiences are integrated into a fighting decision remain unexplored. In this study, individuals of *Rivulus marmoratus* (Cyprinodontidae), a hermaphroditic fish, were given different combinations of two prior fighting experiences to investigate: (1) the effect of penultimate experiences on the probability of winning a subsequent contest; (2) the relative effect of a recent win and loss; and (3) whether the effect of a winning experience was as short lived as observed in other species. Penultimate and recent fighting experiences were given to the test fish approximately 48 and 24 h prior to the dyadic contests, respectively. From the results of the five types of contests staged, we conclude that: (1) penultimate fighting experiences had a significant effect on the probability of winning a subsequent contest; (2) a more recent experience had a more pronounced effect than an earlier experience, which suggested that the effect of a fighting experience would decay and/or the effect of a recent experience would interfere with the effect of an earlier experience; (3) no asymmetric effect between a winning experience and a losing experience was detected; and (4) the effect of both a winning and a losing experience lasted for at least 48 h in *R. marmoratus* which was the maximum time tested in these experiments. The possible reasons for the differences in results among studies of experience effects on contest outcomes are discussed.

Fighting outcomes are considered to be affected primarily by resource value and fighting ability (or resource holding potential) (Maynard Smith 1974; Maynard Smith & Parker 1976). Although the role of past fighting experience in fighting outcomes is still unclear, studies have shown that a prior winning experience tends to increase, and a prior losing experience tends to decrease, the probability of an individual winning a subsequent contest (e.g. McDonald et al. 1968; Bakker & Sevenster 1983; Francis 1983; Abbott et al. 1985; Beacham & Newman 1987; Franck & Ribowski 1987; Beacham 1988; Moore et al. 1988; Bakker et al. 1989; Otronen 1990; Beaugrand et al. 1991, 1996; Chase et al. 1994; Schuett 1997; Whitehouse 1997). Prior winning and losing experiences are not likely to affect how individuals assess resource value to cause such a change in the probability of winning a later contest. Therefore, they are often hypothesized to affect how individuals assess fighting ability (Beacham 1988; Otronon 1990; Beaugrand et al. 1991, 1996; Whitehouse 1997). Individuals may use prior fighting experiences to associate cues, such as size, with the fighting abilities of their opponents, and/or to assess their own fighting ability relative to the population distribution of fighting abilities (Whitehouse 1997). Consequently, individuals with winning/losing experiences assess their own good/poor fighting abilities and expect low/high costs in their future fights. These differences in estimated costs then affect how long individuals with different prior fighting experiences persist in later contests and their probabilities of winning the contests.

Even though a prior fighting experience has been found to affect the probability of winning a subsequent contest in many animal species, three nonmutually exclusive issues regarding the effect of prior fighting experiences remain unclear: (1) the relative importance of multiple prior fighting experiences; (2) the relative effect of a win compared to a loss; and (3) the relative rate of decay of the effect of a win compared to the effect of a loss.

Various theories have been proposed on how nonhuman organisms should incorporate information from multiple past experiences, mainly in the context of foraging decisions (e.g. Killeen 1984; McNamara & Houston

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1987; Mangel & Clark 1988; Todd & Kacelnik 1993; Devenport & Devenport 1994; Mazur 1996). These theories focus on how an individual should adjust its current foraging behaviour based on its past experiences of resource availability and/or foraging costs to maximize its foraging success. The role of information from past foraging depends on the reliability of the experiences in predicting current benefits and costs of foraging. When the environment changes quickly or as the time that has elapsed since the experiences increases, the information from previous experiences becomes less reliable in predicting the current situation, thus, less weight should be given to the past experiences. However, when the environment is temporally stable, but not spatially homogeneous, the information remains reliable longer, and an individual would be expected to distribute weights more evenly among experiences and incorporate more past experiences into its current decision.

The value of past fighting experiences in assisting individuals evaluating their opponent's or their own fighting ability should depend on how fast fighting ability changes over time. If fighting ability does not change over time, all past experiences provide equally reliable information. All experiences should thus be weighted equally. However, if fighting ability does change over time, more recent experiences should be better predictors of the individual's current state. Studies on the effect of prior fighting experience have focused on testing the effect of one experience. The relative importance of different multiple prior experiences in affecting the outcome of a subsequent fight is thus unknown and remains to be investigated.

Even though both winner and loser effects have been observed in previous studies, a loser effect often appears to be more pronounced and to last longer than a winner effect (e.g. Bakker et al. 1989; Chase et al. 1994). In fact, in some studies, a winner effect could not be detected (e.g. Francis 1983; Beacham & Newman 1987; Schuett 1997). Chase et al. (1994) reviewed the literature on winner effects and discovered that a winner effect was usually short lived and thus only noticeable when the effect was examined shortly after the experience. For instance, the effect of a winning experience was observed to last for less than 3 h in sticklebacks (*Gasterosteus aculeatus*, Bakker et al. 1989), 60 min in pumpkinseed sunfish (*Lepomis gibbosus*, Chase et al. 1994) and no effect was detected in copperhead snakes (*Agkistrodon contortrix*, Schuett 1997). In contrast, the effect of a losing experience lasted longer than 6 h in sticklebacks (Bakker et al. 1989), at least 1.5 h in pumpkinseed sunfish (Beacham & Newman 1987), and 7 days in copperheads (Schuett 1997). If a prior fighting experience affects the outcome of a subsequent contest by affecting how an individual assesses its fighting ability as suggested in various studies (Beacham 1988; Otronen 1990; Beaugrand et al. 1991, 1996; Whitehouse 1997), these observations of extremely short-lived effects of a winning experience relative to the effects of a losing experience seem to indicate that it is more important for an animal to learn that it is a poor fighter than to learn it is a good fighter. Nevertheless, more evidence is necessary to test whether this asymmetrical effect from a previous win and loss is a general trend in animal fighting.

The objective of this study was to provide individuals of *Rivulus marmoratus*, a hermaphroditic fish, with two fighting experiences to investigate: (1) whether the probability of winning was affected by more than just the most recent fighting experience; and if so, (2) whether prior winning and losing experiences differ in the magnitude of their effects on the outcome of a subsequent contest; and (3) whether the effect of a winning experience is shorter lived than the effect of a losing experience as observed in other species.

METHODS

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 ($12 \times 8 \times 20$ cm^3) usually establish a dominant–subordinate relationship within an hour (Hsu 1997).

Rivulus marmoratus is completely homozygous for the 31 loci examined by Vrijenhoek (1985) and clonally stable for at least three generations, as demonstrated by single-sequence DNA fingerprinting (Turner et al. 1990). These findings suggest that the fish exist in nature as isogenic, homozygous strains. The strains used in this study were obtained from H. C. Lin in the Department of Biology, Pennsylvania State University. Clone NA (Florida) had been kept in captivity for more than 15 generations. It came originally from R. Harrington, who first described self-fertilizing hermaphroditism in this species (Harrington 1961). Clone B was the first generation from Belize collected by W. Dunson of Pennsylvania State University. Both strains have been maintained and bred at Syracuse University successfully for 3 years (two generations).

Each fish was isolated within a week after it hatched and was kept alone in a $10 \times 10 \times 10$ cm opaque plastic container to eliminate interaction between individuals. Every container was filled with 300–400 ml of approximately 12.5 ppt (ca. 33%) synthetic sea water (Instant Ocean™ powder) and labelled with a unique code for individual identification. Fish were maintained at 26–27°C on a 14:10 h light:dark cycle, and fed newly hatched brine shrimp (*Artemia*) nauplii.

Rivulus marmoratus starts laying eggs within 3–6 months after hatching in the laboratory (Harrington 1975). They can be less than 2 cm in body length when first mature. For ease of handling, subjects were not used for experiments until they were at least 3 cm in total body length (more than 8 months old). The fish used in this study ranged from 3.00 to 4.20 cm. *Rivulus marmoratus* are capable of producing fertilized eggs all year round and do not have obvious oviposition cycles (Harrington 1963, 1971). Hence, we assumed that either all individuals were in the same

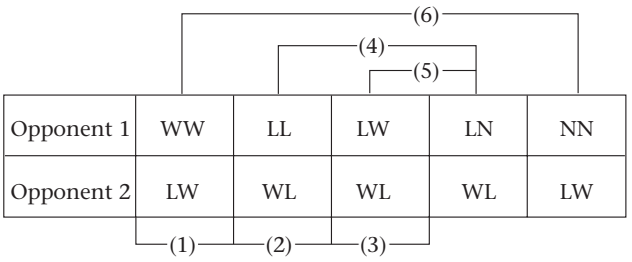

Figure 1. A summary of the experimental design used in the present study. Outcomes of (1) WW–LW and (2) LL–WL contests tested the effect of penultimate experiences. (3) LW–WL contests examined the importance of a penultimate experience relative to the most recent experience on the probability of winning a subsequent contest. The difference in the probability of (4) the LL and LN individuals winning against WL individuals measured the effect of a recent losing experience, and the difference in the probability of (5) LW and LN individuals winning against WL individuals measured the effect of a recent winning experience. (6) The difference in the probability of WW and NN individuals winning against LW individuals measured the effect of two winning experiences.

reproductive state or their oviposition cycles were randomized.

Experimental Design

To test whether a recent fighting experience has a more significant effect than an earlier experience on the probability of winning a subsequent contest, we addressed two questions. (1) Do penultimate fighting experiences have a significant influence on the outcome of a subsequent contest? (2) What is the importance of a penultimate experience relative to the most recent fighting experience in affecting the probability of winning a subsequent contest? To test whether the effect of a winning experience was less significant than that of a losing experience, and whether a winner effect was short lived, we carried out experiments to examine the effect of a recent winning experience relative to the effect of a recent losing experience, and the effects of penultimate winning and losing experiences.

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 an hour as explained below): WW (winning on day 1, winning on day 2), WL, 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. We addressed the following (summary in Fig. 1).

Do Penultimate Fighting Experiences Have Any Significant Influence on the Probability of Winning?

The opponents in WW–LW and LL–WL contests had the same recent experiences, but different penultimate experiences. If penultimate fighting experiences influence the outcome of a subsequent contest, individuals with a penultimate winning experience should have a higher probability of winning than individuals with a penultimate losing experience. We tested the effect of penultimate experiences against both recent winning and losing experiences to examine whether the effect of penultimate experiences depends on the type of recent experience.

What is the Relative Importance of the Penultimate to the Most Recent Fighting Experience for the Probability of Winning a Subsequent Contest?

In LW–WL contests, the opponents had opposite penultimate and recent fighting experiences. If a more recent experience has a more pronounced effect on the probability of winning, LW individuals should have a higher probability of winning than WL individuals.

What is the Magnitude of a Recent Winner/Loser Effect?

To quantify the magnitude of recent winning and losing experiences, we compared the outcomes of LN–WL contests to those of LL–WL and LW–WL contests. In these three sets of contests, LL, LW and LN individuals all fought against WL individuals but differed in their recent experiences. The difference in the probability of winning against the WL individuals by the LL and the LN individuals should be attributable to the effect of a recent losing experience. Similarly, the difference between the LW and LN individuals in their probabilities of winning against the WL individuals should be attributable to the effect of a recent winning experience.

Does a Penultimate Winning Experience Have Any Effect on the Probability of Winning a Subsequent Contest?

To answer our first question, we tested the difference in the effect between a penultimate winning and losing experience. To examine whether the effect of a winning experience lasts at least 2 days, the effect of a penultimate winning experience needs to be tested independently. We did not test the effect of a penultimate winning experience directly. Instead, we examined the effect of two consecutive winning experiences and compared this effect to the effect of a recent winning experience alone, which was measured in answering the previous question. We examined the effect of two consecutive winning experiences by staging NN–LW contests and comparing the outcomes to those of the WW–LW contests staged earlier. In these two sets of contests, the difference in their probabilities of winning against the LW individuals should be due to the two additional winning experiences of the WW individuals relative to the NN individuals.

Procedures

To stage the five types of contests, we measured the total body length of individuals of *R. marmoratus* and

divided them into pairs. A preliminary study showed that a difference of 0–10% in total body length with a difference of 0–7 days in age did not result in an unequal probability of winning between pairs of *R. marmoratus* (25 pairs tested, 12 won by larger opponents, $\chi^2_1=0.04$, $P=0.845$) We thus paired the fish so that the difference in their total body length was smaller than 1 mm (<3.5% of the body length of the smaller fish) and the difference in their 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 (e.g. WW or LW experiences for the WW–LW contests). Each individual was used only once in one type of contest (e.g. WW–LW contests) and was isolated for at least 3 months before it was used for a different type of contest (e.g. LL–WL contests). When fish were used in more than one type of contest, they were subsequently paired with a fish that had the same fighting experiences in earlier experiments. For instance, a WW test fish that won in a WW–LW contest would be paired with another test fish similar in size and age that was also a WW individual that won in an earlier WW–LW contest. Fish were always paired with individuals of the same clone for all contests. Clonal type was found to have no significant effect on any contest behaviours examined or on contest outcomes (Hsu 1997). Therefore, data from the two clones were pooled for subsequent analyses.

For individual identification, we clipped the nonvascularized, 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. All contests, including training the test fish for the predetermined experiences, took place in standard aquaria (12 × 8 × 20 cm) containing gravel 2 cm high and water 16 cm deep. No geographic landmark except the boundaries of the aquarium was available for the fish to defend.

Providing a Losing/Winning Experience

For these experiments, we used 'standard' winners/losers to give the test fish losing/winning experiences, respectively. To generate a standard winner, we staged contests among several large fish and the one that defeated all others was designated a standard winner to provide losing experiences to the test individuals of its clone. To obtain a standard loser, small fish fought among themselves and the one that lost to all others was used as a standard loser to provide winning experiences to the test individuals of its clone. If a test fish was assigned to receive two consecutive winning/losing experiences, two different standard losers/winners were used to provide these experiences.

To produce a losing/winning experience, a standard aquarium was divided by an opaque partition into two equal-sized, symmetrical compartments. The test fish was removed from its maintenance container and placed in one compartment with a standard winner/loser in the other. When fish were first placed into an aquarium, they usually started swimming in less than 15 min. This time was assumed to be required for them to recover from the disturbance of being moved. All fish were given a 15-min acclimation period before the partition was removed to permit the test fish to interact with the standard winner/loser. A losing experience was successful if the test fish retreated first from a contest, continuously avoided the attacks from the standard winner, and did not retaliate for an hour (after it first retreated). A winning experience was successful if the test fish chased/attacked the standard loser for an hour without retaliation. If a test individual failed to receive its predetermined experiences, both the individual and its preassigned opponent were discarded from the experiment.

To minimize the difference in the amount of disturbance received between the test fish that were assigned a winning/losing experience and the test fish that was assigned a 'no experience' treatment, we removed a test fish that was to receive a 'no fighting experience' treatment from its maintenance container and placed it in one of the two equal-sized compartments of a standard aquarium for an hour; there was no fish in the other compartment.

Staging Contests

The test fish received their first fighting experience on day 1 and were returned to their maintenance containers and fed with brine shrimp after their experiences were completed. We carried out similar procedures on the next day for the second set of experiences. After the second experiences were completed on day 2, we placed the preassigned pair of opponents in a standard aquarium with an opaque partition between them to prevent any visual or physical contacts. The two contestants were fed with brine shrimp and allowed to acclimate in the standard aquarium for 24 h. Brine shrimp could swim freely between the two compartments and were never observed to aggregate on either side of the partition. Thus, this feeding procedure did not create a resource value asymmetry between the two contestants. On day 3, a contest began when the partition was lifted. The contestant that first chased/attacked its opponent for 20 min without retaliation was defined as the winner of the contest. All contests resulted in clear winners and losers in an hour. The contestants were returned to their maintenance containers after the contests.

RESULTS

The outcomes of all staged contests are shown in Table 1.

The Effect of Penultimate Fighting Experiences

In total, 27 WW–LW contests were staged, and WW individuals won significantly more contests than LW individuals (chi-square test: $\chi^2_1=4.481$, $P=0.034$). For the 31 WL–LL contests staged, WL individuals won significantly more contests than LL individuals ($\chi^2_1=3.903$, $P=0.048$). These results indicate that penultimate fighting experiences had a significant influence on the fighting

Table 1. The number of contests won by individuals with different combinations of penultimate and recent experiences in the five types of contests staged

Contest type	Number of contests won
WW–LW	19–8
LL–WL	10–21
LW–WL	27–11
LN–WL	13–12
NN–LW	13–19

outcome. Individuals with a penultimate winning experience had a higher probability of winning a subsequent contest than individuals with a penultimate losing experience. A comparison of the fighting outcomes between these two types of contests indicated that the probability of individuals with a penultimate winning experience winning against individuals with a penultimate losing experience was independent of whether the recent experience was a win or a loss (χ^2_1=0.047, P=0.829). With pooled data, the individuals with a penultimate winning experience had a probability of 0.69 of winning against individuals with a penultimate losing experience. Because the expected probability of winning for contestants that also were matched for their penultimate experience is 0.5, this 0.19 (0.69–0.5) deviation should thus have to come from the difference in the effects of a penultimate winning and losing experience.

The Relative Importance of a Penultimate Experience to a Recent Experience

The LW individuals had a significantly higher probability of winning than the WL individuals in the 38 LW–WL contests staged (χ^2_1=6.737, P=0.009). Thus, when contestants were given opposite penultimate and recent experiences, the more recent experience had a greater effect on the probability of winning a subsequent contest.

The Magnitude of the Effect of a Recent Win and a Recent Loss

The overall difference in the probability of winning against a WL individual among the LL (10/31=0.32), LN (13/25=0.52), and LW (27/38=0.71) individuals was significant (χ^2_2=10.339, P=0.006). Nevertheless, the pairwise comparisons revealed that the difference was significant only between LL and LW individuals (χ^2_1=10.332, P=0.001), and not between LW and LN individuals (χ^2_1=2.361, P=0.124) or between LL and LN individuals (χ^2_1=2.229, P=0.136). The conclusions remain the same after adjusting the 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 show that both the recent losing experience of the LL individuals and the recent winning experience of the LW individuals contributed to the significant difference in the probability of winning between them. With a 'no fight' recent experience, the probability of the LN individuals winning against the WL individuals was 0.52. With a recent losing experience, the probability of the LL individuals winning against the WL individuals decreased to 0.32, a decrement of 0.20. Moreover, with a recent winning experience, the probability of LW individuals winning against the WL individuals increased to 0.71, an increment of 0.19. Therefore, no obvious asymmetry in the magnitude of a winner and a loser effect was detected. Because a recent experience was received approximately 24 h before the contest, these results also indicate that the effect of both a winning and a losing experience lasted for at least 24 h in *R. marmoratus*.

The Magnitude of the Effect of a Penultimate Winning or Losing Experience

When fighting against the LW individuals, the WW individuals had a significantly higher probability of winning (19/27=0.70) than the NN individuals (13/32=0.41) (χ^2_1=5.220, P=0.022). The difference in their probability of winning was approximately 0.29 and came from the effect of a penultimate winning experience combined with the effect of a recent winning experience. Previously, a recent winning experience alone was found to increase the probability of winning a subsequent contest by 0.19. These results suggest that a penultimate winning experience received approximately 48 h prior to the contest had a positive effect of 0.10 (=0.29 − 0.19) on the probability of winning a subsequent contest. These comparisons of the effects of experiences assume that the magnitudes of the effects were not influenced by the types of experiences that the opponents had.

We also showed above that the difference between the effect of a penultimate winning experience (=A) and the effect of a penultimate losing experience (=B) was 0.19 (=A − B). Because a penultimate winning experience had a positive effect of 0.10 (=A) on the probability of winning, a penultimate losing experience should thus have a negative effect of 0.09 (=0.10 − 0.19) on the probability of winning. Therefore, no obvious asymmetry in the magnitude of the effect between a penultimate winning experience and a penultimate losing experience was observed.

DISCUSSION

The results of this study demonstrate that a winning experience and a losing experience have effects of similar magnitude in *R. marmoratus* and that the effect of both experiences lasts at least 48 h. The results of this study also indicate that a subject's penultimate experience (received 48 h before the contest) was weighted to be approximately half that of its recent experience (received 24 h before the contest) in affecting its probability of winning a subsequent contest. From these experiments, with only two experiences and equal time intervals between experiences, it is not clear whether the effect of a fighting experience decays over time (time-driven decay; Killeen 1984) or as a result of a new experience (event-driven decay; Devenport & Devenport 1994). The symmetrical effect we observed between a winning and a

losing experience suggests that modifying behaviour after a winning or losing experience may be equally adaptive in *R. marmoratus*. We did not test for effects lasting longer than 48 h, but the change in the probability of winning (ca. ± 0.10) due to a winning or losing experience 48 h in the past indicates that the effect of either experience would persist somewhat longer than 48 h.

The results are somewhat contradictory to the asymmetrical effects of winning and losing experiences reported in previous studies (e.g. Francis 1983; Beacham & Newman 1987; Bakker et al. 1989; Chase et al. 1994; Schuett 1997). However, even though the effect of prior fighting experiences was examined in many studies, only a fraction of them evaluated the effect of a prior winning experience and of a prior losing experience simultaneously (e.g. Bakker & Sevenster 1983; Francis 1983; Beacham & Newman 1987; Bakker et al. 1989; Schuett 1997). In addition, because of methodological differences, the results of some of these studies cannot be compared to ours. In our study, the experiences were preassigned and 'randomly selected' (Chase et al. 1994), and caused no observable physical injuries to the test fish. Some previous studies adopted 'self-selected' procedures for offering the experiences to the test individuals, in which two individuals were matched and the winner and loser were treated as having a winning and losing experience, respectively (Beacham & Newman 1987). Furthermore, some of the studies noted physical injuries of the test individuals (McDonald et al. 1968; Francis 1983; Beacham & Newman 1987). The self-selected procedures have the potential to confound fighting experience with intrinsic fighting ability (Chase et al. 1994). Physical injuries can reduce the fighting ability of the test individuals and thus also may be confounded with the effect of a losing experience.

Two recent studies that examined the effect of a prior winning and losing experience separately, and that adopted experimental procedures comparable to ours are the study of Bakker et al. (1989) on sticklebacks and the study of Schuett (1997) on copperhead snakes. Both winner and loser effects were detected in the male sticklebacks; however, the winner effect was found to be less pronounced and disappeared sooner than the loser effect. In the copperhead study, even though a loser effect was observed, a winner effect was not detected. The results from these two studies and the present study suggested that it is always beneficial for an individual to learn it is a poor fighter and adjust its fighting strategy accordingly, but it is not necessarily adaptive to act like a good fighter after a winning experience. One explanation for an often greater loser effect is that engaging in contests but losing often incurs more costs (time, energy, injuries) than retreating without confrontation (Neat et al. 1998), especially when the benefit of being a winner is not high enough to compensate for the potential costs. These high costs of losing may then select for individuals that adopt a more conservative strategy when incorporating prior fighting experiences into the estimates of their fighting ability such that fighting behaviours are more affected by losing experiences than by winning experiences. The difference in the relative effect between a winning and a losing experience among the three species suggests it might be more costly for a male copperhead to lose a fight than for a three-spined stickleback or a *R. marmoratus*.

Using information from prior experiences presumably reflects the reliability of that information for predicting either an individual's relative ability or how that individual judges an opponent's ability in the absence of information other than general phenotypic cues such as size. How long the effect of a prior experience lasts might be associated with the frequency of social encounters (Schuett 1997). In a population where aggressive interactions occur often, individuals frequently gain more recent and probably more reliable information. It is thus not beneficial for them to retain the information from an experience for a long time. However, when social interactions are not frequent, but information remains reliable for a long time, it would be adaptive for individuals to retain the information longer. In the natural environment, social interactions between male copperhead snakes seem to be infrequent, even during the mating period (Schuett 1997). *Rivulus marmoratus* are hermaphroditic, reproduce by self-fertilization, and live under mangrove leaves, logs, and in crab burrows (Huehner et al. 1985; Taylor 1990). Even though more than one individual could occupy the same burrow, especially when suitable shelters are limited, they never show schooling behaviour (Kristensen 1970). On the other hand, three-spined sticklebacks live in schools during the nonbreeding season. During the breeding season, female sticklebacks still live in groups and males form breeding aggregations and establish individual territories (Wootton 1976; Rowland 1989). Therefore, among the three species, aggressive encounters seem likely to be the most frequent in male sticklebacks, and the least frequent in male copperheads. The observations that the effect of a losing experience was detected after 7 days in copperheads, after at least 2 days in *R. marmoratus*, and after 6 h in sticklebacks support the hypothesis that the frequency of social interactions and the survivorship of the effect of a prior social experience might be correlated.

Other than a difference in decay rate, the difference in how long the effect of an experience lasts among species might also reflect a difference in the magnitude of the initial effect. Unfortunately, the magnitude of the initial experience effects cannot be compared among studies because of methodological differences. Besides a variation in employing 'self-selected' or 'randomly selected' procedures for offering experiences to test individuals, studies of experience effects differed tremendously in how long an experience lasted, ranging from 15 min to 15 days. Also, in these studies, an experience was offered to the test individuals in either one continuous session or multiple interrupted sessions and the effects were allowed to decay for different amounts of time before first being examined (0–24 h). Because no standard procedures were used in testing the effects of experiences, it is not clear how the magnitude of the winner and loser effect differs among species.

The physiological mechanisms underlying the integration of these experiences are still being explored. A winning/losing experience could lead to a change in

some hormone levels (e.g. testosterone; Bernstein et al. 1983; Harding 1983; Leshner 1983; Cardwell & Liley 1991; but see Liley & Kroon 1995; Schuett et al. 1996), differential activation of neuronal receptors (Yeh et al. 1996), and/or differential depletion in muscle energy reserves (Neat et al. 1998). Whether or how these mechanisms are responsible for the changed probability of winning is not known.

Prior experience can also affect the dominance–submissive relationship among familiar individuals (McDonald et al. 1968) and the peck order in groups (Ratner 1961; Dugatkin 1997). The order of opponents an individual encounters in a group could be stochastic, nevertheless, the fighting outcome of an earlier encounter could affect the individual's behaviour in obtaining its subsequent rank order in the group. Therefore, the rank order of an individual in a hierarchical group may not depend strictly on its fighting ability but also on the order of opponents it encounters.

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