

# What sets the odds of winning and losing?

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**Social experience influences the outcome of conflicts such that winners are more likely to win again and losers will more likely lose again, even against different opponents. Although winner and loser effects prevail throughout the animal kingdom and crucially influence social structures, the ultimate and proximate causes for their existence remain unknown. We propose here that two hypotheses are particularly important among the potential adaptive explanations: the ‘social-cue hypothesis’, which assumes that victory and defeat leave traces that affect the decisions of subsequent opponents; and the ‘self-assessment hypothesis’, which assumes that winners and losers gain information about their own relative fighting ability in the population. We discuss potential methodologies for experimental tests of the adaptive nature of winner and loser effects.**

## A general phenomenon lacking explanation

Although winner and loser effects are widespread throughout the animal kingdom, their evolutionary significance is still unknown. Winner and loser effects are usually defined as a higher probability for a winner to win a subsequent encounter and for a loser to lose a subsequent encounter, respectively, regardless of the identity of the opponent [1–3]. The outcome of a contest is thus determined not only by resource holding power (RHP) [4] and resource value [5], but also by the previous contest experience of the opponents. Winner and loser effects have been described for a wide range of animals and, hence, social systems [1]. A survey across several taxa revealed that, when there are no other asymmetries between opponents, the probability of winning a subsequent contest is almost doubled for previous winners, but is reduced more than five times for previous losers (Box 1).

Recent theoretical and empirical evidence reveals that both effects crucially affect hierarchy formation [2,6,7], and that positive feedback of initial victories and defeats is likely to promote linear hierarchies. In spite of their ubiquitous occurrence and extensive effects on social structures [8], it is unknown whether winner and loser effects are adaptive. Why should prior experience affect

subsequent agonistic behaviour? What are the potential fitness advantages for an animal acting upon its prior experience? As an alternative to adaptive causes, winner and loser effects might result from physiological constraints originating from the regulation of preceding escalated contests. Here, we discuss adaptive and by-product hypotheses, and examine whether experimental evidence supports either one or the other.

## Predicting contest outcome

Dominance generates primary access to important resources such as territories, food and mates, but fighting for position also bears costs through increased energy expenditure, injury risk, opportunity costs and vulnerability to predators [5]. Therefore, selection should favour mechanisms that enable animals to maximize their net benefit, taking into account the costs and benefits of a contest. Assessing the probability to win a conflict could optimize this decision-making process. There are two principle, but not mutually exclusive possibilities to estimate the chances of winning. The first is to assess the strengths and weaknesses of an opponent before or during an encounter [9]; prior fighting experience might create cues that could be used by an opponent (‘social-cue hypothesis’). The second is to assess one’s own qualities; prior experience could be used to assess one’s own fighting ability relative to that of others in the population (‘self-assessment hypothesis’) [10]. The importance of self-assessment, which might, for instance, enable individuals to set a cost threshold for any particular contest, has often been underestimated in studies of animal contests [11,12].

## Social-cue hypothesis

The social-cue hypothesis states that prior experience is used as a cue to assess asymmetry between opponents. It assumes that animals can detect a prior victory or defeat of their opponent, for example, by detecting signs of exhaustion or injury in losers [13] or chemical cues emitted by winners or losers [5]. On the proximate level, chemical cues could be related to hormone release that occurs towards the end of an escalated encounter, which might differ between winners and losers and persist for prolonged periods of time. Chemical cues have been found to elicit or inhibit

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### Box 1. How does winning and losing influence the outcome of subsequent contests?

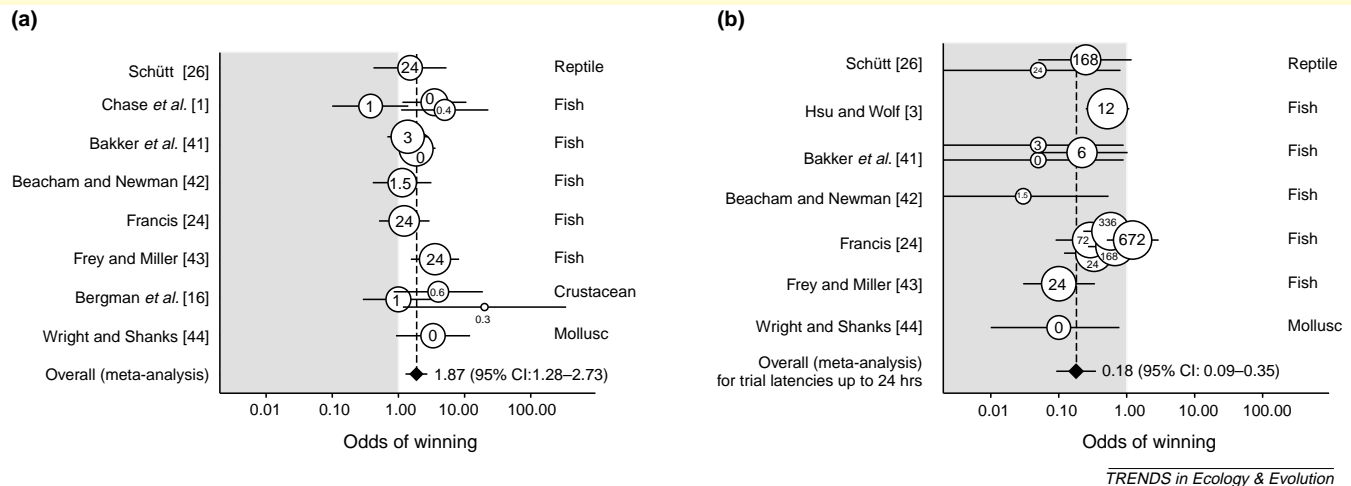
To check for the quantitative effect of fighting experience on subsequent contests, we performed a systematic review and meta-analysis. We retrieved studies that experimentally tested for winner and loser effects by systematically searching the Web of Knowledge (<http://wok.mimas.ac.uk/>) electronic database (keywords: winner, loser, effect, experience, agonistic, prior; search operators: and, or) and by examining the references of the articles retrieved manually.

We included studies that reported the odds of winning and 95% confidence intervals (CIs) (or data to calculate them) for individuals with either a prior winner or a prior loser experience, and which were subsequently tested against a naive individual after a known period of time. Data from nine publications were eligible for the meta-analysis, contributing 13 and 14 tests for winner and loser effects, respectively. Quantitatively, a winner effect is defined as a significant increase in the odds of winning the next contest after a winning experience (odds of winning > 1), whereas a loser effect implies the opposite (odds of winning < 1). In the meta-analysis, we used log-transformed odds of winning and weighted the estimate for each test by the inverse of their variance to obtain fixed-effects and random-effects pooled estimates. All analyses used the statistical package STATA version 8.2 (<http://www.stata.com/>).

Publication bias was assessed on the basis of Egger's funnel plot asymmetry test [40].

The pooled odds of winning for winners were 1.87 (CI=1.28–2.73; Figure 1), whereas there was modest heterogeneity (i.e. variation in effect size attributable to heterogeneity,  $I^2=36\%$ ). Thus, the likelihood of winning nearly doubled after a previous winning experience. The odds of winning across trials involving losers showed substantial heterogeneity ( $I^2=50\%$ ) and this was largely a result of the odds declining with increasing interval length between the initial and the test trial ( $p$  for interaction=0.014). Excluding tests with intervals > 24 h, at which point loser effects might have faded, the pooled odds of winning were 0.18 (CI=0.09–0.35; Figure 1). Thus, losers were more than five times less likely to win the next encounter, and this loser effect was stronger than the winner effect ( $p$  for interaction=0.013).

There was also evidence for a publication bias ( $p<0.01$ ), with studies with smaller sample sizes showing larger effect sizes (Figure 1), suggesting that small studies with small effect sizes remained unpublished. Although their overall effect sizes were therefore somewhat inflated, the results of the larger studies confirm the broad existence of winner and loser effects in animals.



**Figure 1.** Meta-analysis of odds of winning for winners (a) and losers (b) against a naive opponent. Symbol size indicates the relative contribution (inverse variance weight) of study trials to the analysis. Numbers in symbols show the time in hours between the initial and test trials. Estimates (95% CI) in the grey area indicate a reduction in the likelihood of winning (odds < 1), whereas those outside the grey area indicate an increase (odds > 1). The probability of winning a contest is almost doubled for previous winners, but is more than five times reduced for previous losers. Based on results from [1,3,16,24,26,41–44].

attack in species from a wide range of taxa including cockroaches, crayfish, fish, lizards, rats and primates [5]. The big-clawed snapping shrimp *Alpheus heterochaelis*, for example, can recognize the prior fighting experience of an opponent by odour [14]. A former shrimp loser would flee rather than fight against a former winner, whereas it would fight against a naive opponent that had not fought before. Relevant information in this case could be contained in the urine or by a chemical substance carried by the urine [14]. In the crayfish *Orconectes rusticus* (Figure 1), the observed winner effect is also not intrinsic to the winner, but apparently results from information communicated via odour [15]; a winner effect is found only if the opponent can perceive these signals [16].

It remains to be clarified in such cases [14–16] whether information transfer results from inadvertently

produced cues or from intentionally communicated signals. For winners, intentional signals would be adaptive if there were any material consequences of preceding victories that would affect the asymmetry between opponents, and if revealing this asymmetry would increase the probability of winning subsequent encounters or reducing fighting costs. For losers, it might be adaptive to reveal their defeat if losing would have material effects and thereby affect asymmetry between opponents, and if revealing this asymmetry would save fighting costs.

Opponents might also know about each other's previous fighting success or failure by observation [17]. Eavesdropping, where individuals gain information from interactions in which they are not taking part, has been found in several species [18,19]. For example, Siamese



**Figure 1.** Two male crayfish *Orconectes rusticus* performing a series of chelae grabs trying to turn each other on to their backs. Reproduced with permission from Daniel Bergman.

fighting fish *Betta splendens* approach a winner more warily than they do a loser after viewing contests between neighbours [20]; rainbow trout *Oncorhynchus mykiss* settle a conflict faster with opponents whose fighting performance they had previously watched [21]. In the cichlid fish *Oreochromis mossambicus*, androgen levels increase in males while they are watching contests [22]. It has been suggested that androgens are the likely mediators of winner and loser effects that act by modulation of the cognitive mechanisms underlying animal communication [22].

#### Self-assessment hypothesis

The self-assessment hypothesis proposes that prior experience is used to estimate one's own fighting ability in relation to the average fighting ability of other individuals in the population [10]. Because the probability of winning depends on the existence and frequency of weaker and stronger individuals in the population, knowing one's own absolute fighting ability might not be a reliable predictor of contest outcome: a strong individual will still be inferior if all others are even stronger.

A game-theory model suggested that winner and loser effects could evolve through competition among triads of animals taken randomly from a population [23]. In this model, individuals were assumed to revise their subjective perception of RHP in the light of their own experience: a winner effect was combined with animals raising their RHP perception after a victory, whereas a loser effect was combined with animals lowering their RHP perception after a defeat. The strength of an effect of prior experience was unmodified by the RHP of a particular individual, although it depended on the distribution of RHPs in the population. The lack of direct assessment of opponents is consistent with the observed effects of prior experience in the spider *Argyrodes antipodiana* [10], where competing males seem to use prior fighting experience to estimate their position with respect to the fighting ability in the population at large.

The aforementioned game-theory model predicts that loser effects can evolve without winner effects, but not vice versa [23]. This is in accordance with the observation that,

in some species, only a loser effect appears to exist [24–26], but no winner effect was ever found in the absence of a loser effect. For example, in the paradise fish *Macropodus opercularis* [24] and the copperhead snake *Agkistrodon contortrix* [26], only a loser effect was detected 24 h after the initial contest. According to the self-assessment hypothesis, several successive contest experiences should be included when deciding about escalation in an encounter. Accordingly, contest outcome in the fish *Rivulus marmoratus* was influenced by the penultimate as well as by the most recent experience, albeit to a smaller degree [3].

#### The importance of energy and injury

Assessing the chances to win is one way to optimize decision making whether to engage in a contest. The ability to estimate one's own energy reserves and the risk of injury might also be of additional importance.

#### Strategic use of past contest outcomes

A third adaptive explanation for the winner effect is based on the assumption that a winner gains access to a resource that increases its RHP [4]. Individuals are selected to spend this extra energy in further contests because this increases their chances of victory. Correspondingly, a loser whose fighting ability declines owing to a drain of its energy reserves or to an injury might benefit from avoiding escalation in subsequent encounters because its chances of winning are reduced and the risk of getting injured might be increased.

Experience effects based on an RHP increase cannot, however, explain winner effects in cases where winners do not gain access to a resource. Most experimental studies showing a winner effect were performed without any food resource involved [1,16,26]. In *Rivulus marmoratus*, prior experience did not alter the fighting ability of individual fish although they showed winner effects [27]. Also, the explanation of the loser effect resulting from a reduced RHP owing to defeat have not yet been supported empirically. In paradise fish *Macropodus opercularis*, for example, the loser effect lasted for at least three days, although most losers escaped with only 'slightly nipped fins and none of the subjects showed overt signs of physical distress' [24]. Male field cricket *Gryllus bimaculatus* losers will not normally re-engage in a contest for several hours after a defeat, but, after flying, they are reset to an aggressive state immediately [28]. Thus, aggressive behaviour in these loser crickets does not seem to be constrained by the need to recover from exhaustion. In hermit crabs *Pagurus bernhardus*, evicted defenders show low glucose levels [29], which could indicate exhaustion. This decrease, however, is not caused by depletion of energy reserves, but appears to be the result of a strategic decision [29].

#### Reducing risk and saving energy

Winner and loser effects might also reflect economical decisions of animals that are independent of access to resources. If behaving like a winner will settle subsequent encounters more quickly, winners will gain extra time and energy. If losers behaving as such are less likely to be

subject to escalation and injury risk, they can take advantage of this effect. Both described benefits have been demonstrated experimentally in Norway rats *Rattus norvegicus* (S. Lehner *et al.*, unpublished). The importance of contest outcomes in relation to such economical considerations should influence the propensity of animals to behave like either winners or losers. Saving energy and risk is probably not a stand-alone mechanism to explain winner and loser effects, but it could strongly affect fighting propensity in addition to other mechanisms such as the assessment of one's own or the opponent's fighting ability.

### Constraints

A possible alternative to adaptive mechanisms is that winner and loser effects might be by-products of physiological mechanisms. A constraint might either result from regulatory processes induced in escalated conflicts or from a change of body condition owing to material consequences of winning or losing.

#### Constraints imposed by regulative processes

According to this hypothesis that winner and loser effects might be by-products of hormonal mechanisms that regulate agonistic behaviour during contests, escalated contests result in changes of circulating hormone levels that persist for some time before returning to normal [30–32], affecting agonistic behaviour in the process. Although the physiological regulation of aggressive or submissive

behaviour during a contest is probably adaptive, its lasting influence after a fight might not be so.

However, it seems unlikely that winner and loser effects are merely by-products of such a time lag of internal regulatory processes. First, similar winner and loser effects exist in invertebrates and vertebrates (Figure 1 in Box 1), which differ substantially in their physiological regulation of agonistic behaviour. Second, the duration of winner and loser effects does not seem to be obviously related to the persistence of elevated hormone levels after a fight. Male copperhead snake *Agkistrodon contortrix* losers, for example, show elevated levels of plasma corticosterone (a hormone used to assess physiological stress) for only one hour after the fight [32], whereas the loser effect itself lasts for at least seven days in this species [26]. The same study found no difference in testosterone levels between winners and losers. By contrast, winning a conflict is followed by an increase in testosterone in a variety of other male vertebrates [33]. But again, in California mice *Peromyscus californicus*, a change in aggression was measured long after the elevated testosterone had been cleared from the blood [34]. An increase in testosterone levels could, however, form part of the proximate mechanism of winner effects by causing long-term changes in the brain [34]. Third, even if hormonal regulation of aggression and submission during a fight can influence agonistic behaviour in subsequent encounters, natural selection will take effect if winner and loser effects affect fitness significantly and if heritable variation exists

### Box 2. The ultimate causes of winner and loser effects: suggestions for future research

To our knowledge, no study has so far determined experimentally whether acting upon prior fighting experience raises genetic fitness. A straightforward test of the adaptive nature of winner and loser effects would be to measure fitness effects if individuals are prevented from using such prior experience. A suitable candidate for such experiments is the cricket *Gryllus bimaculatus*. These crickets show winner and loser effects [45], but the loser effect is extinguished when a loser is thrown into the air, where, after flying, they are reset to an aggressive state immediately [46]. Do losers behaving as losers do better than those that do not? Another possibility to manipulate social experience is the application of hormones or neurotransmitters in species in which the physiological regulation of agonistic behaviour is sufficiently understood, such as in various invertebrates [47]. In Table 1, we propose some further experimental manipulations to test the adaptive hypotheses outlined here.

When testing winner and loser effects experimentally, some general methodological precautions should be considered. First, focal animals receiving a winning or losing experience should be selected randomly

rather than self-selected. In the former procedure, the experimenter decides which experience an individual receives. Randomly chosen winners or losers can be achieved by staging encounters with an opponent of different fighting ability, or with one that had just lost or won a contest. In the self-selected procedure, two matched individuals are combined without prejudice, and the outcome of the encounter decides which one will be used further as a winner and as a loser. However, this procedure potentially confounds differences in prior experience with other differences in individual attributes [48]. Second, the interval between the experience and the test contest might crucially decide whether an experience effect is found. Our meta-analysis (Box 1) as well as a review of several fish studies [27] showed a negative relationship between interval length and experience effect. Inter-contest intervals should preferably match the frequency of contests in the investigated species under natural conditions. Finally, the opponent of the focal animal in the test encounter should be naïve with respect to prior fighting experience; otherwise the interacting effects of both opponents cannot be disentangled.

**Table 1. Experiments testing for adaptive causes of winner and loser effects**

Hypothesis	Proposed manipulation	Predicted effect
Winner and loser effects are adaptive	Deprive animals of information about former contest outcomes	Test animals should suffer from reduced fitness
Social-cue hypothesis	Impede reception of potential cues by opponents in test encounter	Winner and loser effects should disappear
Self-assessment hypothesis	Provide sequence of several defeats followed by a victory	Test individual should still behave like a loser
	Provide sequence of several victories followed by a defeat	Test individual should still behave like a winner
Strategic use of past outcome	Provide loser with food resource	In comparison with a control situation, the loser effect should vanish
	Prevent winner from obtaining additional resources	In comparison with a control situation, the winner effect should vanish

in these traits (see [7,8]). Therefore, hormonal side-effects are probably of minor importance. In accordance with this, several studies indicate that environmental, social and cognitive variables directly influence aggression to a greater degree than they do via hormone levels [35,36].

#### Constraints imposed by change in fighting ability

Another non-adaptive mechanism is also conceivable: if prior fighting experience results in energy gain, a winner effect might be a by-product of this increase in strength or body reserves. A loser effect might be caused by reduced fighting ability instead, owing simply to exhaustion or injuries inflicted in the previous contest. These non-adaptive mechanisms based on a change in RHP do not involve strategic decisions. They are unlikely, however, to explain winner and loser effects in general. Condition effects should influence strategic decisions to optimize contest behaviour and, hence, they should be subject to natural selection. Also, empirical results demonstrated that winner and loser effects exist even without material consequences ([1,16,26]; see above also).

#### Conclusion

Winner and loser effects are among the most general social phenomena known in animals. Surprisingly, the potential adaptiveness of these ubiquitous traits has not yet been studied. Therefore, it remains unclear if winner and loser effects reflect adaptive behaviour or whether they are mere by-products of physiological processes, even if such non-adaptive explanations seem unlikely. Several possibilities exist to explain why animals might benefit from taking account of their recent fighting history, or of that of their opponents. Rigorous experimental testing (Box 2) is now required to unravel these general and important mechanisms of sociality. Hierarchy and social structures can result from self-regulatory processes [2,6–8,37–39], of which winner and loser effects might be of utmost importance.

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