



## Sex differences in fighting-induced hyperaggression in a fly



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### ARTICLE INFO

#### Article history:

Received 25 November 2014  
Initial acceptance 29 December 2014  
Final acceptance 23 February 2015  
Available online 15 April 2015  
MS. number: 14-00957R

#### Keywords:

aggressive behaviour  
contest  
invertebrate  
learning  
physical fighting  
winner and loser effect

In many animals, after experiencing an intraspecific aggressive interaction, winners are more likely to win again (the winner effect) and losers more likely to lose again (the loser effect). However, the winner and loser effect has been studied in few arthropod models, and comparative approaches between the sexes are hard to find. In this study, we evaluated the role of previous experience in male–male and female–female contests of Mediterranean fruit flies, *Ceratitis capitata* (Diptera: Tephritidae). In this species, lekking males fight for courtship territories, while females fight to maintain single oviposition sites, as well as for mates. We addressed the following questions. (1) Are winners more likely to win again and losers more likely to lose again? (2) Are different interfight intervals critical to detect experience-induced effects on aggression? (3) Are winning and losing probabilities affected solely by the outcome of the previous contests, or is fighting experience itself sufficient to induce the effect? (4) Does experience affect differently aggression displayed by males and females? Results showed reduced fighting success in males and females that experienced a single defeat, while individuals that experienced two previous victories or defeats had higher aggression rates and more wins in subsequent contests (i.e. hyperaggression). This was achieved merely by experiencing a contest, while the actual outcomes of previous fights did not affect the aggressiveness level. Some differences were documented between male–male and female–female contests (e.g. females fought longer than males), showing the value of a comparative approach between the sexes when studying experience-induced hyperaggression. This study highlights that both consecutive victories and defeats enhance fighting performances of fruit fly males and females defending courtship territories and oviposition sites, respectively. To the best of our knowledge, this is the first evidence about how repeated defeat experiences reverse the loser effect in animals, leading to higher fighting success.

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Aggression plays a pivotal role across the animal kingdom (Lorenz, 1966). It enables individuals to acquire and/or defend resources that are often limited (e.g. food, mates and territories; Dierick & Greenspan, 2006). The defence of key resources using aggressive displays enables individuals to survive and pass on their genes through the generations (Dukas, 2008). In this context, the evolution of aggressive traits is shaped by a trade-off between benefits (from access to limited resources) and costs (risk of injuries, time and energy losses) (Hsu, Earley, & Wolf, 2006). Furthermore, the ‘struggle for life’ is usually most severe in intra-specific dynamics, where individuals are more likely to compete for the same resources (Darwin, 1859). Game theory predicts that

evolutionarily stable strategies for conflicts between conspecifics may involve stereotyped contests characterized by the ritualized exchange of agonistic cues (Maynard Smith & Price, 1973; Parker, 1974; Stevenson & Rillich, 2012).

Aggression is a highly flexible behaviour (Dukas, 2008); for example, aggressive motivation is affected by factors such as the presence and quality of resources, social upbringing, physical exertion and learning from previous contests (Hsu et al., 2006; Van Wilgenburg, Clémencet, & Tsutsui, 2010; Yurkovic, Wang, Basu, & Kravitz, 2010). Previous aggression experience affects aggressive performance in subsequent contests in animals (Stevenson & Schildberger, 2013), and losing tends to decrease subsequent aggression intensity, duration and/or fighting success (the loser effect) in many species (Hsu et al., 2006; Iwasaki, Delago, Nishino, & Aonuma, 2006). By contrast, winning tends to increase willingness to escalate a contest and/or the probability of fighting success (the winner effect; Hsu et al., 2006; Rillich & Stevenson, 2011; Rutte,

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Taborsky, & Brinkhof, 2006; Yurkovic et al., 2010). Theoretical models based on this assumption predict that the loser effect can occur with or without occurrence of the winner effect (Fawcett & Johnstone, 2010). By contrast, the winner effect cannot persist alone, at least when contestants lack fighting experience (Mesterton-Gibbons, 1999; but see also Van Doorn, Hengeveld, Weissing, 2003a, 2003b). In addition, when both effects coexist, the loser effect is predicted to be longer and of greater magnitude than the winner effect (Hsu et al., 2006; Kasumovic, Elias, Sivalingham, Mason, & Andrade, 2010). However, a recent study on the parasitoid *Eupelmus vuilleti* (Hymenoptera: Eupelmidae) demonstrated that the winner effect also exists in the absence of any obvious loser effect (Goubault & Decuignière, 2012), and proposed that the winning effect may actually occur through variation in contestants' subjective value of resources rather than via a reassessment of individuals' fighting ability.

Only a few insect models have been tested to study the effect of experience on aggressive behaviour, mainly crickets (Stevenson & Schildberger, 2013) and drosophilid flies (Yurkovic et al., 2010; Zwarts, Versteven, & Callaerts, 2012). True fruit flies (Diptera: Tephritidae) are good insect models for studying aggression. In a number of species, males fight for courtship territories, while females fight to maintain single oviposition sites (Benelli, Daane, et al., 2014; Benelli et al., 2015; Benelli, Giunti, Canale, & Messing, 2014). The occurrence of male–male and female–female combats in the same species allows a comparative approach between the sexes when studying winner and loser effects. Recently, higher aggression levels have been found in experienced males of the olive fruit fly, *Bactrocera oleae* (Diptera: Tephritidae): winners and losers of two consecutive encounters displayed a higher intensity of aggression, fought longer in subsequent contests and achieved higher fighting success than naïve flies (Benelli et al., in press). However, this research was conducted using a self-selection procedure, not ideal for measuring winner and loser effects, since with this approach the particular winning/losing experience cannot be disentangled from intrinsic differences in fighting ability (Hsu et al., 2006).

In this study, we investigated sex differences in the magnitude of winner and loser effects in the Mediterranean fruit fly, *Ceratitis capitata* (also known as the medfly). This species is a tropical polyphagous tephritid with a male dominance polygyny mating system (Benelli, Daane, et al., 2014). In *C. capitata*, highly ritualized aggressive interactions are present in both sexes, and directly related to their reproductive activities. Males establish leks on host and nonhost plants. They fight for courtship territories, then release long-range pheromones that attract females to behavioural exhibition sites. Females discriminate between lek participants and copulate with males performing the best courtship behaviour sequence, which includes wing movements combined with olfactory and tactile cues (Benelli, Giunti, et al., 2014; Briceño, Ramos, & Eberhard, 1999; Gaskin, Futermann, & Chapman, 2002; Shelly, 2000a, 2000b). Females express aggression against siblings to maintain single oviposition sites, thus increasing the chances of their eggs developing successfully (Benelli, Daane, et al., 2014). In addition, it has been reported that female–female aggression may play a role also when they search for mates. Indeed, it has been observed that female aggression against other females is virginity-related and declines strongly after mating (Papadopoulou, Carey, Liedo, Muller, & Senturk, 2009). To study winner and loser effects, we used a random selection procedure, whereby focal individuals are randomly allocated to experimental groups and pitted against either a much stronger or weaker opponent, to deliver the winning or losing experience. Since true predictors of contest outcomes (e.g. male body size, female egg load, Goubault & Decuignière, 2012; Kasumovic et al., 2010) are not available for the majority of tephritid flies (Benelli, Daane, et al., 2014), we evaluated whether prior residence enhanced the fighting success in our *C. capitata* strain (experiment

1). To obtain flies that experienced victories or defeats, we exploited the residence effect as a predictor of fighting success in a random selection procedure (Hsu et al., 2006). We expected *C. capitata* winners to be more likely to win again and losers more likely to lose again. On this basis, in experiment 2 we tested medflies that experienced one or two victories against naïve ones, while in experiment 3 we tested medflies defeated one or two times against naïve individuals. Since winner and loser effects in invertebrates are transient (Rillich & Stevenson, 2011), we tested two interfight intervals (5 and 15 min) to evaluate whether the amount of time elapsed from a previous contest was critical to detect experience-induced effects on aggression. To shed light on the role of physical fighting in increasing aggression rates, in experiment 3 we assessed whether winning and losing probabilities were affected solely by the outcome of the previous contests, or whether the fighting experience itself is sufficient to induce the effect. All experiments were conducted on both sexes, allowing us to estimate whether previous experience affected aggressive interactions displayed by males and females differently.

## METHODS

### *Ethical Note*

This research adheres to the guidelines for the treatment of animals in behavioural research and teaching (ASAB/ABS, 2014). All treatments of the experimental animals complied with the laws of the country (Italy) in which the study was performed (D.M. 116192) and the European Union regulations (European Commission, 2007). All experimental procedures also followed the animal care guidelines of the University of Pisa Ethical Committee. No particular permits were needed by the Italian government for experiments involving *C. capitata*. All the experiments were based on behavioural observations. Flies were treated as gently as possible given the constraints of the experimental design. None were injured or killed during the experiments. Before the test phase, having one animal per Plexiglas cup was not considered stressful, since this is not a group-living species. The health of every animal was constantly assessed by checking that they fed and behaved normally. After the test phase, all flies were kept separately from the rest of the mass rearing, and were not reused.

### *Insect Rearing and General Observations*

We reared *C. capitata* as described in Canale and Benelli (2012). This medfly strain has been reared in our laboratory since 1994, starting from an original stock of about 4000 wild flies collected in fruit orchards (Sicily, Italy). Our strain has been periodically renewed by adding wild flies in 1997, 2003, 2007 and 2012 (about 2000 flies per renewal, sex ratio 1:1). The rearing production unit was composed of cylindrical PVC cages, each containing about 2000 flies (sex ratio 1:1). Adults were fed on a dry diet of yeast extract and sucrose mixture, at a ratio of 1:10 (w:w). Eggs were collected every 2 days and placed into plastic bowls (50 × 15 cm and 2 cm high), each containing 500 g of artificial larval food medium. The resulting pupae were maintained under controlled conditions (21 ± 1 °C, 55 ± 5% relative humidity, 16:8 h light:dark) to wait for adult emergence. Newly emerged flies were gently separated and placed singly in clean Plexiglas cups (diameter: 40 mm; length: 7 mm), using a clean glass vial. They were fed the same diet as adults (see above). Water was provided separately on a cotton wick (Benelli, 2014; Benelli et al., 2015).

Experiments were conducted in the laboratory (21 ± 1 °C, 55 ± 5% relative humidity) during May–June 2014 in a room illuminated with fluorescent daylight tubes (16:8 h light:dark, lights on at 0600). Neon tubes (Philips 30 W/33) were used; light intensity around the test arena was ca. 1000 lx, estimated over the

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