Sex differences in fighting-induced hyperaggression in a fly

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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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Keywords

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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 intraspecific 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 and Price, 1973, Parker, 1974, Stevenson and 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 et al., 2010, Yurkovic et al., 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 et al., 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 and Stevenson, 2011, Rutte et al., 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 et al., 2003a, Van Doorn et al., 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 et al., 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 et al., 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 et al., 2014a, Benelli et al., 2015, Benelli et al., 2014b). 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 et al., 2014b, Briceño et al., 1999, Gaskin et al., 2002, Shelly, 2000a, Shelly, 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 (Papadopoulos, 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 and 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, staring 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 300–1100 nm waveband with an LI-1800 spectroradiometer (LI-COR Inc., Lincoln, NE, U.S.A.), equipped with a remote cosine receptor. Directional light cues were avoided by using diffuse laboratory lighting to reduce reflection and phototaxis. Experiments were performed in a Plexiglas test arena (diameter: 150 mm; length: 200 mm). A fly entrance hole (diameter: 10 mm) was made on the top, in the central part of the arena. Both ends of the arena were covered with transparent chiffon fabric (mesh size: 0.05 mm). The arena contained a twig of apricot, *Prunus armeniaca* cultivar ‘Bella d'Italia’, with 10 leaves and two ripe fruits. The twig and the chiffon fabric used at the ends of the arena were changed every 10 replicates. The arena was carefully washed for about 30 s with warm water at 35–40 °C after each replicate, then cleaned using water plus mild soap for about 5 min, then rinsed with hot water for about 30 s and finally rinsed with distilled water at room temperature (Benelli et al., 2015, Carpita et al., 2012).

Virgin flies (age: 12–20 days old; gonad maturation: 4–6 days; Shelly, 2000b) were used in all experiments. For each replicate, flies were replaced by new ones of the same age. Before beginning, each fly was cooled for 3 min at −10 °C, marked with a small dot of nontoxic colour paint (Polycolor, Maimeri, Italy) on the thorax, and weighed. Only flies with a body mass of 0.005–0.007 g for males and 0.006–0.008 g for females were tested. Preliminary observations showed that cooling and colour tagging did not influence the flies' behaviour. Experiments were performed over about 60 days, to account for any daily variability.

All experiments were carried out from 1000 to 1700 hours. In all experiments, the behaviour of medflies was directly recorded by an observer. The interactions in which both contestants immediately abandoned the territory (e.g. a leaf) were discarded; only interactions in which the winning contestant remained on the territory for at least 30 s after the conclusion of the aggressive interaction were considered for data analysis.

Experiment 1: Does Prior Residence Affect Fighting Success?

We quantified the behaviours displayed by *C. capitata* during male–male and female–female aggressive interactions, evaluating whether prior residence increased the probability of winning following contests. In each replicate, we introduced a male or female *C. capitata* into the test arena using a clean glass vial and waited for 20 min, allowing the fly to establish a territory on a leaf or a fruit. Then, we introduced a second fly of the same sex and observed it exploring the arena for 30 min or until an aggressive interaction with the resident occurred. We considered a contest to occur when, during temporary occupation of the same leaf or fruit, either fly approached the other and displayed wing waving, usually followed by escalating aggressive behaviours as reported in Table 1 (Benelli et al., 2015). For each replicate, the behaviours characterizing contests in both sexes of *C. capitata* were noted (see Table 1 for descriptions of behavioural parameters) and we recorded whether the resident or intruder actively attacked the other. At the end of each contest, we noted which fly (resident or intruder) was dislodged from the leaf or fruit (Benelli, 2014). One hundred replicates were carried out, for both male–male and female–female interactions. To avoid pseudoreplication, only the first aggressive interaction was considered during the observation period for each pair of medflies. If no interaction occurred for 30 min, no data were recorded and the replicate was discarded.

Table 1. Escalating level of aggression that characterizes fighting in males and females of the Mediterranean fruit fly (modified from Benelli et al., 2015)

Level	Behaviour	Description
0	Avoidance (both)	Mutual avoidance: nonaggressive interaction
1	Avoidance (one)	Pre-established dominance: one male attacks, the other retreats

Level	Behaviour	Description
2	Wing waving (one)	Attacker faces the opponent and brings both wings forwards perpendicular to the longitudinal axis of its body, while ventral surfaces of wings are turned to face anterior
3	Wing waving (both)	Both males perform wing waving
4	Chasing	Running towards the opponent
5	Fast head rocking	Rapid head twisting movements before pouncing
6	Pouncing	Lunging at the opponent ending with head butting
7	Labellar (one)	The attacker extends mouthparts to touch the opponent
8	Labellar (both)+head pushing	Both flies extend mouthparts and also try push each other away
9	Wing strike	The attacker brings a wing forwards and strikes the opponent
10	Dive	The fly attacks the opponent and quickly retreats
11	Boxing (one)	Attacker raises forelegs, repeatedly and alternately hitting opponent on the head and thorax
12	Boxing (both)	Both flies fight by boxing

Experiment 2: the Winner Effect

To evaluate the effects of winning we staged aggressive interactions between same-sex pairs of male and female *C. capitata*. We used a random selection procedure, as suggested by Hsu et al. (2006) in which focal individuals were randomly allocated to experimental groups and pitted against either a much stronger or weaker opponent, to deliver the winning or loser experience. Common predictors of fighting success, such as size (Garcia et al., 2014; Kasumovic et al., 2010; Lehner et al., 2011), are not applicable to medflies (Benelli, Daane, et al., 2014). To obtain flies that experienced previous victories, we used a random selection method exploiting the residence effect found in experiment 1 as a predictor of fighting success.

Training phase

For both sexes, three categories of flies were tested in this experiment: winners of a previous contest, winners of two previous contests (twofold winners) and naïve flies. To obtain a winner, we used the same experimental apparatus as described in experiment 1. A naïve (i.e. no previous fighting experience) resident fly was first matched against an intruder naïve fly, easily achieving a victory (this was true, for both sexes, in more than 80% of tested flies, Appendix Figs A1 and A2). To obtain a twofold winner, we used the same apparatus described above; a winner was allowed to establish residence again in the arena, then it was newly matched against an intruder naïve fly, easily achieving a victory. All naïve flies had no fighting experience; during the training of winners and twofold winners, their naïve opponents were allowed to establish previous residency on leaves or fruits of apricot for the same amount of time in another experimental arena without conspecifics.

Test phase

We studied the contests occurring between (1) a twofold winner versus a naïve fly, (2) a winner versus a naïve fly and (3) two naïve flies. In each test, two flies (i.e. twofold winner and naïve, winner and naïve or two naïve individuals) were gently transferred and released simultaneously onto the floor of a separate cylindrical arena and observed for 30 min. Both flies usually started to explore the apricot twig. When they came close to each other, they exhibited aggressive behaviour. We recorded a contest when, during occupation of the same leaf or fruit, a fly approached a conspecific and displayed wing-waving motions, usually followed by escalating aggressive behaviours (Table 1).

The interfight interval between consecutive fights was 5 min or 15 min. For each replicate, the following parameters were recorded: (1) the intensity of aggression (i.e. the escalating level of aggression that characterizes fights in medflies scored from 0 to 12, Table 1; Benelli et al., 2015); (2) the duration of the entire contest; (3) the outcome of the contest (i.e. whether the focal individual or the opponent was dislodged from the leaf/fruit at the end of the contest). The number of replicates for each treatment is shown in Table 2.

Table 2. Number of *Ceratitis capitata* flies observed for each experiment

Experiment		**No. of males**		**No. of females**	
1		100		100	
2	IFI (min)	5	15	5	15
	Naïve	100	100	100	100
	Winner	63	63	68	68
	Twofold winner	48	48	62	62
3	IFI (min)	5	15	5	15

Experiment		No. of males		No. of females	
	Naïve	100	100	100	100
	Loser	69	69	64	64
	Twofold loser	54	56	56	55
4	Naïve	60		60	
	WF	23		38	
	Wf	25		24	
	LF	32		32	
	Lf	20		24	

WF = twofold winners with physical combat; Wf = twofold winners without physical combat; LF = twofold losers with physical combat; Lf = twofold losers without physical combat; IFI = interfight interval between contests.

Experiment 3: the Loser Effect

To evaluate the effects of losing we staged contests between same-sex pairs of male and female *C. capitata*, using a modification of the random selection method described above for the winner effect experiment.

Training phase

For both sexes, three categories of flies were tested in this experiment: losers of a previous contest, losers of two previous contests (twofold losers) and naïve flies. To obtain a loser, we used the same apparatus as described in experiment 2. A naïve intruder fly was first matched against a resident naïve fly and was usually defeated (Appendix Figs A1 and A2). To obtain a twofold loser, a loser was newly matched against a resident naïve fly, easily suffering a second defeat. During the training of losers and twofold losers, their naïve opponents were allowed to spend a similar time as intruders in another experimental arena containing leaves or fruits of apricot, without conspecifics.

Test phase

We studied the contests occurring between (1) a twofold loser versus a naïve fly, (2) a loser versus a naïve fly and (3) two naïve flies. In each test, two flies (i.e. twofold loser and naïve, loser and naïve or two naïve individuals) were gently transferred and simultaneously released onto the floor of a separate cylindrical arena and observed for

30 min. The interfight interval between consecutive fights was 5 min or 15 min. For each replicate, the parameters defined in experiment 1 (see above) were recorded. The number of replicates for each treatment is provided in Table 2.

Experiment 4: Does Physical Combat Increase Aggression?

The aim of this experiment was to test whether the winner and loser effects depend solely on experience of physical combat against a contestant (Rillich & Stevenson, 2011). Here we staged aggressive interactions using the methods described in experiments 1–3.

Training phase

For both sexes, five categories of flies were studied in this experiment: (1) flies that won twice in succession with fighting (WF); (2) flies that won twice in succession without fighting (Wf); (3) flies that lost twice in succession with fighting (LF); (4) flies that lost twice in succession without fighting (Lf); (5) naïve flies. Twofold winners were obtained using the random selection procedure described in experiment 2. For WF flies, 'with fighting' means that physical contact occurred during the contest. For Wf flies, 'without fighting' means that the contest reached wing waving as a maximum and did not involve physical contact. Twofold losers were obtained using the random selection procedure described in experiment 3. For LF flies, 'with fighting' means that physical contact occurred during the contest. For Lf flies, 'without fighting' means that the contest reached wing waving as a maximum and did not involve physical contact. Naïve flies had no previous fighting experience; during the training of losers or twofold losers, their naïve opponents were allowed to spend a similar time as intruders in another experimental arena containing leaves or fruits of apricot, without conspecifics.

Test phase

We studied the contests occurring between (1) a WF fly versus a naïve fly, (2) a Wf fly versus a naïve fly, (3) an LF fly versus a naïve fly, (4) an Lf fly versus a naïve fly and (5) two naïve flies. In each test, the two flies were gently transferred and simultaneously released onto the floor of a separate cylindrical arena and observed for 30 min. The interfight interval between consecutive fights was 5 min for all tournaments. Then, after 5 min, flies in each the five treatments described above were tested in the same experimental conditions against naïve flies. For each replicate, the parameters defined in experiments 1 and 2 were recorded. The number of replicates for each treatment is provided in Table 2.

Data Analysis

In experiment 1, differences in fighting success of resident and intruder males and females were analysed by likelihood chi-square tests with Yates' correction (alpha = 0.05).

In experiments 2 and 3, aggression intensity and fighting duration data were analysed by JMP 7 by using a weighted generalized linear model (GLZ, Poisson distribution) with three fixed factors: $y = X\beta + \varepsilon$ where y is the vector of the observations (e.g. aggression intensity), X is the incidence matrix, ß is the vector of fixed effects (i.e. sex, interfight interval and previously experienced fighting outcome) and ε is the vector of the random residual effects (alpha = 0.05). Differences in fighting success were evaluated using the GLZ described above with a binomial distribution (to model win/loss outcomes; $\alpha = 0.05$).

In experiment 4, aggression intensity and fighting duration data were analysed using the GLZ described above (Poisson distribution), with two fixed factors (i.e. sex and previously experienced fighting outcome; alpha = 0.05). Differences in fighting success were evaluated using the GLZ described above with a binomial distribution ($\alpha = 0.05$).

Results

Experiment 1: Does Prior Residence Affect Fighting Success?

In male and female contests, when an intruder landed on a leaf or a fruit occupied by a resident fly, the aggressive interaction was initiated by the resident or the intruder in equal proportions (Appendix Figs A1 and A2). The resident fly was more successful than the intruder (resident male: 83% success versus 17% displacement; $\chi^2_1 = 42.25$, $P < 0.001$; resident female: 81% success versus 19% displacement; $\chi^2_1 = 37.21$, $P < 0.001$). No main differences between the sexes were detected in the escalating aggression sequence displayed during fighting (Table 1; Appendix Figs A1 and A2). Male and female aggressive interactions started with wing waving, escalated to chasing, followed by fast head rocking and pouncing at the opponent. Then, fighters started labellar displays and wing strikes. The most aggressive behaviours were diving and boxing (Table 1).

Experiment 2: the Winner Effect

Intensity of aggression was affected by experience ($\chi^2_2 = 166.933$, $P < 0.001$), sex ($\chi^2_1 = 32.354$, $P < 0.001$), interfight interval ($\chi^2_1 = 5.556$, $P = 0.018$) and the interaction of experience and interfight interval ($\chi^2_2 = 11.130$, $P = 0.004$), while effects of other interactions were not significant. In male and female contests, intensity of aggression was higher in twofold winners than in naïve flies, while performances of twofold winners and winners were comparable (Fig. 1a).

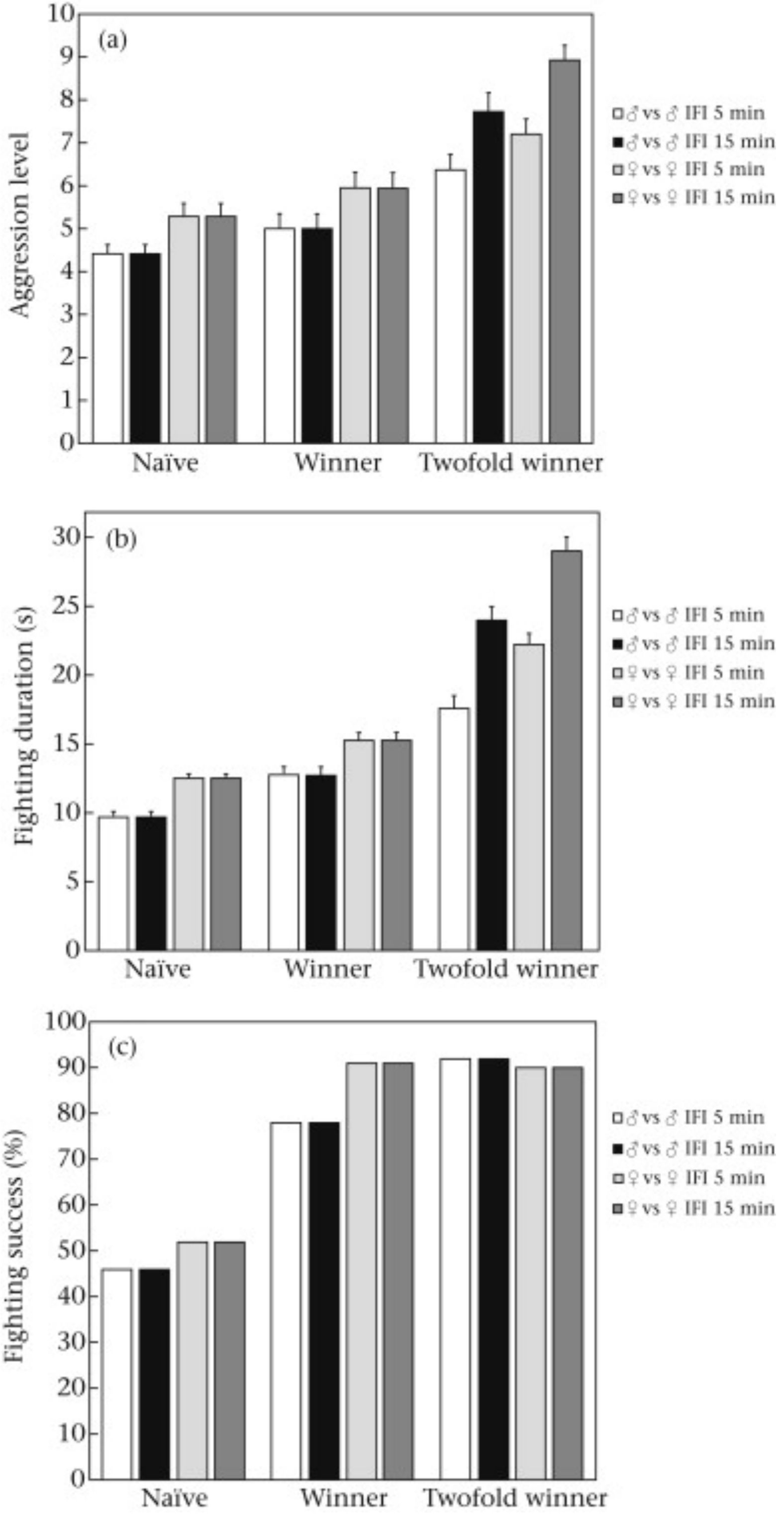

Figure 1. Impact of winning experience on subsequent aggressive interactions. Bar graphs of (a) intensity, (b) duration and (c) success of same-sex contests in Mediterranean fruit flies with different winning experiences. Naïve = fight-inexperienced flies. Winners = winners of one previous encounter. Twofold

winners = winners of two previous encounters. Interfight interval (IFI) was 5 min and 15 min. Vertical lines are SEs.

Fight duration was affected by experience (χ^2_2 = 126.531, *P* < 0.001), sex (χ^2_1 = 148.552, *P* < 0.001), interfight interval (χ^2_1 = 29.102, *P* < 0.001) and the experience*interval interaction (χ^2_2 = 62.421, *P* < 0.001); other interactions were not significant. As a general trend, females had longer aggressive interactions than males. Contest duration was longer in twofold winners than in winners or naïve flies, while there were no duration differences between the latter two at fight intervals of either 5 or 15 min (Fig. 1b).

Fighting success was affected only by experience (χ^2_2 = 216.602, *P* < 0.001), sex (χ^2_1 = 4.289, *P* = 0.038) and the interaction of sex and experience (χ^2_2 = 8.919, *P* = 0.012). It was lower in naïve flies than in winners and twofold winners, regardless of sex and interval. No differences were detected between fighting success of winners and twofold winners (Fig. 1c).

Experiment 3: the Loser Effect

Aggression intensity was affected by experience (χ^2_2 = 158.876, *P* < 0.001), sex (χ^2_1 = 179.984, *P* < 0.001), interfight interval (χ^2_1 = 7.563, *P* < 0.001) and the experience*interval interaction (χ^2_2 = 15.563, *P* < 0.001), while other interactions were not significant. Intensity of aggression was higher in twofold losers than in naïve flies, while performances of twofold losers and losers were comparable. In females, twofold losers showed higher aggression levels after an interfight interval of 15 min than an interval of 5 min (Fig. 2a).

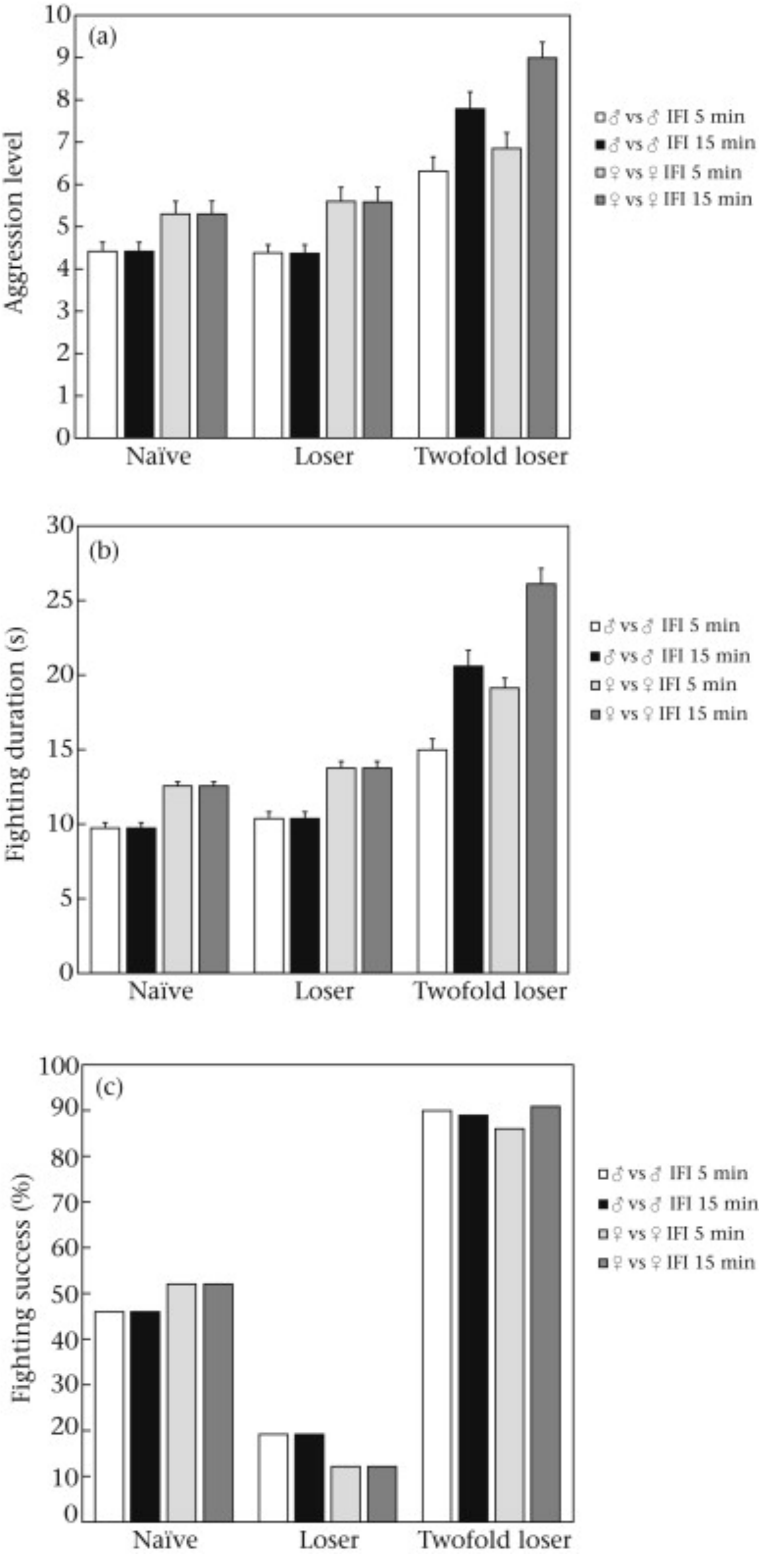

Figure 2. Impact of losing experience on subsequent aggressive interactions. Bar graphs of (a) intensity, (b) duration and (c) success of same-sex contests in Mediterranean fruit flies with different losing experiences. Naïve = fight-inexperienced males. Losers = losers of one previous encounter. Twofold losers = losers of two previous encounters. Interfight interval (IFI) was 5 min and 15 min. Vertical lines are SEs.

Fighting duration was affected by experience ($\chi^2_2 = 790.485$, $P < 0.001$), sex ($\chi^2_1 = 196.956$, $P < 0.001$), interfight interval ($\chi^2_1 = 34.423$, $P < 0.001$) and the experience*interval interaction ($\chi^2_2 = 69.281$, $P < 0.001$); other interactions were not significant. Fighting duration was longer in twofold losers than naïve flies, while duration of contests in naïve flies and losers was comparable. Generally, females fought longer than males. Contests were longer with the 15 min interfight interval only in twofold losers (Fig. 2b).

Fighting success was affected only by experience ($\chi^2_2 = 493.241$, $P < 0.001$). It was lower in naïve flies than twofold losers, while losers achieved less success than naïve flies (Fig. 2c).

Experiment 4: Does Physical Combat Increase Aggression?

Intensity of aggression was affected by experience ($\chi^2_4 = 114.211$, $P < 0.001$), while effects of sex and the interaction of sex and experience were not significant. Intensity of aggression was higher in flies that experienced physical combat than those that had not, and this was true for winners and losers, with no differences due to sex. Aggression intensity in naïve flies was similar to Wf and Lf, but lower than in WF and LF (Fig. 3a).

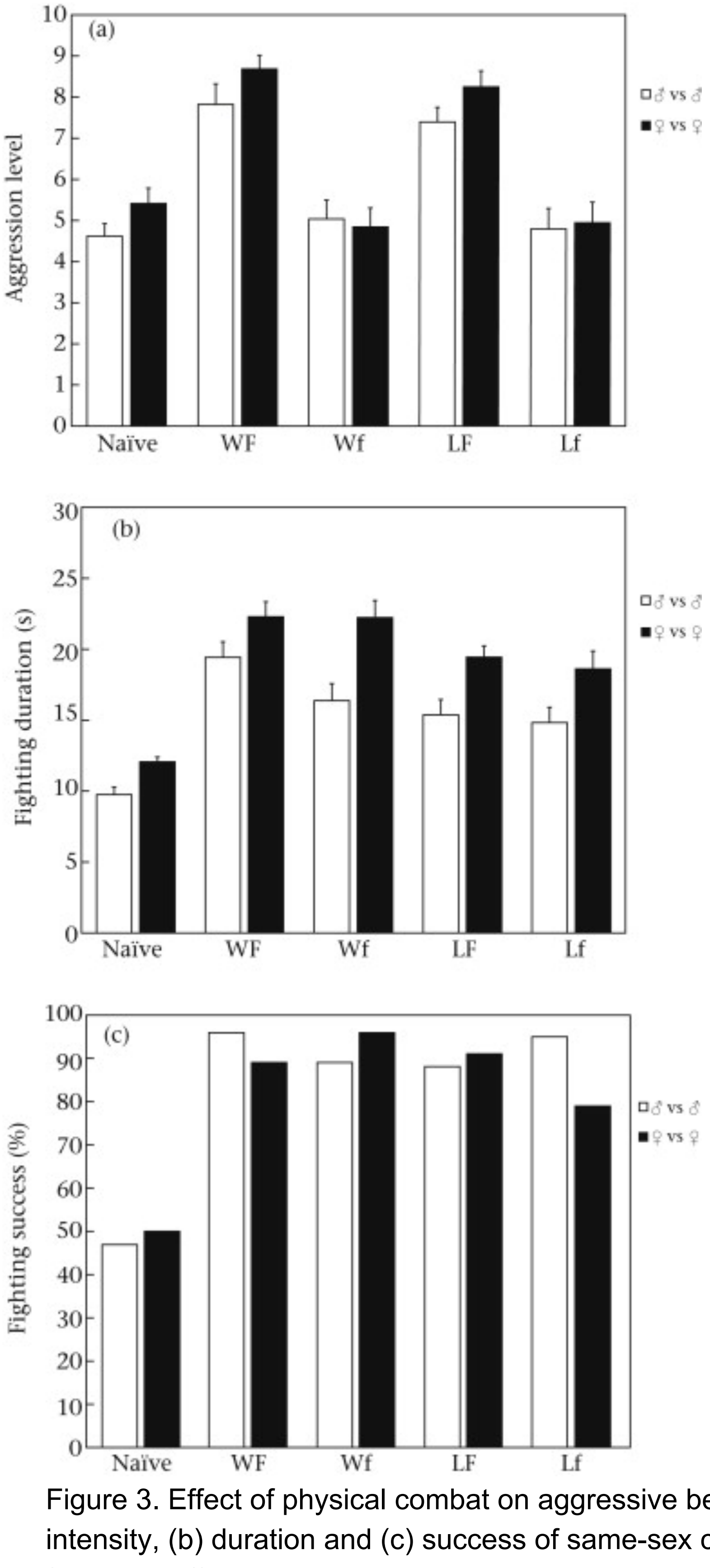

Figure 3. Effect of physical combat on aggressive behaviour. Bar graphs of (a) intensity, (b) duration and (c) success of same-sex contests in Mediterranean fruit flies with different winning and losing experiences. Naïve = fight-inexperienced flies. WF = winners with physical combat. Wf = winners without physical combat. LF = losers with physical combat. Lf = losers without physical combat. Interfight interval (IFI) was 5 min and 15 min. Vertical lines are SEs.

Fighting duration was affected by both experience ($\chi^2_4 = 330.878$, $P < 0.001$) and sex ($\chi^2_1 = 64.302$, $P < 0.001$), while the interaction of sex and experience was not significant. For both males and females, fighting duration was lower in naïve flies than in WF, Wf, LF and Lf. Duration of contests was comparable among WF, Wf, LF and Lf, and was longer in female–female aggressive interactions than those involving males (Fig. 3b). Fighting success was affected by both experience ($\chi^2_4 = 169.516$, $P < 0.001$) and the interaction of sex and experience ($\chi^2_4 = 20.241$, $P < 0.001$), while the effect of sex itself was not significant. Fighting success was lower in naïve flies than in other treatments. No differences in fighting success were detected among WF, Wf, LF and Lf flies (Fig. 3c).

Discussion

Does Prior Residence Affect Fighting Success?

The ownership advantage in contests occurs throughout the animal kingdom (Kemp & Wiklund, 2004). In the present study, the effect of prior residence on fighting success was observed in both sexes (experiment 1), while we found no differences in the escalating aggression sequence displayed in male–male versus female–female contests. Ramos (1991) also found that prior residence increases fighting success in *C. capitata*, at variance with previous studies conducted on other strains (Shelly, 2000a, Whittier et al., 1994), and this may be due to behavioural modifications induced by mass rearing (see Benelli et al., 2014a, Benelli et al., 2014b for recent reviews). More generally, prior residency is known to affect fighting success in several other true Tephritidae species (Benelli, 2014, Benelli, 2015a, Benelli et al., 2014a, Benelli et al., 2014b), although no studies have been carried out to shed light on physiological and ecological mechanisms underlying the residence effect in these flies.

Winner and Loser Effects

In fighting *C. capitata* flies, we observed both a winner and a loser effect after one contest experience. However, while the winner effect remained after two consecutive victories, the loser effect disappeared and reversed after two defeats. Results from experiment 2 showed that winners of two previous encounters displayed a higher intensity of aggression, fought for longer and achieved greater fighting success (i.e. hyperaggressive performances, hereafter) in subsequent contests than naïve males. These findings are consistent with those of previous studies on several invertebrate species (Hsu et al., 2006; Stevenson & Schildberger, 2013), in which aggression intensity, fighting duration and/or probability of winning were higher in previous contest winners than in naïve contestants (i.e. cricket, Adamo & Hoy, 1995; crayfish, Bergman et al., 2003). The winner effect is recognized in a number of vertebrates, including fishes, birds and mammals (see Rutte et al., 2006 and Hsu et al., 2006 for reviews).

Experiment 3 showed reduced fighting success in males and females that experienced a single defeat, while losers of two previous encounters displayed a higher intensity of aggression, fought longer and achieved greater fighting success in subsequent contests than naïve males. This effect lasted at least 15 min. Similar effects have rarely been observed, in either invertebrates (Moore, Ciccone, & Breed, 1988) or vertebrates (Kim and Zuk, 2000, Stamps and Krishnan, 1998). Previous studies in other invertebrate species mostly report decreased intensity of aggression and/or shorter fighting duration in individuals that experienced a defeat in previous contests, compared to naïve individuals or winners (e.g. crickets and *Drosophila* flies; Adamo and Hoy, 1995, Hsu et al., 2006, Iwasaki et al., 2006, Khazraie and Campan, 1999, Yurkovic et al., 2010). Similar findings have been reported for vertebrates, such as fish, reptiles, birds and mammals (Hsu et al., 2006, Lan and Hsu, 2011). In *C. capitata*, the higher aggressive level and fighting success observed in twofold losers could be because after two consecutive defeats the flies placed a much higher value on the defended resource. We hypothesize that they would be willing to pay higher costs to get access to the resource during further contests. Further studies are needed to quantify the fighting performances of naïve and winner/loser males at the individual level. Why medflies show such a divergent response to prior social experience compared to other invertebrate and vertebrate species is still unclear. Additional research is required to understand whether previous fighting experience can modify the contestants' subjective value of a given resource (i.e. male courtship territory or female oviposition site) in flies.

Effect of Aggression Experience on Males and Females

A comparative approach between the sexes when studying aggression is hard to find, and mostly concerns behavioural lateralization of aggressive displays (see Ariyomo and Watt, 2013, Benelli et al., 2015, Bianki and Filippova, 2001, Reddon and Hurd, 2008). In experiments 2, 3 and 4, experiencing previous aggression led to some behavioural differences between the sexes in *C. capitata*. As a general trend, females fought longer than males. Aggressive interactions are of pivotal importance for males and females in the medfly, as well as in a number of other tephritids relying on both male dominance polygyny and resource defence polygyny as mating systems (Benelli, 2015a). However, the amplified effect of experience on consecutive contests we found in females relative to males (e.g. longer fighting duration) may be connected with the fact that female flies rely on aggression for more than one purpose in their life, while this has not been ascertained for males. Indeed, it has been reported that *C. capitata* females express aggression against siblings when competing for mates (Papadopoulos et al., 2009) and for oviposition sites (Benelli, Daane, et al., 2014). Conversely, calling males fight only when searching for mates, to defend territories in leks (Benelli, 2015a, Shelly, 2000a, Shelly, 2000b).

Does Physical Combat Increase Aggression?

Experiment 4 showed that longer fighting duration and higher success of winning and losing males relative to naïve ones were mainly due to experience in a previous contest, while the outcome and the experience of physical combat did not affect subsequent aggressiveness level any more than an aggressive interaction without physical contact. In contrast, we found that aggression intensity was increased only in winning or losing experiences that had physical contact during contests; in Wf and Lf treatments the aggression level was similar to that of naïve individuals. Concerning fighting duration, in *C. capitata* the experience of winning without physical combat led to a behavioural effect similar to that shown in crickets; in both taxa this experience alone is sufficient to prolong fight duration in subsequent male–male contests (Rillich and Stevenson 2011). In some vertebrates (e.g. East African cichlids), it has been proved that fighting experience itself (coupled with an androgen response) increases the subsequent likelihood of winning, even in the absence of a prior winning experience (Dijkstra, Schaafsma, Hofmann, & Groothuis, 2012). We showed that experiencing two consecutive defeats without physical contact induced a similar effect in both sexes of *C. capitata* (Lf), which achieved higher fighting success in subsequent combat to a level comparable to flies that had experienced two consecutive defeats with physical interaction (LF). Fighting success in LF and Lf flies was also comparable to that of WF and Wf individuals, demonstrating that experiencing either consecutive victories or defeats, with or without physical contests, led to hyperaggression in this fly and increased fighting success in subsequent contests.

Conclusions

Our research highlighted that male and female *C. capitata* experiencing a single defeat suffered lower fighting success in the following contest, while flies that experienced two previous victories or defeats had higher aggression rates and more wins in further combats. This effect was due to merely experiencing a contest, while the actual outcomes of previous fights did not affect the aggressiveness level. To the best of our knowledge, this is the first evidence that consecutive defeats can reverse the loser effect, leading to higher fighting success. Although extensive research has been conducted to understand the role of social experience in affecting the outcomes of aggression, the ultimate and proximate causes for the existence of the winner and loser effects are unknown (Hsu et al., 2006, Rutte et al., 2006, Stevenson and Schildberger, 2013). Rutte et al. (2006) formulated two adaptive hypotheses to explain these effects, namely the 'social-cue hypothesis' (i.e. victory and defeat leave traces that affect the decisions of subsequent opponents) and the 'self-assessment hypothesis' (i.e. winners and losers gain information about their own relative fighting ability in the population). In this latter scenario, it appears conceivable that *C. capitata* males and females are able to gain information from previous fighting experience to refine their future performances, regardless of previous outcomes (see also Fawcett & Johnstone, 2010).

Can this knowledge help to improve pest management strategies against fruit fly pests? To our mind there are some connections. The sterile insect technique is one of the most reliable nondisruptive control tools against tephritids. However, sterile males have lower mating competitiveness than wild ones, owing to mass-rearing procedures as well as to damage/stress occurring during sterilization, shipping and release (Hendrichs, Robinson, Cayol, & Enkerlin, 2002). Our findings outline the possibility of inducing hyperaggression in sterile males by manipulating the flies' density in cages, thus increasing the number of contests, and providing small potted host plants to create a semifield environment during the prerelease phase. This may help sterile males to refine their fighting skills and achieve better subsequent contest outcomes against wild ones (Benelli, 2015a, Benelli, 2015b).

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Appendix

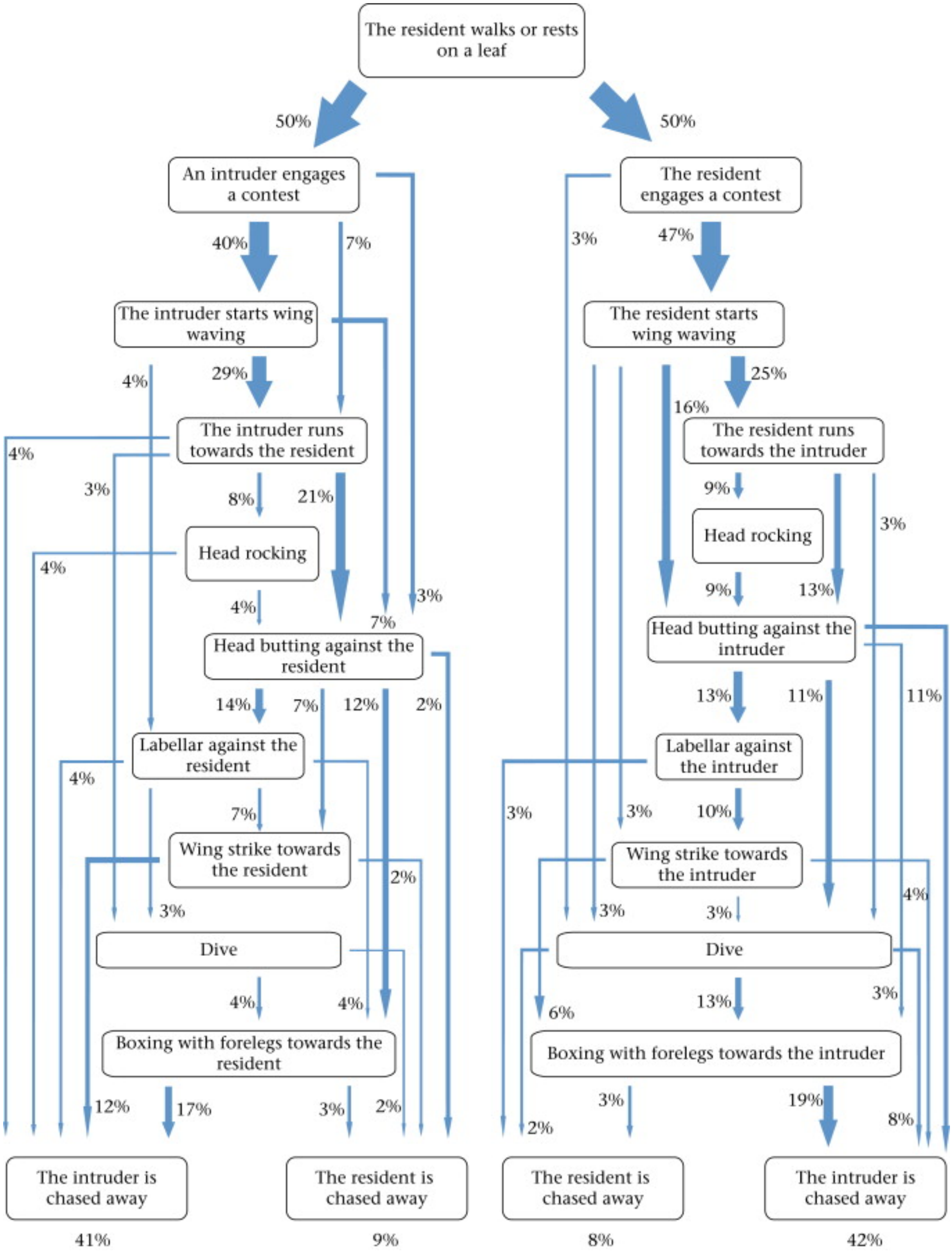
The resident walks or rests on a leaf
50%
50%
An intruder engages a contest
The resident engages a contest
40%
7%
3%
47%
The intruder starts wing waving
The resident starts wing waving
4%
29%
25%
16%
The intruder runs towards the resident
The resident runs towards the intruder
4%
3%
8%
21%
9%
3%
Head rocking
Head rocking
4%
4%
3%
7%
9%
13%
Head butting against the resident
Head butting against the intruder
14%
7%
12%
2%
13%
11%
11%
Labellar against the resident
Labellar against the intruder
4%
7%
3%
3%
10%
Wing strike towards the resident
Wing strike towards the intruder
2%
3%
3%
3%
4%
Dive
Dive
4%
4%
6%
13%
3%
Boxing with forelegs towards the resident
Boxing with forelegs towards the intruder
12%
17%
3%
2%
2%
3%
19%
8%
The intruder is chased away
The resident is chased away
The resident is chased away
The intruder is chased away
41%
9%
8%
42%

Figure A1. Effect of previous residence on male–male contests of Mediterranean fruit flies. The thickness of the arrows indicates the percentage of individuals displaying different behavioural phases; 100 males were observed.

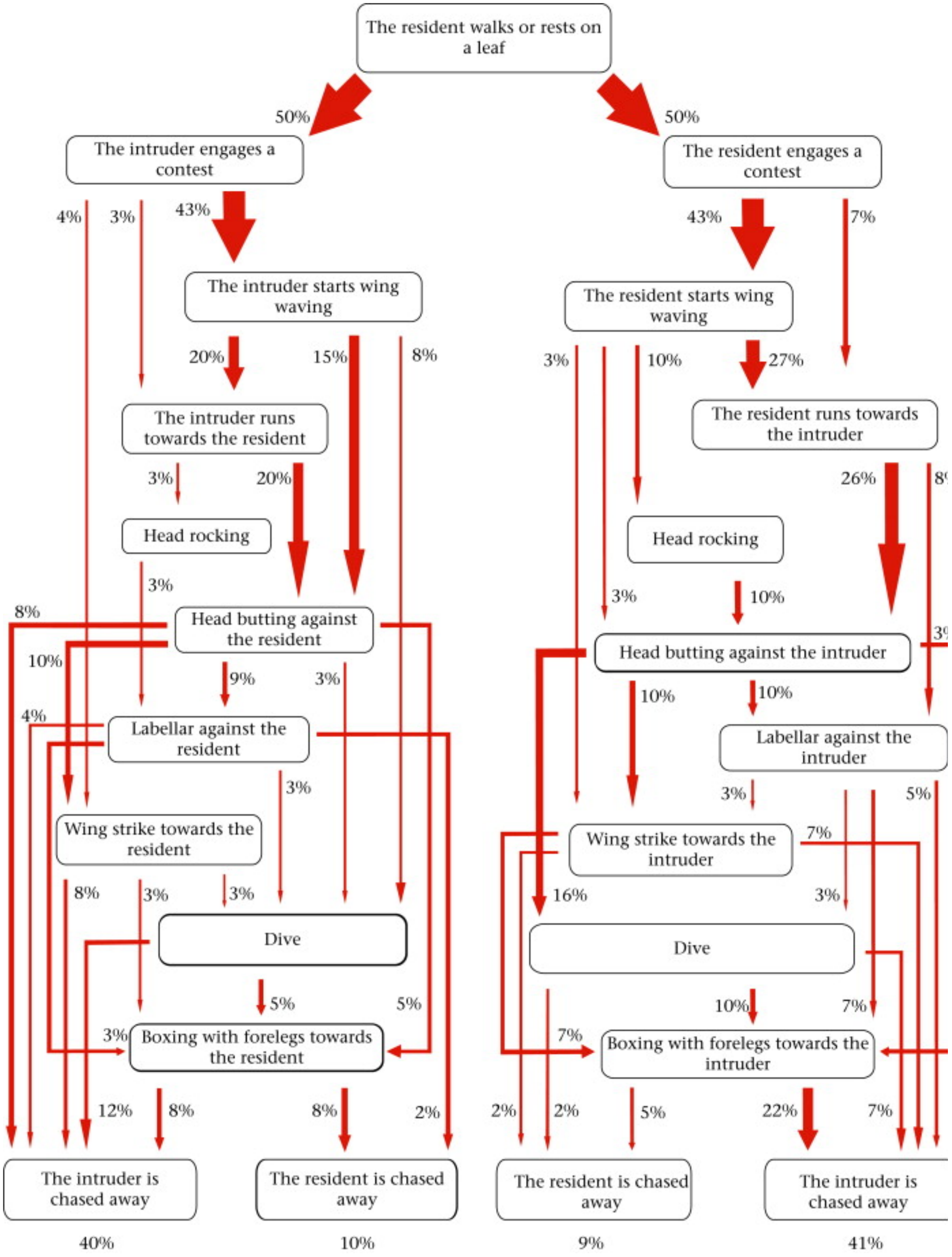
The resident walks or rests on a leaf
50%
50%
The intruder engages a contest
The resident engages a contest
4%
3%
43%
43%
7%
The intruder starts wing waving
The resident starts wing waving
20%
15%
8%
3%
10%
27%
The intruder runs towards the resident
The resident runs towards the intruder
3%
20%
26%
8
Head rocking
Head rocking
3%
3%
10%
8%
Head butting against the resident
Head butting against the intruder
3
10%
9%
3%
10%
10%
4%
Labellar against the resident
Labellar against the intruder
3%
3%
5%
Wing strike towards the resident
Wing strike towards the intruder
7%
8%
3%
3%
16%
3%
Dive
Dive
5%
5%
10%
7%
3%
7%
Boxing with forelegs towards the resident
Boxing with forelegs towards the intruder
12%
8%
8%
2%
2%
2%
5%
22%
7%
The intruder is chased away
The resident is chased away
The resident is chased away
The intruder is chased away
40%
10%
9%
41%

Figure A2. Effect of previous residence on female–female contests of Mediterranean fruit flies. The thickness of the arrows indicates the percentage of individuals displaying different behavioural phases; 100 females were observed.

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