



Population-level lateralized aggressive and courtship displays make better fighters not lovers: evidence from a fly



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ABSTRACT

Lateralization (i.e., left–right asymmetries in the brain and behavior) of aggressive and courtship displays has been examined in many vertebrate species, while evidence for invertebrates is limited. We investigated lateralization of aggressive and courtship displays in a lekking tephritid species, the olive fruit fly, *Bactrocera oleae*. Results showed a left-biased population-level lateralization of aggressive displays, with no differences between the sexes. In both male–male and female–female contests, aggressive behaviors performed with left body parts led to greater fighting success than those performed with right body parts, while no differences in fighting duration were found. Olive fruit fly males also showed a side bias during courtship and mating behavior, courting females more frequently from the left than the right, front, or back sides. No differences were detected between courtship duration and copulation duration following the different male directional approaches. Male mating success was comparable whether females were approached from the left, right, front, or back side. Lateralized aggressive and courtship displays at the population-level may be connected to the prolonged social interactions occurring among lekking flies. Further research is needed on possible benefits arising from lateralization of courtship traits in insects.

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1. Introduction

Lateralization (i.e., left–right asymmetries in the brain and behavior) occurs in all vertebrate classes (Bisazza et al., 1998a; Vallortigara, 2000; Vallortigara et al., 1999, 2011; Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; MacNeillage et al., 2009; Rogers et al., 2013a). Recently, evidence begins to emerge in invertebrates, pointing out that lateralization of the nervous system may be a feature of simpler brains as well (Rogers and Vallortigara, 2008; Anfora et al., 2009; Frasnelli et al., 2012). Interestingly, lateralized animals have been found to outperform non-lateralized ones in many circumstances, supporting the hypothesis that lateralization contributes to biological fitness (Vallortigara and Rogers, 2005). Ghirlanda and Vallortigara (2004) reported that alignment of the direction of behavioral asymmetries in a population can arise as an evolutionarily stable strategy when individual asymmetrical organisms must coordinate their behavior with that of other asymmetrical organisms. This supports the hypothesis that lateralization at the population-level is more likely to evolve in social species, while lateralization at an individual-level is more likely to

evolve in solitary species (Vallortigara and Rogers, 2005; Ghirlanda et al., 2009).

Lateralization of aggressive behavior has been examined in many animal species, with special reference to vertebrates, and individual- and population-level behavioral asymmetries have been reported (Vallortigara and Rogers, 2005). Good examples are found in cichlids (Reddon and Hurd, 2008; Arnott et al., 2011), zebra fishes (Ariyomo and Watt, 2013), Siamese fighting fishes (Cantalupo et al., 1996; Takeuchi et al., 2010) and other teleosts (Bisazza and de Santi, 2003), lizards (Hews and Worthington, 2001; Hews et al., 2004), fallow deer (Jennings, 2012, 2014), and horses (Austin and Rogers, 2012, 2014). Conversely, lateralization of aggressive behavior has been investigated in few invertebrates (Frasnelli et al., 2012), mainly spiders (Ades and Ramires, 2002), fiddler crabs (Backwell et al., 2007), Mediterranean fruit flies (Benelli et al., 2015a), mosquitoes (Benelli et al., 2015b), blowflies (Romano et al., 2015), and honeybees (Rogers et al., 2013b). Also lateralization of courtship and mating behavior has rarely been investigated in invertebrates (Kamimura, 2006; Davinson et al., 2009), though some examples are available for vertebrates, including fish (e.g., Workman and Andrew, 1986; Cantalupo et al., 1996; Amcoff et al., 2009), amphibians (e.g., Green, 1977; Marzona and Giacomini, 2002, 2004), birds (e.g., Rogers et al., 1985; Ventolini et al., 2005; Templeton et al., 2014), and mammals (Bisazza et al., 1998a; Vallortigara and Rogers, 2005; Rogers et al., 2013a).

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In this research, we investigated asymmetries of aggressive and courtship behavior in the olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae), a worldwide pest of olive groves (Benelli et al., 2014a). *B. oleae* is a lekking species, forming aggregations in which males fight to defend a small territory (usually an olive leaf) where they court females and mate. Females display aggressive behavior to maintain single oviposition sites and reduce larval competition for food (Benelli et al., 2014a,b; Benelli, 2015). In both sexes of *B. oleae*, aggressive interactions are highly ritualized and composed of various displays, including wing waving, chasing, pouncing, and boxing (Benelli, 2014). Boxing acts represent the culminating event of aggressive bouts, and can be performed using left or right prothoracic legs, allowing the comparison of sex differences in lateralization (Bianki and Filippova, 2001; Reddon and Hurd, 2008, 2009; Benelli et al., 2015a). On this basis, in Experiment 1 we investigated if males and females of the olive fruit fly showed population-level lateralization of boxing displays and if this led to enhanced fighting success. After having established a territory, males perform courtship displays that include sex-specific olfactory cues and wing vibrations, then attempt copulation with females (Benelli et al., 2012; Canale et al., 2013). In Experiment 2 we evaluated if olive fruit fly males showed any side bias in courtship approaches toward females, and if this had any effect on male courtship duration, mating success, or copulation duration.

2. Materials and methods

2.1. Ethics statement

This research adheres to the guidelines for the treatment of animals in behavioral research and teaching (ASAB/ABS, 2014). All treatments of the experimental animals complied with the laws of the country (Italy) in which it 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 Italian government for experiments involving *B. oleae*. All the experiments were based on behavioral observations. Flies were treated as gently as possible given the constraints of the experimental design. None of them has been injured or killed during the experiments. The health of every animal was constantly assessed by checking that they fed and behaved normally. After the testing phase, all flies were kept separately from the rest of the mass-rearing, and were not reused.

2.2. Olive fruit fly rearing

Olive fruit flies used in this study were obtained from field-derived pupae (collected in a Tuscan olive-mill in Pisa, Italy) during October and November 2014. Pupae were maintained in laboratory conditions ($24 \pm 1^\circ\text{C}$, $45 \pm 5\%$ R.H. and natural photoperiod) to wait for adult emergence. To obtain coeval virgin specimens, emergent flies were sexed, stored singly in clean glass vials (diameter 3 cm, length 7 cm) and fed on a dry diet (yeast and sugar at ratio 1:10) and water until the testing phase.

2.3. General observations

All experiments were carried out in laboratory conditions ($24 \pm 1^\circ\text{C}$, $45 \pm 5\%$ RH) in a room illuminated with overhead fluorescent daylight tubes (Philips 30W/33) [16:8 (L:D) photoperiod, lights on at 06:00]. The light intensity in close proximity of the testing arena was approximately 1000 lux, estimated over the 300–1100 nm waveband using a LI-1800 spectroradiometer (LI-COR Inc., Lincoln, NE, USA), equipped with a remote cosine receptor. Directional light cues were avoided by using diffused laboratory

lighting to reduce possible reflection and phototaxis. No differences in spectroradiometer measurements conducted in different points of the arena were found. Environmental cues (e.g., the position of the observer) were prevented by shielding the sidewalls of the testing arena with screens of white filter paper (42 ashless, Whatman Limited, Maidstone, Kent, United Kingdom). All experiments were carried out from 15:00–18:00 h. Virgin sexually mature males and females (10–15 days old) were used in all observations (Benelli et al., 2012).

Experiments were conducted from November to December 2014, using the Plexiglas testing arena (diameter: 400 mm; length: 250 mm) described in Benelli (2014). An entrance hole (diameter: 50 mm) was made on the top, in the central part of the arena. Both ends of the arena were covered with transparent chiffon fabric (diameter of openings: 0.05 mm). The arena contained a twig of olive, *Olea europea* L. cultivar “Leccino”, with about ten leaves and four ripe fruits. The twig and the chiffon fabrics used at the ends of the arena were changed at each replicate. After each replicate, the arena was carefully washed for 30 s with water at $35\text{--}40^\circ\text{C}$, cleaned using water plus mild soap for about 5 min, rinsed with hot water for about 30 s and finally rinsed with distilled water at room temperature (Benelli et al., 2015a).

2.4. Experiment 1: lateralization of aggressive displays

Here we investigated if males and females of the olive fruit fly showed population-level lateralization of boxing displays and if this led to enhanced fighting success. For each sex, two flies were transferred to the cylindrical arena using clean glass vials, released on opposite ends of the olive twig, and observed for 40 min. Flies usually started to explore the olive twig and when they came in close proximity to one another they exhibited aggressive behavior (Benelli et al., 2015a). We recorded an “aggression” when a fly approached a conspecific (distance: less than 20 mm) and performed the escalating aggressive displays described in Benelli (2014). If aggression escalated to boxing (i.e., the attacker raises a foreleg, hitting the opponent on the head and/or thorax), both in male–male and female–female contests, we recorded: (i) which foreleg was used to box against the opponent, (ii) duration of the contest, (iii) number of boxing acts performed with the foreleg per fighting event, and (iv) outcome of the fight (i.e., which male was displaced from the twig at the end of the contest). For each sex, 100 *B. oleae* fighting pairs escalating to boxing during contests were tested. For each observation period, only the first contest was recorded. No repeated testing of individuals was carried out. After a boxing event, the contest usually terminated, with the immediate displacement out of the territory by one of the two flies.

2.5. Experiment 2: lateralization of courtship displays

Here, we evaluated if the olive fruit fly males showed a left- or right-side bias during courtship approaches toward females, and if bias had any effect on male copula duration and mating success. A *B. oleae* male was transferred to the cylindrical arena described in Experiment 1 using a glass vial, then observed during exploration of the olive twig; when the male established a territory and stationed on an olive leaf for more than 3 min, we released a female on the opposite end of the arena, and both flies were observed for 60 min. When the male observed the female, he moved toward her and started courtship wing vibration, then attempted copulation (Benelli et al., 2012).

For each male courting a female, we recorded: (i) the side of the female approached by the male (i.e., left, right, front, or back side, Fig. 1), (ii) duration of the male courtship (i.e., wing vibration plus directional walking toward the female), (iii) male mating success (i.e., if successful intromission of the aedeagus occurred and

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