Behavioural Processes 121 (2015) 33–36

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Target-invariant aggressive display in a tephritid fly

Samuel Aguilar-Argüello [1], Francisco Díaz-Fleischer, Dinesh Rao *

INBIOTECA, Universidad Veracruzana, Av. Culturas Veracruzanas No.101, Col. E. Zapata, CP 91090 Xalapa, Veracruz, Mexico

ARTICLE INFO

Article history:
Received 20 May 2015
Received in revised form
10 September 2015
Accepted 10 October 2015
Available online 23 October 2015

Keywords:
Aggression
Jumping spiders
Salticidae
Supination
Tephritidae

ABSTRACT

Fruit flies of the family Tephritidae (Diptera) use specialized wing displays in aggressive encounters with conspecifics and predators. These displays, called supination displays, have been thought to deter attacks from one of their main predators, spiders of the family Salticidae. However, there is no information whether the display is qualitatively or quantitatively different when the target is a conspecific or a predator. In this study, we sought to determine whether flies vary their displays depending on the display target. Using the Mexican fruit fly *Anastrepha ludens*, we compared the characteristics of the display that male and female flies use against conspecifics and spiders. Flies did not distinguish between spiders and conspecifics in terms of display rates and bout duration. In general, flies are more likely to retreat faster from spiders after performing a display. We suggest that supination is a generalized aggressive behavior that is independent of the target.

1. Introduction

Fruit flies of the family Tephritidae (Diptera) use their wings during several behaviors such as courting, mating and aggression (Benelli, 2015). The family is very diverse with more than 4000 species found worldwide (van Houdt et al., 2010; Benelli, 2015). A majority of the flies in this family have some sort of markings on the wings; they can be banded, stellate or shouldered (Sivinski and Pereira, 2005).

Flies exhibit different forms of wing display namely lofting, enantion, hamation, arching and supination (Headrick and Goeden, 1994). These displays are usually context specific. Supination, a display commonly used in aggressive encounters, is defined as when a wing is brought forward "perpendicular to the long axis of the body while the ventral surface of the wing turned to face anterior such that the costal margin of the wing is dorsal" (Headrick and Goeden, 1994). Supination can be asynchronous or synchronous, and has been recorded in a wide variety of species. Both males and females perform this display. Although there are several flies which show 'boxing' and 'ramming' behaviors (e.g., in the tephritoid superfamily Richardiidae (Becerril-Morales and Macías-Ordóñez, 2009)), especially in the context of male–male contests, tephritid flies are known to use the wing itself to strike their opponent (Briceno et al., 1999; Benelli, 2015).

Despite the interest in fly displays in terms of courtship and mating strategies (for reviews see Cayol, 2000; Benelli et al., 2014a), aggressive displays have not been afforded a similar level of attention (Briceno et al., 1999; Benelli, 2015). However, a recent study by Benelli et al. (2014b) showed that in *Ceratitis capitata*, male and female flies were more likely to win contests when they used the left wing strike compared to the right one suggesting that there is lateralization of aggressive displays. Since tephritid flies are a major pest species, studies have generally focused on applied behavior rather than basic biology. For example, till date there is no comprehensive study of variation in displays across species even though tephritid flies account for some of the most diverse set of displays seen in nature.

Many tephritid species have been shown to use aggressive wing displays to deter one of their main predators, i.e., spiders of the family Salticidae (Greene et al., 1987; Hasson, 1995; Mather and Roitberg, 1987; Rao and Díaz-Fleischer, 2012). The wing bands are thought to resemble the leg patterns of salticids, and the combination of the appearance and the display is thought to deter the spiders from attacking. However there still remain unresolved questions about the predator mimicry hypothesis, given that salticids are deterred even by non-mimicking flies (Hasson, 1995; Rao and Díaz-Fleischer, 2012). Furthermore, in a study comparing the efficacy of supination against different predators, salticids were deterred by the display but mantids, non-salticid spiders, assassin bugs and lizards were not deterred (Greene et al., 1987).

* Corresponding author.
E-mail address: dinrao@gmail.com (D. Rao).
[1] Current address: Instituto de Ecología, A.C, Apartado Postal 63, CP, Xalapa, Veracruz 91000, Mexico.

http://dx.doi.org/10.1016/j.beproc.2015.10.006
0376-6357/

Males and female flies can use supination for different reasons. In lekking species such as in the genera *Anastrepha*, *Ceratitis* and *Bactrocera*, males may display to conspecifics in order to defend their territory while they await females (Benelli, 2015). Wing displays are often accompanied by aggressive behaviors such as chasing, head-butting and boxing (Benelli, 2015). Females may use these displays to defend oviposition sites on fruits (Benelli, 2015). The proximate trigger for supination is the movement of the opponent and it does not depend on the identity of the opponent (Hasson, 1995; Aguilar-Argüello et al., 2015).

In this study we focused on supination displays in *Anastrepha ludens* (Diptera: Tephritidae). *A. ludens* is a major pest species and has been extensively studied in the context of control. Many behavioral aspects of *A. ludens* are governed by wing displays including mating and aggression (Aluja et al., 2000).

In particular, we sought to determine if male and female flies can distinguish between their conspecifics and a salticid predator and alter their aggressive displays accordingly. We analyzed the frequency of flies displaying to other flies (male and female) and spiders. We further evaluated if the type of display was similar across the treatments and recorded the outcome of such displays.

2. Methods

2.1. Study species

A. ludens flies were obtained from the MoscaFrut plant in Metapa de Dominguez, Chiapas. Flies were acquired as pupae and were allowed to emerge in wooden cages (30 × 30 × 30 cm) covered in mesh cloth within the laboratory. Flies were fed yeast hydrolysate and sugar (proportion 3:1) ad libitum. *Phidippus audax* (Araneae: Salticidae) is distributed all across North America (Edwards, 2004) and is frequently found in citrus orchards, where it is likely to encounter tephritid fruit flies. Spiders were collected from an abandoned maize plantation on the outskirts of Xalapa, Veracruz, Mexico. They were brought to the laboratory of the Inbioteca campus of the Universidad Veracruzana in Xalapa and housed in small plastic containers. Spiders were fed grasshoppers weekly and watered every three days.

2.2. Experimental design

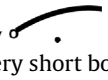
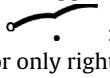
All experiments were carried out in the laboratory under natural light conditions from 10 am to 4 pm. We did not control for temperature or humidity within the laboratory. Flies were chosen randomly from a holding cage for each experiment and each fly was used only once. In all experiments, flies were introduced into the test arena (a petri dish 14 cm diameter, 3 cm tall with an opaque partition in the middle) first and allowed to acclimatise for 1 min. The partition was subsequently removed and trials proceeded for 3 min. In case of treatments with spiders, trials continued for 3 min or till the fly was captured. Only the first bouts were used for the analysis. We considered the start of the bout when the flies faced the opponent and started performing supination display, and the bout ended with the cessation of the display (following Rao and Díaz-Fleischer, 2012). All experiments were recorded with a Sony HDR-XR260 video camera from above.

2.3. Data analysis

All data analysis were done with the statistical software package R ver 2.15.2 (R Core Team, 2014)

To compare bout duration among treatments and fly sex, we performed a two-way ANOVA, with fly sex the first factor with two levels: female and male; and opponent as the second factor, with three levels: female flies, male flies and spiders. Bout duration was log transformed to fit the normality assumptions of ANOVA. We evaluated the interaction between both factors. For display rates (number of displays per bout), we used a GLM with a normal distribution and an identity link function and fly sex and opponent (male flies, female flies, spiders) as the factors. One outlier was removed from the analysis.

We categorized the types of displays and compared the frequencies of each type among display targets with a Generalized Linear Model with binomial distribution with a logit link function. Male and female flies were analysed separately. The different display types are described below with schematic representations. In these representations, the fly display starts at the open circle, and is directed towards the display target (shown as a filled circle). For a detailed representation of display characteristics, see Rao and Díaz-Fleischer (2012).

1. Truncated Display  : a couple of displays or even one display, being a very short bout;
2. Lateral 'a'  : when displaying, the fly gets closer;
3. Lateral 'b'  : a series of lateral movements but at the same distance from opponent;
4. Lateral 'c'  : a series of displays in just one direction, only left or only right, drawing consecutive waves;
5. Frontal  : like Lateral 'a' but the lateral movements are very short and there is a tendency to approach the opponent.

For the outcome after display, we obtained the frequencies of each behavior after displaying and compared them among treatments separately. Male and female flies were analyzed separately. The three possible outcomes were: fly away, walk away and stay. We used a Generalized Linear Model (GLM) with the binomial distribution and a logit link function.

3. Results

3.1. Display characteristics

There was no significant effect of the treatments (fly sex or display target) on the display rates (Whole Model: GLM; Normal Distribution, Identity link, df = 5, $X^2 = 5.56$, $p = 0.35$). Display rates were not significantly different among the different display targets (GLM; Normal Distribution, Identity link, df = 2, $X^2 = 3.4$, $p = 0.17$) or fly sex (GLM; Normal Distribution, Identity link, df = 1, $X^2 = 0.04$, $p = 0.83$). The interaction between these factors (fly sex and display target) was not significant (GLM; Normal Distribution, Identity link, df = 2, $X^2 = 1.15$, $p = 0.56$). There was no significant difference in bout duration between the fly sexes (ANOVA; $F_{1,192} = 0.079$, $p = 0.779$) and across display targets ($F = 0.001$, df = 1, $p = 0.999$). The interaction between both factors was not significantly different ($F = 0.170$, df = 2, $p = 0.844$).

3.2. Display type

There was no significant difference in the frequencies of female flies that performed different displays against males or against spiders in comparison to displays that targeted female flies (Table 1, Fig. 1). Similarly, there was no significant difference in the frequencies of flies that performed different displays against males or against spiders in comparison to displays that targeted female flies (Table 1).