



The influence of male wing shape on mating success in *Drosophila melanogaster*



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ARTICLE INFO

Article history:

Received 6 September 2012

Initial acceptance 8 October 2012

Final acceptance 14 February 2013

Available online 13 April 2013

MS. number: A12-00687R2

Keywords:

body size

courtship behaviour

courtship song

Drosophila melanogaster

fruit fly

mate choice

selection

wing morphology

Drosophila melanogaster males court females through a series of steps. In one of these steps, the male vibrates his wings to produce a courtship song that is species specific. Variation in the shape of *Drosophila* wings has been described among populations and species, but it is still unknown whether this variation influences the courtship process. In our laboratory, replicate strains were obtained from a natural population of *D. melanogaster* by artificial selection for rounded or elongated wing shapes. We used those strains and a nonselected strain to test the influence of wing shape on male mating success. We observed significantly higher success by males from strains with elongated wings when competing with those with rounded or nonselected wings, regardless of the female type. In addition, smaller males were more successful. We also recorded the courtship songs produced by males of different wing shape strains. We detected some variation among the courtship song produced by males depending on the original strain. However, this difference did not fully explain the success of males with elongated wings. Our results therefore show that wing shape has to be considered as influencing male mating success in *Drosophila*.

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Drosophila sexual behaviour is characterized by a series of steps involving acoustic (courtship songs), chemical (pheromones) and visual signals that can influence mating success (Greenspan & Ferveur 2000; Markow & O'Grady 2005; Lasbleiz et al. 2006). Morphological traits are also associated with mating success; body size is often the focus in sexual selection studies (reviewed in Markow & O'Grady 2005). The advantage of large males in mating competition has been extensively reported. Among the hypotheses to explain this advantage, large males may be able to win fights or find females faster (Partridge & Farquhar 1983; Partridge et al. 1987; Prasad et al. 2008).

Wing length has also been used in sexual selection studies of *Drosophila* as a proxy for body size (Sokoloff 1966). In addition, the

fundamental involvement of the wing in courtship behaviour has also made wing length a topic of study, since wing movement has been correlated with species-specific recognition through acoustic signals that produce love song (Bennet-Clark & Ewing 1970; von Schilcher 1976). Covariation between wing length and mating success has been described for multiple *Drosophila* species (Monclus & Prevosti 1971; Wilkinson 1987; Naseerulla & Hedge 1992; Hedge & Krishna 1997; Yenissetti & Hedge 2003).

However, a complete understanding of the relationship between morphological traits and sexual behaviour requires complex analysis that includes many aspects. Steele & Partridge (1988) observed that if males of *Drosophila subobscura* are prevented from producing a drop of regurgitated food during courtship, small males have greater courtship success than large males, which suggests that small males perform some other aspect of courtship better than large males. Aspi & Hoikkala (1995) demonstrated the importance of male wing morphology in sound production in *Drosophila littoralis* and *Drosophila montana*. Males with larger wing length mated more frequently than males with smaller wing length. Despite this finding, these authors detected no size effect in *D. littoralis* mating success, but they found that small *D. montana* males have a mating advantage in the field.

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Regarding wing morphology, length is not the only aspect of the wing that should be considered in studies of male mating success. Several works have described wing shape variation within and among multiple species of *Drosophila* (Klaczko & Bitner-Mathé 1990; Bitner-Mathé et al. 1995; Hoffmann & Shirriffs 2002; Loh et al. 2008; Hatadani & Klaczko 2008; Gidaszewski et al. 2009; Matta & Bitner-Mathé 2010). It is possible that this variation might also be a target for sexual selection as a visual signal. In addition, it is also conceivable that changes in wing shape might affect the acoustic signal produced by males during courtship (Tauber & Eberl 2003).

In this work, we tested the influence of male wing shape in mating success and courtship song production. We used strains of *D. melanogaster* selected for divergence in the wing width/wing length ratio, and we compared flies with elongated versus rounded wings.

METHODS

Ethical Statement

This study was approved by the Ethics Committee on Animal Use in Scientific Experimentation (CEUA) from the Centro de Ciências da Saúde of the Universidade Federal do Rio de Janeiro (UFRJ) under reference number IBO04, and classified with one degree of invasiveness (little or no discomfort or stress), according to the Conselho Nacional de Controle de Experimentação Animal (CONCEA) resolutions, disposed on 11.794 Brazilian Federal Law. Professor Blanche Bitner-Mathé has a permanent license (31053-1) from Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) to collect *Drosophila* species for research. All the flies utilized in this work were sedated in ethyl ether before the euthanasia.

Lineages

The flies used in this work were previously established by B. C. Bitner-Mathé, D. Tesseroli & B. F. Menezes (unpublished data), as described below.

A sample of 135 *D. melanogaster* females was collected from a natural population to generate laboratory isofemale lines. One male and one virgin female were taken to form pools of each sex from the first generation of each isofemale line. From these flies, a wing shape index (W_{SH}), which was measured as the wing width/wing length ratio (W_W/W_L), was obtained. The 10 females with the highest shape index (the most rounded wings) and the 10 females with the smallest shape index (the most elongated wings) were selected for mass mating with 10 males randomly taken from the male pool to start divergent selection strains; these strains were named 'round' (R) and 'long' (L), respectively. Ten other couples were randomly selected to start the control strain (C). This procedure was repeated four times, producing four biological replicates (denoted as 1, 2, 5 and 6) that were maintained at 22 °C. Each biological replicate has one 'L' strain, one 'R' strain and one 'C' strain from the same initial pool.

From each generation of each selection line, up to 50 females were collected and measured. Depending on the direction of selection, the 10 females with the most extreme shape indexes were transferred to a new bottle. In the control lines, 10 females were randomly taken. This procedure was performed for 21 generations. At the 22nd generation and beyond, L and R strains were maintained as described for C strains, although the respective selection was applied intermittently.

Therefore, we use the label L for the strains selected for elongated wings, R for the strains selected for rounded wings and C for the control strains. The flies used in this work were obtained from the 50th to 58th generation.

Measurements

The wing measurements were taken with a micrometric ocular in a stereoscope microscope (at 40 times enlargement) after the flies were sedated with ethyl ether.

The wing length (W_L) measurement was defined as the distance from the winglet opening with the wing proximal border to the intersection of the third longitudinal vein with the wing distal border. The wing width (W_W) was defined as the distance from the perpendicular straight line to the line that describes the W_L (Fig. 1). These values were used to estimate a measure of general wing shape ($W_{SH} = W_W/W_L$). Wings with higher W_W/W_L values are rounder because they have higher W_W and/or lower W_L values. A measure of the general size of the wing (W_{SI}) was estimated as the geometric mean of $W_L/2$ and $W_W/2$. W_{SH} and W_{SI} are in vivo surrogates of the wing shape and wing size indexes (Klaczko & Bitner-Mathé 1990) derived from the fitting of an ellipse to the wing contour.

A measure of body size separate from the wing was obtained by measuring the distance from the anterior margin of the thorax to the most distant point of the scutellum, the thorax length (T_L).

Mating Experiments

We performed five experiments to test the mating success of males with different wing shapes. In every experiment, the trials included two males from strains with different wing shapes (L × R, L × C or R × C) and a virgin female (L, R or C). The flies used were 5–7 days old. Males were housed individually and females were kept in small groups. This procedure aimed to guarantee the sexual maturation of each individual.

Trials were performed in vials with standard culture medium and observed for up to 120 min until mating began. At that moment, the couple was collected with an aspirator and placed into another vial for identification of the male that had successfully mated based on his wing shape measures. There was no overlapping of wing shape measures between the male competitors. Additionally, the W_L , W_W and T_L of the competing males were measured, and the W_{SH} and W_{SI} values were estimated. Over 82% of all pairs successfully mated in all experiments, and there were no significant differences between experiments in the proportion of successful matings.

We first compared the mating success of males from the L and R strains when competing for virgin females coming from any of the three different wing shape type strains (L, R or C). Experiment 1 included only flies from biological replicate 1, since this replicate had the best response to the selection programme in both directions. One hundred 1L × 1R trials were performed for each female type (1L, 1R or 1C). To verify that the results obtained in

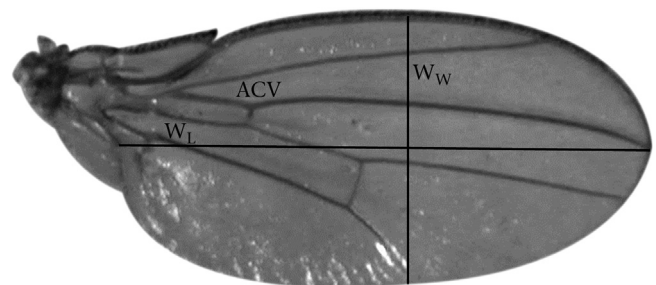


Figure 1. The left wing of *D. melanogaster* showing the axis positions utilized to estimate the length (W_L) and width (W_W) measures of the wings and the anterior crossvein (ACV).

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