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**THE EFFECT OF MANIPULATING THE MALE FACE COLOR IN
COURTSHIP SUCCESS IN *CERATITIS CAPITATA*
MALES (DIPTERA, TEPHRITIDAE)**

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Abstract.—The effect of the sexually dimorphic face color as a visual stimulus during courtship was tested by painting male faces of laboratory-reared *Ceratitis capitata*. Experimental males were less successful copulating, due to their lower courtship activity. However, female responses in all the courtship steps were similar to both experimental and control males. Dimorphic face color may have lost relevance in sexual selection by the females of this species during courtship. Examination by scanning electron microscopy and a light stereoscope suggest that this sexually dimorphic character is caused by differences in cuticle color between males and females and is not related to structural differences or microtrichia density of the male face.

Key words: *Ceratitis capitata*, courtship, sexual dimorphism, sexual selection.

Despite the fact that the reproductive behavior of the Mediterranean fruit fly (*Ceratitis capitata* Wiedemann), a pest in many crops, has been studied extensively, little is known about the aspects that determine success or failure of a given courtship (Eberhard, 1999). Visual communication is one such poorly understood aspect. Many sexually dimorphic aspects in the behavior and morphology of medflies are presumed to visually stimulate and elicit crucial female responses during courtship (Eberhard, 1999).

Active female cooperation is necessary for the progression of the normal stages of medfly courtship (i.e., advancing from continuous wing vibration to intermittent buzzing, and finally to mounting) (Eberhard, 1999). Some studies have suggested the effect of visual stimuli displayed by males when courting a female. Females separated from males by glass walls turned toward courting males (Fèron, 1962). This behavior indicated that visual stimuli may be important, although it was not clear which male signal induced the female response. Another study in which flies were kept in total darkness for three days, found that the insemination rate was reduced approximately 90% (Keiser et al., 1973). However, it was not clear if the reduction was due to a decrease in courtship activity, in the female acceptance rate, or both.

Sexual dimorphisms that could possibly affect visual stimuli during courtship in *C. capitata* include eye color and the capitate anterior orbital head bristle (Mendez et al., 1998). Another sexual dimorphism in male medflies is the intense white color of the face, extending to the frontogenal suture of the head. This bright white surface could be displayed to the female during head rocking (Fèron, 1962), since almost all visual signals are associated with some kind of movement to intensify detectability (Fleishman, 1988). To date, the possible effect of this character on female responses has not been directly evaluated.

The present study focuses on manipulating the dimorphic male face color and analyzes its effect on female acceptance during courtship. It also explores how sexual dimorphism in medflies is related with structural differences or microtrichia density.

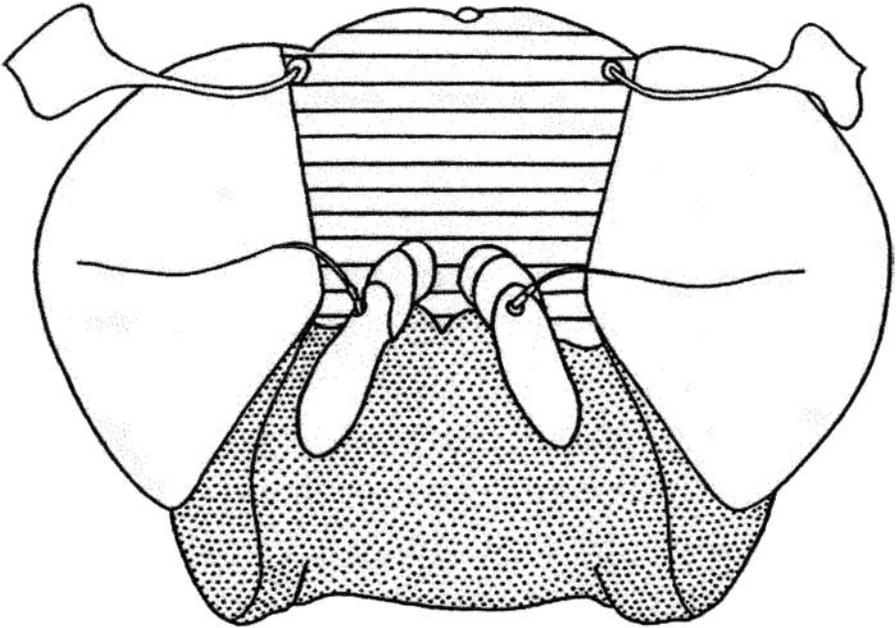


Fig. 1. Frontal view of the head of male *Ceratitis capitata*. Dots indicate the area that was painted with black ink in the first experiment. Stripes correspond to the area painted in the second experiment.

MATERIALS AND METHODS

The flies used in this study were from a colony that had been mass-reared for approximately 5 years at the Estación Experimental Fabio Baudrit, Alajuela, Costa Rica, originally derived from wild adults captured in the Central Valley of Costa Rica. Males were separated from the females before they were four days old to ensure that they were virgins. Males were painted 24 hours before being observed with an indelible fine point (0.1) black marker (edding 1880®). The white face (*sensu* White et al., 1999) was painted with the black marker under a stereoscope by holding each fly unaenesthetized with foam padded forceps, leaving only the head uncovered (Fig. 1). The area near the antennal insertion was painted using a single-hair paintbrush. The flies were held by the forceps until the paint was dry (about 10 minutes). The control males were held by the forceps the same length of time. Both groups were separated from each other and from the females until they were observed.

Before starting observations, the painted males were checked under a stereoscope to assure the white area remained completely covered by black ink. The flies were placed in 8.5 cm × 1.8 cm deep clear petri dishes. Each dish contained a female, and one control and one painted male, all of the same age (5 to 8 days). New flies were used for each observation period. A total of 25 petri dishes were observed for four hours beginning at 9:00 am. The number of times each male performed continuous wing vibration courtship, intermittent wing vibration courtship, mounted or copulated were registered for 432 males. Some pairs copulated without their courtship being observed. In these cases it was assumed that the previous courtship steps had occurred.

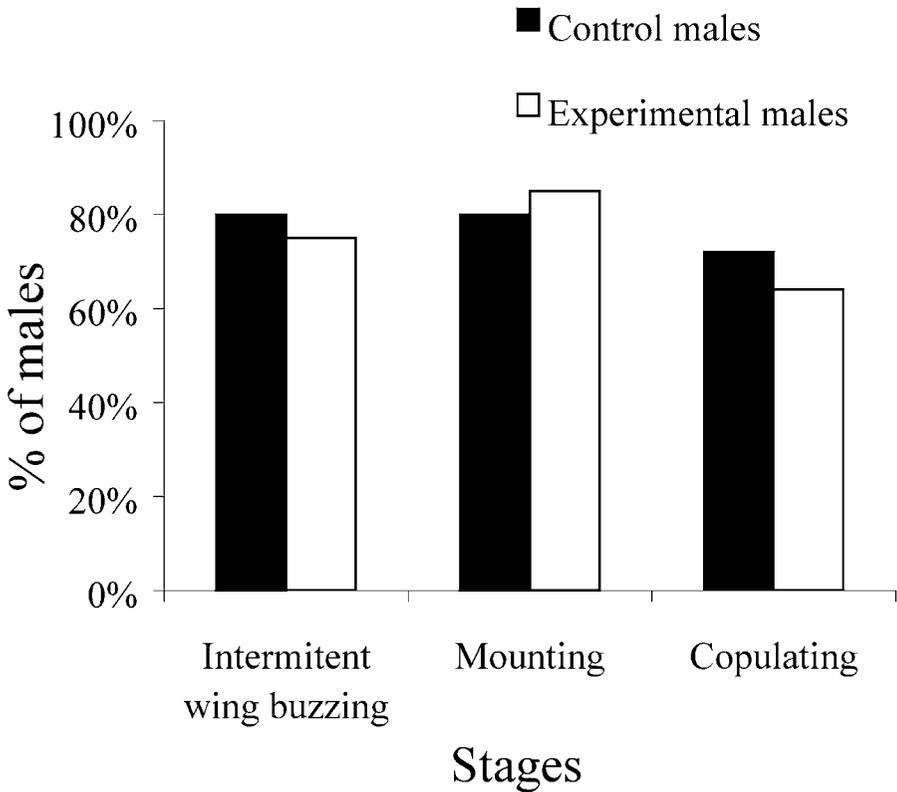


Fig. 2. Percentage of males successfully advancing from one courtship stage to another and finally copulating.

The possible effect of the blank ink on courtship behavior was evaluated by painting males on the superior part of the head (Fig. 1). Control males were treated as described above. Head photographs were taken with a scanning electronic microscope using air-dried specimens.

RESULTS

Control males were more successful copulating than the painted ones. Of the 115 males that copulated, 68% were control males ($\chi^2 = 5.23$, $P = 0.022$, $df = 1$). Control males also mounted more females than experimental males; 59% of a total of 168 males that mounted a female were control males ($\chi^2 = 54.71$, $P = 0.03$, $df = 1$).

However, there was no difference between treatments when comparing the probability of advancing from one courtship step to another. Advancing from continuous wing vibration to intermittent wing vibration occurred similarly in males of both treatments ($\chi^2 = 1.13$, $P = 0.29$, $df = 1$, $N = 118$, Fig. 2). Moving on from intermittent wing buzzing to mounting showed the same tendency for both control and experimental males ($\chi^2 = 0.66$, $P = 0.42$, $df = 1$, Fig. 2), and finally copulating after mounting the female ($\chi^2 = 0.99$, $P = 0.32$, $df = 1$, $N = 73$, Fig. 2). Combining the intermediate courtship steps, 46% of a total of 147 males that initiated

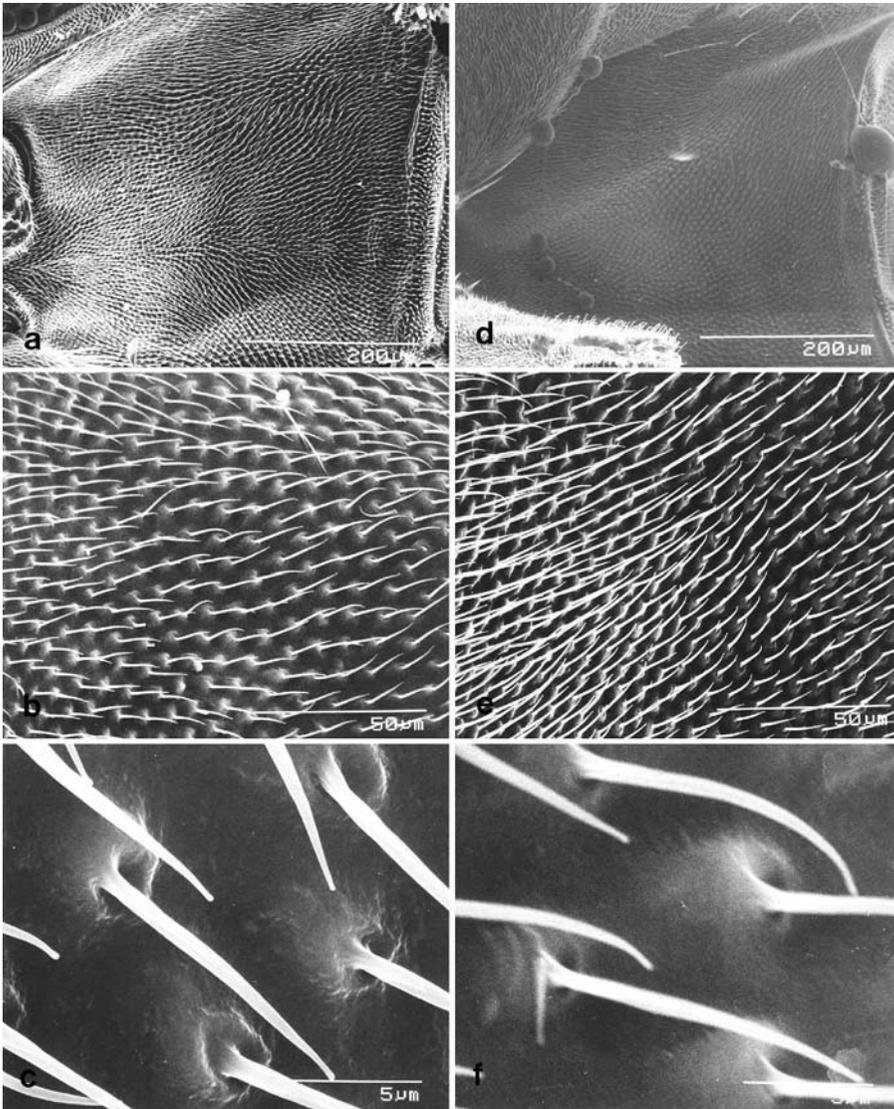


Fig. 3. Face of male (a, b, c) and female (d, e, f) of *Ceratitis capitata*.

continuous wing buzzing were able to copulate with a female; 41% of these were experimental males ($\chi^2 = 1.03$, $P = 0.48$, $df = 1$). Thus, the courtship of males from both treatments was similarly successful in inducing the female to copulate.

Female age did not affect the probability that courtship would advance from one step to another. There was no difference between females with ages of 5–6 and 7–8 days that courtship would advance from continuous to intermittent wing buzzing ($\chi^2 = 0.73$, $P = 0.39$,

df = 1, N = 200). Similarly, the chance of advancing from intermitent wing buzzing to mounting females ($\chi^2 = 0.066$, $P = 0.80$, df = 1, N = 155), and finally copulating after mounting did not change with female age ($\chi^2 = 0.506$, $P = 0.48$, df = 1, N = 199).

In the second experiment, a total of 43 control males and 43 experimental males were observed. No effect of the ink was noticed, males of both treatments had similar probabilities of performing both continuous wing buzzing ($\chi^2 = 0.78$, $P = 0.38$, df = 1) and intermitent wing buzzing ($\chi^2 = 0.47$, $P = 0.49$, df = 1). They also showed similar tendencies to mount females ($\chi^2 = 0.51$, $P = 0.48$, df = 1) and copulate ($\chi^2 = 0.081$, $P = 0.78$, df = 1).

Examination by scanning electron microscopy suggested that the sexual dimorphism in face color does not relate to structural differences, and microtrichia density is also apparently similar in both sexes (Fig. 3). Observations with a light stereoscope suggest that, it is apparently due to differences in the color of the cuticle of the face. The cuticle of males is bright white and of females is more opaque with a brownish coloration on the inferior margin of the face.

DISCUSSION

Experimental males were less successful in copulating, but apparently this disadvantage was due to their reduced sexual activity. This suggests that female response to male courtship was not affected by the elimination of the white face dimorphism. The low courtship activity in experimental males may be due to a harmful effect of the ink, since the painted area is close to the mouthparts of the flies and paint may have penetrated these tissues. The results of the second experiment support this idea, since covering the frons with black ink did not have an effect on the male tendency to court.

The data suggests the unexpected conclusion that the white dimorphic face does not influence sexual selection by female *C. capitata*. Possibly this sexual dimorphism is a vestigial character of an ancestor with a more dimorphic face. Other *Ceratitidis* species, including the closely related *C. catoirii* and others in the subgenus *Ceratalapsis*, such as *C. cosyra* and *C. discussa* (De Meyer, 1999), have an intense white face in males. In *C. catoirii*, the male face is directed toward the female during courtship as a possible display signal (Briceño, Eberhard and Quilichi, in prep.).

Another possible explanation is that in *C. capitata* there is a tendency in males of mass reared strains to perform a shorter courtship than in natural conditions and for head rocking movements to be reduced (Briceño and Eberhard, 1998). This could influence the functionality of the white face as a visual stimulus during courtship.

The sexual dimorphism in male face color is apparently not related to obvious structural differences or differences in microtrichia density. It appears to be caused by a difference of color between the cuticle of the face of males and females. This fails to explain a previous description of it as a highly reflective white area of pubescence on the anterior surface of the head (Holbrook et al., 1970; Landolt et al., 1992).

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