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COURTSHIP BEHAVIOR OF DIFFERENT WILD STRAINS OF *CERATITIS CAPITATA* (DIPTERA: TEPHRITIDAE)

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ABSTRACT

This study documents differences in the courtship behavior of wild strains of *Ceratitis capitata* (Wiedemann) from Madeira (Portugal), Hawaii (U.S.A.), Costa Rica, and Patagonia (Argentina). Some traits showed large variations and others substantial overlaps. The angle at which the male faced toward the female at the moment of transition from continuous wing vibration and intermittent buzzing changed very little during the course of courtship in all strains, but males from Madeira tended to face more directly toward the female than other males. Females tended to look more, and more directly, toward the males as courtship progressed in all strains. The distance between male and female tended to decrease as courtship proceeded in all strains, but the distances at which males initiated continuous vibration, intermittent buzzing, and jumped onto the female were relatively less variable between strains, except for the strain from Costa Rica. Flies of Madeira courted for longer and the male moved his head and buzzed his wings longer than the other strains.

Key Words: courtship behavior, wild flies, medfly, geographic differences, Madeira, Costa Rica, Argentina, Hawaii

RESUMEN

Este estudio documenta diferencias en el comportamiento de cortejo de cepas silvestres de *Ceratitis capitata* (Wied.) provenientes de Madeira (Portugal), Hawaii (Estados Unidos de Norte América), Costa Rica y Patagonia (Argentina). Algunas características mostraron grandes variaciones y traslape substancial. Los ángulos a los cuales los machos miraron hacia las hembras cambiaron muy poco en el momento de la transición de la vibración continua al zumbido intermitente durante el curso del cortejo en todo las cepas, pero los machos de Madeira tendieron a enfrentar más directamente a la hembra que otros machos. Los ángulos de las hembras disminuyeron claramente durante el cortejo en todas las cepas. La distancia entre el macho y la hembra tendió a disminuir conforme el cortejo continuaba en todas las cepas, pero las distancias a las cuales los machos iniciaron la vibración continua, el zumbido intermitente, y el salto sobre la hembra eran relativamente menos variables entre cepas excepto la cepa de Costa Rica. Moscas de Madeira cortejaron más tiempo y el macho movió su cabeza y zumbaba sus alas mas prolongadamente que las otras cepas.

Translation provided by the author.

The use of sterile males for the integrated control populations of *Ceratitis capitata* (Wiedemann) makes it economically important to understand which male stimuli induce females to mate, in order to design appropriate quality control measures for mass-reared males (FAO/IAEA/USDA 2003;Calkins & Parker 2005). Because it is difficult to induce wild flies to reproduce in the laboratory (Rössler 1975), some strains have been maintained under mass-rearing conditions for many years. These conditions differ from those in the wild in a number of respects (Cayol 2000). Briceño & Eberhard (1998) found that males from mass-reared strains court for shorter periods before attempting to mount the female, apparently due to the crowded conditions in mass rearing cages which result in frequent interruptions of courtships. There are at least five differences between the sexual behavior of mass-reared males and wild males (Briceño & Eberhard 2002a).

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Mass-reared males are generally less able to induce wild females to copulate than wild males. Although several aspects of male courtship behavior are known to have changed in at least some mass-reared strains (Zapien et al. 1983; Limatainen et al. 1997; Briceño & Eberhard 1998; Calcagno et al. 1999; Briceño et al. 2001), it is not clear whether these or other male traits are more important in producing this inferiority (Eberhard 2000). Such differences in male behavior may result in partial reproductive isolation between strains (Lux et al. 2002).

This paper explores the possibility that there are differences in courtship behavior among four wild *C. capitata* populations from Costa Rica, Patagonia (Argentina), Hawaii (USA) and Madeira (Portugal). Differences between wild strains may have important implications for development strategies for SIT implementation (Dyck et al. 2005).

Materials and Methods

Flies of each strain were separated by sex within 48 h of emergence as adults, and kept in buckets topped with screen, with *ad libitum* access to water and hydrolyzed yeast and sugar (1:3). Wild flies from Costa Rica were raised from larvae that emerged from infested tangerines collected at the Estación Experimental Fabio Baudrit near Alajuela, Costa Rica. Wild flies from Argentina were a laboratory F_2 derivative from flies raised from fruit collected in the field in the Alto Valle region of Patagonia. Wild flies from Hawaii were raised from larvae collected from coffee fruit on Kauai. Wild flies from Madeira were collected from infested mixed hosts.

Flies in Costa Rica and Hawaii were videotaped in plastic chambers that were 13.7 cm diam. and 1.8 cm tall. They were videotaped from below through a transparent glass table (Briceño & Eberhard 1998) with a Sony Hi8 camcorder equipped with +6 close-up lenses. Pairs from Patagonia and Madeira wild flies were videotaped in a clear plastic cylinder 7.3 cm high and 9.0 cm in diameter. Each morning a fresh leaf from a citrus tree was attached to the ceiling of the cage, and a male was released in the cage (or mating chamber). Five min after the male began emitting pheromone, a female was released into the cage, and the behavior of the 2 flies was recorded for 30 min or until they copulated. Flies in mating trials were sexually mature, 10 days old, and each fly was used only once.

Measurements of different aspects of courtship behavior that led to a mounting attempt by the male were made from frame by frame analyses of videotapes. Only a single courtship was analyzed for each male to avoid pseudoreplication. Durations of the following male behaviors were analyzed: (1) continuous wing vibration (wings directed postero-laterally and vibrated rapidly dorso-ventrally); (2) intermittent buzzing (wings moved back and forth from being directed posteriorly over to the abdomen to anteriorly and also vibrated rapidly); for detailed descriptions of both these wing movements, see Briceño & Eberhard (2000b); (3) head rocking (head was rotated from side to side and turned and laterally just before intermittent buzzing began); (4) the total time the female remained immobile (no walking) before the male launched his mounting attempt; (5) and total courtship duration from the start of continuous vibration until the mounting attempt.

The directions the 2 flies were facing with respect to the midpoint of the other fly's prothorax and the distances between them were determined at 3 stages of the courtship (initiation of continuous wing vibration; initiation of intermittent buzzing; and launch of the male's jump onto the female) with 0° indicated that one fly was facing directly toward the other. The "male angle" was the angle between the direction the male faced and the orientation directly toward the female; the "female angle" was the equivalent for the female.

In Madeira and Hawaii strains the time during which the male's aristae touched those of the female was measured because contact with the male's sexually dimorphic aristae during head rocking and buzzing appears to be and important part of medfly courtship (Briceño & Eberhard 2002b). The number of bouts of wing buzzing was counted in 2 strains. All means are followed by + SD. Statistical tests were Mann-Whitney *U* Tests unless otherwise specified.

Results

Data in Table 1 show that there were differences between at least 1 pair of geographic strains in 12 of the 14 variables measured (the female angle when the male jumped, and the amount of time the female was quiet before the male jumped, are exceptions). There were also large differences in most variables (especially males vibrating and wing buzzing), and substantial overlaps between different strains in most behavioral traits. Madeira males rocked their heads and buzzed their wings significantly longer, and their total courtship was also longer.

The male angles at the moment of transition between wing vibration and wing buzzing changed very little during the course of courtship in all strains, but males from Madeira tended to face more directly toward the female than other males. Female angles clearly decreased during courtship in all strains. The distance between the male and female tended to decrease as courtship proceeded in all strains. The distances at which males initiated continuous vibration, intermittent buzzing, and jumped onto the female were

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TABLE 1. MEANS AND STANDARD DEVIATIONS OF COURTSHIP BEHAVIOR OF *CERATITIS CAPITATA* FLIES FROM DIFFERENT GEOGRAPHIC AREAS, AND SIGNIFICANCE DIFFERENCES WITH MANN-WHITNEY *U* TESTS. VALUES IN THE SAME ROW FOLLOWED BY THE SAME LETTER AND NUMBER ARE SIGNIFICANTLY DIFFERENT (A = $p < 0.05$; B = $p < 0.01$; C = $p < 0.001$, NS = NO SIGNIFICANT DIFFERENCE).

	Madeira	Costa Rica	Hawaii	Patagonia
Angles (°)				
contmal	1.8 ± 2.6 b_1a_1	6.8 ± 9.1 $b_{1,2}$	0.8 ± 0.9 b_2a_2	5.9 ± 4.5 $a_{1,2}$
confem	22.1 ± 29.0 c_1	43.9 ± 31.4 $a_1c_{1,2}$	5.4 ± 3.2 a_1b_1	36.5 ± 39.9 c_2b_1
intermal	1.2 ± 2.7 $a_{1,2}$	3.5 ± 4.1 a_1	2.7 ± 4.6	4.4 ± 4.7 a_2
interfem	7.8 ± 7.9 ns	13.1 ± 16.6 ns	6.2 ± 5.4 c_1	13.7 ± 14.8 c_1
jumpmal	1.4 ± 2.2 c_1	3.8 ± 5.1 c_1	3.5 ± 3.7 c_2	2.7 ± 5.2 c_2
jumpfem	6.1 ± 7.7 ns	8.8 ± 13.9 ns	10.3 ± 8.4 ns	7.6 ± 10.8 ns
Distances (cm)				
distcont	6.7 ± 4.3 a_1	1.6 ± 2.1 $a_{1,2,3}$	6.7 ± 3.7 a_2	9.1 ± 5.7 a_3
distinter	1.71 ± 0.9 a_1c_1	0.3 ± 0.1 $a_{1,2,3}$	3.0 ± 0.9 $a_2b_1c_1$	1.8 ± 1.1 a_3b_1
distjump	0.09 ± 0.03 ns	0.1 ± 0.3 ns	0.15 ± 0.4 ns	0.10 ± 0.03 ns
disthead	3.3 ± 1.8 ns		3.1 ± 1.0 ns	
Duration (seconds)				
femquiet	8.0 ± 6.3 ns	5.9 ± 3.7 ns	5.8 ± 4.9 ns	5.9 ± 5.6 ns
buzz	18.1 ± 19.6 $b_{1,2}$	10.6 ± 8.3 b_1	12.3 ± 10.6	8.2 ± 6.2 b_2
vibrate	17.2 ± 20.7 ns	14.8 ± 19.8 ns	5.7 ± 8.2 c_1	8.6 ± 6.8 c_1
head rocking	3.9 ± 4.6 c_1	0.77 ± 0.45 c_2	3.3 ± 4.8 $c_{2,3}$	1.4 ± 1.3 $c_{1,3}$
court	29.4 ± 27.1 c_1	19.8 ± 20.3 $c_{1,2}$	15.7 ± 113.5 c_2	16.8 ± 10.6
antenna touches	9.4 ± 8.7 ns		5.6 ± 4.3 ns	
number buzzes	21.3 ± 13.7 ns			28.7 ± 16.2 ns
N	32	56	17	38

contmal =male angle when continuous vibration began
contfem = female angle when continuous vibration began
intermal = male angle when intermittent buzzing began
interfem = female angle when intermittent buzzing began
jumpmal = male angle when male jumped onto female
jumpfem = female angle when male jumped onto female
distcont = distance in cm between flies when male began continuous vibration
distinter = distance in cm between flies when male began intermittent buzzing
distjump = distance in cm between flies when male jumped onto female
disthead = distance in cm between flies when male began head rocking
femquiet = time in s female was motionless prior to the male's jump
vibrate = duration in s of continuous wing vibration
buzz = duration in s of intermittent buzzing
court = duration in s of entire courtship
antenna touches = duration in s of the antenna touches by the male during intermittent buzzing
head rocking = duration in s for head rocking

relatively less variable among strains, except for the strain from Costa Rica.

DISCUSSION

Our results confirm several conclusions from previous studies regarding possible female acceptance variables. The gradual reduction in the distance between male and female, the increase in the female's tendency to look more directly toward the male, and her relative immobility prior to the male's jump are in accordance with the idea that one result of successful male courtship behavior is to induce the female to approach him, to look directly toward him, and to remain immobile (Briceño & Eberhard 2002a).

Lux et al. (2002) measured average duration of vibration and buzzing in 3 wild populations, and reported that in flies from Israel and Patagonia these activities lasted longer than in flies from Kenya (likely to be more similar to the original ancestor of this African species) but failed to present data or statistical tests. The values for wing vibration in the Kenyan populations we studied were much lower, i.e., 8.6-17.2 compared to 57.9 (Lux et al. 2002). One behavior (head rocking) that was absent in one of the wild strains (Israel) studied by Lux et al. (2002) was present in all the strains we studied.

There are several possible reasons for geographic differences in courtship behavior, including founder effects and divergent sexual selection

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in different populations. The behavioral differences between wild flies indicate that there is appreciable genetic variation for these male courtship traits in field populations. The question of whether variation exists in male traits under sexual selection in natural populations has been controversial. Our results are in accord with the trend for genetic variation seen in other groups (Anderson 1994). On a practical level, the variance we found means that relatively large samples of courtships are needed to test for significant differences among strains. The differences between strains documented here involved males interacting with females of the same strain. Given the probable effects of the behavior of one sex on that of the other (Briceño & Eberhard 2002b), it is not possible to attribute differences to one sex or the other until cross-strain pairs are studied.

There was an apparent tendency of the wild Madeira males to rock their heads and buzz their wings significantly longer, and to court for longer before mounting. Because it appears that Madeira females are the "choosiest" among populations studied (Cayol et al. 2002), this could suggest that males with this suite of behaviors would be good candidates for medfly SIT operations world-wide.

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