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Aggressive Behavior in Medflies (*Ceratitis capitata*) and Its Modification by Mass Rearing (Diptera: Tephritidae)

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ABSTRACT: Male and female *Ceratitis capitata* employ at least nine different behavior patterns during aggressive interactions that include possible visual, auditory, and tactile stimuli. Male flies of a 4.5 year old mass-reared strain were less aggressive in some respects than wild flies.

Males of the medfly *Ceratitis capitata* Wied. form leks on the undersides of leaves, where mating occurs (Prokopy and Hendrichs, 1979; Hendrichs and Hendrichs, 1990; Shelly et al., 1994). Each male in a lek occupies a leaf, where he releases an attractant pheromone, and courts and copulates with females which arrive there (Prokopy and Hendrichs, 1979). Aggressive interactions involving both males and females occur at leks and at oviposition sites (Hendrichs and Hendrichs, 1990; Whittier et al., 1992). Medflies are unusual among lekking animals (Höglund and Alatalo, 1995; Shelly and Whittier, 1997) in that males defend their territories only weakly (Whittier et al., 1992; Hendrichs et al. 1996).

Despite the fact that millions of dollars are spent annually to combat this species, which is a serious agricultural pest, there is apparently no detailed description of its aggressive behavior. Arita and Kaneshiro (1989) mention sustained head-to-head contact of up to 5 min between males contesting a leaf, and also lunging, pushing, and "slashing" with the wings. Rolli (1976) briefly mentioned that sounds are associated with aggressive behavior in both males and females. The use of video recordings makes possible more detailed and complete observations of the sometimes quite rapid and subtle movements associated with aggression. The recent extensive descriptions of aggression in other tephritids (Headrick and Goeden, 1994) permit numerous comparisons.

Medflies offer an unusual opportunity to study the effects of sexual selection on microevolution. The widely used sterile male technique to control medflies involves rearing huge numbers of flies for many generations under conditions that are very different from those in nature. These conditions can result in inadvertant changes in the selection that acts on different aspects of male sexual behavior (e.g. Calkins, 1984; Kaneshiro, 1991; Briceño and Eberhard, 1998). Because mass-reared strains are somewhat difficult to establish, many have been kept for several years. The possible effects of mass-rearing conditions on their behavior can be determined by comparing the behavior of mass-reared strains with that of wild flies of the strain from which the mass-reared strain was derived. Since the effectiveness of the control technique depends on the behavior of sterilized males, changes in the behavior of mass-reared strains can have serious economic consequences.

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This paper provides the first detailed descriptions of aggressive behavior and aggressive sounds in medflies, and also compares, under both laboratory and semi-natural conditions, the relative frequencies of different types of aggressive behavior in males and females of wild and mass-reared flies.

Materials and Methods

The mass-reared flies whose behavior was taped were from a 6 year old strain (approximately 100 generations in captivity) that had been maintained in 2.4 × 0.7 × 0.35 m cages (approximately 60,000 flies/cage) in the Laboratorio de Investigación de la Mosca del Mediterráneo in San José, Costa Rica. Wild flies were raised from fallen oranges and tangerines at the Estación Experimental Fabio Baudrit near Alajuela, Costa Rica, the site where flies that founded the mass-reared strain were collected. Males and females of both strains were separated one day after eclosion. Because mass-reared flies matured more rapidly, they were observed at ages between 5–10 days, while wild flies were observed when they were 10–19 days old. Flies of both strains were kept in plastic cups (7.3 cm tall, 9.0 cm in diameter) until the day of observation, when they were aspirated (two males, two females) into plastic petri dishes (13.7 cm in diameter, 1.85 cm deep). Several petri dishes were placed on a revolving glass plate, and those in which aggression was occurring were taped using a Sony Hi8 video camera (CCD V-801) equipped with +6 closeup lenses that allowed closeups in which a single fly filled the screen. Sound was recorded simultaneously using a Sennheiser MZK 802V microphone inserted through a hole in the side of the petri dish and coupled to the video camera. The number and duration of different types of movement were determined to the nearest 0.03 sec with frame-by-frame analyses of the videos. Durations and fundamental frequencies of sounds were analyzed with the 2.5 version of Avisoft-SONOGRAPH Pro software. Fundamental frequencies were estimated using the first strong peak in Fourier analyses. These determinations were only approximate, because the signals were very short and the resolution of such analyses is reduced with short signals. All drawings are based on video images. Body parts that were not clear (out of focus or moving rapidly) are omitted. Average durations are followed by one standard deviation.

Observations in a semi-natural setting were made on sunny days during the dry season (January–May) in a screen field cage (3 × 2 × 2 m) in which three small potted orange frees (1.3 m fall) were placed together to form a single canopy. Two mature fruit were placed at the forks of branches of each tree. At 8:00 each of 12 mornings males and females were released into the cage. Wild flies were used on four days, mass-reared flies on four, mass-reared males with wild females on two, and males and females of both strains (marked with different colors of nail polish on the pronotum) on two.

Aggressive interactions were defined in the following way: at least one of the flies turned to face toward the other, and then moved toward the other without performing the courtship wing vibration display (Feron 1962, Briceño et al. 1996). Names of behavior patterns follow, when possible, those of Headrick and Goeden (1994).

Results

No qualitative differences were noted in the behavior of wild and mass-reared flies. Unless specified otherwise, all numerical data are for mass-reared males.

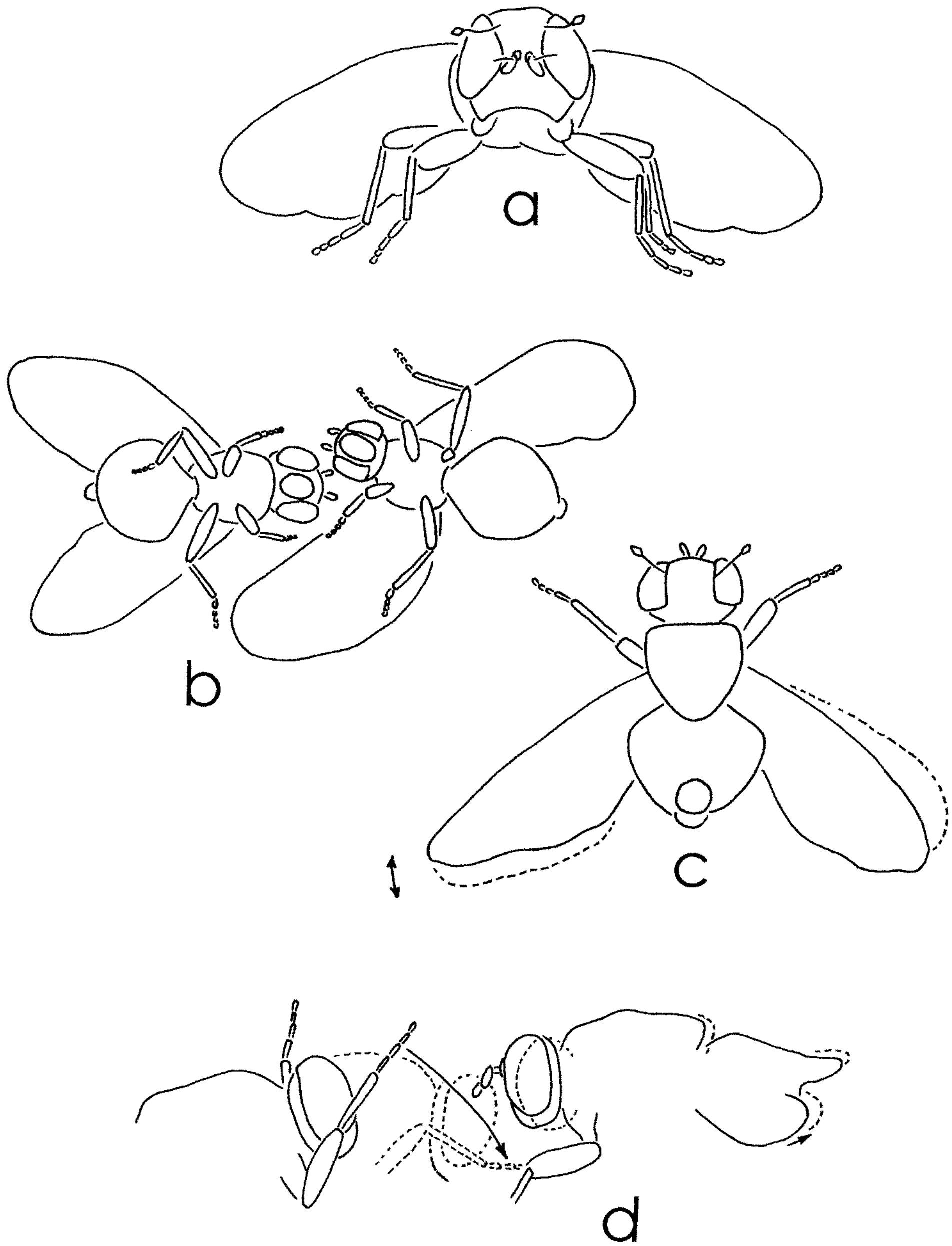
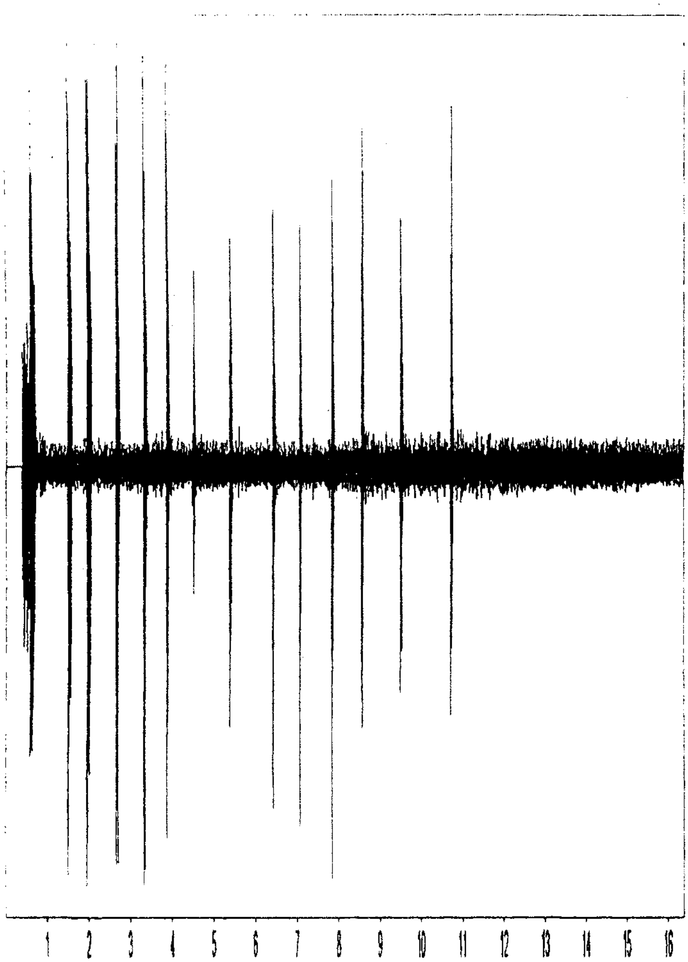


Fig. 1. Aggressive behavior patterns of male medflies. A. Arching wings. The wings were brought forward to be perpendicular to the longitudinal axis of the fly, and twisted so the costal margin was dorsal and the tip nearly touched the substrate; B. Wing strike. One wing was brought forward by the fly on the right to strike his opponent; C. Wing vibration. Both wings moved but too rapidly to be resolved in video images; D. Tap with front legs. The male on the left caused his opponent to retreat, after raising his front legs in an apparent defensive response to being approached.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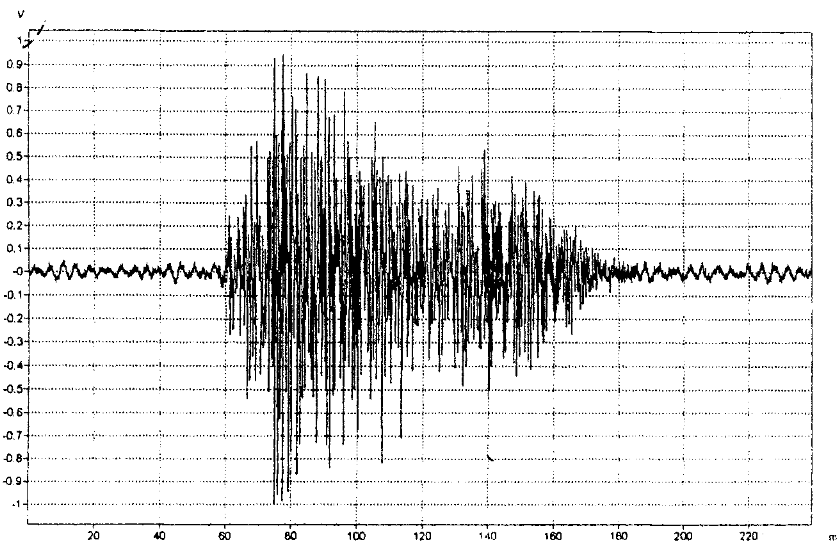
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A. Behavior associated with aggression

Wings (folded). The wings were held horizontally over the dorsum of the body with their posterior surfaces partially overlapping. This behavior commonly occurred as one fly approached another (32% of 179 cases), often before an aggressive movement was made.

Arching wings (present wings). Both wings were extended perpendicular to the longitudinal axis of the fly, and twisted so that the costal margin was dorsal and the tip nearly touched the substrate (Fig. 1a).

Synchronous supination (wave wings). Arched wings moved rhythmically up and down while the fly faced the other fly. Often the fly walked in more or less a semicircle in front of its opponent during supination (mean angle moved 75 ± 70°, N = 43), and sometimes the supinating individual moved toward or away from the other. The duration of synchronous supination averaged 24.2 ± 13.2 sec (N = 13), and the mean distance between the flies when supination began was 7.4 ± 3.4 mm (N = 25).

Wing strike. The body and one or both wings moved forward rapidly a short distance (body movement averaged 1.6 ± 0.5 mm, N = 15) and one or both wings swung forward to strike the opponent with its anterior border (Fig. 1b). Wing strikes were rapid (av. duration 0.09 ± 0.06 sec, N = 48), and were sometimes repeated several times in quick succession. A sound was produced during each strike that lasted an average of 0.106 ± 0.075 sec and a fundamental frequency of 1.5 ± 0.7 KHz (N = 20) (Fig. 2). Wing strikes sometimes occurred simultaneously with head butts.

Short wing vibration. The wings vibrated rapidly for a brief period, sometimes moving slightly forward and back (Fig. 1c). These movements were associated with sounds that were shorter than the intermittent wing buzzing during courtship (average 0.06 ± 0.04 sec, N = 11 vs. 0.0982 ± 0.0710 sec—Briceño and Eberhard in prep.), and had a fundamental frequency of 3.1 ± 0.7 KHz (N = 14). The short wing vibration sound included a "click" at the first followed by vibration (Fig. 3).

Tap with front legs. One or both front legs were extended forward in an apparent defensive "fending" response to a rapidly approaching opponent. When the two individuals were sufficiently close, they sometimes touched each other in alternation with their front legs. No sound was associated with leg tapping. When flies pushed with their heads or mouthparts (below), the front leg movements may have been attempts to trip the opponent. Occasionally a fly struck forward rapidly and its front legs touched the head or legs of the opponent briefly before retreating (Fig. 1d).

Enantion (body jerk). The fly made a short, rapid forward movement of its body, and simultaneously spread its wings to form an angle of about 90° with its longitudinal axis, sometimes vibrating them, and then immediately returned body and wings to their original positions. These movements were very brief (av. duration 0.08 ± 0.03 sec), and occurred when the flies were relatively far from each other (mean 4.9 ± 2.5 cm, N = 49). Enantion was associated with a sound that lasted an average of 0.049 ± 0.065 sec and had a fundamental frequency of 2.6 ± 2.1 KHz (N = 2) that was associated on video recordings with wing movements. Enantion also occurred when the opponent was close enough to be butted (Fig. 5a). Usually the opponent

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Fig. 2. Sounds produced during a series of wing strikes. The record below is the second sound in the series above.

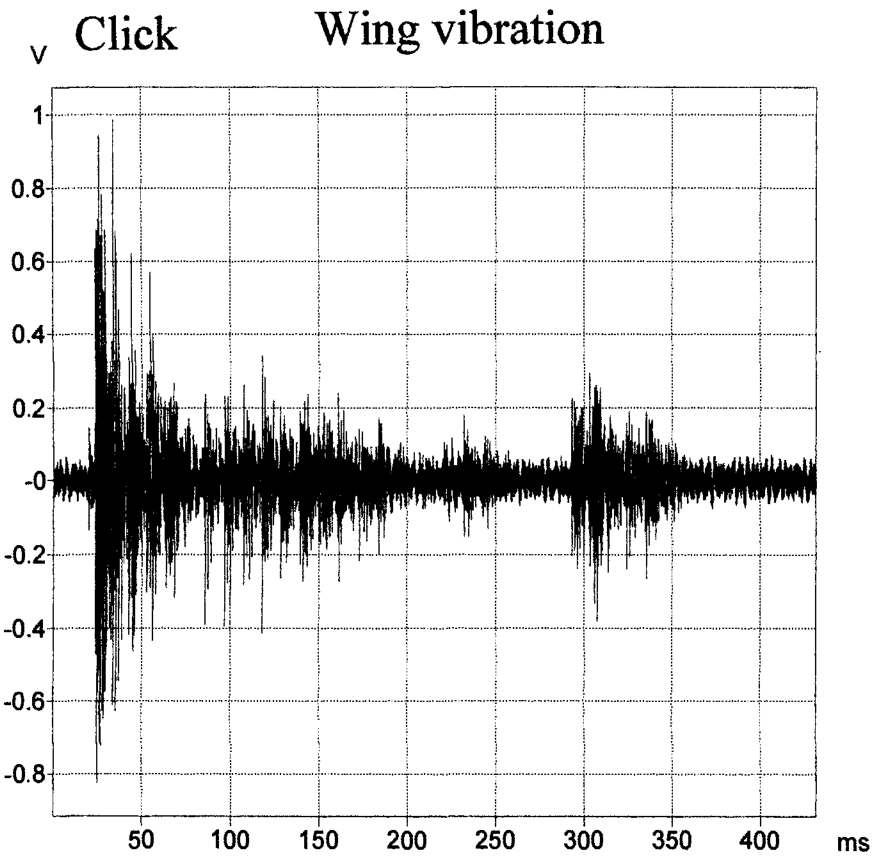

Fig. 3. Sounds produced during short wing vibration. There was an early "click", followed by one or more periods of vibration.

was butted on the head, but sometimes on other parts of its body. The duration of butts averaged 0.10 ± 0.03 sec (N = 99), and the butting fly then returned to its original position. Sometimes several butts were given in succession, and butts were sometimes combined with wing strikes. The duration of acoustic signals associated with butts averaged 0.110 ± 0.054 sec and the fundamental frequency averaged 2.8 ± 1.3 KHz (N = 12).

Labellar display (mouthpart extension). When close to the other fly, the labellum was extended and maintained erect, sometimes for extended periods (av. duration 11.5 ± 7.4 sec. N = 15) (Fig. 5b). No sound was associated with labellar displays. Females performing the labellar display often contracted and extended the labellum rapidly, touching different parts of the male's body including his head, thorax, and abdomen.

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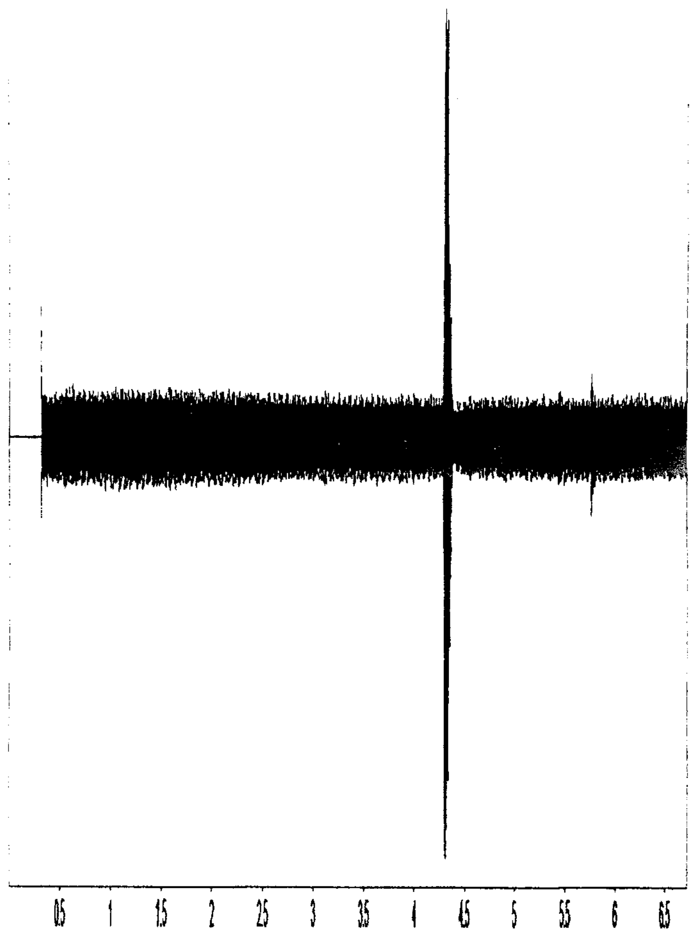
Fig. 4. Sounds produced during enantion.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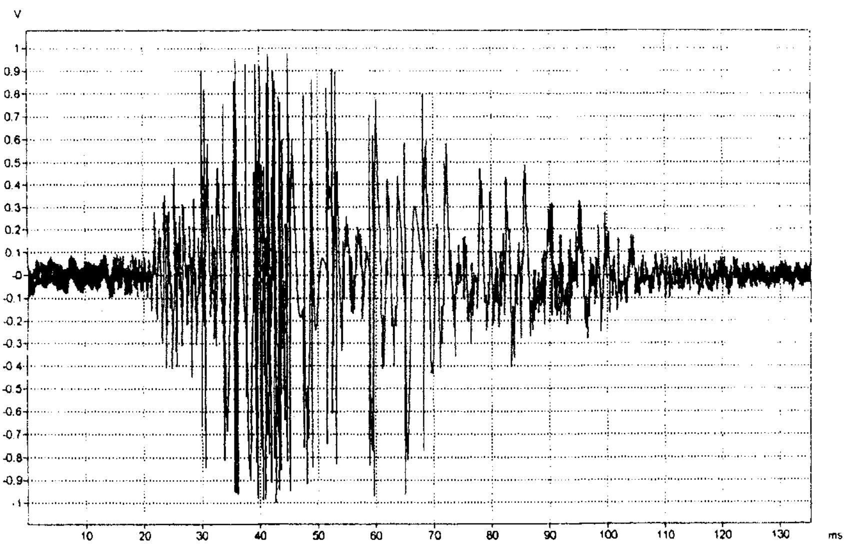
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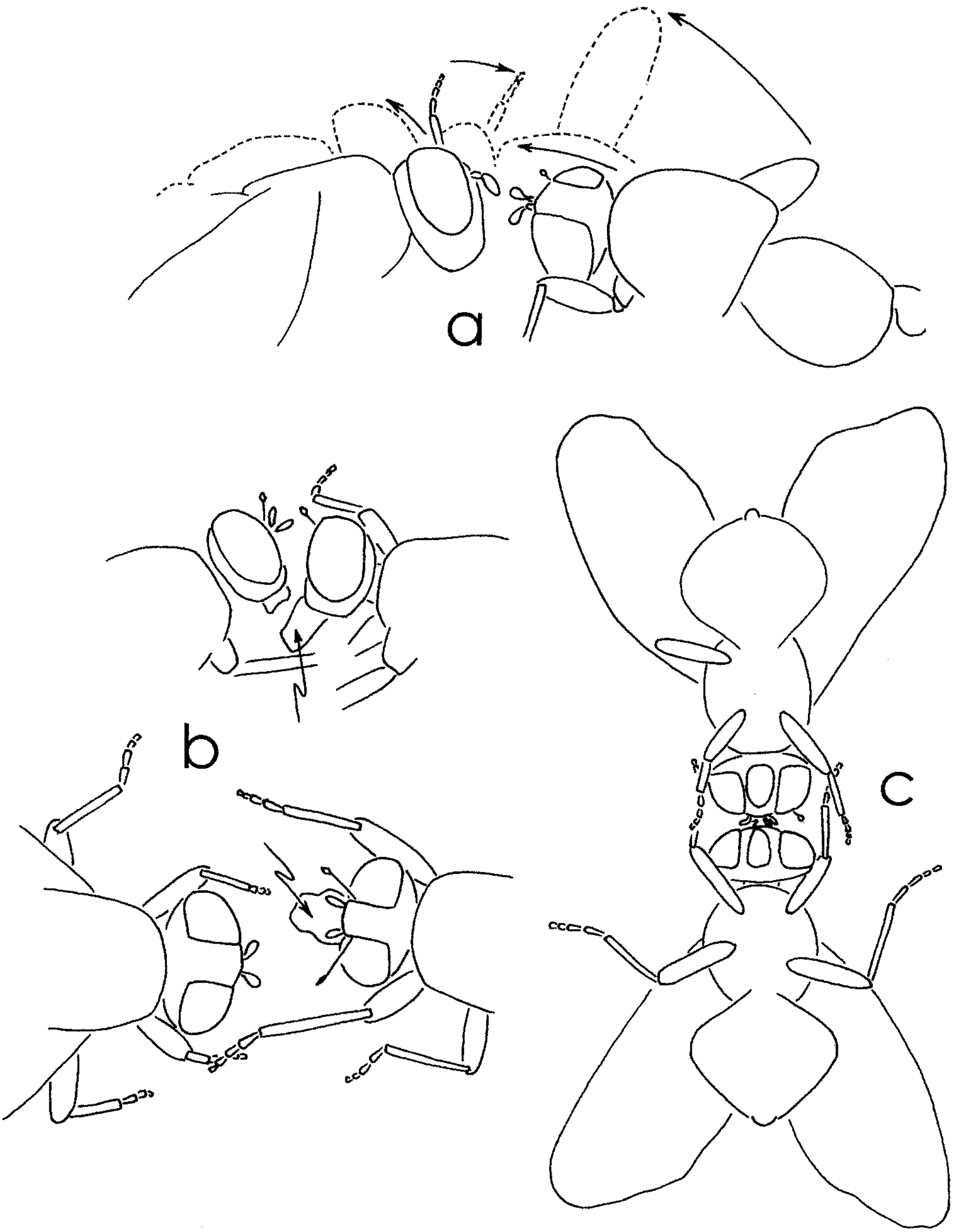

Fig. 5. Aggressive behavior patterns of male medflies. A. Butting. The male on the right lunged forward and also brought his right wing forward as his opponent leaned rearward but brought his raised leg down in a tap. B. Labellar display in lateral and dorsal view. C. Head pushing in ventral view. The flies' front legs were intermeshed, and they may have been used to upset the other's balance.

Push with head and mouthparts. When two flies extended their mouthparts to touch each other, they may have pushed each other in some cases, since their heads remained slightly separated and one fly leaned slightly rearward. Flies often subsequently touched heads and proceeded to push (Fig. 5c). Head pushing lasted on av-

Table 1. Frequency of different aggressive behavior patterns in male–male interactions of different strains in petri dishes. Asterisks indicate values which differed between wild and mass-reared flies (X^2 tests).

	Wild strain			Mass-reared strain		
	% of interactions	Number of events per interaction	% of all behavioral events	% of interactions	Number of events per interaction	% of all behavioral events
Enanation and butt	33	2.6	24	46	0.57	16
Enanation without butt	33	1.4	10.3	25	0.21	6
Wing strike	50**	1.0	14.5	2.5	0.14	12
Push with head and mouthparts	83**	0.52	8.2	12	0.20	6
Tap with front legs	92**	0.6	8.2	31	0.28	8
Wings over dorsum	17	0.24	1.7**	31	0.35	10
Labellar display	83**	0.64	16.2	50	0.42	12
Arching wings	33	0.16	14.0	25	0.14	12
Short wing vibration	8.3	0.08	0.0**	12.5	0.28	8
Synchronous supination	8.3	0.16	1.9**	12.5	0.35	10
N (interactions or behavioral events)	25	—	295	42	—	150

erage 6.11 ± 6.39 sec (N = 10) in wild flies, and 0.36 ± 0.59 sec (N = 24) in mass-reared flies ($p < 0.01$ with Mann Whitney U Test). No sound was associated with head pushing. Frequently head pushing ended when one of the flies mounted the other and attempted to mate (36%, N = 25). During pushing one male bent his legs and lowered his body toward the substrate, introducing his head below that of the other and thus provoking mounting. The mounted male then lowered his abdomen as if to achieve genitalic coupling. Eventually the mounted male climbed off, or was thrown off by the other.

B. Differences between males of different strains

In petri dishes the mix of different behavior patterns performed by wild and mass-reared males was similar ("% of all behavioral events" in Table 1), but aggressive interactions between wild males more often included forceful behavior such as labellar displays, wing strikes, and head and mouthpart pushing ("% of interactions" in Table 1). Aggressive interactions were more often initiated with wing strikes in mass-reared flies, and head butting in wild flies. Aggressive interactions lasted longer in wild flies (25.8 ± 60.9, N = 14) than mass-reared flies (12.5 ± 14.4, N = 28) ($p < 0.05$ with Mann Whitney U Test).

In the field cage, the maximum percentage of males present in the cage which participated in a lek during a day of observation was similar in wild (24%) and mass-reared males (20% with mass-reared females, 18% with wild females). Resident wild males were much more likely to win aggressive interactions in leks than were mass-reared males (win in 81.8% of 43 interactions, versus 5.7% of 35 interactions; $p < 0.001$ with X^2). When mass-reared males were in the cage, two males called with pheromones from the same leaf in six cases, while calling wild males never shared the same leaf. Mass-reared males only once defended a leaf with head butting, while this behavior occurred 21 times in wild males.

C. Female aggressive behavior

Females also interacted aggressively with other females in both petri dishes and the field cage. Mass-reared females performed all of the behavior patterns described above. Males generally reacted to females by courting them with continuous wing vibrations (e.g. Feron, 1962; Briceño et al., 1996). Males usually only behaved aggressively toward females after the female had attacked (62% of male-female aggressive interactions were initiated by the female, 38% by the male, N = 60).

Discussion

All the aggressive behavior patterns seen in *C. capitata* also occur in other tephritids (Headrick and Goeden 1994). The head pushing, enanation, and wing strikes we observed probably correspond to the head-to-head contact, lunging, and wing slashing reported by Arita and Kaneshiro (1989) in Hawaii. There were no qualitative differences in the aggressive behavior patterns of the two Costa Rican strains, or between mass-reared males and females. Wild flies were, however, quantitatively more aggressive in several aspects both in petri dishes and in field cages. They were more likely to contact the opponent directly, less likely to cede an occupied leaf to an invader in the field cage, and more likely to head butt in the field cage. Presumably reduced aggression has been favored under the highly crowded conditions of mass-rearing. Increased crowding results in facultative lowering of the frequency and intensity of aggressive behavior in many other animals (e.g. Andersson 1994, Thornhill and Alcock 1983). The differences observed in medflies probably represent evolutionary responses to selection pressures in mass-rearing cages. This interpretation must be tentative, however, in light of other patterns seen elsewhere: resident wild males were frequently displaced in leks in the field in Hawaii (Whitter et al., 1992); there were no differences in successful defense of leaves between wild males and those of an old mass-reared strain in Hawaii (T. E. Shelly, pers. comm.); and mass-reared *Vienna-42* males were successful in defending leaves nearly 50% of the time (Hendrichs et al. 1996).

The similarity between the sounds and the behavior of body vibration and head butting makes it seems likely that the sound produced during body vibration constitutes threat behavior. Determinations of fundamental frequencies were only approximate. It is clear, however, that aggressive sounds are substantially higher in pitch (around 1–3 KHz) than the sounds produced during courtship, which are in the range of 0.16–0.35 KHz (Webb et al., 1983). In general, the aggressive auditory stimuli may function as threats of physical attack, and to accentuate the effectiveness of attacks.

The adaptive significance of aggression in medfly leks is not clear. Losing males generally simply move to a nearby leaf and continue calling (Whittier et al., 1992; Shelly et al., 1993, 1994), and mating seems not to occur preferentially on particular leaves (Whittier et al., 1992). The variety of male aggressive behavior patterns shared with females and with other tephritids nevertheless suggests that aggression is probably selectively important.

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