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VARIATION IN THE INTERMITTENT BUZZING SONGS OF MALE MEDFLIES (DIPTERA: TEPHRITIDAE) ASSOCIATED WITH GEOGRAPHY, MASS-REARING, AND COURTSHIP SUCCESS

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ABSTRACT

Many aspects of the temporal pattern of sounds produced during the intermittent buzzing displays of pre-copulatory courtship by male medflies varied between wild flies from Costa Rica, Argentina, and Hawaii, and between mass-reared flies from Costa Rica, Argentina, Mexico, and Hawaii. There were no consistent differences when mass-reared strains were compared with the wild strains from the area where they originated in Costa Rica, Argentina and Hawaii. Buzzing sounds produced prior to successful mounting attempts did not differ consistently from those preceding unsuccessful mounts in flies from Costa Rica and Argentina. In strains from all sites, however, courtships in which buzzes were interrupted were more likely not to result in mounting of the female. There was a weak tendency for interruptions to be more common in mass-reared strains.

Key Words: Courtship sounds, medfly, geographic differences

RESUMEN

Varios aspectos de los patrones temporales de los sonidos del zumbido intermitente producido durante el cortejo pre-copulatório de los machos de la mosca del Mediterráneo variaron entre moscas silvestres de Costa Rica, Argentina y Hawaii, y entre moscas de sepas de cría masiva de Costa Rica, Argentina, Mexico y Hawaii. No se presentaron diferencias consistentes cuando se compararon las sepas de cría masiva en Costa Rica, Argentina y Hawaii con moscas silvestres de los sitios de origen. Los sonidos producidos durante cortejos que terminaron en cópulas no difieron de los sonidos producidos durante cortejos que llevaron a montas que fracasaron en moscas de Costa Rica y Argentina. Pero en sepas de todos los sitios los zumbidos intermitentes que incluyeron pequeñas pausas tuvieron una mayor probabilidad de no terminar en un intento de monta. Los zumbidos intermitentes de las moscas de las crias masivas tuvieron una tendencia leve a interumpirse mas frecuentemente.

Male medflies (*Ceratitis capitata* Wied.) produce two types of wing vibration during premount courtship (Féron 1962, Rolli 1976, Webb et al. 1983, see review of behavior in Briceño et al. 1996, Briceño & Eberhard 2002). During an early stage of courtship, the male produces the "calling song" with an average fundamental frequency of about 350 Hz (Webb et al. 1983), by vibrating his wings continuously while he looks toward the female and holds his abdomen bent ventrally so that the pheromone-producing everted rectal epithelium is ventral to the rest of his body. Probably a plume of pheromone is thus wafted toward the female. After an average of about 6 sec of continuous wing vibration, the rectal epithelium is retracted, and the male begins a series of intermittent wing buzzes (Fig. 1) which continue until he leaps onto the female or abandons courtship. Each buzz is associated with a more intense sound that has a lower average fundamental frequency of about 165 Hz (Webb et al. 1983). A single buzz lasts on the order of 0.1 sec and is produced during the time wings are vibrated rapidly with a large amplitude, from anterior of the male's head to back over his body (Briceño & Eberhard 2000). The softer calling song continues during the intervals between buzzes. During intermittent buzzing behavior the male often also rocks his head rapidly from side to side, often tapping the female with his aristae (Briceño & Eber-

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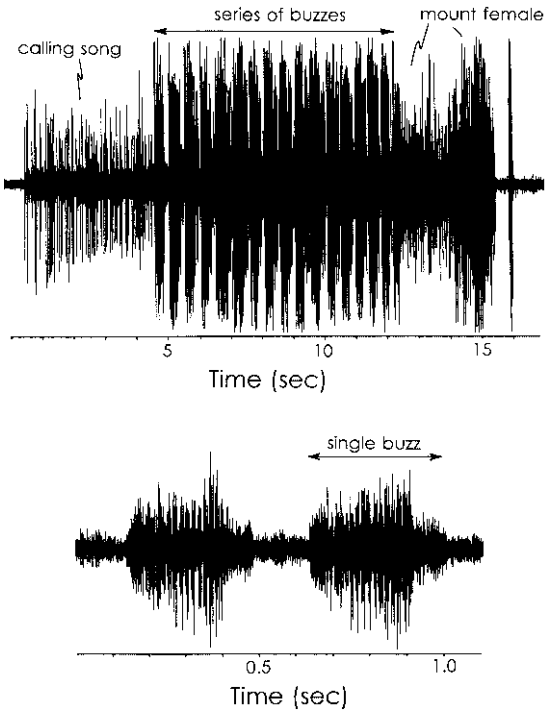


Fig. 1. Sounds produced by a male *Ceratitis capitata* during courtship and mounting.

hard in press). Finally the male leaps onto the female, shakes his body briefly rapidly forward and backward while producing another strong buzzing sound (Fig. 1). Sound production ends as the male then attempts to turn and establish genitalic contact; males do not resume sound production during copulation.

The significance of sounds produced during courtship in medflies is as yet unclear. Possible effects of sounds produced during courtship on copulation success, and of changes in the female's ability to perceive them have been investigated experimentally. Keiser et al. (1973) found that the percentage of females that were inseminated when male wings were removed dropped by about half, and Nakagawa et al. (1973) and Levinson et al. (1987) found that removal of the female antennae nearly completely eliminated copulation. However, the first experiment also modified possible visual stimuli, the second also modified possible tactile stimuli from the male's aristae, and both may have also modified chemical stimulation of females. There are thus as yet no conclusive demonstrations that any sounds are functionally important in courtship; it is possible that they are all only incidental consequences of other activities (i.e., creation of air currents) (see review in Eberhard 2000).

There are several reasons to expect that present day populations of medflies may not have uniform courtship songs. The geographic range of the species, which is native to Africa, has increased dramatically, and several population bottlenecks have probably occurred in recent times (Huettel et al. 1980, Fuerst 1988). Thus both drift and divergence under sexual selection in geographically isolated populations may have occurred. In addition, mass rearing of sterile males has often been used in attempts to control pest populations of medflies, and mass-reared strains have often been conserved for many years. Reproduction in these strains occurs under conditions that differ sharply from those in nature in several respects. Old mass-reared strains thus represent the results of inadvertent experiments in which several environmental conditions have been changed. It is not obvious, however, which song traits would be more advantageous under mass-rearing conditions. Rolli (1976) reported a lack of differences between the songs of wild medflies from Tunis and Morocco and mass-reared males in Germany (the age of the mass-reared strain was not specified). The sample sizes were small, however, and it is not clear which song characters were compared.

This paper tests the possibility of geographic divergence and of changes under mass-rearing in the temporal pattern of the intermittent buzz and the mounting songs of males of seven strains of flies: wild flies from Costa Rica, Argentina and Hawaii; mass-reared strains derived from these strains 6.5, 10, and more than 40 years previously; and a three-year old mass-reared strain from Mexico. Songs of successful and unsuccessful courtships are also compared.

Materials and Methods

Mass-reared flies from Costa Rica were from a strain which had been initiated in 1990 using wild flies collected near Alajeula, Costa Rica, and maintained subsequently at the Laboratorio de Manejo Integrado de la Mosca de la Fruta mass-rearing facility. Wild flies were raised from larvae that emerged from infested tangerines collected in Jan-April, 1997, at the Estación Experimental Faubio Baudrit near Alajuela, Costa Rica.

Argentinian mass-reared flies came from the Mendoza strain, which had been derived from flies collected about 10 years before our observations in Mendoza province, Argentina. Wild flies were a laboratory G2 derived from flies raised from fruit collected in the field in the Alto Valle region of Patagonia. Mass-reared flies in Mexico were from a three year-old strain derived from flies collected as larvae from coffee in Costa Cuca, Quetzaltenengo, Guatemala. Hawaiian mass-reared flies were from the Hilab strain derived from wild flies more than 40 years previously, while wild flies were reared from coffee fruit collected on Kauai.

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Adult flies of all strains were separated by sexes when they were less than two days old, and fed mixtures of sugar and protein hydrolysate. Male-female pairs of mass-reared flies were placed together for video taping when they were five days old; male-female pairs of wild flies, whose sexual maturation is more delayed, were placed together only after they were 10 days old.

Pairs of flies in Costa Rica and Hawaii were videotaped in 13.7 cm diameter and 1.8 cm deep mating chambers (clear Petri dishes) on a glass table using a Sony CCD Video Hi 8 camera equipped with + 6 closeup lenses. The camera was below the table, allowing taping from below (most courtships occurred on the ceiling of the mating chamber). A small microphone (Sennheiser System MZK 80ZU) was inserted through a hole in the side of the chamber and connected to the camera. Pairs in Argentina and Mexico 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. Five minutes after the male began emitting pheromone, a female was released into the cage, and the flies' behavior was recorded for 30 min or until they copulated.

All recording environments were noisier than that used by Webb et al. (1983), and both types of mating chambers produced strong echoes. Other than verifying that the apparent fundamental frequencies of the songs of the Costa Rican flies were similar to those observed by Webb et al. (1983), we did not attempt to analyze the frequencies or power spectra of songs. Instead we concentrated on the temporal patterns of the songs. There are indications in other flies that temporal patterning may be an especially important aspect of songs (Bennet-Clark & Ewing 1969, Kyriacou & Hall 1982, Tomaru & Oguma 1994, Aspi & Hoikkala 1995, Neems et al. 1997, and Hoikkala & Kaneshiro 1997 on *Drosophila*).

Recordings of sounds were imported from video recordings into a PC 486dx2 computer using a 16 bit card. The mean durations of buzzes and intervals between buzzes were measured using the real time display in the program Avisoft® when cursors marked the beginning and the end of the envelope curve displayed in the main window of the program (Fig. 1). The precision of these measurements was determined by re-measuring the duration of 10 buzzes and 10 intervals in each of 8 different courtships. The average differences were 2.0 ms in buzz duration, and 2.2 ms in interval duration. In addition, the number and duration of interruptions during the buzzes was determined. An interruption was defined as any interval between buzzes that was more than twice the mean of the intervals immediately preceding and following it (Fig. 2).

We examined two different sets of buzzes in Costa Rican flies: the first 10 buzzes in the courtship of a male; and the last 10 buzzes before the male either leapt onto the female or ceased courting, to determine whether the characteristics of buzzes varied systematically during courtship.

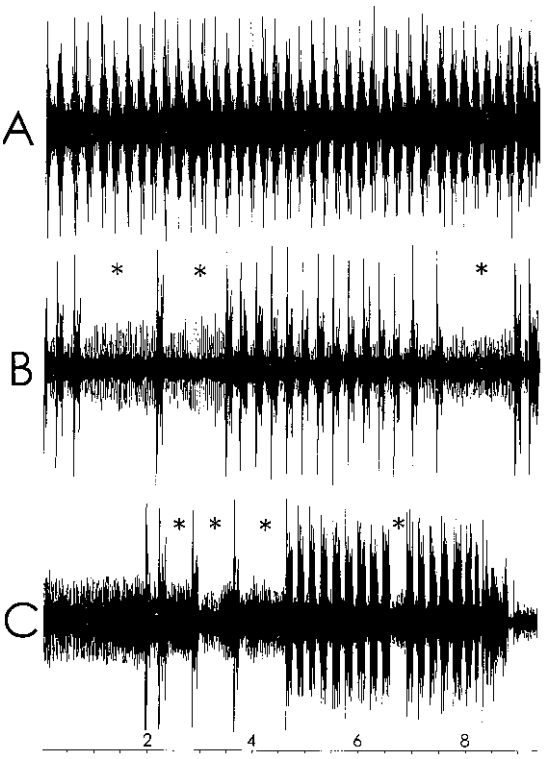


Fig. 2. Three intermittent buzzing courtships in which interruptions (*) were absent (A) and present with slower (B) and more rapid buzzing (C) (all with same time scale).

Courtship outcome was classified in three classes: *no mount*—the male ceased courting without attempting to mount the female (failure to mount is often associated with failure of the female to align herself properly with the courting male and to remain still—Briceño et al. 1996, Briceño & Eberhard 2002); *failed mount*—the male mounted but was dislodged within 10 s when the female struggled; and *successful mount* - the male mounted the female and achieved genitalic contact.

All statistical tests were non-parametric Mann Whitney U Tests due to the highly skewed distributions of many variables. Means are presented followed by one standard deviation for illustrative purposes only.

Results

There was no clear, consistent tendency for buzz duration or interbuzz duration to differ between the first and last 10 buzzes of a courtship in Costa Rican or Argentinian flies (Fig. 3). Wild flies

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from Costa Rica, Argentina, and Hawaii differed significantly in all five pre-mount song traits (Table 1). Comparing wild flies, those from Argentina produced longer buzzes, those from Hawaii produced the largest number of buzzes/courtship, and those from Costa Rica had longer intervals between buzzes and a lower overall rate of buzzing. Wild Hawaiian flies had the longest mount buzzes. Mass-reared flies from the three sites also differed in many traits. When mass-reared and wild flies from the same site were compared, no traits showed the same trends at all three sites.

In an attempt to understand the possible selective factors which might influence song characteristics, we compared several aspects of intermittent buzzes in courtships that led to copulation as compared with those that ended in female rejection of a mount or a failure to mount in different strains (Tables 2 and 3). There were no consistent directional differences for traits related to durations and frequencies of intermittent buzzing (Table 2). The duration of the mount buzz was marginally longer in successful mounts in the mass-reared strain from Costa Rica, but there were no similar trends in wild Costa Rican flies or in strains from Argentina and Hawaii.

In contrast, there was a consistent trend in each of the six strains with good sample sizes for interruptions in intermittent buzzing to be more frequent in courtships that did not lead to a mounting attempt (first two columns in Table 3); combining the data from all strains, the frequency with which buzzing was interrupted was 72.3% of 166 courtships which did not lead to mounting, 39.2% of 263 in which the male mounted but was then rejected, and 28.4% of 81 in which the male mounted and succeeded in copulating. Hawaiian flies were more likely to interrupt buzzing. Among the other sites, mass-reared males in Costa Rica were less likely to interrupt their courtships than mass-reared males from Argentina or those from Mexico, but there was no difference in this respect between wild flies from Costa Rica and Argentina. There were no differences when mass-reared flies were compared with their respective wild counterparts in Costa Rica, Argentina, and Hawaii with respect to the proportion of courtships in which buzzing was interrupted, the number of interruptions, or their durations. But there were similar trends for more interruptions to occur in mass-reared strains, and when data from different sites were combined, mass-reared flies were slightly more likely to interrupt buzzing (52.7% of 262) than were wild flies (41.7% of 156) ($P = 0.0297$ with Chi Squared Test).

The apparent female bias against interrupted buzzing did not extend to events that occurred after mounting. There was no significant association in any strain between the occurrence of an interruption, the number of interruptions, or the mean duration of interruptions and the likelihood that the female would reject the male once he had mounted. Similarly, when all courtships in which mounts occurred were combined for all strains, there was no significant relation between male copulation success and whether or not buzzing had been interrupted.

When song parameters were correlated with male body size (estimated by the maximum width of the head in dorsal view), there was only one significant relationship, with the total number of buzzes/courtship ($r = 0.26$ with log-transformed numbers, $P < 0.05$). Other correlation coefficients were -0.01 ($P = 0.99$) for the mean duration of each buzz, -0.12 ($P = 0.29$) for the mean duration of interval between buzzes, -0.06 ($P = 0.62$) for the number of buzzes/s, 0.22 ($P = 0.20$) for the log of total duration of buzzing, and 0.17 ($P = 0.41$) for the duration of the mount buzz.

Discussion

Although there were several differences between mass-reared and wild Costa Rican flies in duration and number of buzzes, similar differences did not occur between mass-reared and wild flies from Argentina and Hawaii. This suggests that the differences in the Costa Rican flies may not be due to mass-rearing per se. This result is in accord with a less-detailed study of flies from Tunis and Morocco (Rolli 1976), and with the lack of obvious differences in selective pressures on the details of intermittent buzzing behavior under mass-rearing conditions.

Similarly, there were no consistent differences between successful and unsuccessful courtships in Costa Rican, Argentinian and Hawaiian flies in many of the song variables that we measured. However the possibility of stabilizing sexual selection on these traits cannot be excluded until further analyses are performed. We also did not measure additional aspects of the song, such as its intensity and basic frequency, and there are other ways that vibrations may be transferred to the female, such as through substrate and near field medium motion (Markl 1983). Song intensity is an important determinant of female acceptance in the tephritid *Anastrepha suspensa* (Loew) (Sivinski et al. 1984). Thus while presently available data do not support the idea that song traits influence courtship success, the possibility cannot be ruled out.

The strongest association we found with the eventual outcome of courtship was that between interruptions of intermittent buzzing behavior and failure to mount (Table 3). The significance of this association is not clear. On the one hand, our criterion for distinguishing interruptions was obviously arbitrary. The strength and consistency of the association we found with failure to mount leaves little doubt that there is an association of some sort with the pattern of buzzes, but it is uncertain whether or not the biologically relevant criterion is the one which we used.

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TABLE 1. SONG CHARACTERISTICS FOR COURTSHIPS THAT LED TO BOTH SUCCESSFUL AND UNSUCCESSFUL MOUNTS IN WILD AND MASS-REARED MEDFLIES FROM COSTA RICA, ARGENTINA, MEXICO, AND HAWAII (MEAN ONE STANDARD DEVIATION). VALUES IN THE SAME ROW FOLLOWED BY THE SAME LETTER AND NUMBER I DIFFER SIGNIFICANTLY WITH MANN-WHITNEY U TESTS ($a = P < 0.05$; $b = P < 0.01$; $c = P < 0.001$).

	Costa Rica		Argentina		Mexico	Hawaii	
	Wild	Mass-reared	Wild	Mass-reared	Mass-reared	Wild	Mass-reared
Intermittent buzzes:							
Duration of each buzz (ms)	113 ± 16 $c_1c_2c_3$	152 ± 70 $b_2c_1c_4c_8$	127 ± 26 $c_2c_5c_7$	135 ± 16 $a_1c_3c_4c_9$	113 ± 16 $a_1b_2c_5c_{10}$	114 ± 12 c_6c_7	95 ± 12 $c_6c_8c_9c_{10}$
Duration of each interval between buzzes	178 ± 108 b_1	173 ± 52	145 ± 44 b_1	149 ± 47	182 ± 167	152 ± 46	151 ± 102
Total number of buzzes/courtship	34.7 ± 19.0 c_1b_1	29.1 ± 14.6 b_2c_3	24.6 ± 14.0 b_3c_1	25.5 ± 15.5 $b_1c_2c_4$	45.8 ± 31.1 $b_2b_3c_2$	55.0 ± 43.4	47.4 ± 21.4 c_3c_4
Rate (number/sec)	3.57 ± 0.67 a_1c_1	3.03 ± 0.95 $b_1c_1c_2c_3c_5$	3.75 ± 0.85 $a_1b_1b_2c_3$	3.65 ± 0.84 b_2c_4	4.11 ± 0.65 c_2c_4	4.04 ± 0.53	4.30 ± 1.30 c_5
Total duration of buzzing (s)	9.64 ± 5.98 a_1b_1	11.07 ± 8.49 $a_2b_1b_2$	7.58 ± 5.16 $a_1b_2b_3$	7.16 ± 4.31 $a_2c_1c_2$	15.03 ± 12.65 c_1b_3	14.2 ± 11.2	11.7 ± 10.3 c_2
N (courtships)	90	142	66	46	55	11	44
Mount buzz:							
Duration (s)	1.77 ± 0.41 $a_1a_2c_1$	2.76 ± 0.41 $a_1b_1c_2$	1.23 ± 0.44 c_1	1.58 ± 0.86 b_1	1.10 ± 0.52 b_2	3.22 ± 2.70 a_2	4.86 ± 4.52 c_2
N (courtships)	37	36	40	30	36	9	28

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TABLE 2. SONG CHARACTERISTICS PRECEDING SUCCESSFUL (S) AND UNSUCCESSFUL (U) MOUNTS BY MASS-REARED AND WILD COSTA RICAN, ARGENTINIAN, AND HAWAIIAN FLIES (MEAN ± STANDARD DEVIATION). VALUES IN THE SAME ROW FOLLOWED BY THE SAME LETTER AND NUMBER DO NOT DIFFER SIGNIFICANTLY WITH MANN-WHITNEY U TESTS ($A = P < 0.05$).

	Costa Rica				Argentina				Hawaii	
	Mass-reared		Wild		Mass-reared		Wild		Mass-reared	
	S	U	S	U	S	U	S	U	S	U
Intermittent buzzes:										
Duration of each buzz (ms)	156 ± 71	152 ± 69	114 ± 16	113 ± 16	137 ± 18	135 ± 15	134 ± 22	125 ± 25	105 ± 14 $\underline{a_1}$	92.4 ± 10.5 $\underline{a_1}$
Duration of each interval between buzzes (ms)	164 ± 51	175 ± 52	155 ± 59	184 ± 118	138 ± 40	155 ± 50	132 ± 41	148 ± 45	115 ± 32	159 ± 110
Total number of buzzes/courtship	24 ± 10	30 ± 15	35 ± 16	37 ± 26	28 ± 16	24 ± 16	26 ± 17	26 ± 18	39 ± 19	49 ± 22
Rate (number/s)	2.5 ± 0.7	3.0 ± 0.9	3.7 ± 0.4	3.5 ± 0.7	3.9 ± 0.9	3.5 ± 0.8	3.6 ± 1.0	3.6 ± 0.9	4.4 ± 1.7	4.3 ± 1.1
Total duration of buzzing (s)	9.7 ± 3.6	11.2 ± 8.9	9.0 ± 4.0	9.7 ± 6.4	7.6 ± 4.6	6.9 ± 4.2	8.6 ± 6.7	7.3 ± 4.8	7.5 ± 4.6	12.5 ± 6.5
N	32	110	30	60	15	31	13	53	18	30
Mount buzz:										
Duration (s)	6.9 ± 4.3 $\underline{a_2}$	2.6 ± 1.8 $\underline{a_2}$	1.5 ± 1.9	1.8 ± 0.5	1.2 ± 0.4	1.9 ± 1.0	1.4 ± 0.5	1.2 ± 0.4	1.2 ± 0.1	1.3 ± 0.4
N	14	22	17	20	15	31	13	53	8	25

TABLE 3. ASSOCIATION BETWEEN THE OCCURRENCE OF AN INTERRUPTION IN INTERMITTENT BUZZING, AND THE NUMBER AND DURATION OF INTERRUPTIONS WITH THE OUTCOMES OF COURTSHIPS IN DIFFERENT STRAINS. MEANS WERE CALCULATED ONLY FOR THOSE COURTSHIPS IN WHICH INTERRUPTIONS OCCURRED, AND ARE FOLLOWED BY ± ONE STANDARD DEVIATION. THE SAMPLE SIZES (IN PARENTHESES) FOR MEAN NUMBER OF INTERRUPTIONS REFER TO THE NUMBER OF COURTSHIPS; FOR MEAN DURATION THEY REFER TO THE NUMBER OF INTERRUPTIONS. MC = MOUNT AND COPULATE; MF = MOUNT BUT FAIL TO COPULATE DUE TO FEMALE RESISTANCE; NM = NO MOUNT. ASTERISKS DENOTE NM INTERRUPTION FREQUENCIES THAT WERE SIGNIFICANTLY LOWER THAN THE FREQUENCIES FOR MC AND MF IN THE SAME STRAIN USING A CHI^2 OR A FISHER EXACT TEST (F). IN NO STRAIN DID MC FREQUENCY DIFFER SIGNIFICANTLY FROM MF FREQUENCY, NOR WAS THE FREQUENCY FOR ALL MC (DATA FROM ALL STRAINS COMBINED) DIFFERENT FROM THAT FOR ALL MF (CHI^2 TEST). VALUES FOLLOWED BY THE SAME LETTER ARE SIGNIFICANTLY DIFFERENT (a AND * = $P < 0.05$, B AND ** = $P < 0.01$, *** = $P < 0.001$).

Strain and outcome		Interrupt? Yes	Interrupt? No	Mean number of interruptions	Mean duration of each interruption
Costa Rica					
Mass-reared	MC	0	15	—	—
	MF	15	45	2.8 ± 3.29 (15)	1.46 ± 2.19 (43)
	NM***	15	9	4.07 ± 3.24 (14)	1.40 ± 1.35 (39)
	Total $\underline{a_1}\underline{b_1}\underline{c_4}\underline{c_5}$	30	69	3.36 ± 3.20 (20)	1.44 ± 1.75 (82)
Wild	MC	1	9	2.0 (1)	1.80 ± 1.64 (2)
	MF	9	34	1.66 ± 1.65 (9)	1.98 ± 4.33 (15)
	NM***(F)	10	2	2.36 ± 1.93 (10)	0.81 ± 0.43 (26)
	Total $\underline{c_3}\underline{c_6}$	20	45	2.15 ± 1.87 (20)	1.26 ± 2.60 (43)
Argentina					
Mass-reared	MC	8	12	2.00 ± 1.15 (7)	1.81 ± 1.75 (15)
	MF	15	18	2.23 ± 1.42 (13)	1.93 ± 3.30 (30)
	NM*(F)	11	2	1.92 ± 2.60 (11)	1.47 ± 1.24 (31)
	Total $\underline{a_4}\underline{b_1}\underline{b_2}$	34	32	2.34 ± 1.84 (31)	1.72 ± 2.33 $\underline{b_2}$ (76)
Wild	MC	4	9	1.75 ± 0.95 (4)	1.47 ± 0.67 (7)
	MF	14	30	1.37 ± 0.71 (14)	1.47 ± 1.94 (27)
	NM**(F)	8	2	2.15 ± 1.35 (8)	1.10 ± 1.09 (17)
	Total $\underline{c_2}\underline{c_7}$	26	41	1.64 ± 0.98 (26)	1.34 ± 1.56 (51)
Mexico					
Mass-reared	MC	0	3	—	—
	MF	23	21	3.30 ± 4.07 (23)	1.08 ± 1.28 $\underline{a_3}$ (80)
	NM***	20	25	5.31 ± 5.44 (20)	1.27 ± 1.30 $\underline{a_3}$ (116)
	Total $\underline{a_1}\underline{b_3}\underline{c_1}$	43	49	4.28 ± 4.82 (43)	1.19 ± 1.29 $\underline{b_2}$ (196)
Hawaii					
Mass-reared	MC	9	9	3.75 ± 2.75 (4)	0.375 ± 0.22 (4)
	MF	19	11	5.10 ± 4.86 (19)	1.02 ± 1.21 (19)
	NM	46	3	3.80 ± 2.62 (46)	1.17 ± 1.50 (46)
	Total $\underline{b_2}\underline{c_{1\text{-}4}}$	74	23	4.15 ± 3.40 (69)	1.08 ± 1.40 (69)
Hawaii					
Wild	MC	1	1	3 (1)	1.13 (1)
	MF	8	1	3.25 ± 2.86 (8)	1.20 ± 1.23 (8)
	NM	10	3	4.00 ± 2.58 (10)	0.77 ± 0.45 (10)
	Total $\underline{a_4}\underline{b_3}\underline{c_{5\text{-}7}}$	19	5	3.63 ± 2.60 (19)	1.01 ± 0.94 (19)

In addition, cause and effect relations in this association are uncertain. Further analyses will be required to distinguish between two possibilities. Interruption of buzzing may be a cue used by females, and they may exercise selection against those males whose buzzes are interrupted, failing to allow the male to mount by positioning themselves properly. Alternatively, females may not use interruption of the buzz as a cue, but rather the male may interrupt his buzzing when he per-

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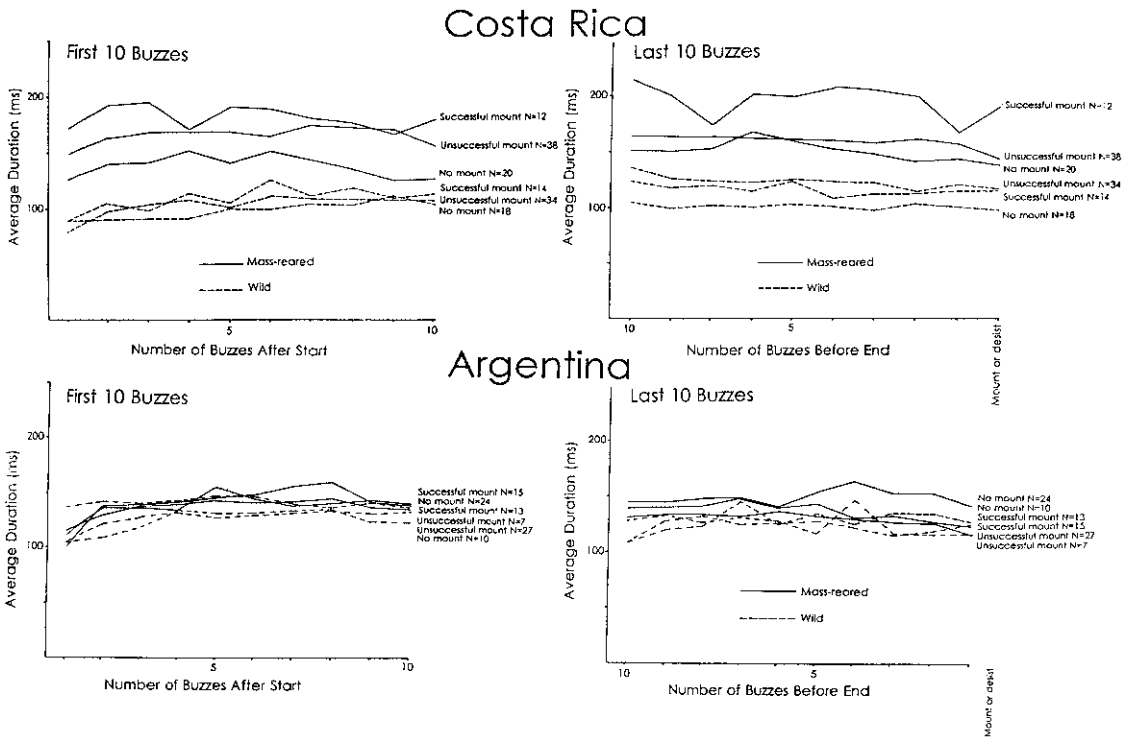


Fig. 3. Durations of the first and last 10 buzzes in courtships of wild and mass-reared Costa Rican and Argentinian flies that led to successful mounts (copulation), unsuccessful mounts (female rejection), and failure to mount (n = number of courtships).

ceives from the female's behavior that she is about to reject him. However this question is resolved, it does not appear that our results will help explain the common inferiority of mass-reared males as compared with wild counterparts, as we found only a weak difference in interruption frequencies between mass-reared and wild males from the same site.

There were several geographic differences between both wild and mass-reared strains in the details of intermittent buzzing. Possible causes of divergence include founder effects and divergent sexual selection in different populations. The lack of consistent association between these details of male songs and copulatory success argues against the possible significance of sexual selection.

Sizes of mass-reared males from Hawaii showed little sign of strongly influencing the different song parameters we measured in this study.

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