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DECISIONS DURING COURTSHIP BY MALE AND FEMALE MEDFLIES (DIPTERA, TEPHRITIDAE): CORRELATED CHANGES IN MALE BEHAVIOR AND FEMALE ACCEPTANCE CRITERIA IN MASS-REARED FLIES

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Abstract

Analyses of more than 300 videotaped courtships of wild and mass-reared medflies from Costa Rica showed that the tendency for male and female to align themselves facing directly toward each other increased, and that the distance between them decreased as courtship proceeded. More direct alignments and shorter distances between the flies at the moment the male jumped onto the female were correlated with greater female acceptance of copulation. There were no consistent differences in durations of components of intermittent buzzing songs or male size between successful and unsuccessful courtship in either strain. Several possible cues may release different courtship responses: males of both strains tend to initiate both continuous vibration and intermittent buzzing after reduction of the distance to the female; slow creeping toward the female was associated with longer courtships that had failed to lure the female close; and females tended to turn to face more directly toward the male soon after the male began continuous vibration, and especially after he began intermittent buzzing. Females became progressively more immobile as courtship progressed, especially soon after intermittent buzzing began. There were numerous differences between strains. Mass-reared males were more likely to mount females without previous courtship than were wild males. Wild males initiated continuous wing vibration when farther from the female and when the female was looking less directly toward them, but the two strains did not differ in the distances and angles at which males initiated intermittent buzzing and jumped. Wild males were more likely to creep toward the female during intermittent buzzing. Mass-reared females but not wild females were more likely to copulate when the proportion of time the male had spent in intermittent buzzing was low, and if the courtship began when the flies were nearer each other. Wild but not mass-reared females were less likely to copulate if courtship was shorter. Possible coevolution of female responses with the five different male courtship traits that differ between mass-reared and wild flies are discussed.

Key Words: medfly, sexual selection, courtship behavior, mass-rearing, female choice

Resumen

Análisis de más de 300 cortejos video-grabados de moscas del Mediterráneo silvestres y criadas en masas de Costa Rica demostraron que la tendencia de los machos y las hembras de alinearse cara a cara el uno frente al otro aumentó, y que la distancia entre ellos ha disminuó a medida que el cortejo procedía. Alineaciones más directas y distancias mas cortas entre las moscas en el momento en que el macho salta sobre la hembra se correlacionaron con mayor aceptación por parte de las hembras. No hubo diferencias consistentes en la duración de los componentes de los zumbidos intermitentes de las canciones o el tamaño del macho, entre los cortejos efectivos y no efectivos en ninguna de las dos razas. Varios estímulos posibles podrían inducir diferentes respuestas en el cortejo: machos de ambas razas tienden a iniciar vibraciones tanto continuas como intermitentes que después de se reduce la distancia a la hembra; un lento acercamiento hacia la hembra se asoció con cortejos más largos que no lograron inducir el acercamiento de la hembra; y hembras que presentaron la tendencia de girar y encarar más directamente al macho pronto después de que el macho inició las vibraciones continuas, y especialmente después de que iniciaron los zumbidos intermitentes. Las hembras se hicieron progresivamente más inmóviles a medida que el cortejo continuaba, especialmente poco tiempo después que el zumbido intermitente se inició. Existieron numerosas diferencias entre las razas. Los machos criados en masa montaron a las hembras sin ningún tipo de cortejo previo, con mayor frecuencia que los machos silvestres. Los machos silvestres iniciaron vibración continua cuando se encontraban a mayor distancia de la hembra y cuando las hembras se orientaron menos directamente hacia ellos, pero las dos razas no difirieron en las distancias y ángulos a los cuales los machos iniciaron su zumbido intermitente y saltaron. Los machos silvestres se acercaron lentamente hacia las hembras con mayor frecuencia durante el zumbido intermitente. Las hembras criadas en masa, a diferen-

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cia de las hembras silvestres presentaron mayor tendencia a copular cuando la proporción de tiempo que el macho utilizó en el zumbido intermitente fue baja, y si el cortejo comenzó cuando las moscas estaban mas cerca las unas a las otras. Hembras silvestres a diferencia de las hembras criadas en masa, tendieron a copular menos si el cortejo era mas corto. La posibilidad de coevolución en las respuestas de la hembra hacia los cinco rasgos del cortejo que difieren entre las moscas criadas en masas y las mosca silvestres se discuten.

The success of the massive efforts to control pest populations of the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann using mass-reared sterile males depends on the abilities of these males to successfully induce wild females to copulate with them. Nevertheless, current understanding of why it is that some courtships result in copulation, while the majority do not, is only fragmentary. The commonly observed mating inferiority of mass-reared males as compared with wild males when they are paired with wild females (e.g., Rössler 1975b, Calkins 1984, Shelly et al. 1994, Hendrichs et al. 1996) is apparently due to their inadequate courtship per se, rather than to inferior abilities to find and attend leks, or to attract females pheromonally and begin to court them once they are at a lek (Shelly et al. 1994, Shelly & Whittier 1996, Hendrichs et al. 1996, Liimatainen et al. 1997, Lance et al. 2000.). Differences in courtship behavior between wild and mass-reared males are, however, only starting to be studied (Briceño et al. 1996, Liimatainen et al. 1997, Briceño & Eberhard 1998, 2000 in press).

Courtship in medflies was first studied in detail by Feron (1962) and current knowledge was reviewed by Eberhard (2000). Usually courtship follows a relatively standard sequence of events, during which the male courts actively but stays more or less in one place. The female performs little if any overt courtship behavior, but moves toward the male and aligns herself facing him. Active male behavioral courtship begins when the male (usually while he is in the pheromone releasing posture—stage I of Feron) responds to the presence of the female (apparently on the basis of visual cues—Feron 1962, Kaneshiro 2000) by turning toward her. He bends his abdomen ventrally and starts to vibrate his wings (stage II of Feron, "continuous wing vibration" of Eberhard 2000). The abdominal pleura and the rectal sac, which are everted during stage I and presumably release pheromone (e.g., Nation 1981, Headrick & Goeden 1994 on other tephritids with similar structures), remain everted, and the wing vibrations, which involve rapidly twisting the wings on their longitudinal axes, presumably causes pheromone to be wafted toward the female (Arita & Kaneshiro 1989, Briceño & Eberhard 2000). The abdominal pleura often pulse during continuous wing vibration (unpublished data). After a variable amount of continuous wing vibration, the male switches abruptly to a second type of wing movement. He moves his wings rhythmically forward and back while continuing to vibrate them rapidly, and he also intermittently rocks his head from side to side and forward and backward (stage III of Feron, "intermittent wing buzzing" and "head rocking" of Eberhard 2000). In some cases the male "creeps" slowly toward the female with small steps that are taken each time he initiates a buzz (Briceño & Eberhard in press). Chemical signaling is probably altered and may be suspended during stage III, since the rectal sac is retracted when intermittent wing buzzing begins (Figure 3-3 of Feron 1962, Briceño et al. 1996). Head rocking often results in contact between the male's aristae and those of the female (Briceño & Eberhard in press).

After a variable amount of intermittent wing buzzing, the male jumps onto the female if she is appropriately positioned in front of him. If she does not dislodge him by flying or falling, as frequently occurs (Eberhard 2000, Lance et al. 2000), he aligns himself on her dorsum, and, if she everts her aculeus from the tubular eversible membrane, he grasps it with his genitalic surstyli and intromits (Eberhard & Pereira 1995). Males also perform apparent courtship movements during copulation itself (Eberhard & Pereira 1995), suggesting that the male also attempts to influence further female decisions (e.g., transport sperm—Yuval et al. 1996) after his genitalia have entered the female's body (Eberhard 1991). This stage of the male-female interaction will not be considered further here, and the term "courtship" will refer only to precopulatory behavior. There is at least one alternative male behavioral sequence. The male does not court, but simply jumps onto the female and immediately attempts to copulate (Prokopy & Hendrichs 1979).

These descriptions show that both the male and the female make a series of behavioral "decisions" or transitions during courtship. The male makes at least five decisions: whether to begin courtship or to jump immediately; when, if he is going to court, to begin continuous wing vibration; when to switch from continuous vibration to intermittent wing buzzing; whether to creep toward the female during intermittent buzzing; and when to terminate intermittent buzzing and jump onto the female. Females also make decisions, although some are less easily characterized. Indirect data (Briceño et al. 1996) indicate that female behavior which results in her being immobile, directly in front of the male and facing directly toward him, increases the chances that he will jump onto her. Such female responses may include turning or not turning, and walking or not walking. Once the male jumps, two further female decisions are

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more easily categorized: whether or not to dislodge the male; and whether or not to evert her aculeus (and thus allow him to intromit).

Understanding the factors that influence the decisions of both males and females will probably help clarify why some courtships succeed and others fail. One attractive possibility is that males and females exchange signals during courtship (Lux & Gaggl 1996, Liimatainen et al. 1997). For instance, the male decisions to switch from continuous wing vibration to intermittent buzzing or to jump could be triggered by some particular female behavior indicating that she is receptive. A review of available data showed, however, that there is no quantitative evidence that any particular female behavior has a triggering effect on male behavior (Eberhard 2000). Briceño & Eberhard (1998) found three possible female signals that showed significant associations with eventual mounting attempts (strike the male with her head; lean slowly rearward and sometimes crouch; and tap the male's legs with her front legs); but none had a significant effect on the likelihood that the male would mount after the female performed them. In other words, males appeared not to pay attention to these possible signals from the female.

One possible cue that could be used in male-female dialogues is the female's position with respect to the male. There were differences between positions at the moment the male jumped onto the female as compared with positions when the courting male desisted from courting (Briceño et al. 1996). The present study constitutes an attempt to use similar correlational evidence, in this case from a much larger sample of courtships. Not only the male's decision to jump, but also his decision whether to court rather than jump immediately, when to initiate courtship, and when to switch from continuous wing vibration to intermittent buzzing, as well as the female's decision whether or not to allow a male to mate after he has mounted her are analyzed.

Materials and Methods

Wild flies were raised from fallen tangerines and oranges collected at the Estación Experimental Fabio Baudrit of the Universidad de Costa Rica, el. about 900 m near Alajuela, Alajuela Province, Costa Rica. Mass-reared flies were from a strain that had been founded about three years previously with flies collected in the same area, and kept as adults thereafter (about 51 generations) in $2.30 \times 0.35 \times 0.50$ m breeding cages with approximately 60,000 flies/cage. Flies were separated by sex the day after emergence, and kept in $32 \times 32 \times 32$ cm cages with free access to water and a mixture of sugar and hydrolyzed protein. Immediately before taping sessions flies were aspirated into mating chambers (9.5 cm diameter plastic Petri dishes with millimeter ruled paper on the top of the lid) that had either one pair/dish or that were divided into four equal sectors by cardboard walls with one pair/sector. A subset of the males was preserved by freezing, and later measured using an ocular micrometer at 30× (maximum width of head, maximum length and width of the thorax in dorsal view).

All data came from analyses of videotaped courtships in which the male mounted the female. To avoid pseudoreplication, only the first courtship of each pair of animals was analyzed, and the only courtships included were those in which the male performed a single episode of continuous wing vibration followed by a single episode of intermittent wing buzzing and then leapt onto the female (i.e., courtships in which, for example, the male resumed continuous vibration after intermittent buzzing and then eventually mounted were excluded). Each animal was used only once. Several variables were measured at each of seven moments that were associated with three transitions in male behavior: one s before and one s after the male initiated continuous wing vibration as well as the moment when he initiated this behavior; one s before, one s after, and the moment when the male initiated intermittent buzzing; and the moment when the male jumped onto the female. Data preceding and following transitions were analyzed to elucidate stimuli associated with particular decisions. For instance, a change in the female's position from one s prior to the initiation of buzzing to the moment when buzzing began could be the stimulus used by males to trigger buzzing. In contrast, only data from the moments that transitions occurred were used in analyses involving female acceptance of copulation.

Three variables that were measured to estimate the flies' relative positions are illustrated in Fig. 1: the distance between the centers of the two animals' prothoraces; the orientation of the female with respect to the direction in which the male was oriented (the angle she made with his longitudinal axis—"male angle" in Fig. 1); and the orientation of the male with respect to the direction in which the female was oriented (the angle he made with her longitudinal axis—"female angle" in Fig. 1). These variables were measured using the NIH Image program (public domain software) by grabbing a frame from the video with a Genius videocapture card (Pro II series) and importing it into a computer. Walking behavior was counted as forward movements, and did not include when the fly turned but the center of its thorax was immobile.

Other variables measured included the duration of each stage of courtship, and the length of time the female had been immobile preceding the moment the male leapt onto her. When the male jumped onto the female, the time elapsed until the female began to resist, whether or not she re-

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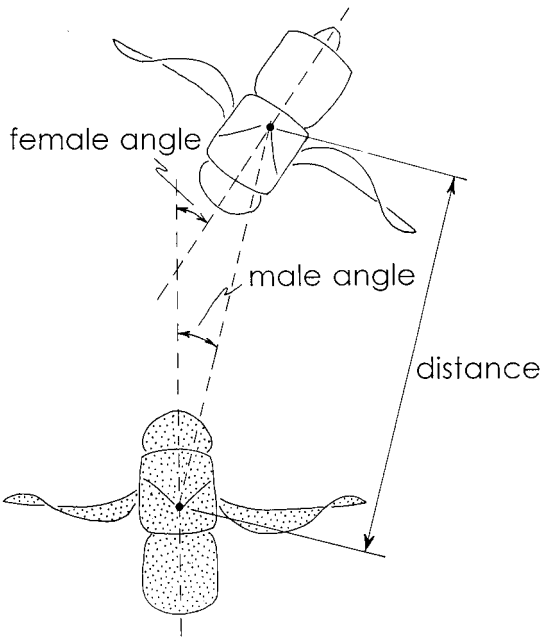


Fig. 1. Angles and distances measured (male stippled).

sisted, and the time the male took to turn and align himself facing in the same direction as the female, were also measured. Successful mounts were those in which the immobile female did not dislodge the male within 60 s of his having landed on her.

The sounds produced during intermittent buzzing were recorded using a small, Sennheiser MZK 80ZU, microphone inserted through a hole in the side of the mating chamber and connected to the camera. Recordings of sounds were imported from video recordings into a PC 486dx2 computer using a 16 bit card. Durations of buzzes and the intervals between buzzes were measured using the real time display in the program Avisoft® using cursors to mark the beginning and the end of the envelope curve displayed in the main window of the program (see Briceño et al. in press for further details). The precision of these measurements was determined by remeasuring the durations 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.

Most variables were not normally distributed, and means and standard deviations are presented for illustrative purposes only. Except where noted otherwise, all statistical tests of differences employed two-tailed Mann-Whitney U Tests.

We performed three types of analysis. First we made simple, variable by variable comparisons between strains and between unsuccessful and successful courtships that led to successful mounts. For instance, we compared the length of intermittent buzzing preceding unsuccessful and successful mounts within both strains, and between strains. These analyses had the possible problem that some independent variables are probably correlated. For instance, an apparently significant effect of variable A on the female decision to copulate rather than reject the mounted male, might actually result from this variable's association with another independent variable B that truly does affect the female's decision. This possible dependence was tested with additional analyses, using the statistics program SYSTAT. These were organized into three questions:

1. Which aspects of the female's behavior during courtship are associated with increased probability that she will allow the male to mate when he mounts?
2. Which aspects of male courtship behavior may have induced this female receptivity?
3. Which cues are used by males to initiate continuous wing vibration to intermittent buzzing?

For those questions with a discontinuous response variable (e.g., unsuccessful, successful), we used stepwise logistic regressions (SYSTAT forward stepwise option). For the others we used ordinary multiple regressions. For each analysis we provided the program with a list of variables with possible effects, on the basis of the stimuli likely to be available to the fly making the response that was being tested. The program first selected from this list the variable that had the largest effect on the response variable, and calculated this effect. It then repeated the process with the remaining variables on the list while correcting for the effect of the first variable, and it continued this process until none of the remaining variables had significant effects on the response variable ($P < 0.05$). In each round the effects of all variables that had already been selected in previous rounds were held constant.

An additional complication is that flies may have multiple threshold criteria for some decisions. Thus, for instance, the female may only allow a mounted male to copulate when the distance between them is below some critical value and in addition the duration of his courtship is above some other critical value. Such interactions could impede detection of decision criteria. We thus performed an additional set of logistic regressions in which we tested for interactions between pairs of independent variables in their effects on the response variable. Regression models were constructed for different questions as before, but in this case we checked for significant interactions between each of the variables that

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had been found to have a significant effect in the first model when each was combined with all of the other variables in the list which had not had significant effects in the original model. These interactions analyses were performed separately from other analyses because even with our large sample sizes it was not possible to find significant effects for more than about 4 variables at a time with these regression techniques.

It is important to keep in mind that a given behavioral variable may be influenced by both the male and the female. Consider, for example, the length of time the female was immobile before the male jumped onto her. The male clearly makes the decision to jump, and it would thus seem reasonable to include this time in the model for question 2 (male effects on female receptivity to copulation), but not in the model for question 1 (female indicators of receptivity). But it is also obvious that the female herself determines whether or not she moves, and female movement probably inhibits jumping by the male. This kind of interdependence sometimes made it difficult to decide which variables should be included which models. In some cases the same variable was included in different lists.

RESULTS

Table 1 and Figures 2, 4, and 6-8 present variable-by-variable analyses of behavioral traits with respect to strain and male copulation success. Figures 3 and 5 illustrate changes just before and just after male initiation of continuous vibration and intermittent buzzing behavior. Table 2 presents the results of regression analyses testing for independence of the effects of different variables. Table 3 gives the results of logistic regression analyses of the interactions between those variables with significant effects in the models in Table 2 and the rest of the variables that did not have significant effects in these models. In general, the regression analyses confirmed the results of the variable-by-variable analyses, but did not reveal many additional relationships. We will discuss the results variable by variable.

Distances between the Male and Female

The distance between the male and female tended to decrease as courtship proceeded in both mass-reared and wild flies (Fig. 2) ($P < 0.0001$ with Kruskal-Wallis Test for each strain; a posteriori Duncan tests showed that differences between all three pairs of values at the moment of transition were significant in both strains $P < 0.001$). Wild males initiated continuous vibration at significantly greater distances females than did mass-reared males (Figs. 2 and 3, Table 1). Combined values for successful and unsuccessful courtships differed by more than a factor of 2 between the two strains (0.64 ± 0.40 cm vs. 1.60 ± 2.12 cm, $P < 0.001$). Distances when the male initiated subsequent stages in courtship did not differ between the two strains (Figs. 2 and 3, Table 1), even when successful and unsuccessful courtships were combined ($P > 0.05$). The distance from which the male jumped onto the female was relatively less variable within each strain than the other distances (e.g., error bars in Fig. 2; Barlett's homogeneity of variances test showed significant differences between the variances in all three variables in both strains, $P < 0.001$).

In both strains the distance between male and female decreased significantly during the s prior to initiation of continous vibration, and during the s prior to initiation of intermittent buzzing (BC vs. C and BI vs. I in Fig. 3), suggesting that reduction in the distance may be a cue used by males to trigger both behavior patterns. Distances did not decrease significantly during the s after continuous vibration began, nor during the s after intermittent buzzing began, suggesting that these male activities did not immediately induce the female to approach him. There was no significant difference associated with successful vs. unsuccessful mounts in either strain with respect to any of the distances measured (Table 1).

Male Angles

The male angles at the moments of transition changed very little during the course of courtship in both strains (Fig. 4) ($P = 0.021$ with Kruskal-Wallis Test on mass-reared flies, but no pairs were significantly different with a posteriori Duncan Tests; the male's angle at the start of continuous wing vibration was slightly larger than either of the other two in wild flies with similar tests). There was, however, a tendency in both strains for the male to turn to face more directly toward the female in the s preceding initiation of both continuous vibration and intermittent buzzing (Fig. 5). The strains did not differ consistently (Figs. 4 and 5, Table 1).

Mounts by both mass-reared and wild males were more likely to be successful when the male angle was lower at the moment the male jumped (Table 1), although in mass-reared flies this effect was not significant in regression analyses (Table 2, Model 2). The male angle at the moment he jumped was clearly smaller preceding successful as compared with unsuccessful courtships when data from the two strains were combined ($2.8 \pm 6.7°$ vs.$4.6 \pm 5.3°$; $P < 0.001$). Male angles at other stages showed less consistent effects (Fig. 4, Table 1), and were not significant in regression analyses (Table 2, Model 2). Summarizing, the male remained oriented looking more or less directly toward the female during the entire courtship, and he turned to face her even more directly just before beginning both continuous vibration and intermittent buzzing. A male's mount was more

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TABLE 1. MEANS AND STANDARD DEVIATIONS OF VARIABLES MEASURED IN COURTSHIPS OF MASS-REARED AND WILD FLIES, AND SIGNIFICANCE OF DIFFERENCES WITH MANN-WHITNEY U TESTS. VARIABLES ARE DESIGNATED AS FOLLOWS: *CONTFEM*—FEMALE ANGLE AT MOMENT CONTINUOUS VIBRATION BEGAN; *CONTMAL*—MALE ANGLE AT MOMENT CONTINUOUS VIBRATION BEGAN; *INTERFEM*—FEMALE ANGLE AT MOMENT INTERMITTENT BUZZING BEGAN; *INTERMAL*—MALE ANGLE AT MOMENT INTERMITTENT BUZZING BEGAN; *JUMPFEM*—FEMALE ANGLE AT MOMENT MALE JUMPED ONTO FEMALE; *JUMPMAL*—MALE ANGLE AT MOMENT MALE JUMPED ONTO FEMALE; *DISTCONT*—DISTANCE BETWEEN FLIES WHEN MALE INITIATED CONTINUOUS VIBRATION; *DISTINTER*—DISTANCE BETWEEN FLIES WHEN MALE SWITCHED FROM CONTINUOUS TO INTERMITTENT BUZZING; *DISTJUMP*—DISTANCE BETWEEN FLIES WHEN MALE JUMPED ONTO FEMALE; *FEMQUIET*—TIME FEMALE WAS MOTIONLESS PRIOR TO THE MALE'S JUMP; *VIBRATE*—DURATION OF CONTINUOUS WING VIBRATION; *BUZZ*—DURATION OF INTERMITTENT WING BUZZING; *COURT*—DURATION OF ENTIRE COURTSHIP

	Mass-reared (m)		Wild (w)		Significance of differences			
	ms Successful (N = 36)	mu Unsuccessful (N = 204)	ws Successful (N = 34)	wu Unsuccessful (N = 68)	ms-mu	ws-wu	ms-ws	mu-wu
Angles (°)								
contmal	2.4 ± 2.7[a]	6.3 ± 8.8[b]	10.2 ± 9.2[e]	5.4 ± 8.5[f]	**	ns	**	ns
contfem	39.4 ± 65.7[a]	29.3 ± 33.3[b]	52.6 ± 33.2[e]	38.9 ± 30.4[g]	*	ns	***	*
intermal	4.2 ± 3.3[a]	4.7 ± 4.6[b]	2.8 ± 3.6	3.7 ± 4.3	ns	ns	ns	*
interfem	9.3 ± 6.2[a]	11.5 ± 12.4b	7.3 ± 9.9	14.9 ± 12.4	ns	*	*	ns
jumpmal	4.0 ± 8.5[a]	4.5 ± 5.3[c]	1.1 ± 2.1	4.6 ± 5.5	**	*	ns	ns
jumpfem	4.0 ± 6.6[a]	11.0 ± 11.6[c]	3.9 ± 4.2	10.3 ± 15.6	***	*	ns	ns
Distances (cm)								
distcont	0.61 ± 0.35[a]	0.64 ± 0.41[c]	1.36 ± 0.81[e]	1.69 ± 2.44[g]	ns	ns	**	***
distinter	0.29 ± 0.12[a]	0.32 ± 0.15[c]	0.30 ± 0.12	0.31 ± 0.14	ns	ns	ns	ns
distjump	0.12 ± 0.02[a]	0.15 ± 0.08[c]	0.14 ± 0.02	0.13 ± 0.03	ns	ns	*	ns
Durations (sec)								
femquiet	4.07 ± 4.61[a]	7.26 ± 8.00[d]	5.78 ± 3.63	5.8 ± 3.77	**	ns	*	ns
buzz	7.53 ± 8.09	11.36 ± 9.21	10.7 ± 6.6	10.92 ± 8.92	**	ns	***	ns
vibrate	9.05 ± 15.70	6.23 ± 7.70	18.7 ± 23.8	13.2 ± 17.97	ns	*	ns	*
court	16.08 ± 16.30	15.76 ± 11.85	23.2 ± 22.2	18.0 ± 19.45	ns	*	*	ns

[a]N = 32.
[b]N = 134.
[c]N = 178.
[d]N = 172.
[e]N = 16.
[f]N = 44.
[g]N = 42.

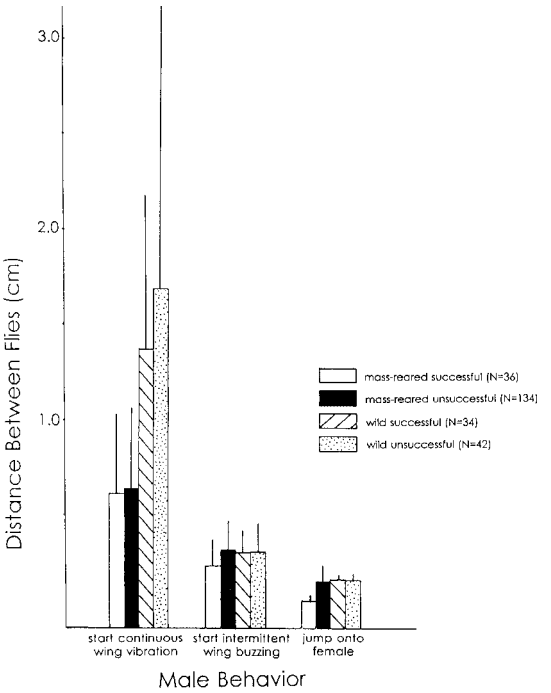


Fig. 2. Distances between male and female at different stages during male courtship in mass-reared and wild flies during successful and unsuccessful courtships. The flies gradually came closer together as courtship proceeded. Distances when courtship began were significantly greater in wild flies.

likely to be successful if he launched his jump while looking more directly toward the female.

Female Angles

Female angles clearly decreased during courtship (Figs. 5 and 6) ($P < 0.0001$ with Kruskal-Wallis Test in each strain comparing angles at the initiations of continuous vibration, intermittent buzzing, and the male's jump in combined data from successful and unsuccessful courtships). A posteriori Duncan tests showed that the female angle when the male began continuous wing vibration was significantly larger than each of the other angles in both strains (all $P < 0.001$). Females of both strains turned to face more directly toward males during the s following initiation of intermittent and continuous buzzing, but this trend was only weak in wild flies (Fig. 5).

Courtship was more likely to be successful in both strains when the female was looking more directly toward the male at the moment he jumped (Fig. 6, Table 1), though in wild flies this effect was not significant in regression analyses (Table 2, Model 1). The mean female angles for both strains combined at the moment the male jumped were 4.0 ± 5.6 vs. $10.8 \pm 12.8°$ comparing successful and unsuccessful mounts ($P < 0.001$). The female angles at earlier stages of courtship did not show significant differences between successful and unsuccessful courtships in mass-reared flies, and only inconsistent differences in wild flies (Tables 1 and 2). Combining successful and unsuccessful courtships, mass-reared males initiated courtships when females were facing more directly toward them (female angle 31.2 ± 41.5 vs. 42.7 ± 31.6 in wild flies, $P < 0.001$). Summarizing, the female looked more directly toward the male later in courtship, and mounts that occurred when she was looking more directly toward him were more likely to result in copulation. Initiation of continuous and intermittent buzzing apparently induced the female to turn toward the male, the trend was weak in wild flies. Mass-reared males initiated courtship when females were looking more directly toward them.

There was a positive correlation in both strains between male and female angles, so when the male was looking more directly toward the female, she tended to be looking more directly toward him (Fig. 7). This correlation seemed stronger later in courtship, but the changes were not significant.

Female Immobility

Females were nearly always immobile when the male jumped. The amount of time the female had been quiet before the male jumped was significantly shorter in successful courtships of mass-reared flies than in those preceding unsuccessful mounts, but there was essentially no difference in wild flies (Fig. 8, Table 1). This difference was independent of the effects of other variables in mass-reared flies (Table 2, Model 1).

Female immobility was significantly shorter when the distance between the flies at the moment of the jump was larger, and it was larger when the distance at the beginning of intermittent buzzing was larger in mass-reared but not in wild flies (Table 3, Model 1). Mass-reared females that were successfully mounted had been motionless for a marginally shorter time than wild females that were successfully mounted ($P = 0.03$), but there was no difference between strains for the females that were unsuccessfully mounted ($P > 0.05$). Combining successful and unsuccessful courtships in each strain, the mean durations of female immobility did not differ significantly between strains (6.76 ± 7.65 s vs. 5.84 ± 3.71 s for mass-reared and wild flies ($P > 0.05$).

Absolute and Relative Durations

As was found previously using different flies and a different, older mass-reared strain from Cost Rica (Briceño & Eberhard 1998), several aspects of courtship by mass-reared males were shorter than those by wild males (Table 1). The

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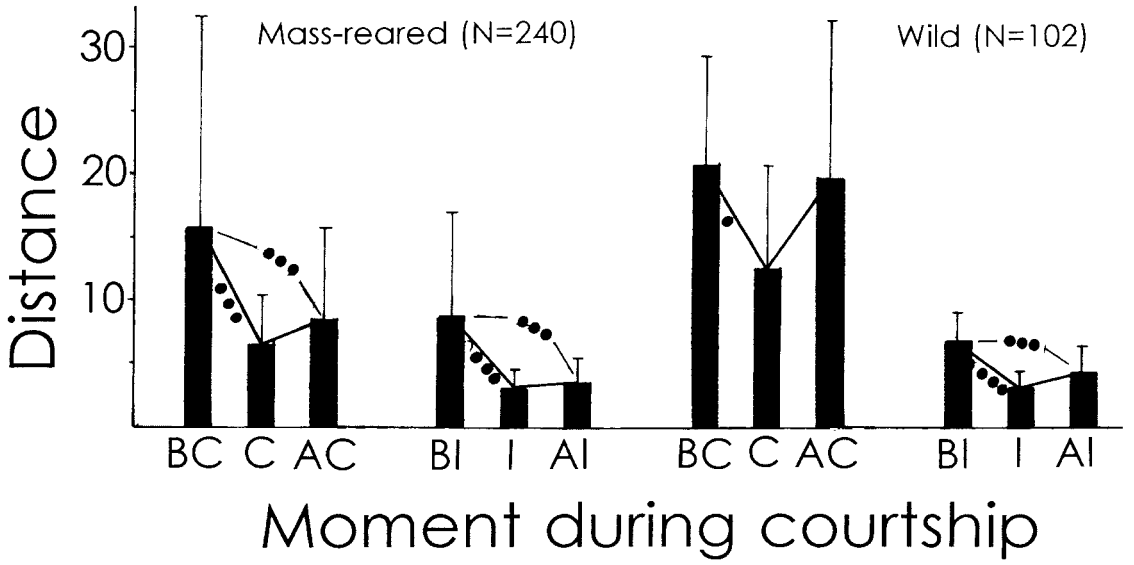


Fig. 3. Distances between male and female 1 s before initiation of continuous vibration (BC), at the moment continuous vibration began (C) and 1 s after it began (AC), and 1 s before (BI), 1 s after (AI), and at the moment of initiation (I) of intermittent buzzing in two strains. Dots accompanying lines between bars indicate significant differences between the two bars (one dot $P < 0.05$; two dots $P < 0.01$; three dots $P < 0.001$).



Fig. 4. Male angles at different stages during male courtship in mass-reared and wild flies during successful and unsuccessful courtships. Males tended to be oriented toward the female throughout courtship. Differences between strains, and between successful and unsuccessful courtships were not significant.

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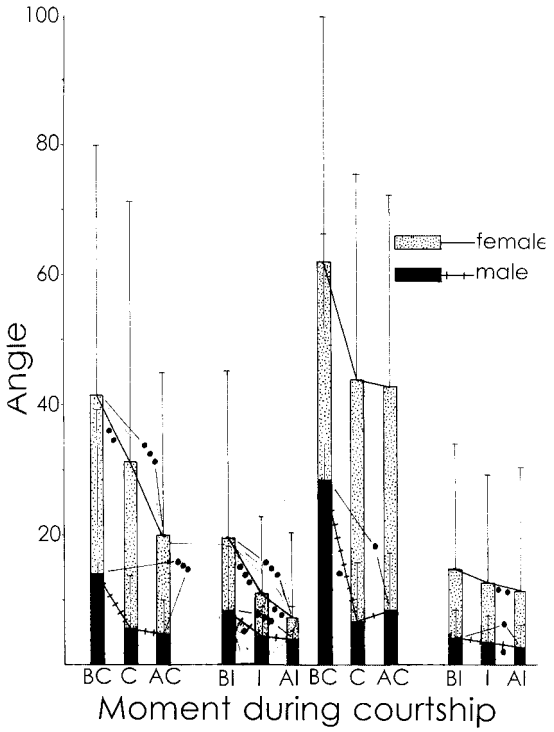


Fig. 5. Male and female angles 1 s before initiation of continuous vibration (BC), at the moment continuous vibration began (C) and 1 s after it began (AC), and 1 s before (BI), 1 s after (AI), and at the moment of initiation (I) of intermittent buzzing in two strains (mass-reared on left, wild on right). The dots accompanying lines between bars indicate significant differences between the two bars (one dot $P < 0.05$; two dots $P < 0.01$; three dots $P < 0.001$).

difference in total courtship duration between mass-reared and wild flies when successful and unsuccessful courtships were combined was also significant (15.81 ± 12.50 s vs. 20.18 ± 20.70 s, $P < 0.05$). This difference was due to different durations of continuous vibration (6.68 ± 9.77 s vs. 15.86 ± 20.20 s, $P < 0.001$) rather than differences in intermittent buzzing ($P > 0.05$). The time spent in intermittent buzzing was shorter in successful courtships than in unsuccessful courtships of mass-reared flies, but not in wild flies (Table 1), while longer continuous vibration and total courtship led to greater success in wild flies but not in mass-reared flies (Table 1). Combining data from mass-reared and wild flies, the mean time spent in intermittent buzzing in successful courtships was less than that in unsuccessful courtships (8.80 ± 7.63 and 11.08 ± 9.14 s, ($P < 0.001$). The corresponding difference in durations of continuous vibration was not significant.

Mass-reared females showed a strong tendency to copulate when the proportion of time during the courtship that was spent in intermittent buzzing was especially low. The mean proportion of time spent buzzing prior to successful mounts was 57.0%, while the corresponding value prior to unsuccessful mounts was 77.6% (Student's t comparing arcsine transformations of these proportions was 4.38, $P < 0.00002$). This effect was both independent of and stronger than the effects of the other durations (Table 2, Model 2). Although wild flies showed the same trend to copulate when the proportion of the time spent in intermittent buzzing was lower (66.4% vs. 74.7%), the difference was not significant (Tables 1, 2). The decrease in this proportion in mass-reared flies was due in large part to the decrease in the duration of intermittent buzzing preceding successful mounts rather than to longer durations of continuous vibration (Table 1). In wild flies, however, there was not even a hint of a similar difference (Table 1).

There was a weak negative correlation in both strains between the total duration of courtship and the percentage of courtship dedicated to intermittent buzzing (r = -0.29, -0.60 in mass-reared and wild flies respectively; in both cases $0.01 < P < 0.05$). There was no correlation in either strain between the absolute duration of intermittent buzzing and continuous vibration.

Durations of Individual Buzzes and the Rate of Buzzing

A comparison of the mean durations of the last 10 individual buzzes during intermittent buzzing before the male jumped onto the female in a subsample of the courtships of mass-reared and wild flies that led to copulation (N = 19 and 25 respectively) with those in courtships that did not lead to copulation (N = 121 and 109 respectively) showed that buzz duration did not differ between successful and unsuccessful courtships in either strain (respective means were 156 ± 71 ms vs. 152 ± 70 ms for mass-reared flies, and 114 ± 16 ms vs. 113 ± 16 ms for wild flies; $P = 0.80$ and 0.76 respectively) (the durations of buzzes did not change significantly during intermittent buzzing – unpublished data). Similarly, comparisons between the average intervals between buzzes during successful and unsuccessful courtships in these same pairs also failed to show consistent significant differences (respective means were 164 ± 50 ms vs. 175 ± 52 ms for mass-reared flies, and 155 ± 60 ms vs. 184 ± 117 ms for wild flies; $P = 0.10$ and 0.03 respectively). Similar comparisons showed no differences in the overall rates of intermittent buzzes (number/sec) in successful and unsuccessful courtships (respective means 2.51 ± 0.7 buzzes/s vs. 3.0 ± +1.0 buzzes/s for mass-reared flies, and 3.73 ± 0.40 buzzes/s vs. 3.52 ± 0.71 buzzes/s for wild flies; $P = 0.25$ and 0.42 respectively).

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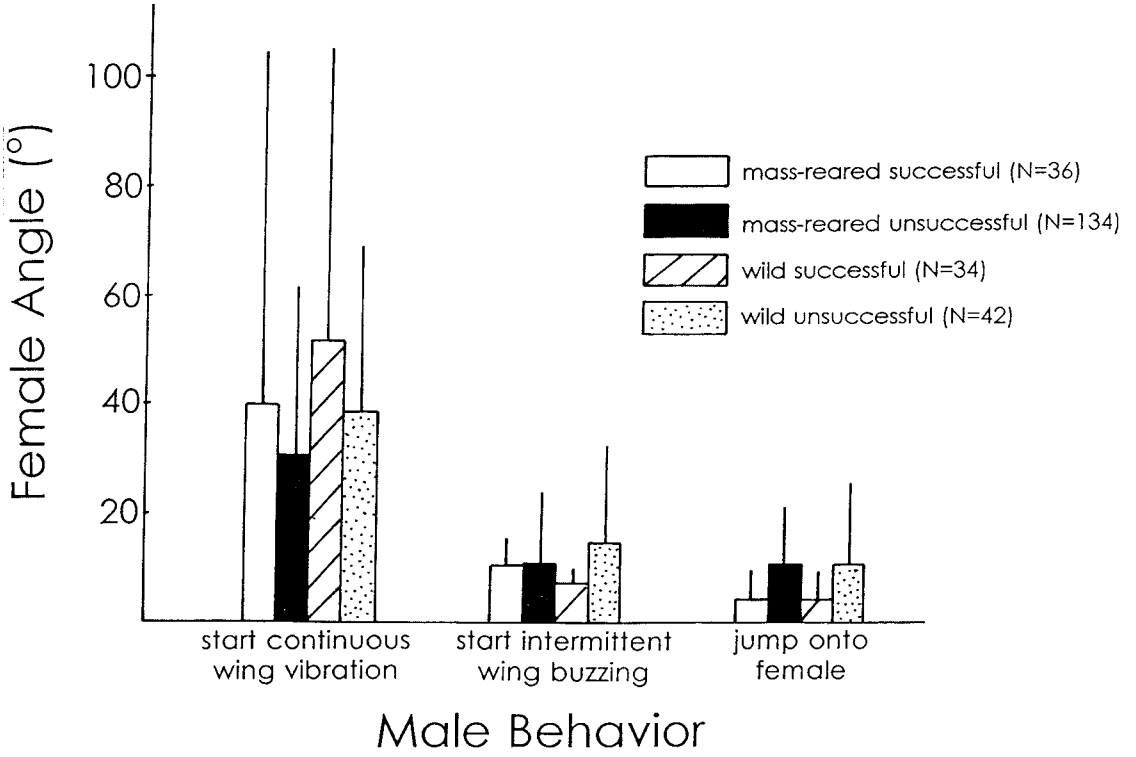


Fig. 6. Female angles at different stages during male courtship in mass-reared and wild flies during successful and unsuccessful courtships. The female tended to turn to face more toward the male after continuous wing vibration began and before intermittent wing buzzing. Differences between strains and between successful and unsuccessful courtships were not significant.

Walking Behavior

There were no consistent differences between successful and unsuccessful courtships with respect to whether the female or the male was immobile (= not walking) when continuous vibration or intermittent buzzing began, or one s before or afterward. In both strains female immobility increased as courtship progressed. The female was more likely to be immobile when intermittent buzzing began than she had been when continuous vibration began ($P < 0.0001$ with Chi^2 for both), and to be immobile one s after buzzing began than she had been 1 s before it began ($P < 0.0001$ with Chi^2 for both). There was a similar, but inconsistent trend for females to be immobile more often one s after continuous vibration began than they had been one s before ($P = 0.002$ for mass-reared flies; $P = 0.45$ for wild flies).

There were several between-strain differences. Mass-reared females were less likely to be immobile after continuous vibration began ($P = 0.0003$ with Chi^2), and one s after intermittent buzzing began ($P = 0.006$). Mass-reared males were less likely to be immobile during the s after intermittent buzzing began ($P = 0.001$ with Chi^2), but were less likely to creep slowly toward the female during intermittent buzzing ($P = 0.0001$ with Chi^2).

In general, courtships were shorter in both strains when the female was immobile one s before or one s after continuous vibration began (means were smaller in all eight within-strain comparisons; differences were significant in five). There was also a significant association between longer courtships and male creeping behavior during intermittent buzzing (P = 0.008 and 0.01 in mass-reared and wild flies respectively). Thus males apparently decided to creep toward the female when relatively long courtships failed to lure her close enough.

Male Size

Mass-reared males were smaller than wild males in head width 0.85 ± 0.06 vs. 0.89 ± 0.06 mm), thorax length (2.63 ± 0.15 vs. 2.81 ± 0.13 mm), and thorax width (1.73 ± 0.10 vs. 1.83 ± 0.09 mm) (all $P < 0.001$ with t tests). Although mass-reared males performed more mounting attempts than wild males (respective means were 8.3 and 3.7; $P = 0.019$), there was no consistent relation within either strain between male body size and

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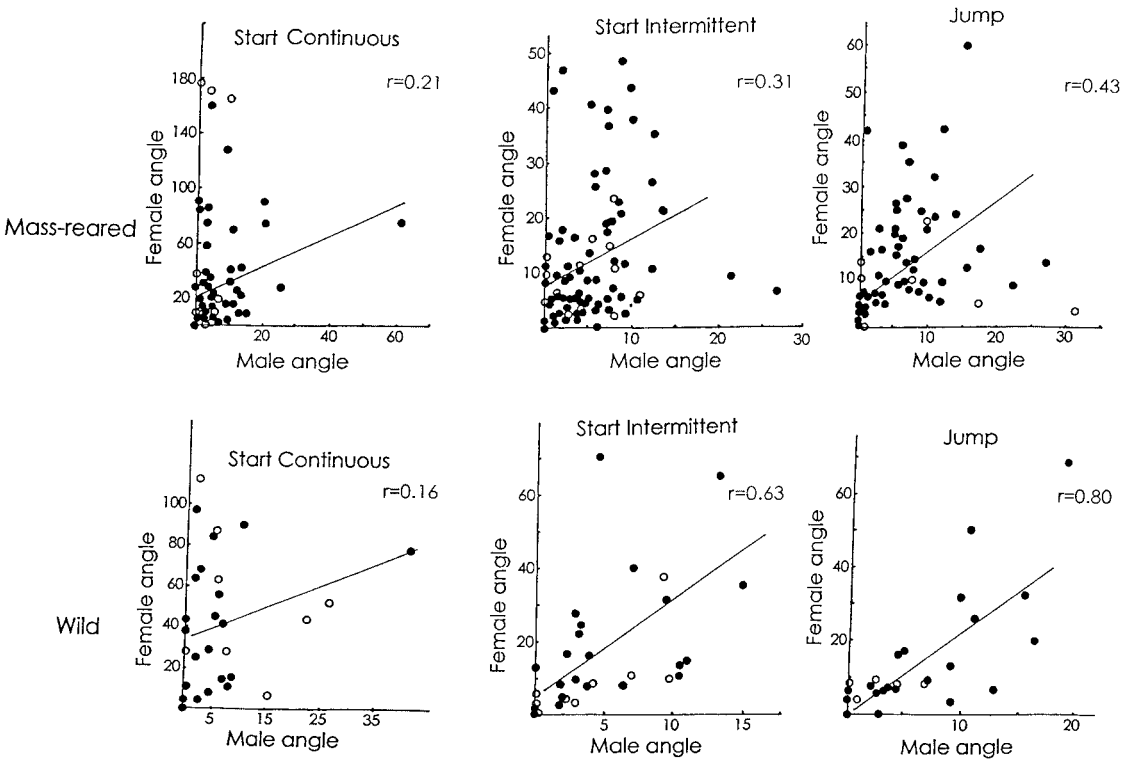


Fig. 7. Relationships between male and female angles in mass-reared and wild flies at different stages of courtship.

the rate of mounting failure (number of mounts that led to copulation/ total number of mounts). The p values for linear regression slopes of the rate of failure on the three size measurements were 0.047, 0.149 and 0.479 for wild flies (N = 21), and 0.472, 0.606 and 0.939 for mass-reared flies (N = 48). Males that copulated were not larger than those that did not copulate among either mass-reared or wild flies.

Mounts without Prior Courtship

Males and females frequently encountered each other as they walked about in the confines of the Petri dish. Mass-reared males were more likely to jump onto the female during such an encounter without previous courtship (40.8% of 142 mounts were not preceded by courtship) than were wild males (22.0% of 109 mounts without prior courtship) (Chi^2 = 9.9, df = 1, p = 0.0016). Mounts without a previous courtship were less likely to result in copulation in mass-reared flies (6.9% of 58 mounts without previous courtship vs. 19.0% of 84 with previous courtship; Chi^2 = 4.24, df = 1, $P < 0.05$), There was no difference in acceptance rates in wild flies (corresponding values were 20.8% of 24 vs. 24.7% of 85; $P > 0.05$).

Discussion

Cues associated with Courtship Decisions

The data presented here are probably related at two different levels of causation to the decisions made by males and females during courtship. The difference between levels involves cause-and-effect relations as opposed to simple correlations. Some measurements, such as the distance between the flies (which is largely a function of whether or not the female approached the male), are probably "indicator variables" that represent the probability that a particular decision has been or will be made. They may constitute, for instance, indicators from the female's overt behavior of the likelihood that she will eventually accept the male's copulation attempt when he jumps onto her. These variables may have little or nothing to do with *why* the female made the decision to accept or reject the male, but rather be consequences of her having made a decision. A second set of possible "cue" variables represent possible stimuli that trigger particular decisions by males or females. For example, the male's size and his song characteristics, represent possible cues that might be used by females in making the

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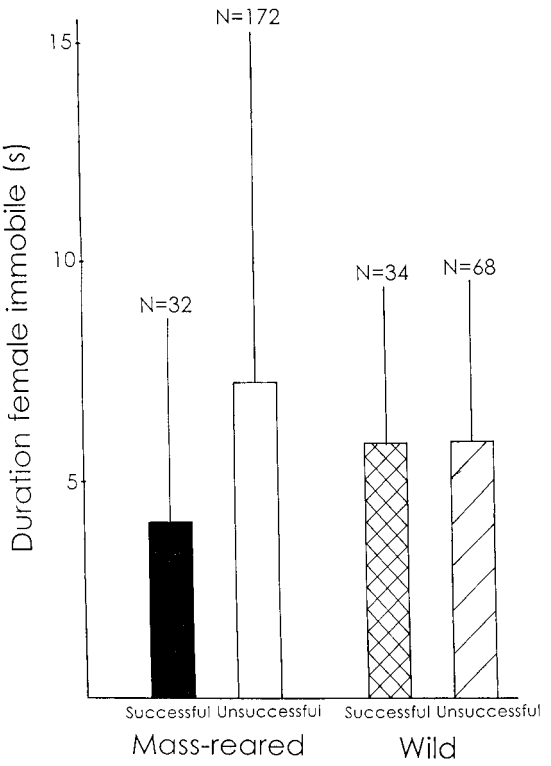


Fig. 8. Length of time female was immobile before the male mounted her in successful and unsuccessful courtships of mass-reared and wild flies. Mass-reared females were immobile for significantly shorter periods preceding successful mounts as compared with unsuccessful mounts; and successful mounts of mass-reared flies were preceded by significantly shorter periods of female immobility than successful mounts of wild flies.

decision whether or not to accept copulation. These two questions are discussed separately, although it is possible that some variables may play more than a single role. For instance, female behavior that is associated with likely acceptance may be used as a cue by the male to trigger particular courtship behavior of his own. These differences have not always been clear in previous discussions of medfly courtship.

Possible Indicator Variables. Our results confirm and quantify several conclusions regarding possible female "acceptance" variables from previous studies. 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 increased immobility in the later stages of courtship are in accord with the idea that one result of successful male courtship behavior is to induce the female to approach him (or allow him to approach her), to look directly toward him, and to remain still. Feron (1962) derived these ideas from qualitative observations of the relative mobility of females compared to courting males, but gave no quantitative support. Briceño et al. (1996) came to similar conclusions from comparing A) the positions of flies at the moment a male leapt onto the female (both successful and unsuccessful leaps were included), and B) positions when males decided to abandon courtship (presumably relatively extremely unfavorable conditions).

The present data are much more extensive and quantitative. They are also more convincing regarding the biological importance of male and female angles and the distance between the two flies at the moment that the male jumps, because they establish correlations with the likelihood that the female will allow copulation to occur, rather than just whether or not the male will jump. It must be kept in mind, however, that the data are only correlations, and thus do not allow confident deductions regarding cause and effect. It is thus not yet certain whether male-female alignment and close proximity is a cause of female acceptance of copulation, or whether it is correlated with female receptivity that is due to other causes.

It is entirely possible that we have documented here only manifestations of the female's likelihood of accepting copulation, and not the reasons why sometimes they were receptive and sometimes not. On the other hand, our results call into question the usefulness of studies of male-female interactions and possible interchanges of signals that do not take the angles and distances between the flies into account (e.g., Lux & Gaggl 1996, Liimatainen et al. 1997). It is now clearer than before that these factors are indeed associated with the success and failure of male courtships.

The tendency for the female to have spent less time moving prior to courtships that terminated with successful mounting is also in accord with the idea that male courtship functions to arrest female movement. The correlation between male and female angles may be due to the difficulty of continuing to look directly toward the female when the female is looking (and perhaps moving) in a direction other than toward the male.

Possible Cue Variables. The changes in distances and angles that occurred just before and after males began continuous vibration and intermittent buzzing suggest the following interpretation. Males are stimulated to begin continuous vibration when the female approaches, and to begin intermittent buzzing when she approaches still closer. The male may also be induced to initiate these behavior patterns when the female is oriented facing more directly toward him. Mass-reared males began both types of behavior when the female was facing them more directly, while similar trends in wild flies were not significant. Female decisions may be affected by stimuli from continuous vibration and intermittent buzzing by the male.

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TABLE 2. SUMMARY OF RESULTS FROM LOGISTIC REGRESSIONS. VARIABLES ARE DESIGNATED AS IN TABLE 1.

Model 1. Female behavioral variables that were associated with altered probability that the mount would be successful (copulation) instead of failure (female rejection). Variables included: 1. angles: contfem, interfem, jumpfem; 2. distances: distcont, distinter, distjump; 3. durations: femquiet.

	Mass-reared flies				Wild flies			
	Estimate	S.E.	t ratio	*P* value	Estimate	S.E.	t ratio	*P* value
Constant	0.148	0.460	0.322	0.747	-1.10	0.74	-1.49	0.135
jumpfem	-0.105	0.035	-3.03	0.002	No significant effect			
femquiet	-0.177	0.066	-2.69	0.007	No significant effect			
interfem	No significant effect				-0.41	0.14	-2.84	0.005
contfem	No significant effect				0.074	0.025	2.93	0.003

Model 2. Male behavioral variables that were associated with altered probability that the mount would result in copulation rather than in female rejection of the male. Variables included: 1. angles: contmal, intermal, jumpmal; 2. distances: distcont, distinter, distjump; 3. Durations: vibrate, buzz, vbuz, femquiet.

	Mass-reared flies				Wild flies			
	Estimate	S.E.	t ratio	*P* value	Estimate	S.E.	t ratio	*P* value
Constant	2.15	0.92	2.32	0.02	1.85	1.29	1.43	0.15
vbuz	-3.02	0.92	-3.27	0.001	No significant effect			
distcont	-2.19	0.94	-2.34	0.02	No significant effect			
jumpmal	No significant effect				-2.63	1.10	-2.40	0.017
intermal	No significant effect				-0.69	0.32	-2.14	0.032
contmal	-0.14	0.07	-1.95	0.05	0.22	0.10	2.11	0.035

Model 3 (Multiple regression). Female behavioral variables that were associated with altered distance at which the male switched from continuous vibration to intermittent buzzing. Variables included: 1. angles: contfem, interfem; 2. distances: distcont; 3. Durations: vibrate.

	Mass-reared flies				Wild flies			
	Estimate	S.E.	t ratio	*P* value	Estimate	S.E.	t ratio	*P* value
Constant								
contfem	-0.001	0.00	-0.23	0.005	No significant effect			

Model 4. Variables associated with differences in distance at which continuous wing vibration was initiated. Variables included: 1. angles: contmal, contfem.

	Mass-reared flies				Wild flies			
	Estimate	S.E.	t ratio	*P* value	Estimate	S.E.	t ratio	*P* value
Constant	No significant effect				No significant effect			

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Although neither type of male behavior was associated with reductions in the distance between the two flies, females tended to turn to orient themselves more directly toward the male in the s after intermittent buzzing began, and, less consistently, in the s after continuous vibration began.

These interpretations must be evaluated carefully. They assume that reductions in the distance between the flies are due to female rather than male movements (nearly always true prior to and during continuous vibration and the early stages of intermittent buzzing, but not later in buzzing). They also attribute cause and effect relations to what are at present only correlations (above).

Our results shed little light on the cue or cues that trigger female acceptance of a male, other than ruling out several possibilities. The durations of individual buzzes and the intervals between them during intermittent buzzing, the rate of buzzing, the duration of the intermittent buzzing stage, the duration of the continuous wing vibration stage, and the male's size all failed to show significant differences between successful and unsuccessful courtships. There was a weak tendency in wild flies for successful courtships to have been longer than unsuccessful courtships; the lack of such a female criterion in mass-reared flies may be due to selection on females in mass-rearing cages (Briceño & Eberhard 2000), where males with shorter courtships are favored (Briceño & Eberhard 1998). The significance of the very strong tendency for increased female acceptance of copulation in mass-reared flies when the proportion of time during the courtship spent in intermittent wing buzzing was low with respect to the time spent in continuous wing vibration is not clear, especially in view of the lack of a significant trend in wild flies

Our finding that male size does not affect female acceptance is similar to the results of several studies in Hawaii (Arita & Kaneshiro 1988, Whittier et al. 1992, 1994, Whittier & Kaneshiro 1995), but differs from the equally clear tendency for larger males to be more readily accepted in Israel (Blay & Yuval 1997). It appears that there may be geographic variation in this trait. Female choice criteria are known to vary geographically in other species (e.g., Andersson 1994).

Differences between Mass-reared and Wild Flies

Our results constitute the second set of observations showing that courtship duration is reduced in a mass-reared strain compared with the wild strain from which it was derived (Briceño & Eberhard 1998). Males of two other mass-reared strains also perform relatively short courtships, but in one case the behavior was recorded under different conditions, and in the other nothing is known of behavior of the wild flies from which it was derived (Briceño & Eberhard 1998). The degree of reduction in the present study of a 3 year-old strain (78% of wild flies) is somewhat less than that seen previously with older, 4.5 year-old mass-reared strain (69%), as would be expected if inadvertent selection due to interruptions under mass-rearing conditions produced a gradual shift toward shorter courtships.

The tendency for mass-reared males to initiate continuous wing vibration when the female was closer and when she was facing more directly toward him may represent additional adaptations by mass-reared males to the crowded conditions of mass-rearing cages. High thresholds for initiating courtship may well be advantageous in a cage containing 60,000 flies. These changes may be accompanied on the female side by a greater tendency in mass-reared but not wild females to accept courtships that were initiated at a shorter distance. This difference was not significant in the variable-by-variable analyses in Table 1, but was significant in regression analyses of mass-reared flies when the effect of relative duration of intermittent buzzing was held constant (Table 2, Model 2), and also showed a significant interaction with the female angle when the male jumped (Table 3, Model 1). Thus the acceptance criteria of mass-reared females may have coevolved in accord with a reduction in the distance at which the male begins courtship.

The greater selectivity in mass-reared males with respect to when to initiate courtship was not accompanied by a possibly coevolved preference by females favoring courtships that began with smaller female angles. However the selectivity shown by wild females with respect to the effects of the female's angle at the moment when continuous and when intermittent wing vibration began was absent in mass-reared females (Table 2, Model 1). The loss of such selectivity in mass-reared females would thus favor males that initiate courtship at smaller female angles, which is the trend found when mass-reared and wild males are compared. Thus this female acceptance criterion may also have changed in mass-reared flies (via abandonment of a former bias) in step with changes in male behavior that probably resulted from selection in crowded mass-rearing cages, just as greater acceptance of shorter courtships has also coevolved with abbreviated courtship in mass-reared flies (Briceño & Eberhard 2000). Males in cages may thus be under selection to respond only to females at shorter distances to avoid interruptions; and female criteria may have evolved to favor males whose sons were more likely to perform uninterrupted courtships. Further data are needed to test these ideas.

One further point regarding differences and similarities in distances concerns the uniformity, both between and within strains, in the distance between male and female when the male initiated his jump onto the female. It might have been

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TABLE 3. SUMMARY OF RESULTS OF INTERACTIONS BETWEEN VARIABLES IN LOGISTIC REGRESSIONS. VARIABLES ARE DESIGNATED AS IN TABLE 1. INTERACTIONS WITH THE OTHER VARIABLES IN THE LIST WERE TESTED SEPARATELY FOR EACH OF THE VARIABLES THAT HAD A SIGNIFICANT EFFECT IN THE REGRESSIONS IN TABLE 2.

Model 1. Female behavioral variables that were associated with altered probability that the mount would result in copulation rather than in female rejection of the male. The variables which showed significant effects in previous regression analysis, and with which other the variables (Table 2) were combined to test for interactions, were jumpfem, femquiet, and distcont.

	Mass-reared flies				Wild flies			
	Estimate	S.E.	t ratio	*P* value	Estimate	S.E.	t ratio	*P* value
Interactions with jumpfem								
constant	0.38	0.46	0.82	0.412	-1.25	0.64	-1.98	0.048
distcont* jumpfem	-0.25	0.075	-3.33	0.001	-0.10	0.05	-1.85	0.064
femquiet	-0.19	0.068	-2.83	0.005	0.18	0.12	1.50	0.13
Interactions with femquiet								
constant	0.76	0.51	1.48	0.14	-1.05	0.48	-2.21	0.027
jumpfem	-0.11	0.034	-3.13	0.002	-0.10	0.05	2.10	0.036
distjump* femquiet	-4.64	1.53	-3.03	0.002	0.59	0.65	0.90	0.37
distinte* femquiet	0.86	0.41	2.10	0.035	0.065	0.31	0.21	0.84
Interactions with contfem	No significant effect				No significant effect			
Interactions with interfem	No significant effect				No significant effect			

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TABLE 3 (CONTINUED). SUMMARY OF RESULTS OF INTERACTIONS BETWEEN VARIABLES IN LOGISTIC REGRESSIONS. VARIABLES ARE DESIGNATED AS IN TABLE 1. INTERACTIONS WITH THE OTHER VARIABLES IN THE LIST WERE TESTED SEPARATELY FOR EACH OF THE VARIABLES THAT HAD A SIGNIFICANT EFFECT IN THE REGRESSIONS IN TABLE 2.

Model 2. Male behavioral variables that were associated with altered probability that the mount would result in copulation rather than in female rejection of the male. The variables which showed significant effects in previous regression analysis, and with which other variables (Table Variables which had not showed significant effects previously and were combined to check for interactions included the angles contfem, interfem and the distances: distinter, distjump. 2) were combined to test for interactions, were vbuz and distcont.

	Mass-reared flies				Wild flies			
	Estimate	S.E.	t ratio	*P* value	Estimate	S.E.	t ratio	*P* value
Interactions with vbuz								
Constant	0.083	0.43	0.19	0.85	-1.87	0.58	-3.23	0.001
vbuz* court	-0.18	0.054	-3.20	0.001		No significant effect		
vbuz* contmal		No significant effect			0.27	0.11	2.43	0.015
Interactions with distcont								
Constant	-0.17	0.38	-0.44	0.66	-0.61	0.83	-0.74	0.46
distcont* buzz	-0.26	0.083	-3.14	0.002		No significant effect		
distcont* jumpmal		No significant effect			-3.54	18.40	-0.19	0.85#
distcont* femquiet		No significant effect			0.86	0.32	2.68	0.007
distcont* intermal		No significant effect			-0.73	0.29	-2.56	0.01
Interactions with jumpmal								
Constant	-1.31	0.27	-4.93	0.000		No significant effect		
jumpmal* vibrate	0.006	0.004	1.73	0.083				
jumpmal* buzz	-0.034	0.016	-2.12	0.034				
jumpmal* intermal	0.048	0.017	2.84	0.005				
jumpmal* contmal	0.035	0.016	-2.13	0.033				

#Was significant at $P = 0.024$ when first entered the model.

thought that the shorter courtships of mass-reared males (e.g., Briceño & Eberhard 1998; above) occurred because the males fail to wait until the distance to the female has decreased, and jump onto the female from farther away. This seems not to be the case. The probable reason is that male stimulation by the female using his aristae (Briceño & Eberhard in press) cannot occur until the flies are quite close together.

Summarizing the results of this and previous studies, there are now five differences known between the sexual behavior of mass-reared males and wild males. Mass-reared male courtship prior to mounting is shorter, is initiated at a shorter distance from the female and when the female is looking more directly toward the male, the male is less likely to creep toward the female during intermittent buzzing, and the male is more likely to attempt to mount a female they have encountered without prior courtship. Acceptance criteria in mass-reared females appear to have changed to favor the first two and possibly also the third of these male changes, but to act against the fifth. The first two changes fit a Fisherian sequence of evolution by sexual selection (see Briceño & Eberhard 2000). Changes in female criteria have also been documented in other mass-reared insects (Liu & Haynes 1994, Zhu et al. 1997).

The data documenting differences between strains must be interpreted cautiously, because only pairs of flies of the same strain were observed. Given the probable effects of the behavior of one sex on that of the other, it will not be possible to attribute differences to one sex or the other with certainty until cross-strain pairs are studied.

Limitations of These Analyses

Many male courtships do not end in a mount; the male terminates courtship when the female moves away or otherwise fails to respond appropriately (Feron 1962, Briceño et al. 1996). Courtships that do not lead to a mounting attempt could obviously affect a male's success, but were omitted in the present analyses. Also omitted were those courtships in which the male returned to continuous wing vibration after having begun intermittent wing buzzing. Perhaps additional answers to why some courtships succeed and others fail will be revealed by analyses of these types of interaction.

This study revealed several strong trends with respect to probable male and female cues and responses during the course of courtship, and also demonstrated several clear behavioral differences between mass-reared and wild flies. But it was much less fruitful in uncovering clear differences between successful and unsuccessful courtships. The critical reader cannot help but be struck by the large standard deviations and substantial overlaps in nearly all of our data. Indeed, large variations are ubiquitous in nearly all quantitative data on medfly courtship behavior (Briceño et al. 1996, Liimatainen et al. 1997, Briceño & Eberhard 1998, Quilici in press; an exception is behavior involving contact between male and female aristae—Briceño & Eberhard in press). It is clear, for instance, that when the distance to the female is shorter and when she is facing more directly toward the male, there is a greater likelihood that the male will jump (Briceño et al. 1996), and that the female will accept copulation with him when he does (Figs. 2 and 6). But there were numerous rejections when both the distance and the female angle were low, and acceptances when they were both high. Similar variation also occurs at earlier stages of courtship (see large error bars in Figs. 2 and 6).

These large variations and substantial overlaps have several consequences. On a practical level, they mean that relatively large samples of courtships are needed to document significant differences between successful and unsuccessful courtships or differences between strains. They also signal our lack of detailed understanding why some courtships are successful and others are not. There are several possible explanations of this failure. Perhaps we simply have not yet focused on the male trait or traits that have the most powerful effects on female acceptance. Such "mystery traits" could involve factors that cannot be measured in videotapes (e.g., sound intensities in male songs, male pheromones).

A second possibility is that the basic approach of searching for triggering stimuli is not biologically appropriate. Perhaps female acceptance is sometimes "spontaneous", and does not depend on the presence of particular stimuli. The consistent superiority of wild males over mass-reared males (above) and of some males over others (e.g., Whittier & Kaneshiro 1995) argues, however, that this cannot be the complete explanation. Another possibility is that each particular stimulus only slightly increases the probability of acceptance, rather than guaranteeing that it will occur. Discriminating between the possibilities of mystery traits and small incremental effects may be especially difficult in medfly courtship, where a large variety of possible stimuli are involved. Experimental manipulation of traits may be the best tactic for future studies.

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