

# Acoustical Behavior and Sexual Success in the Caribbean Fruit Fly, *Anastrepha suspensa* (Loew) (Diptera: Tephritidae)

J. C. WEBB, J. SIVINSKI,<sup>1</sup> AND C. LITZKOW

Insect Attractants, Behavior, and Basic Biology Research Laboratory,  
Agricultural Research Service, U.S. Department of Agriculture,  
Gainesville, Florida 32604

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**ABSTRACT.** Male *Anastrepha suspensa* (Loew) produce two female-directed sounds, the calling and precopulatory songs. Aspects of these were correlated to factors thought important in male sexual success and compared in males that copulated and males that failed to mate. Both sounds became more intense with male size. Larger males tended to have calling songs of lower fundamental frequency, but frequency of precopulatory songs and size was uncorrelated. The calling song's fundamental frequency bandwidth was broader in unsuccessful flies, perhaps reflecting physical disability. Precopulatory songs may be the last acoustic opportunity for males to demonstrate their "quality" and receive further cooperation from females they have mounted. Unsuccessful precopulatory songs were not as loud and had a broader bandwidth than successful songs. Greater distortion in unsuccessful songs appeared to be due to female movement during rejection. The longer a precopulatory song, the shorter the subsequent mating. This may have been due to males making greater efforts toward less sexually responsive mates. Larger males copulated longer, suggesting a potential conflict of interest between the sexes over copulation duration that bigger males are more apt to win.

MANY TEPHRITIDAE have rich repertoires of sexual signals. Because of the economic importance of certain fruit flies and the extensive use of sterile-male release for their control, studies were undertaken of the communicative qualities that make fruit flies sexually competitive or attractive (Burk and Calkins 1983). In view of their economic importance, surprisingly little is known in this basic area, because limited research resources have been spent on control efforts.

Male *Anastrepha suspensa* (Loew), Caribbean fruit flies (caribflies), aggregate ("lek") on larval host plants, e.g., guava, *Psidium guajava* L., or Surinam cherry, *Eugenia uniflora* L., in late afternoon. They compete for single-leaf territories on which they emit pheromone, produce repeated bursts of wing-generated sound—the "calling song," and semaphore with patterned wings. When a male has mounted a female, he makes a relatively constant, sustained sound—the "pre-mating or precopulatory sound" (Webb et al. 1976, Dodson 1982, Burk 1981, 1983). Mating lasts an average of 35 min, after which call-singing may begin again. The known bases of male success within the lek are prior residency, an advantage in territory defense, and large size, which aids in disputes and is fa-

vored by females (Dodson 1982, Burk 1983, Burk and Webb 1983).

We have added details to the description of *A. suspensa* acoustic signals, correlated features of their sounds to male attributes likely to be reproductively important, and compared the songs of males having various degrees of sexual success. The result is an acoustic library that may identify qualities that tephritid breeders wish to study, and perhaps establish, in their stocks. At the same time, this unique compilation of sounds and sexual fates will interest those studying animal signals and their role in courtship.

## Materials and Methods

Caribflies used in this study were from a colony kept in domestication for ca. 1 year at the Insect Attractants, Behavior and Basic Biology Research Laboratory, Gainesville, Fla. Flies were segregated by sex 2 days after eclosion, and kept in plastic screen mesh cages (20 by 20 by 20 cm) containing water and yeast hydrolysate. Temperature was 20 to 22°C, with a photoperiod of L:D 12:12. Both males and females were selected for sexual maturity by the method of Burk and Webb (1983). At 10 to 13 days of age, calling songs were recorded. Males were then individually placed in 7.5-cm-diameter, 8-cm-high fiber glass screen cages. During the next 1 to 3 days, a female was added to the cage. Sexual behaviors were noted, and re-

<sup>1</sup>Employed through a cooperative agreement between the Department of Entomology and Nematology, University of Florida and the Insect Attractants, Behavior and Basic Biology Research Laboratory, Agric. Res. Serv., USDA, Gainesville, FL 32604.

**Table 1.** Means ( $\pm$ SE) for each of the measured variables for the calling and precopulation songs and the biotic factors

Song	Variable	n	Mean	$\pm$ SE	Units
Calling	FF-c	169	148.8	1.4	Hz
	EUC-c	169	84.4	4.2	volts
	% WD-c	168	70.1	0.5	%
	$\Delta$ F-c	168	79.6	1.2	Hz
	PTD	168	419.0	28.4	msec
	PTI	168	423.0	11.4	msec
Precopulation	SPL (pc)	119	61.6	0.4	dB
	SPL (pcum)	25	58.8	0.9	dB
	FF (pc)	107	167.0	1.2	Hz
	FF (pcum)	16	162.6	4.1	Hz
	EUC	107	277.8	18.5	V
	EUC (pcum)	16	165.9	29.2	V
	% WD-pc	106	35.7	1.2	%
	% WD (pcum)	16	47.6	3.7	%
	$\Delta$ F-pc	106	28.1	0.8	Hz
	$\Delta$ F (pcum)	16	37.9	3.1	Hz
Biotic factors	Female wt	248	14.0	0.0001	mg
	Male wt	289	10.0	0.0001	mg
	Male:female wt	248	0.74	0.01	Ratio
	DOP	143	2.7	0.3	min
	DOM	177	34.8	1.0	min
	TTM	162	19.8	1.4	min
	TTR	234	34.2	3.3	sec
	TTB	186	23.5	0.8	No

Abbreviations are as follows: Calling song: FF-c, fundamental frequency; EUC-c, energy under the curve; % WD-c, waveform distortion;  $\Delta$ F-c, bandwidth; PTD, pulse train duration; PTI, pulse train interval. Precopulation song: SPL-pc, sound pressure level; SPL (pcum), unsuccessful song sound pressure level; FF-pc, fundamental frequency; FF (pcum), fundamental frequency of unsuccessful songs; EUC, energy under the curve; EUC (pcum), energy under the curve of unsuccessful songs; % WD-pc, percent waveform distortion; % WD (pcum), percent waveform distortion of unsuccessful songs;  $\Delta$ F-pc, bandwidth;  $\Delta$ F (pcum), bandwidth of unsuccessful songs. Biotic: DOP, duration of precopulatory song; DOM, duration of mating; TTM, time between introduction of female and mating; TTR, seconds required to record 11 calling song bursts; TTB, number of calling song bursts produced until an evenly spaced series of 11 was recorded.

Recordings were made of the calling and precopulatory songs (similar to Burk and Webb [1983]). The sound pressure level (SPL) of the calling song was not determined, because in general, the pulse train (PT) duration was shorter than the response time of the SPL meter, a problem that did not occur with the relatively continuous precopulatory song. The SPL of the precopulation song was measured at a distance of 12 mm from the fly. Flies were killed after mating and weighed.

After 30 min of observation, we placed males into four categories of sexual success: copulated on first attempt; copulated after an initial failure(s) to mount, attempted mounting(s) but failed, and never attempted to mate. When analysis of variance comparisons demanded, we discarded data from sexually successful flies that had mated only after 30 min.

Statistical tests included correlation, analysis of variance, paired and unpaired *t* tests, and stepwise multiple regression. Correlated relationships that failed to be included in stepwise regression models were considered spurious and were discarded.

Recordings were made in an anechoic chamber. Only the microphone was located in the chamber, all other recording and analysis equipment were in an adjacent laboratory. A 25-mm Brüel & Kjaer (B&K) model 4145 condenser microphone with a frequency response of 5 Hz to 20 kHz  $\pm$  3 dB

with an open-circuit sensitivity of  $-25.5$  dB re mV per Pa was used. The microphone was coupled through a cathode follower to a B&K model 2608 microphone amplifier and SPL meter. The amplifier output was fed into a Hewlett-Packard 3964A tape recorder where the analog data were stored. Data were analyzed with a Nicolet 660A dual-channel Fast Fourier Transform (FFT) computing spectrum analyzer. Mass storage was accomplished with a Nicolet 160C 5.25-in., double-sided, double-density floppy disk drive. The following factors were calculated from the analysis of the recorded data: fundamental frequency (FF), total voltage under the spectrum analysis curve, percent waveform distortion, bandwidth, or frequency spread of the FF, pulse train duration (PTD), and pulse train interval (PTI) (Webb et al. 1983). See the glossary of terms below for the definitions of these factors.

## Results and Discussion

### Calling Song

Before pair formation and during pheromone release, male flies periodically produce bursts of sound a few msec to several sec in length (Webb et al. 1976). These sounds are attractive to virgin females, although associated wing movements may aid pheromone dispersal as well (Webb et al.



1983a). Virgin, but not mated, females become more active in the presence of certain male songs (Sivinski et al. 1984). Large males are more likely to call per minute of observation than small ones (Burk and Webb 1983).

The statistics for each of the factors of the calling, precopulation, and biotic songs are shown in Table 1, and their correlation with other factors is shown in Table 2.

Estimates of PT productivity, i.e., the time required to record a continuous series of 11 PTs and the number of PTs generated up to and including the continuous series of 11 PTs, bear no relationship to size ( $r = -0.003$ ,  $n = 203$ ,  $P = 0.97$ ;  $r = 0.027$ ,  $n = 158$ ,  $P = 0.73$ ). The songs of large males tend to have lower FF than small males ( $r = 0.29$ ,  $n = 168$ ,  $P < 0.0001$ ) and a higher power (EUC) ( $r = 0.40$ ,  $n = 168$ ,  $P = 0.0001$ ). This frequency relationship has been recorded in deer, toads, and frogs, and is sometimes used as a clue to male size by females preferring large mates (e.g., Wilbur et al. 1978). There is no correlation between bandwidth of the FF and size, and we found little support for a previous finding that bigger males produced shorter PTIs (Burk and Webb 1983). The correlation was negative as expected, but only bordered on significance ( $r = -0.14$ ,  $n = 167$ ,  $P = 0.08$ ). Songs with long PTDs also tend to have narrower FF bandwidths, less distortion, and higher FFs ( $r = -0.25$ ,  $n = 167$ ,  $P = 0.0007$ ;  $r = -0.26$ ,  $n = 168$ ,  $P = 0.0006$ ;  $r = 0.18$ ,  $n = 167$ ,  $P = 0.02$ ).

Males with the four degrees of sexual success had but one difference in their calling songs (the categories being: mated immediately, failed then mated, failed and never mated, never attempted to mount). Bandwidth of the FF was wider in males that called but never mounted a female compared with those that copulated successfully on their first attempt. Expanded bandwidth of FF may be a reflection of physical disability, and has been noted in irradiated (droopy-wing) Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Webb, unpublished data).

### Precopulatory Sounds

When males mount females, they generally beat their wings and produce a "precopulatory" sound of relatively constant intensity for a period of a few seconds to 25 min. Besides their lack of PTs, precopulatory sounds differ from calling songs in their higher FF (mean difference = 19.2 Hz,  $t = 10.4$ ), voltage under curve (mean difference = 199 mV,  $t = 11.8$ ,  $P < 0.0001$ ), narrower bandwidth of the FF (mean difference = 48 Hz,  $t = 29.14$ ,  $P < 0.0001$ ), and relative lack of distortion (mean difference = 34.8%,  $t = 24.53$ ,  $P < 0.0001$ ) (see Tables 1 and 3). The term "precopulatory" or "pre-mating" is something of a misnomer, because the sound typically continues after the ovipositor is lifted and the aedeagus is in contact (although generally not threaded through the female into its

**Table 3. Comparisons of aspects of precopulatory song and calling song**

Determination	Mean difference	P
Fundamental frequency	+19 Hz	<0.0001
Voltage under FFT curve	-199 mV	<0.0001
% Waveform distortion	-35%	<0.0001
Range of fundamental frequencies	-49 Hz	<0.0001

Mean difference is the average of the value of an individual copulatory song minus the value of its calling song.

final position). Also, Dodson (1978) observed that wild flies, but not flies of a laboratory strain, make periodic repetitions of precopula-like sounds during mating. We frequently observed precopula-like sounds toward the end of mating when females became restless, and Burk (unpublished data) noted that male buzzes followed female movement throughout copulation. Males that do not produce precopula songs (3% of our sample) have shorter mating durations (Sivinski et al. 1984). In another tephritid, *C. capitata*, mating duration was correlated with the number of sperm transferred so that abbreviated copulations may not have been as successful from the male's perspective (Farias et al. 1972, Burk and Calkins 1983).

The apparent signalling of male to mate led Burk and Webb (1983) to postulate that precopulatory sounds were sexually selected advertisements of male quality that could result in further female cooperation in the coupling, and that low SPL would lead to a male's rejection. We found support for their theory in the greater mean SPL of successful versus rejected males' precopulatory songs (mean successful = 61.6 dB,  $n = 115$ , mean unsuccessful = 58.8 dB,  $n = 25$ ,  $t = 2.64$ ,  $P = 0.009$ ; see also greater sexual success with greater intensity in male crickets [Forrest 1983]). However, there was no evidence of a minimum SPL below which males could not couple. The lowest successful and unsuccessful songs were both 50 dB, and 19% of successful songs were less than the mean of those produced during failed attempts. Nor was high SPL a guarantee of copulation; 20% of rejected males sang louder than the mean successful male.

Because rejection typically involves vigorous female movement, it is possible that characteristics of songs made during rejection are due to the refusal, rather than being its cause. However, successful and unsuccessful sounds produced by the same males were not significantly different in SPL, demonstrating that rejection does not necessarily mute an otherwise loud sound ( $t = 0.85$ ,  $n = 11$ ,  $P = 0.42$ ; see Table 4). As would be expected, a similar pattern occurs in the EUC. The EUC of successful songs were 1.7-fold greater than unsuccessful (mean = 280 versus 166 mV,  $t = 3.3$ ,  $P = 0.0027$ ), but the latter were made by males that showed no significant difference between their

**Table 4. Comparisons of precopulatory songs that preceded mating and rejection**

Determination	Mean	<i>P</i>	<i>P</i> (paired)
Successful male intensity (SPL)	61.6 dB	<0.009	NS
Unsuccessful male intensity (SPL)	58.8 dB		
Successful male EUC	280 mV	<0.003	NS
Unsuccessful male EUC	166 mV		
Successful male bandwidth	28 Hz	<0.0009	NS
Unsuccessful male bandwidth	37 Hz		
Successful male % distortion	36%	<0.002	<0.03
Unsuccessful male % distortion	47%		

*P* refers to the results of unpaired *t* tests; *P* (paired) refers to the results of paired *t* tests.

successful and unsuccessful efforts. Bandwidths of FF were wider in unsuccessful songs generally but not specifically (mean = 37 versus 28 Hz,  $t = 3.4$ ,  $P = 0.0009$ ). However, rejection appeared to increase the distortion of a male's song, perhaps due to female movement. Sounds produced during a failed mounting were generally more distorted (mean = 36 versus 47%,  $t = 3.2$ ,  $P = <0.002$ ), and a male, on average, sang 16% more distorted (% WD) song during rejection ( $t = 2.8$ ,  $P = <0.03$ ). A remarkably distortion-free, unsuccessful song occurred during the one rejection that involved little female movement.

If coupling sounds serve as displays of male quality, it is interesting that precopula-like sounds made near the end of mating by a male were significantly less intense than his precopula song *sensu stricto* (mean = 62.7 versus 58.9 dB,  $t = 2.54$ ,  $n = 7$ ,  $P = 0.04$ ). Males may invest more energy in manipulating females early in pairing, before all or most sperm are transferred.

Larger males tended to have louder precopulatory songs ( $r = 0.37$ ,  $n = 114$ ,  $P < 0.0001$ ), so females have a potential means of estimating male size by the intensity of the song. Recall that larger males are more apt to mate than smaller competitors when presented simultaneously to females (Burk and Webb 1983), though we found no difference in the mean weights of males that mated or failed to mate when placed singly with females and failed to find any correlation between male size and a possible measure of male acceptability (time taken to achieve coupling after female introduction). Whereas male size was significantly and negatively related to the FF of the calling song, it was conspicuously uncorrelated to the FF of the precopulatory sound ( $r = -0.09$ ,  $n = 106$ ,  $P = 0.34$ ). It may be that females "demand" (or best hear) a very specific signal from this last acoustic element of courtship which all males strive

to produce. This would be consistent with lower variance of FF in precopulatory song (coefficient of variation [*v*] calling song/*v* precopulatory song = 1.75,  $F = 2.4$ ,  $P < 0.0001$ ).

The SPL of the precopulatory song was positively correlated to its duration ( $r = 0.257$ ,  $n = 101$ ,  $P = 0.009$ ). If precopulatory song duration is an advertisement of male quality, as SPL is supposed to be, perhaps some sexually unresponsive females require both longer and louder male efforts before acquiescing. In this context, it is notable that the longer the precopulatory song (i.e., the more reluctant the female), the shorter the subsequent mating. A conflict of interest may exist between male and female over copulation duration (see Sivinski 1983). In *A. suspensa*, the larger the male relative to its mate, the longer the mating ( $F = 5.98$ ,  $P = 0.004$ ). Because copulation duration may be related to the number of sperm transferred and female propensity to remate, males may wish to extend coupling, and larger males might be more able to accomplish the extension. Also suggestive of greater male effort expended on less cooperative females is the shorter mean duration of songs sung by males who mated immediately compared with those who had previously mounted but failed to copulate with their mate (mean = 139 versus 209 sec). Whereas these means were not significantly different, the variances of the two groups were ( $F = 3.34$ ,  $P = 0.0001$ ), due to the singing of a few very long songs by the initially unsuccessful.<sup>2</sup> The songs of immediately and eventually successful males did not differ in FF, distortion, or bandwidth.

#### **Caveats and a Summary of the Role of Sound in Caribfly Courtship**

Recall that our females could not choose between males but only copulate with or reject a single companion. It would be misleading to assume that an acoustic attribute that did not vary among our males with different degrees of sexual success does not have a form preferred by females. For example, we found no difference in the weights of males that mated or failed to couple, yet larger male caribflies are known to copulate more often than smaller males when in competition (Burk and Webb 1983). Other difficulties arise from the inevitability of sexual contact. For instance, a hypothetical calling song with extended broadcast range has no chance to show its advantage when caged females can never be more than 10 cm away.

With all the possible omissions in our data in mind, we propose and reemphasize the following roles for acoustic signals in caribfly courtship.

**Calling Song.** Females orient toward or become

<sup>2</sup> In a separate experiment in which the precopula song of immediately and eventually successful males were recorded a similar result was obtained, a much higher but not significant mean duration with a highly significant difference in variances.

more active in the presence of calling song (Webb et al. 1983a). Virgin, but not mated females react differently to different songs and may discriminate among males on the basis of song qualities correlated to male value; e.g., large males' calling sounds are lower in FF and have shorter PTIs (Burk and Webb 1983, Sivinski et al. 1984). Males with broad-bandwidth calling song may be injured, malformed, or weak, and may be less vigorous in courtship or less attractive to females or both.

**Precopulatory Song.** Females may gather information about male quality from this last acoustic performance before insemination and decide whether to accept the ejaculate. The effort males put into its production appears prodigious (3.3-fold as powerful as calling song, assuming equal efficiency in the production of each). Males with lower SPL, lower EUC, and broader bandwidth precopulatory songs are less likely to mate, and those that do not sing at all have shorter mating durations. Females may prefer (or hear best) songs within a relatively narrow band of FFs. The longer a precopulatory song lasts, the greater its SPL and the shorter the subsequent mating. These relationships may be the result of males making greater efforts to gain the cooperation of sexually less responsive females. Longer matings by relatively larger males suggest conflict between the sexes over copulation duration. The SPL of precopula-like sounds produced during coupling decreases over time, perhaps due to the decreased value of further female cooperation.

#### Glossary of Terms

**Sound.** A variation in the atmospheric pressure propagated in a wave motion which occurs when a sound source sets the nearest airborne particles into motion. This motion spreads in air at a speed of ca. 340 m/sec (Anonymous 1972, 1982, Graf 1970).

**Sound pressure level (SPL).** A measure of the relative intensity of a sound expressed in decibels (dB). It is a scalar quantity that only has magnitude. The terms "intensity of a sound" and "sound intensity" should not be confused. Sound intensity is the sound energy flux per unit area, a vector with both magnitude and direction. It cannot be measured on an SPL meter. The term "level," e.g., "sound pressure level," indicates that the quantity being measured is a logarithmic ratio and is expressed in dB. For the term SPL to be meaningful, two variables must be stated: (1) the distance the microphone is from the source, and (2) the reference pressure. The reference pressure is normally 20  $\mu$ Pa for most SPL meters, and the standard notation is 0 dB re 20  $\mu$ Pa, or 0 dB re 20  $\mu$ bar, or 0 dB re 0.0002 dynes/cm<sup>2</sup>, or 0 dB re  $2 \times 10^{-5}$  n/m (Anonymous 1972, 1982, Beranek 1949).

**Decibel (dB).** One-tenth of a bel; the standard unit used in expressing relative power levels, e.g., SPL, where the dB expresses the relative power

level between the pressure measure by a microphone and a reference pressure. The dB for the SPL is 20 times the logarithm of the ratio of the measured pressure of the sound to the reference pressure. The reference pressure must be stated (Anonymous 1972, 1982, Thumann and Miller 1974, Tremaine 1969).

$$\text{SPL (dB)} = 20 \log_{10} \frac{P}{P_{\text{ref}}}$$

where  $P$  = sound pressure (RMS) in  $\mu$ Pa and  $P_{\text{ref}} = 20 \mu$ Pa.

**Fundamental frequency (FF).** The principal component of a wave, and normally the first spectral peak to occur in a frequency analysis. It is also called the first harmonic. Because our data were averaged with an FFT analyzer, we selected the spectral line with the highest amplitude occurring in the first spectral band as the FF (Anonymous 1972).

**Bandwidth ( $\Delta$ F).** The range of fundamental frequencies included in the averaged frequency spectrum. The band is limited on the lower side by the lowest detectable FF and on the upper side by the highest FF (Anonymous 1972, Graf 1970, Webb et al. 1983b). Bandwidth is related to the variance of the wing beat; i.e., relatively uniform wing movement results in relatively narrow bandwidth.

**Voltage under the curve EUC.** Total RMS voltage that lies under the spectral analysis curve.

**Percent waveform distortion (%WD).** A measure of the harmonic distortion of waveform. It is calculated by the FFT frequency analyzer technique and is equal to 100 times the ratio of the total (RMS) voltage under the frequency curve (EUC) to the peak RMS voltage of the fundamental frequency (FF).

$$\% \text{ WD} = \frac{\text{EUC}}{\text{FF}} \times 100$$

**Pulse.** An abrupt change in voltage (or current) either positive or negative and is characterized by a rise and a decay line of a finite duration.

**Pulse duration (PD).** Also called the pulse length or pulse width. The interval of time between the points at which the instantaneous value on the leading and trailing edges bears a specified relationship to the peak pulse amplitude.

**Pulse train (PT).** A group of pulses of similar characteristics.

**Pulse train duration (PTD).** The duration of a group of pulses of similar characteristics.

**Pulse train interval (PTI).** The time interval between pulse trains.

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