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THE FORM AND FUNCTION OF ACOUSTIC COURTSHIP SIGNALS OF THE PAPAYA FRUIT FLY, *TOXOTRYPANA CURVICAUDA* (TEPHRITIDAE)

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ABSTRACT

The male papaya fruit fly, *Toxotrypana curvicauda* Gerstäcker, makes two acoustic signals during courtship: (1) the approach song consists of one to five pulse trains (sound bursts) and is directed at females prior to mounting; (2) the precopulatory song consists of one to seven pulse trains produced immediately after mounting the female. Unlike the somewhat similar "calling song" of the Caribbean fruit fly, the papaya fruit fly's approach song is monotonic, a character which may be due to an absence of selection for escaping vegetation-filtering. Virgin females, but not males, become less active in the presence of broadcast approach sounds, suggesting that the proximate effect of the song is to depress locomotion in the female. Large males pair more often than small and the sound pressure level of large male approach songs is louder. Females may detect the size/vigour of a singer by his song, and such sounds may have evolved as sexually selected male advertisements rather than a means of species isolation.

RESUMEN

El macho de la mosca de la papaya, *Toxotrypana curvicauda* Gerstacker, hace dos señales acústicas durante el cortejo: (1) el canto de acercamiento consiste de una a cinco pulsaciones (estallidos de sonido) y es dirijido a las hembras antes de montarlas; (2) el canto pre-copulatorio consiste de una a siete pulsaciones producidas inmediatamente después de montarlas. Aunque el canto de llamada de la mosca de frutas del caribe es algo similar, el canto de acercamiento de la mosca de la papaya es monotónico, una característica que puede ser debida a la ausencia de selección para escapar filtraciones vegetativas. Las hembras vírgenes, pero no los machos, se vuelven menos activos en la presencia de sonidos de acercamiento diseminados, sugiriendo que el efecto inmediato del canto es para reducir la locomoción de la hembra. Los machos grandes se aparean más a menudo que los pequeños, y el nivel de presión del sonido del canto de acercamiento de los machos grandes es más alto. Las hembras pueden detectar el tamaño/vigor de un cantante por su canto, y tales sonidos pueden haberse desarrollado como un anuncio de selección sexual en vez de un medio para aislar especies.

A number of Tephritidae include acoustic signals in their courtships (Burk 1981). For example, in the Caribbean fruit fly (caribfly), *Anastrepha suspensa* (Loew), the form and intensity of two male produced songs are important criteria of female mate choice (Burk and Webb 1983, Sivinski et al. 1984, Webb et al. 1984). Similar wing generated acoustic signals have been recently found in the papaya fruit fly, *Toxotrypana curvicauda* Gerstäcker (Landolt et al. 1985).

Unlike many tropical fruit flies that tend toward polyphagy, *T. curvicauda* is a papaya (*Carica papaya* L.) specialist, although larvae are occasionally found in mango (*Mangifera indica* L.). Males have been observed on fruit attempting to copulate with ovipositing females. Little courtship behavior was noted so that the discovery in the laboratory of relatively complex off-fruit male/female interactions, including acoustic signals, was somewhat unexpected (see Landolt and Hendrichs 1983, Landolt et al. 1985). It is supposed that these displays are performed at as yet undiscoverd sites away from hosts (Landolt et al. 1985).

We describe two courtship songs and demonstrate a female reaction toward the one most frequently produced. We suggest that the greater sexual success of large male flies is correlated to the higher sound pressure levels of their signals, and we discuss differences and similarities between the songs of papaya fruit flies and those of other tephritids.

Methods

Flies were obtained as late instar larvae from papaya fruits grown in the vicinity of Homestead, Florida. Upon eclosion the flies were sorted by sex and kept in a 20 x 20 x 20-cm screen wire cage provisioned with dilute sugar water. Females were not used in experiments until they reached sexual maturity at an age of 6 days (see Landolt and Hendrichs 1983).

Recordings of sounds were made in an anechoic chamber. A 25-mm Brüel & Kjaer® Model (B&K) 4145 condenser microphone with a frequency response of 5 Hz to 20 kHz ± 3 dB and an open-circuit sensitivity of –25.5 dB re mV per Pa was coupled through a cathode follower to a B&K 2610 amplifier whose peak holding feature allows measuring the highest amplitude of short duration sound bursts (pulse trains). Data were analyzed for frequency content with a Nicolet® 660A fast Fourier transform computing spectrum analyzer. Male flies whose songs were to be recorded were placed in 7.5 x 7.5-cm screen wire cylinders along with a virgin female. The microphone was held at a distance of 1.3 cm from the surface directly under the fly. The songs of 35 males were recorded and analyzed.

In order to detect the response of females to male-produced sounds, recorded songs were broadcast at 25 virgin females placed in a 20 x 20 x 20-cm screen wire cage. Sound pressure level (SPL) was 90 dB (20 dB re 20 μPa) at cage top. Their activity was determined by counting the number of times flies crossed a line bisecting the cage during 40 alternating 90-sec periods of broadcast and silence (see Sivinski et al. 1984). In order to demonstrate that any effect was not an indiscriminate response to noise, the experiment was repeated with 25 males. We believed that since males would likely have different sexual interests their reaction to sexual signals would differ as well.

In another tephritid, the Caribbean fruit fly, the intensity of an acoustic signal is both important to probability a male will mate and correlated to male size. We were curious as to whether larger male papaya fruit flies enjoyed greater sexual success and whether size was related to the SPL of their songs. We chose our largest and smallest males ($\bar{X}$ weight large = 0.040 g; $\bar{X}$ weight small = 0.022 g) and placed them with a virgin female in 7.5 x 7.5-cm screen wire cages. We observed 20 matings and measured the peak SPL for the songs of five small and six large males. SPL was obtained by holding a 25-mm B&K Model 4145 condenser microphone 13 mm over a singing fly. The microphone was coupled to a B&K Model 2610 amplifier that measured the peak SPL of the signal.

RESULTS

Descriptions of acoustic signals.—Males approached females from the side before attempting to mount. When nearly in contact, they buzz their wings to produce what we have dubbed an "approach song." Of a sample of 58 encounters, we noted such a song in 45. Less frequently, males produced a sound within seconds after mounting the females' dorsum that we have called the "precopulatory song" (so named because it is produced under circumstances similar to those surrounding precopulatory song in Caribbean fruit flies (Webb et al. 1984)). In one 44-attempt sample, we heard eight precopulatory songs (Fig. 1).

The approach song consisted of one to five pulse trains ($\bar{X}$ = 1.6) with a pulse train duration of 0.23 sec and a mean pulse train interval of 0.14 sec. Occasionally much larger series of pulse trains occurred but it was our impression that these were due to an uncooperative female being constrained by the cage to remain near the male and that such lengthy broadcasts would not occur naturally (Table 1). One notable characteristic of the approch song is that, unlike the similar pulse trains produced by Caribbean fruit flies in their calling song, there was no frequency bimodality (see Fig. 2).

Precopulatory songs were produced by mounted males as they attempted to position the extremely long female ovipositor and insert their aedeagus. The song consisted of one to seven pulse trains. The fundamental frequency was generally lower than that of the approach song (see Table 1, Fig. 3).

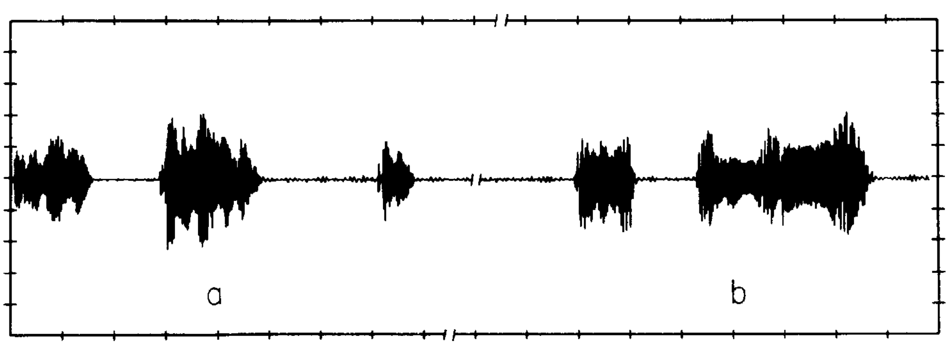

Fig. 1. Sonograph of a male approach song (a) and precopulatory song (b). Each hash mark on the baseline represents 0.25 sec. Eight sec elapsed from the first to last pulse train.

TABLE 1. THE MEAN, STANDARD DEVIATION AND MINIMUM AND MAXIMUM VALUES FOR CHARACTERISTICS OF APPROACH AND PRECOPULATORY SONGS.

	Mean	Std. deviation	Maximum	Minimum
	Approach song			
Fundamental frequency	200 Hz	26.4	285	150
Bandwidth[1]	135 Hz	38.2	228	82
Distortion[2]	45%	12%	71%	27%
Pulse train duration	.23 sec	.17	.93	.09
Pulse train interval	.14 sec	.05	.210	.60
	Precopulatory song			
Fundamental frequency	155 Hz	54	260	120
Bandwidth	87 Hz	38	137	45
Pulse train duration	.38 sec	.22	.58	.12

[1]The frequency range of the first harmonic containing the fundamental frequency.
[2]The proportion of the total energy of a sound that lies in its first harmonic.

Female reaction to approach song.—Virgin female papaya fruit flies became less active in the presence of broadcast approach song (1.1 movements/fly per min *vs*. 1.3 movements/fly per min; Wilcoxon rank sum test; $p = 0.002$). The relative female quiescence during broadcasts was opposite the reaction of virgin female caribflies, which increase their activity in the presence of calling song. There was no difference in the reaction of males.

Size, sound, and sexual success.—Large males are more likely to mate than smaller rivals (15 *vs*. 5 copulations; $X^2 = 5.0$; $p < 0.05$). There was a significant difference in the approach song sound pressure levels of large and small males (91 dB *vs*. 83 dB; Mann Whitney test; $p < 0.05$).

DISCUSSION

Acoustic signals in tephritids appear to occur in three categories: (1) calls produced in the absence of females that may serve to attract mates, (2) sounds made at close range and directed toward particular females, and (3) sounds made by mounted males as they attempt intromission or during mid-copula periods of female restlessness. The Mediterranean fruit fly (medfly), *Ceritatis capitata* (Wied.), makes three distinct sounds in the three contexts (Webb et al. 1983a) while the Caribbean fruit fly produces a distinct precopulatory (type 3) song but uses similar sounds in contexts 1 and 2 (calling song pulse train intervals shorten when singing males orient toward females at close range; [Sivinski and Webb, unpublished data]). We found no evidence of long range noncourtship singing in the papaya fruit fly. However, there are close-range and mounted songs. Such songs may function in species identification or as sexually selected self-advertisements of size/vigor, i.e. genetic quality, investment potential, resource holding power, etc. (see Thornhill 1980).

Large male mating advantages, such as occurs in *T. curvicauda*, have been found in a growing number of Diptera (e.g. Burk and Webb 1983, Borgia 1981, Sivinski 1984). In at least some of these cases, female mate choice is partially responsible for the bigger competitors having greater sexual success. While we have no direct evidence that female choice is the cause of large male advantage in papaya flies, there is substantial

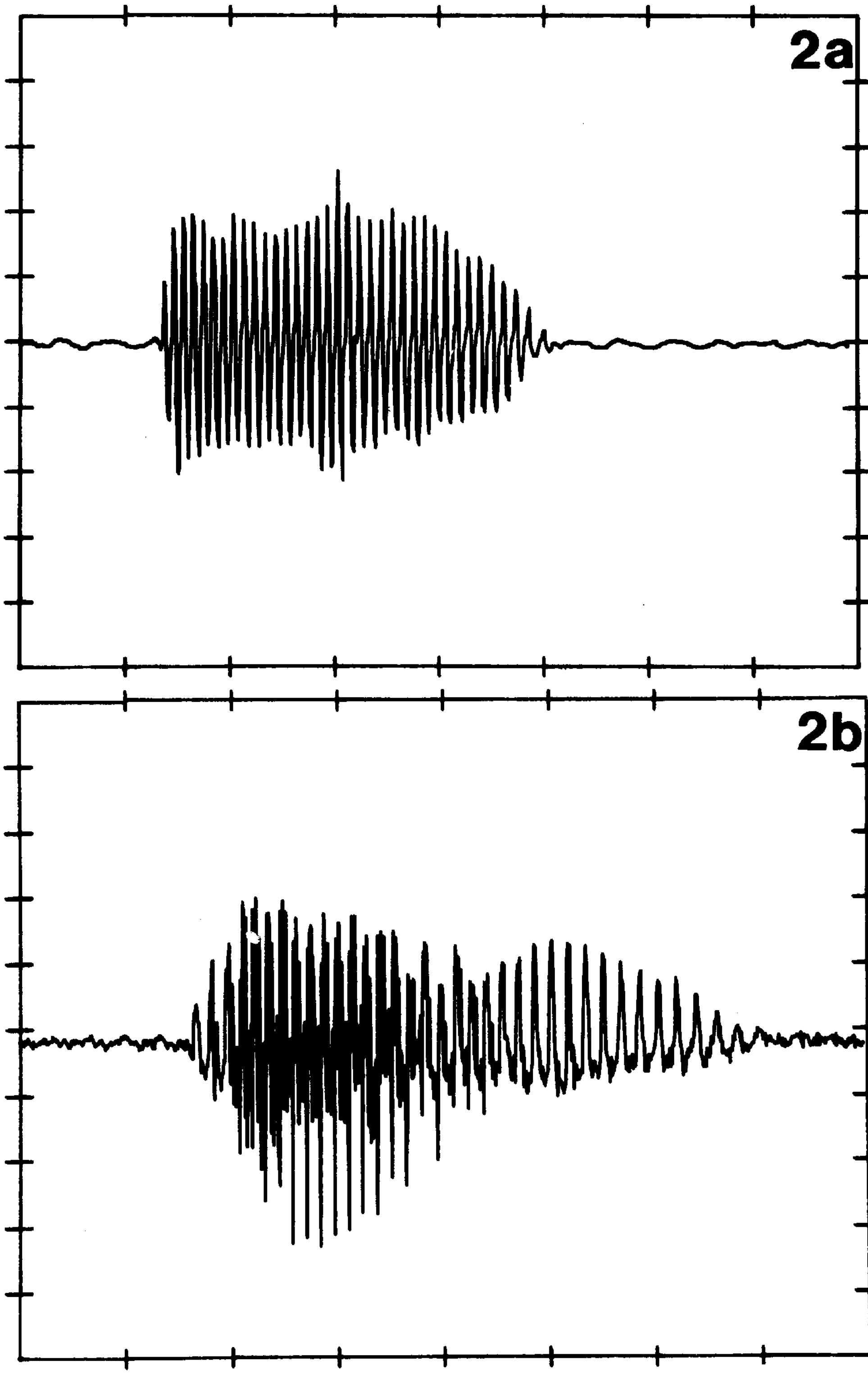

Fig. 2. A pulse train from the calling song of: A) papaya fruit fly and B) the Caribbean fruit fly. Note the lower frequency in the later half of B and the more homogeneous frequency of A. Base line in both cases represents 0.4 sec; each division 0.05 sec.

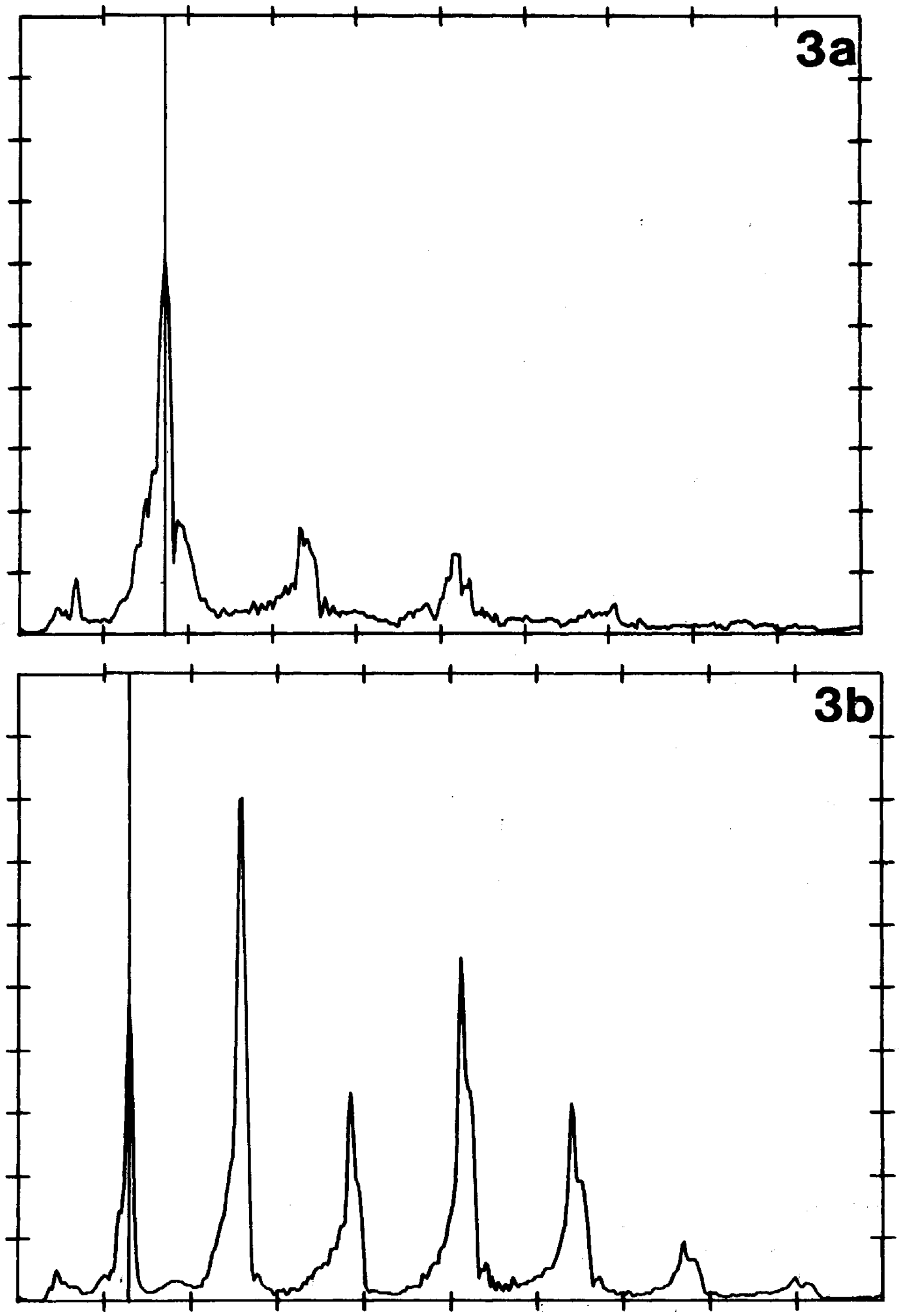

Fig. 3. A frequency spectrum analysis of: A) the papaya fruit fly approach song (fundamental freq. = 173 Hz), and B) the papaya fruit fly precopulatory song (fundamental freq. 128 Hz. Base line in both cases represents 1 kHz; each division = 100 Hz).

evidence for such choice in another tephritid, the Caribbean fruit fly (Webb et al. 1983b, Sivinski et al. 1984). In this instance song SPL, a correlate of size, is a determinate of sexual success. The similar relationships in papaya fruit fly could allow females to use the SPL of the song to estimate the size of the singer.

Papaya fruit fly and Caribbean fruit fly females have opposite reactions to broadcast song. The former becomes less active, while the latter becomes more active. Thus, the proximate function of these superficially similar songs may be as different as the context of their production. Recall that caribfly calling song is used as relatively long-range attractant that might plausibly result in the greater activity of a mate-searching female (Webb et al. 1983b). The papaya fruit fly produces a close-range courtship song directed at a particular female. Here perhaps a signal holds a choosing female in place until she can ascertain the quality of the emitter. Like papaya fruit flies, *Drosophila melanogster* Meigan sings a close-range song and females become relatively inactive in its presence (e.g. Von Schileher 1976).

The relatively monotonic nature of papaya fruit fly approach song bears comparison with the bimodal frequency of caribfly calling song. The function of producing two frequencies in the latter is unknown. It may aid females in locating emitters through the differentiated attenuation of the two frequency components (see Morris et al. 1975), or perhaps serves to avoid vegetation filtering that decreases broadcast range (see Michelsen, et al. 1982, Webb et al. 1985). Either explanation is consistent with finding two frequencies in the caribfly calling song, which is broadcast in the absence of females apparently as an attractant, and the monomorphic quality of papaya fly signals directed at very near females. Also note that the multiple pulse train wing generated "courtship song" of Mediterranean fruit flies is directed at particular females at close range and is monotonic (Webb et al. 1983a). The medfly "'calling song" is a more continuous (several sec to several min) sound produced by stridulation and is relatively monotonic. However, its very low amplitude and relatively high frequency cast doubts on its ability to reach receivers at distances comparable to caribfly calling song and its role is somewhat ambiguous. *Dacus* spp. stridulate a pulsed, fairly monotonic calling song (Webb et al., unpublished data). So little is known of courtship and signal function in *Dacus* spp. that it is premature to judge whether their monofrequent pulse trains are consistent with our distance signaling argument or not.

ENDNOTE

Mention of a commercial or proprietary product does not constitute an endorsement by the USDA.

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BAIT STAKE DETECTION OF THE FORMOSAN TERMITE IN SOUTH FLORIDA

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ABSTRACT

The Formosan termite, *Coptotermes formosanus* Shiraki, was detected in Florida in a Hallandale (Broward Co.) condominium in July, 1980. A two year (1981-1983) bait stake survey was undertaken. Of 41 building lots included in the survey, grounds, 14 were infested with Formosan termites, 4 with *Retiticulitermes flavipes* (Kollar), and 2 by both species. A stake location was rarely abandoned once found by termites, and the number of infested stakes increased with successive inspections. A stake occupied by one subterranean species was seldom subsequently occupied by the other.

RESUMEN

El comején de Formosa, *Coptotermes formosanus* Shiraki, fue descubierto por primera vez en la Florida en un condominio de Hallandale (Condado de Broward) en Julio de 1980. Se inició un estudio de dos años (1981-1983) con estacas cebadas colocadas cerca de los cimientos de edificios. De los 41 lotes incluidos en el censo, 14 terrenos estaban infestados con comején de Formosa, 4 con *Reticulitermes flavipes* (Kollar), y 2 por las dos especies. Una vez que la estaca era localizada por el comején, raramente era abandonada, y el número de estacas infestadas aumentaba con inspecciones sucesivas. Una estaca ocupada por una especie subterránea era raro que posteriormente fuera ocupada por la otra especie.