Changes in a Caribbean Fruit Fly Acoustic Signal with Social Situation (Diptera: Tephritidae)[1]

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ABSTRACT *Anastrepha suspensa* (Loew) males produce a wing-generated calling song from leaf territories in leks. Virgin females discriminate between songs on the basis of pulse-train interval (PTI) (the interval between sound bursts) with short-PTI songs eliciting more reaction. Males were found to shorten their pulse-train intervals in the presence of females and produce longer pulse trains with a higher frequency when near males. While males sing short-interval songs near potential mates, the amount of singing declines. This is due to the addition of another signal, wing semaphoring. Males are relatively quiescent when long pulse-train/high frequency sounds are broadcast toward them. There is a similar reaction to the obviously agonistic "aggression song."

MALE *Anastrepha suspensa* (Loew), the Caribbean fruit fly (caribfly), have an acoustic signal that varies in its effect on females. Males hold leaf territories in mating aggregations (leks) (Burk 1983). While on the leaves, they evert pheromone glands and, by fanning their wings, produce a calling song consisting of sound bursts (pulse trains). This behavior is initiated in the absence of females but continues as the male orients toward arriving females. Under seminatural (field-cage) conditions, this song is attractive to females (Webb et al. 1983). In the laboratory, virgin but not mated females increase their activity (flying and walking) when certain recorded calling songs are played to them. However, a song conspicuous for its long pulse-train interval (PTI) (the interval between sound bursts) elicits no reaction (Sivinski et al. 1984). Shorter PTI's are correlated with large male size, a trait much preferred by females (Burk and Webb 1983; see, however, the much weaker relationship between size and interval in Webb et al. 1984). Mate-choosing females may estimate male size and vigor on the basis of the calling song PTI.

In corroboration of earlier data that found short-interval songs are preferred by females (Sivinski et al. 1984), we show that males shorten their PTI's in the presence of females, perhaps appearing as attractive as possible. In addition, we discover that males produce longer, higher frequency PTI's when near sexual rivals. The effect of those changes on the behavior of potential competitors is similar to that produced by the clearly agonistic "aggression song."

[1] This article reports the results of research only. Mention of a proprietary product does not constitute an endorsement or the recommendation for its use by USDA.

Methods and Results

Flies were removed as 1- to 2-day-old virgins from a colony at the Insect Attractants, Behavior, and Basic Biology Research Laboratory in Gainesville, Fla. They were kept in groups of 50 in plastic screen-mesh cages (20 cm^3) until sexual maturity (10 days of age). Temperatures averaged 26°C (±1°C SD). Recordings were made in an anechoic chamber with a 25-mm condenser microphone (Brüel and Kjaer 4145) equipped with a 2619 cathode follower, Brüel and Kjaer sound pressure level meter (Model 2608), and a tape recorder (Hewlett-Packard 3964). Data were analyzed for frequency content with a computing spectrum analyzer (Nicolet 660A FFT). Pulse-train duration and PTI were determined by recording the calling song on an oscillograph (Honeywell, Model 2106) and measuring the traces.

Social Changes in Song. Twenty replications of the songs of individual males were recorded under all three of the following conditions. 1) In the cages described previously, males were in frequent contact with one another; calling individuals typically orient toward passing neighbors and are often within several centimeters of singing competitors. 2) Alone in a screen cylinder (7.5 by 7.5 cm). 3) In the cylinder, but with the addition of a smaller screen cylinder (6 by 4 cm) holding three virgin female flies. An additional five comparisons were made between flies alone and in the presence of females. Results were analyzed by random block analysis of variance by rank and Wilcoxon's paired *t* test.

Results. Males modified their songs under the three conditions (Fig. 1). PTI was shortest when males were caged with females. Pulse-train durations produced around other males were on average nearly double those made by males alone or

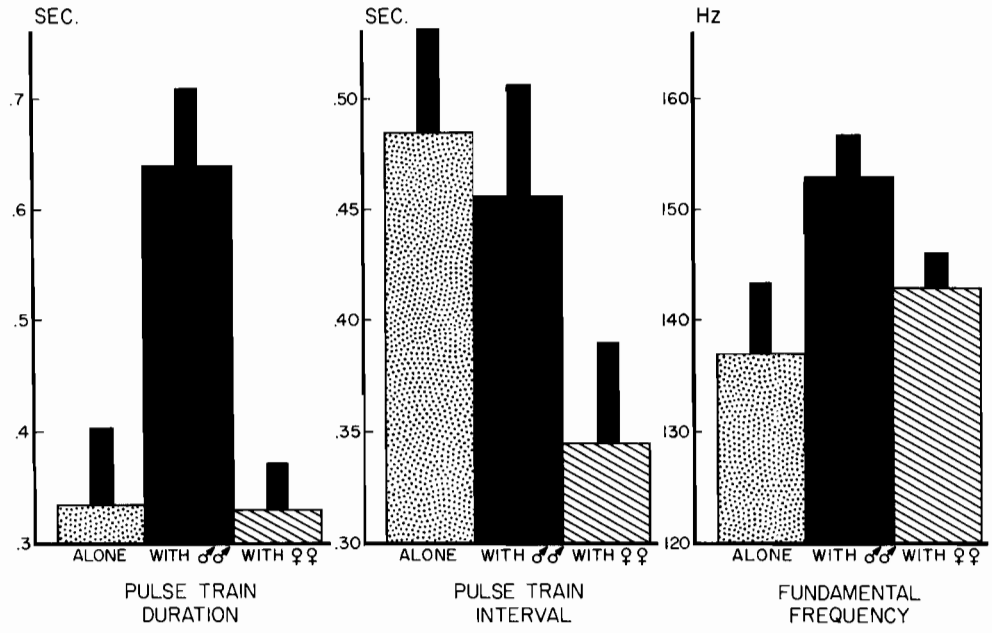

Fig. 1. Mean pulse-train duration, pulse train interval and fundamental frequency of males as they sang alone, with other males and near females. The narrow bars represent standard errors. The significance of the following comparisons is given by the notations * ($P < 0.05$) and NS ($P > 0.05$).

Pulse-train duration		PTI		Fundamental frequency	
Alone < with ♂♂	*	Alone *vs.* with ♂♂	NS	Alone < with ♂♂	*
Alone *vs.* with ♀♀	NS	Alone > with ♀♀	*	Alone *vs.* with ♀♀	NS
With ♂♂ > with ♀♀	*	With ♂♂ *vs.* with ♀♀	NS	With ♂♂ > with ♀♀	*

with females. The mean frequency was more than 10 Hz higher in songs sung near sexual competitors than when sung near females or when alone.

Calling Song Production near Females. Because songs are different near females, the propensity of males to sing might be expected to change as well. Males were caged in screen cylinders (7.5 by 7.5 cm) that contained 3-by-5-cm cylinders. These smaller cylinders either held three females or were kept empty. The number of pulse trains produced in 5 min were counted in the 10 replicates of each treatment. Statistical analysis was by Student's *t* test.

Results. Males alone produced more pulse trains than those with females (mean alone 168 pulse trains/5 min versus 116 pulse trains/5 min; $P = 0.01$; s = 51.3 versus 41.5).

Semaphoring and Calling. It was noted that males in the presence of females semaphored (i.e., wings were alternately brought forward and then pulled back by flies as they stood oriented toward another individual or slowly turned in circles).

We thought that this movement might be another signal and that the drop in song production was an effect of escalated signaling using two media rather than a mere decline in acoustic self-advertisement. To determine whether males spend more time semaphoring near females, males were placed in a wire screen cage (7.5 by 7.5 cm) first alone and then with three females enclosed in smaller cages as described above. The proportion of the two 5-min observation periods that the males spent semaphoring was determined with a stop watch. Ten replicates were made. Statistical analysis was by Wilcoxon's paired test.

Results. Males did not semaphore when caged alone, but all males semaphored when placed with females (mean = 35% of the observation period; $P < 0.0025$). Note that males with females produced 75% as many pulse trains as males by themselves. However, since semaphoring took 35% of their time, the rate of signaling (both acoustic and visual) was the same or higher in the presence of females.

Effect of Long Pulse-train Duration and High Frequency on Males. The extended pulse-train duration and higher frequency of males singing near males may either be attempts to sound different than one's neighbor and so establish an identity to potential mates, or be an agonistic variation directed at rival males. To observe the effect of different frequencies and durations on other

males, the recorded songs that a particular male sang alone and in the company of competitors were alternately broadcast toward a cage (20 cm^3) containing 20 males (a lone broadcast, mean pulse-train duration = 0.24 s, frequency = 117 Hz; with females broadcast mean pulse train = 1.19 s, frequency = 155 Hz). Peak sound pressure level of the broadcast was ca. 70 dB (0 dB re 20 pa) at cage top is measured with the previously mentioned microphone and SPL meter. A calling song has a peak SPL of ca. 12 mm from the fly. Previous work suggests males do not distinguish among different pulse-train intervals (Sivinski et al. 1984). During 5-min broadcasts of the two songs, the activity of the males was determined by counting the number of times flies crossed a line bisecting the cage. Ten replicates were made. Statistical analysis was by Wilcoxon's paired test.

Results. There was a small but relatively consistent difference in activity rate. Males moved less frequently during the broadcast of the long duration, high frequency sound (mean = 0.34 versus 0.36 movements/min per fly; $P < 0.05$, s = 0.14 versus 0.12). While apparently this demonstrates that flies distinguish between the signals, it is difficult to interpret the significance of this lower rate in terms of behavior in the field. Perhaps males are less likely to explore surrounding territories in the presence of a formidable ("vigorous") signal.

Male Reaction to Aggression Song. Given the ambiguity of the above result, we wished to compare it to the reaction of males to a clearly agonistic acoustic signal. As before, males in a cage were counted as they crossed a bisecting line. The two acoustical conditions were silence, and the raspy, aggression song produced by males in head to head conflicts. The song was played at 90 dB, an estimated intensity for a receiving organ (arista) ca. 1–2 mm from the fanning wings. Ten replicates were made. Statistical analyses were by Wilcoxon's paired test.

Results. As in the previous experiment, males moved more during periods of silence (0.68 movements per fly per min versus 0.79 movements per fly per min; $P < 0.01$; s = 0.85 versus 0.87). Again the significance of this difference is unclear, but the similarity in the reaction of males to the long duration–high frequency and aggression songs is consistent with a similar function.

Discussion

When a sexual signal has a form "preferred" by the responding sex, it is reasonable to ask why the more attractive version is not universal. One explanation is that, rather than being communications concerning species' identity and reproductive status, such broadcasts are self-advertisements of fitness elaborated by sexual selection. Their message may be contained in the expense and difficulty of their production, which ultimately reflects on the genetic quality, investment potential, resource holding power, etc., of the sender (Trivers 1972, Thornhill and Alcock 1983). Variance in these attributes generates variety in the broadcasts. If this is the case, individuals may be selected to expend more resources under conditions that best justify the expense. That is, frugal repertoires might evolve with appropriate signals for different receivers or different probabilities that receivers are within range. The same argument applies to the discouragement of rivals. If signals can, with effort, exaggerate size formidableness then a conditional use of resources may be superior to undirected and exhausting broadcasts. The elongation and acceleration of calling song in the presence of competitors and potential mates are consistent with such frugality.

Other perhaps similar social effects on dipteran signals are known. Caribflies in the presence of neighboring flies emit pheromone earlier during the afternoon broadcasting period (Burk 1985). Perhaps a closer parallel to the modification of caribfly song is the increased wing vibration in the courtship of *Drosophila melanogaster* Meigen when smaller males are confronted with larger sexual rivals (Ewing 1961). The braconid *Biosteres longicaudatus* (Ashmead) makes an intermittent buzzing sound as it approaches conspecifics. Pulse trains made in the presence of females are longer than those made near males (J. Sivinski, unpublished data). Crickets often produce different calls under different circumstances (calling, aggression, courtship) but these are frequently distinct to human observers and not subtle modifications of what would appear to be a single display (e.g., Alexander 1961).

Social changes complicate the concept of the normal–species-specific signal. Breeders of tephritids for sterile male release who consider monitoring courtship signals for quality control of their stocks should standardize the social conditions under which they gather their information. While males may exaggerate their size and vigor through decreasing PTI's, calling song may not be completely uninformative. A short-interval song need not be the product of a large and vigorous male, but a long-interval song may be more indicative of an inferior one.

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