Comparison of Acoustic Properties of Tethered Flight
Sounds for Wild, Mass-Reared, and Irradiated
Melon Flies, *Dacus cucurbitae* COQUILLET
(Diptera: Tephritidae)¹

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Acoustic properties of tethered flight sounds produced by the male melon fly, *Dacus cucurbitae* COQUILLET in wild (W-), mass-reared (M-), and irradiated (I-) strains were analyzed. Properties included fundamental frequency (FFQ), peak power density of FFQ (PPD), overall root mean square value (ORMS), total harmonic RMS (THRMS), total harmonic distortion (THDIST), bandwidth of FFQ (BWFF), and the number of harmonics and wing-strokes. M- and I-strains developed FFQ 3 days earlier than the W-strain. The W-strain had a greater variance in the mean, and overall lower values for FFQ, PPD, and ORMS than M- and I-strains. The fluctuation of acoustic properties of wild strain with aging was markedly different from that of the laboratory strains. The fact that values of these parameters for laboratory strains developed at earlier adult age and continued relatively high may be due to selection effects. No significant differences were observed between laboratory strains resulting from effect of irradiation. There were, however, significant differences among the 6 parameters in 8 age groups which were recognized for 12 cases between W- and I-, 8 between W- and M-, and 4 between M- and I-strains.

INTRODUCTION

BOLLER (1972) reviewed problems of behavioral modification in mass-reared and irradiated colonies for suppression of fruit fly populations by sterile-male release. Behavioral research to compare the quality of mass-reared stock with wild strain or to check on the deterioration of quality under artificial treatments has been conducted in tephritid flies (reviewed by CHAMBERS, 1977; MOORE et al., 1985).

Flight-mills have often been used as a method in tephritid flies for the laboratory

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assay of flight ability to detect the effects of artificial treatments, or to compare the quality of populations (reviewed by BOLLER and CHAMBERS, 1977). However, data of the parameters associated with flight propensity and distance by means of flight-mill performance of tethered flight insects usually showed considerable variability and often one could not obtain significant difference (KISHABA et al., 1967; SHARP et al., 1975; SHARP and CHAMBERS, 1976; REMUND et al., 1976; CHAPMAN, 1982, 1983; COOTER, 1982; NAKAMORI and SIMIZU, 1983; NAKAGAWA et al., 1984).

Acoustic parameters involved in flight sounds also reflect various physiological backgrounds and are estimated as a qualitative parameter of behaviour, because the properties show direct relationships between fly maturity and flight ability (WEBB et al., 1976). Data of the sound analyses for tethered flight remained relatively constant in specimens and had a rather narrow range of variation within a single group in contrast to flight-mill performance (WEBB et al., 1976; WARD and BAKER, 1982). WEBB et al. (1976) objectively measured acoustic parameters of the wingbeat frequency, the sound pressure level, and the harmonic contents of the tethered flight sounds of *Anastrepha suspensa* (LOEW), and obtained signature of the power spectral density plots by using an effective acoustic apparatus.

The present study was carried out to determine whether the acoustic properties of tethered flight sounds could be used as a measure for detecting the change of quality in strains by age or the treatment effects between wild, laboratory reared, and irradiated populations of melon flies, *Dacus cucurbitae* COQUILLET.

MATERIALS AND METHODS

Experimental stocks. Adult males of mass-reared laboratory strains (I-: irradiated and M-: non-irradiated strains) used in this research were colonies of the 49–51st releases (about 13 generations) from mass-reared colonies at the Melon Fly Eradication Project Office of Kagoshima Prefecture in Amami-oshima Island. The sterilized males were those mass-reared flies irradiated with Cobalt-60 at a dose rate of 7 krad 3 days before adult eclosion. The wild strain (W-) was 1st generation flies obtained from the infested plant, *Cucurbita moschata* DUCH. as larvae at Yoron-jima Island in Kagoshima Prefecture, except for 22-day-old flies which were 1st generation flies obtained from the infested plant, *Momordica charantia* L. as larvae at Kasari in Amami-oshima Island. Three blocks, wild (W-), mass-reared (M-), and irradiated (I-) strains were prepared for the test.

Preparation of samples. About 20 males each of 3, 5, 7, 10, 13, 16, 19, and 22 days old after adult eclosion were used respectively in these three blocks. Three to 5 days after adult eclosion, eight-day old populations of each of the three blocks were isolated in wooden cages (25 × 25 × 27 cm) and reared in a room maintained at $27 \pm 1^\circ\text{C}$, 70–80% R.H. and a photoperiod adjusted to an almost natural condition (L=8: 00–17: 30). The flies were adequately supplied with a mixture of yeast hydrolysate and sugar (1: 5), and water.

Sampling procedure. Before each test, the required number of flies were aspirated randomly from the cages into a glass tube and anaesthetized with carbon dioxide for 2–3 sec. After the anaesthesia, a fly was placed on the surface of a refrigerant (Icenon®) to keep it immobile for 1–2 min. During this time, the fly was attached by the middle of the scutum to a sharpened tip (0.6–0.7 mm) of balsa wood (50 × 1.5 × 1.5 mm) using

Fig. 1. Block diagram of recording and analysis system.

a small amount of instant glue (Alon-alpha, Toa Gosei, Japan). During this attachment an insect needle pierced the base of the balsa wood through India rubber, and held it at an appropriate position between the scutum and the balsa tip until the glue dried. After the tethered fly recovered from the anaesthesia, it was positioned so that the wings were 10 mm above the microphone, and was stimulated to initiate flight by a slight puff of mouth air from the rear to move its wings. Sounds of the first 5 min flight were recorded. If the first flight did not continue for at least one minute, the fly was discarded.

Recording system. A block diagram of the sound recording and analyzing systems is shown in Fig. 1. Two recording systems were adopted to record the required samples rapidly and without interruption. A soundproof chamber was used to cut the environmental factor of acoustic noise (10–12 dB cut). It was composed of double boxes made of 9 mm thick triple-plywood, the external one H=35 cm, W=40 cm, D=40 cm, the interior one H-W-D=13 cm. The space between the two boxes was filled with high density cellulose fiber. The interior box was covered with a double lid made of 6 mm thick acrylic board to allow observation of flight activities. A one inch condenser microphone (Type VC-25, Rion, Tokyo) with a frequency of 10 Hz–20 kHz ± 1 dB (FLAT) and dynamic range 40–130 dB (0 dB=1 V/Pa) was used as a sound transducer. The output signals were coupled through a sound level meter (Type NA20, Rion, Tokyo). Outputs from the two level meters were respectively fed into two channels of a data recorder (Model R-80, TEAC, Tokyo) simultaneously.

Parameters measured. The following acoustic parameters of tethered flight were calculated from the power spectral density plots recorded by the FFT-analyzer:

1. Fundamental frequency (FFQ: Hz): Average first spectral peak frequency (first harmonics), principal component of the wingbeat stroke.
2. Average peak power density (PPD: dBV): Average peak power density of the fundamental frequency (P-Ps, 1 Vrms re 0 dB).
3. Overall root mean square value (ORMS: dBV): Average overall RMS voltage in the spectrum of analyzing frequency band (2 kHz).
4. Total harmonic RMS voltage (THRMS: dBV): Average RMS voltage of the total harmonic contents except for the 1st harmonics,

$$\text{THRMS} = \sqrt{E_2^2 + E_3^2 + \dots + E_n^2}$$

$$E_2 - E_n = \text{average RMS of the 2nd to } n\text{th harmonics}$$

5. Total harmonic distortion (THDIST: %): Total average RMS voltage of the 2nd– n th harmonics to the average RMS voltage of the 1st harmonics in the 2 kHz frequency range,

$$\text{THD} = \frac{\sqrt{E_2^2 + E_3^2 + \dots + E_n^2}}{E_1^2} \times 100\%$$

E_1 = average RMS voltage of the 1st harmonics

6. Bandwidth of the fundamental frequency (BWFF: Hz): From the automatic peak spectral sweeping in the real time mode, the difference between minimum and maximum fundamental frequency was calculated; the value shows the degree of variation of the temporal wingbeat stroke.

In addition to the above 6 acoustic parameters measured by automatic averaging procedure, the number of wing-strokes and harmonics, and the periodicity of harmonic order were examined. The number of wing-strokes was calculated individually by age at the last sampling frame (128th) on CRT of a FFT-analyzer. The number of harmonics and periodicity of harmonic order were measured by average power spectral density plots obtained individually from Analysis II as explained in the Sample Procedure. Periodicity of harmonics order is the average rate of disorder in respective harmonic contents up to the 6th harmonics. The amplitudes of harmonics decrease gradually with the greatest at the 1st harmonics in the normal periodic waveform. The distortion of harmonics order is believed to be caused by an asynchronous wing-stroke by the two wings (WEBB et al., 1976).

Analyzing system. In the sound analysis, the output signals from the data recorder were filtered through a 70 Hz high-pass filter, multi-function decade filter (Model E-3201, NF Circuit Design Block, Tokyo), then processed through a digital spectrum analyzer (TR-9305, Advantest, Tokyo) in automatic trigger and averaging mode. The digital spectrum analyzer (FFT-analyzer) performs narrow constant band and real-time frequency analysis using a program based on the Fast Fourier Transform algorithm with a high-speed spectral processing. The TR-9305 calculates 1,024 real-valued time samples, transforms 512 points of a complex finite number of Fourier coefficients representing negative frequency less than Nyquist frequency, and displays the first 400 points which provide a guarantee for the dynamic range. The full scale frequency adopted was 2 kHz, so that 5 Hz (1/400) frequency resolution was obtained in a 200 msec frame time. A Hanning window was adopted in the Fourier transformation of the time window in order to eliminate the discontinuity of the continuous wing vibration.

Sampling procedure. In the acoustic analysis, the following three sampling and displaying procedures were used:

Analysis I: Sound signals of about 20 samples of the respective age of days and block were totalled and averaged using three kinds of program through a personal computer (M23, Mark III, Sord Computer System, Tokyo) to control the GP-IB interface of the FFT-analyzer and plotter (Myplot WX4671, Logitec, Tokyo). In this averaging, the first 10 samples were succeedingly processed by each 102 integrations up to a 1,024 averaging number, and the mean was pooled in the computer. After the mean of the next 10 samples was obtained by the same process, the two mean values measured by 2,048 integration were combined to produce a total mean of 20 samples and stored in the computer. The power spectral density plots were demonstrated by 3-dimensional representation through a plotter. The 3-dimensional comparison was made among different ages of the same strain or between different strains of the same age.

Analysis II: Sound signals of about 20 samples were individually processed and each mean of six acoustic parameters was obtained respectively by 128 integration so

that 2,678–4,165 strokes per fly were measured. A mean of respective age and strain was obtained by $1/20$ of the sum total. One merit of this procedure is that the mean of respective samples has the same value on each parameter, whereas, in Analysis I, the mean is influenced by the samples which have higher sound pressure level. Analysis II requires much time and laborious work, whereas Analysis I is effective to compare the difference of age or strain through a 3-dimensional graphical representation with automatic high speed processing by the computer systems.

RESULTS

I. Comparison by graphical displaying

Mean power spectrums of every age group of W-, M-, and I-strains are respectively demonstrated by 3 dimensional displaying in Fig. 2. The W-strain showed wider dispersion of FFQ and harmonic contents, especially at 3 and 5 days old than those of M- and I-strains. Harmonic contents for W-strain appeared with distinct peaks only at 7, 10, and 13 days old. For M-strain the 2nd harmonic contents were less distinct than those of I-strain. The peaks of each harmonics was most distinct in I-strain, with those of the 2nd to 4th harmonics between 7 and 19 days old especially being more distinctive than those for M-strain.

II. Comparison by statistical analysis

Mean values of six acoustic properties in the eight age groups for the three strains measured by Analysis II were calculated and figured (Figs. 3–8). Significant difference among ages in the same strain and between different strains were measured by *t*-test ($p < 0.05$).

1. FFQ: The FFQ (Fig. 3) remained relatively low at 3 and 5 days old for W-strain, significantly increased at 7 days, and decreased to a minimum at 13 days with a significant difference from that of M- and I-strains. The FFQ of M-strain was lower than that of I-strain at 3 days, significantly increased at 5 days, significantly higher than that of W-strain at 5, 10, 13, and 19 days old, and maintained higher value up to 10 days than that of I-strain, then gradually decreased. The FFQ of I-strain maintained a high level between 3 and 7 days, significantly higher than that of W-strain at 3, 5, and 13 days old.

2. PPD: The PPD (Fig. 4) of W-strain was lower than that of M- and I-strains at 3 days old as in the case of the FFQ, decreased to a minimum at 10 days, significantly lower than that of I-strain at 3 and 10 days old. The PPD of I-strain increased high at 7 and 10 days, then suddenly decreased at 13 days with significant differences between 10 and 13, and 13 and 16 days old. It showed no prominent decrease at 13 days old for M-strain.

3. ORMS: The ORMS (Fig. 5) showed more distinct fluctuation by age groups than the PPD. The ORMS of W- and I-strains remained low at 3 days old, and increased to a peak at 7 days, then decreased at 10 days. The ORMS of M-strain was high at 3 days old with a significant difference from that of W-strain. The ORMS of all strains rose to a peak at 7 days old, then gradually decreased to a minimum at 13 days for W- and I-strains, but it maintained a constant high level between 10 and 16 days old for M-strain. There were significant differences at 3 and 13 days old between W- and M-strains, and at 10 days between W- and I-strains.

Fig. 2. Mean power spectral density plot for W-, M-, and I-strains by age.

Fig. 3. Mean wingbeat frequency for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard errors.

Fig. 4. Mean peak power density in the fundamental frequency for W- (□), M- (●), and I- (▲) strains. Vertical bars indicate standard errors.

Fig. 5. Mean overall RMS voltage in the spectrum of 2 kHz frequency range for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard errors.

Fig. 6. Mean total harmonic RMS voltage in the 2 kHz frequency range for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard errors.

Fig. 7. Mean rate of harmonic distortion in the 2 kHz frequency range for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard errors.

Fig. 8. Mean bandwidth of the fundamental frequency for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard errors.

4. THRMS: The THRMS (Fig. 6) showed a peak at 7 days old and decreased at 10 days old for all strains, then gradually increased again. Succeeding peaks were at 13 days for M-strain, 16 days for I-strain, and 19 days for W-strains. The THRMS of I-strain was significantly higher than that of W-strain at 16 and 22 days old.

5. THDIST: The THDIST (Fig. 7) also showed distinct fluctuation by age as in the ORMS. It was low at 3 days for all strains, then increased at 5 days old. For M- and I-strains it showed a decrease at 10 days and an increase at 13 days old. From 16 to 22 days old it showed quite different curves between M- and I-strains. For W-strain it showed a peak at 7 days old, then gradually decreased to a bottom at 16 days old. The THDIST of W-strain was significantly higher than that of I-strain at 7 and 19 days old.

6. BWFF: The BWFF (Fig. 8) of W-strain was relatively low from 3 to 7 days old, greatly decreased at 13 days, with a significant difference from M-strain at 3 days and from I-strain at 13 days. The BWFF of M- and I-strains was slightly decreased at 7 days old, then showed a peak at 10 days for M-strain and 13 days for I-strain.

The line of the average number of wing-strokes for each strain (Fig. 9) was quite identical with that of the FFQ, even though the former were obtained from single data on the last frame of the FFT analyzer. W-strain had peaks at 7 and 10 days old and a minimum at 13 days. M- and I-strains already had much higher values at 3 and 5 days old, and maintained relatively higher constant values than of W-strain. On the contrary, the number of harmonics (Fig. 10) was relatively higher for W-strain than for

Fig. 9. Mean number of wing-strokes in the last frame of CRT (0.2 sec) for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard errors.

Fig. 10. Mean number of harmonics in the power spectral density plot for W- (□), M- (●), and I- (▲) strains by age. Vertical bars indicate standard deviations.

M- and I-strains. This appears to be partially coincident with the THDIST. Periodicity of harmonic order showed similar, complete periodic harmonics order for all strains except for their 4th and 5th harmonics which were often reversed, and had no significant difference between strains.

Significant differences by age within the same strain were compared by *t*-test. Significant differences ($p < 0.01$) were enumerated as 14 pairs for W-, 5 for M-, and 7 for I-strains. Days which showed significant differences ($p < 0.05$) from other days in the same strain were in total 34 cases for 3 days, 19 for 5 days, 22 for 7 days, 12 for 10 days, 17 for 13 days, 16 for 19 days, and 16 for 22 days old. Significant differences ($p < 0.05$) of each parameter by age were 17 cases for the ORMS, 15 for the THDIST, 14 for the FFQ, 11 for the THRMS, 10 for the PPD, and 9 for the BWFF.

Among pair comparisons of days for all strains, many significant differences were observed between 3 and 7 days (10 cases), 3 and 9 days (6), 3 and 22 days (6), and 3 and 16 days (5). Each mean of six acoustic parameters between the three strains was also compared by *t*-test, and significant differences ($p < 0.05$) were listed (Table 1). Significant differences were observed for 8 pairs between W- and M-strains, 12 between W- and I-strains, and for 4 between M- and I-strains. Significant differences of six acoustic parameters between different strains were 9 cases for the FFQ, 6 for the THDIST, 3 for the ORMS, 2 for the PPD, 2 for the BWFF, and 2 for the THRMS.

Table 1. Summary of the comparative results obtained by *t*-test on different strains for all ages

Strains compared	Variable	Age in days							
		3	5	7	10	13	16	19	22
W-M	FFQ	—	**	—	*	**	—	*	—
	PPD	*	—	—	—	—	—	—	—
	ORMS	*	—	—	—	*	—	—	—
	THRMS	—	—	—	—	—	—	—	—
	THDIST	—	—	—	—	—	—	—	—
	BWFF	*	—	—	—	—	—	—	—
W-I	FFQ	*	*	—	—	**	—	—	—
	PPD	—	—	—	**	—	—	—	—
	ORMS	—	—	—	*	—	—	—	—
	THRMS	—	—	—	—	—	*	—	*
	THDIST	—	—	*	—	—	*	*	**
	BWFF	—	—	—	—	**	—	—	—
M-I	FFQ	—	**	—	—	—	—	—	*
	PPD	—	—	—	—	—	—	—	—
	ORMS	—	—	—	—	—	—	—	—
	THRMS	—	—	—	—	—	—	—	—
	THDIST	—	—	*	—	—	**	—	—
	BWFF	—	—	—	—	—	—	—	—

*: significant $p < 0.05$, **: $p < 0.01$.

DISCUSSION

The mechanical characteristics and power requirements of flying insects directly affects the level of energy metabolism of an insect during flight (WEIS-FOGH, 1972). The difference of power spectral density plots resulting in wing-stroke activities can, therefore, be indicative of the difference of physical characteristics of thorax and wings, and physiological characteristics of flight metabolism and contraction of flight muscles. The rate of energy metabolism during flight may be most closely related to the wingbeat frequency and amplitude of wing-strokes. WEBB et al. (1976) showed that the wingbeat frequency and sound pressure level varied with fly maturity, namely, there were differences between young 1- to 4-day-old and other older flies of *A. suspensa* (LOEW). Our data also showed significant increase of acoustic properties at 3 and 5 days old. Similar results were obtained in other fruit flies (SHARP, 1972, 1978; SHARP et al., 1975; SHARP and CHAMBERS, 1976; REMUND et al., 1976; NAKAMORI and SIMIZU, 1983; NAKAGAWA et al., 1984). The tendency of thus marked increase in properties of flight activities early in adult life was also recognized in other Diptera as follows: ROCKSTEIN and BHATNAGAR (1966, wingbeat frequency in Muscidae), TRIBE (1966, flight duration in Calliphoridae), KUTSCH and HUG (1981, wingbeat frequency in Calliphoridae), and COOTER (1982, flight duration in Simuliidae). The marked increase of flight properties of post-teneral flies may be correspondent with the growth of muscles (development of mitochondrial protein and myofibrils) as confirmed by the studies of aging in muscles

of Glossinidae and Calliphoridae (reviewed by FINLAYSON, 1975). The different rate of muscle development is indicated here by the distinctive difference of wingbeat frequency between W-, M-, and I-strains. Significant differences were observed in the FFQ at 3 days old between W- and I-strains, and at 5 days old between W- and M-strains because of M- and I-strains already maintaining high value of the FFQ at 3 days. We believe this result reflects the earlier development of the flight muscles in M- and I-strains.

The fluctuation of acoustic properties by aging also revealed marked difference between W-, M-, and I-strains. For W-strain the FFQ, PPD, ORMS, THRMS and THDIST rose to a peak at 7 days old, then gradually decreased to reach a minimum at 13 days old (except for the THDIST at 16 days old). For M- and I-strains this tendency was not coincident with W-strain, namely, the FFQ, PPD, and ORMS maintained rather constant higher values than those of W-strain. By the two-tailed F test (at $p=0.05$), W-strain had the most abundant cases of heterogeneous variance and significant differences of the means between ages. Greater variance of the mean values of six acoustic parameters for W-strain is well recognized in Figs. 3–10. In the comparison of ages for each strain, there were 15 cases of heterogeneous variance in W-, 12 in M-, and 10 in I-strains. In the comparison of ages between different strains, there were 15 cases of heterogeneous variance between W- and M-strains, 18 between W- and I-strains, and 10 between M- and I-strains. These data show the difference of variance by strain, and suggest the effect of selection by domestication and irradiation. It was noted that selection pressure and conditioning during the process of mass-rearing might alter the behaviour of the organisms produced under artificial conditions and cause a failure of field-release (BOLLER, 1982). It is uncertain whether or not the overall stability of acoustic properties in M- and I-strains observed in our experiments is ultimately a good effect. It is probable that the high value of the FFQ for M- and I-strains indicates the high value of flight velocity, and the high value of the THDIST and the number of harmonics for W-strain may indicate the high value of flight propensity, as was true of similar results obtained in mass-reared and wild strains of *D. cucurbitae* by flight-mill experiments (NAKAMORI and SIMIZU, 1983).

There were a few parameters that significantly distinguish between M- and I-strains in contrast with W-strain to M- and I-strains. In the comparison between strains, there were only 4 cases of significant differences (2 each in the FFQ and THDIST) between M- and I-strains and, on the contrary, 8 cases between W- and M-strains, and 12 cases between W- and I-strains. This may suggest the existence of homogeneity in the M- and I-strains due to selection pressure during the long mass-rearing process.

Gamma irradiation effect can be examined by the various properties of flight activities. SCHROEDER et al. (1973) recognized the significant change of flight propensity on the I-strain of *Ceratitis capitata* (WIED.) as compared with M-strain under 10 krad dose of irradiation 2 days before adult eclosion. SHARP and CHAMBERS (1976) also showed significant difference in flight distance, velocity, and duration between M- and I-strains of *D. dorsalis* HENDEL under 20 krad dose of irradiation. In our experiments there were no prominent differences in acoustic parameters between M- and I-strains in contrast to the comparison of W-strain against M- and I-strains. The same result was recognized by SHARP (1972) on *D. dorsalis* under 10 krad dose of irradiation, and by BOLLER and CALKINS (1984) on *C. capitata* under 10 krad dose of irradiation as long as 2 days before adult eclosion. These may be due to their optimal dose of

irradiation. In spite of the absence of a distinctive difference between M- and I-strains, there was a tendency of higher values associated with the factor of sound amplitude (PPD, ORMS, THRMS) at 3 days old for M-strain than those for I-strain. This may possibly suggest the effect of irradiation.

The bio-acoustic evaluation of quality on the properties of flight sounds can be effectively performed on selected ages and parameters by using acoustic apparatus equipped with an automatic averaging function and the necessary software for control of the apparatus and a computer.

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