Flight Mill and Stroboscopic Studies of Oriental Fruit Flies[1] and Melon Flies,[1] Including Observations of Mediterranean Fruit Flies[1, 2, 3, 4]

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A flight mill system was constructed in 1969 at the Hawaiian Fruit Flies Investigations Laboratory, Honolulu, to study the flight performance of 3 Hawaiian tephritids, *Dacus cucurbitae* Coquillett, *D. dorsalis* Hendel, and *Ceratitis capitata* (Wiedemann). The unique system allowed simultaneous measurements of 18 individual flies, and data were automatically recorded on magnetic tape and computer analyzed (Chambers et al., unpublished data). The parameters measured with the system were: time in flight and at rest, distance flown, flight velocity, percentage of time flying and resting, and number of flights/hr.

Standards were established for flight of both sexes of *D. cucurbitae* and *D. dorsalis* at various ages using the flight mills. These data were augmented by wingbeat and weight studies for the 3 fruit flies, and the results are presented in this paper.

MATERIALS AND METHODS

About 1000 pupae each of the melon fly, oriental fruit fly, and Mediterranean fruit fly (obtained from the domestic stock at the USDA Hawaiian Fruit Flies Investigations Laboratory in Honolulu) and an adequate amount of hydrolyzed protein, sugar, and water (Mitchell et al., 1965; Keiser and Schneider, 1969) were placed in $(2.8\ dm)^3$ wooden cages and maintained in an insectary. Mean low and high temperature and RH inside the insectary were 23.5 ± 1.2 and 25.7 ± 0.1°C and 74.5 ± 0.4 and

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$78.4 \pm 0.2\%$, respectively. Adults of both sexes of each species were randomly selected at appropriate ages from these cages, inactivated for handling with low temperatures, and tested. Testing was done in a 3.05 $\times$ 3.05 $\times$ 3.05-m room illuminated with a mean of 8.2×10^{-3} lumens/cm^2 of fluorescent light; mean temperature and RH were 25.4 ± 0.2°C and $58.3 \pm 0.6\%$.

All statistical tests were based on Student's *t*-test for significance of the differences between sample means.

Flight Mill Studies. Replicated tests, 4 each for both sexes of both the melon fly and the oriental fruit fly were performed with 1-, 2-, 4-, 8-, 16-, and 32-day-old adults to determine the earliest age at which maximum flight ability was demonstrated. For each test, 18 randomly selected flies, 9 normal ♂ and 9 normal ♀ (ca. equal size) were fastened individually on the dorsal thorax region with nontoxic neoprene rubber cement to a small, lightweight L-shaped wire harness which was then fastened to a lightweight, stiff horizontal wire rotor arm 31.85 cm long which was attached to a magnetically suspended hub modified from a design previously described (Chambers and O'Connell, 1969).

The manner in which flies are harnessed and fastened influences test results. Thus, in our tests each fly was aligned at right angles to the rotor arm tangential to the circle it circumscribed; the body angle of each, fastened so its head tilted downward and abdomen upward, was ca. 10° with respect to the horizontal.

In the replicates, we alternated the sequence of attachment and the positions (mill nos. 1-9 vs. 10-18) of the sexes tested in the 2 mill systems. After each fly had been fastened to the rotor arm, gentle puffs of air stimulated flight. Those not responding and not turning the rotor arm were replaced. Tests lasted from 2-2.4 and 2-2.8 hrs for *D. cucurbitae* and *D. dorsalis,* respectively, during which time the flies were not provided food or water. At the end of each test, all flies were discarded.

Wingbeat Frequency Studies. The studies of wingbeat frequency were made with a General Radio Company Strobotac® type 1531-AB with a rate of flash ranging from 110 to 25,000 flashes/min and an accuracy of $\pm 1\%$.

Males and females of all 3 species (sexes not isolated) were selected at random from their cages when they were 1, 3, 5, 9, 17, 33 and 48 days old, inactivated with low temperatures, and fastened to the wire harness as previously described, except that the free end of the harness was inserted into a stationary mount to simplify the stroboscopic observations. Wingbeat frequencies of the tethered flies were recorded immediately after 2 min of sustained flight. Flies not remaining in sustained flight for a minimum of 2 min were replaced.

Weight Studies. An apparent direct relationship existed between improved flight ability and increased weight. Therefore, pupae and adults of appropriate ages of both sexes of all 3 species were selected randomly from the cages, killed with ethyl acetate vapor, and immediately weighed on a torsion balance.

RESULTS

Flight Mill Studies. Tables 1 and 2 show the means for 4 criteria of flight performance for males and females of *D. cucurbitae* and *D. dorsalis.* Age, sex, and weight were important. Females are larger and better fliers.

TABLE 1.—*Mean distance (m) and flight rate of* ♂ *and* ♀ D. cucurbitae *and* D. dorsalis.[a]

Age of flies (days)	D. cucurbitae ♂	D. cucurbitae ♀	D. dorsalis ♂	D. dorsalis ♀
		Distance (m)		
1	3333.4	3931.1	1781.3	1792.7
2	2992.6	4334.2*	1590.1	1966.2
4	4405.1	4826.4	3516.0	3167.7
8	4706.7	6058.4*	4297.5	4430.0
16	2950.7	4007.1*	5723.6	3981.9*
32	3469.6	3837.4	2980.0	3232.2
		Flight rate (m/sec)		
1	0.55	0.63	0.40	0.39
2	0.57	0.68*	0.43	0.42
4	0.63	0.68	0.59	0.54
8	0.73	0.76	0.67	0.67
16	0.71	0.82*	0.79	0.70*
32	0.71	0.85*	0.63	0.61

[a] *Denotes significant differences between sexes within species at the 95% level of probability based on Student's *t*-test. Based on 4 replications (9 ♂ and 9 ♀/replicate).

TABLE 2.—*Mean number and duration of flights of* ♂ *and* ♀ D. cucurbitae *and* D. dorsalis.[a]

Age of flies (days)	D. cucurbitae ♂	D. cucurbitae ♀	D. dorsalis ♂	D. dorsalis ♀
		Number of flights/hr		
1	3.6	3.0	5.0	5.1
2	3.2	3.1	3.5	4.3
4	3.4	3.3	2.7	2.8
8	2.4	2.9	2.6	3.2
16	3.0	2.7	1.4	2.3*
32	2.2	2.2	3.6	4.1
		Percentage of time flying		
1	66.7	70.6	53.5	54.0
2	60.4	74.0*	43.7	52.8
4	70.2	71.3	76.3	77.9
8	62.0	74.9*	71.5	74.9
16	58.8	68.7	78.4	66.4
32	67.8	64.7	53.9	59.5

[a] *Denotes significant differences between sexes within species at the 95% level of probability based on Student's *t*-test. Based on 4 replications (9 ♂ and 9 ♀/replicate).

However, significant (95% probability by t-test) differences between sexes were not common for either species of fly. Most flies flew more than 50% of the time (Table 3), and at least 83% of both sexes of *D. cucurbitae* flew more than 1000 m (Table 4). Maximum distances flown by individual males of *D. cucurbitae* were 9867 m (4 days old) and 9845 m (8 days old) at velocities of 0.7 and 0.9 m/sec while flying 92.7 and 96.7% of the time, respectively. Maximum distances flown by individual females were 10,246 m (4 days old) and 13,000 m (8 days old) at flight speeds of 0.8 and 1.1 m/sec., respectively. The 4-day-old female flew 100% of the time, and the 8-day-old female flew 98.5% of the time.

TABLE 3.—*Percentage of ♂ and ♀* D. cucurbitae and D. dorsalis *flying a given percentage of time.*[a]

Age of flies (days)	Percentage 100 ♂	100 ♀	80-99.9 ♂	80-99.9 ♀	50-79.9 ♂	50-79.9 ♀	<50 ♂	<50 ♀
				D. cucurbitae				
1	16.6	11.1	30.6	36.1	16.7	30.5	36.1	22.2
2	5.7	14.3	25.7	40.1	28.6	22.9	40.0	22.9
4	13.9	2.8	36.1	22.2	22.2	22.2	27.8	27.8
8	5.6	2.8	27.8	55.6	33.3	25.0	33.3	16.7
16	0.0	5.6	22.2	33.3	44.5	38.9	33.3	22.2
32	8.3	2.9	38.9	20.0	30.6	51.4	22.2	25.7
				D. dorsalis				
1	5.9	8.6	23.5	22.9	14.7	14.3	55.9	54.3
2	0.0	2.9	25.7	25.7	11.5	28.6	62.9	42.9
4	25.0	22.2	36.1	38.9	19.5	19.5	19.4	19.4
8	16.7	8.3	30.6	44.4	25.0	36.1	27.8	11.1
16	33.3	13.9	33.3	25.0	13.9	33.4	19.4	27.8
32	2.8	8.3	16.7	19.4	41.7	36.1	38.9	36.1

[a] Based on 4 replications (9 ♂ and 9 ♀/replicate).

Female *D. dorsalis* tended to achieve maximum flight ability earlier than males. However, the only significant differences between sexes were recorded at 16 days of age; males flew greater distances, flew faster and had fewer flights/hr. Most flies of both species, except the youngest *D. dorsalis,* flew more than 50% of the time (Table 3), and 16-day-old males and 8-day-old females had the greatest percentage of flies flying distances more than 5000 m (Table 4). Maximum distances flown by individual male *D. dorsalis* (16 days old) were 10,081 and 10,794 m, and these males flew 89.5 and 99.9% of the time, respectively, at speeds of 1.0 and 1.1 m/sec. Maximum distances flown by individual females (8 days old) were 8025 and 8301 m by 2 which flew 91.2 and 100% of the time, respectively, at velocities of 0.9 m/sec.

TABLE 4.—*Percentage of ♂ and ♀* D. cucurbitae *and* D. dorsalis *flying a given distance (m).*[a]

Age in days	>5000 ♂	>5000 ♀	3000-4999 ♂	3000-4999 ♀	1000-2999 ♂	1000-2999 ♀	<1000 ♂	<1000 ♀
				D. cucurbitae				
1	33.3	36.1	16.7	30.6	33.3	19.4	16.7	13.9
2	11.4	40.0	37.1	34.3	37.1	17.1	14.3	8.6
4	44.4	47.3	19.4	22.2	30.6	25.0	5.6	5.6
8	47.2	61.1	27.8	22.2	19.4	13.9	5.6	2.8
16	13.9	33.3	30.6	30.6	44.4	30.6	11.1	5.6
32	22.2	20.0	36.1	48.6	27.8	25.7	13.9	5.7
				D. dorsalis				
1	2.9	8.6	20.6	14.3	35.3	28.6	41.2	48.6
2	2.9	8.6	20.0	17.1	22.9	42.9	54.3	31.4
4	19.4	2.8	36.1	52.8	38.9	41.7	5.6	2.8
8	44.4	44.4	22.2	27.8	27.8	22.2	5.6	5.6
16	69.4	33.3	5.6	36.1	16.7	22.2	8.3	8.3
32	22.2	16.7	22.2	25.0	38.9	44.4	16.7	13.9

[a] Based on 4 replications (9 ♂ and 9 ♀/replicate).

Wingbeat Frequency Studies. The wingbeat frequencies of both sexes of *D. cucurbitae* increased significantly with advancing age up to 9 days (Table 5). Thereafter, they remained essentially constant. Only 5-day-old

TABLE 5.—*Mean wingbeat frequencies (Hz) of ♂ and ♀* D. cucurcitae, D. dorsalis *and* C. capitata.[a]

Age of flies (days)	D. cucurbitae ♂	D. cucurbitae ♀	D. dorsalis ♂	D. dorsalis ♀	C. capitata ♂	C. capitata ♀
1	95.4	90.6	106.6	103.5	107.8	107.5
3	105.9	102.3	117.8	114.8	147.4	150.2
5	113.7	107.8*	127.1	129.7	139.8	150.6*
9	123.6	121.0	137.6	140.7	148.4	152.2
17	121.2	118.8	138.7	138.9	149.1	158.3*
33	118.8	119.2	141.1	148.8*	155.4	158.7
48	121.0	117.2	142.9	141.2	......	......

[a] *Denotes significant differences between sexes within species at the 95% level of probability based on Student's *t*-test. Each mean based on 3 replications (10 ♂ and 10 ♀/replicate); measurements made after 2 min of sustained flight.

males had higher frequencies than females the same age. Also, 9-day-old *D. cucurbitae* males and females had different wingbeat frequencies than 1-, 3-, or 5-day-old flies of the same sex. The minimum and maximum frequencies for individual male flies were 73.3 and 145.0 Hz at ages of 1 and 48 days; for females, they were 68.3 and 143.3 Hz at ages of 1 and 9 days, respectively.

In both sexes of *D. dorsalis,* wingbeat frequencies also increased with advancing age (Table 5). Only 33-day-old females had significantly higher frequencies than males of the same age. In addition, 9-day-old males and females had significantly higher frequencies than 1-, 3-, or 5-day-old males and females. The minimum and maximum individual wingbeat frequencies were 76.7 and 166.7 Hz for males and 80.0 and 190.0 Hz for females, at 1 and 33 days, respectively.

Both male and female *C. capitata* showed sharp increases in wingbeat frequencies between 1 and 3 days of age (Table 5). Thereafter, females showed a gradual increase with advancing age; however, males showed a decrease at day 5 and then a gradual increase with advancing age. The statistically significant differences included: Females at ages of 5 and 17 days had higher wingbeat frequencies than males of the same ages; 1-day-old males and females had the lowest frequencies; 5-day-old males had lower frequencies than at other ages except 1 day. The minimum and maximum individual wingbeat frequencies were 86.7 and 186.7 Hz for males and 83.3 and 176.7 Hz for females at ages of 1 and 9 days, respectively.

Weight Studies. The mean weight of *D. cucurbitae* pupae 2 days before eclosion was 12.6±0.2 mg. Adult males dropped slightly to 10.4 mg at 1 day after emergence, increased to a maximum of 16.8 mg at day 8, and then dropped (Table 6). Thus, the 8- and 16-day-old males weighed

TABLE 6.—*Mean weights (mg) of* D. cucurbitae, D. dorsalis, *and* C. capitata.[a]

Age of flies (days)	D. cucurbitae		D. dorsalis		C. capitata	
	♂	♀	♂	♀	♂	♀
<1	10.6	13.8*	9.4	9.8	6.1	6.3
1	10.4	12.4*	10.2	10.7*	6.4	7.2*
2	11.3	13.3*	11.9	12.5*	6.8	7.4*
4	15.2	18.2*	15.6	16.6*	7.2	8.7*
8	16.8	23.0*	16.4	19.8*	7.0	9.0*
16	16.7	22.2*	16.1	20.1*	6.8	8.7*
32	15.7	22.3*	14.9	18.6*	6.1	8.0*

[a] *Denotes significant differences between sexes within species at the 95% level of probability based on Student's *t*-test. Weights based on 10 replications (10 ♂ and 10 ♀/replicate), each fly individually weighed.

significantly more than younger or older males. Similarly, the weights of females which averaged 13.8 mg soon after emergence decreased slightly to 12.4 mg at day 1 and then increased to a maximum of 23.0 mg at day 8. The females 8 days old or older therefore weighed significantly more than younger females. Also, females weighed significantly more than males at all ages.

The mean weight of *D. dorsalis* pupae 2 days before eclosion was 12.0±0.1 mg. Adult males increased from a low of 9.4 mg at <1 day after emergence to a maximum of 16.4 mg at day 8 (Table 6), and males 4 days old or older weighed significantly more than younger males. The mean weights of females increased from a low of 9.8 mg at <1 day after emergence to a maximum of 20.1 mg at day 16. Females 8 days old or older weighed significantly more than younger females. Also, females at all ages except <1 day weighed significantly more than males of comparable ages.

The mean weight of *C. capitata* 2 days before eclosion was 7.6 ± 0.0 mg. After eclosion, the weights of males increased from emergence to a maximum of 7.2 mg at day 4 (Table 6). Thereafter, losses occurred with advancing ages, and a minimum weight of 6.1 mg was recorded at 32 days. Thus, 4-day-old males weighed significantly more than <1-day, 1-, 2-, 16- and 32-day-old males. The weight of females increased from a low of 6.3 mg at <1 day after emergence to a maximum of 9.0 mg at day 8; thus, females 4 days old or older weighed significantly more than younger females. Females at all ages except <1-day weighed significantly more than males.

Discussion

The flight mill system and electronic stroboscope showed age and sex differences in the flight ability of the 3 tephritid fruit flies. Young flies performed poorly on the mills, and young adults of all 3 species had low wingbeat frequencies and minimum weights. Older flies performed better and were heavier. Eight-day-old males and 8-16-day-old females of the melon fly and 16-day-old males and 8-day-old females of the oriental fruit fly had the best performance in most flight categories and weighed the most whereas <1 and 1-day-old flies were poor fliers and had the lowest weights. Our data show significant differences in body weight occur between sexes and among ages, and these changes are related to flight ability. Thus, in tests of flight ability, consideration to age and weight of test insects should be given so it can be controlled or accounted for when appropriate.

Wingbeat increased to a maximum for *D. cucurbitae* at 9 days; for *D. dorsalis,* males reached a maximum at 48 days, females at 33; *C. capitata* reached a maximum at 33 days. Very high frequencies were recorded from 9-33 days and 48 days. It was lowest for young flies. Teneral flies are in a critical physiological condition when they emerge from the puparia, and they must ingest suitable food and water within a short period of time or die since they have little or no stored energy resources and must be supplied sugar daily (Keiser and Schneider, 1969). They remain sedentary for several hours while their wings and body cuticle harden and other processes occur; wings expand rapidly, but the soft body cuticle apparently does not harden completely for several days. These observable changes plus weight gains with time appear to be related to improved flight ability in these flies.

Clark and Rockstein (1964) reported postemergence maturation in *Musca domestica* L., *Phormia regina* (Meigen), and *Drosophila funebris* (F.). With all species, flight improved gradually after emergence as it did with the tephritids to a certain age.

The flight data indicate that young flies lack the ability to fly well. Improved flight performances were demonstrated as the flies aged and became heavier. These tests provide standards and guidelines for the conduct of tests of flight performance and behavior and for programs involving the release of adult flies.

Summary

An automatically recording flight mill system consisting of 18 individual mills was developed at the USDA Hawaiian Fruit Flies Laboratory in Honolulu and used to study the flight ability of 1-, 2-, 4-, 8-, 16- and 32-day-old male and female melon flies, *Dacus cucurbitae* Coquillett and oriental fruit flies, *D. dorsalis* Hendel. Determinations of wingbeat frequencies and body weights were also made. Female melon flies were significantly better fliers than males except at ages of 1 and 4 days; male oriental fruit flies were significantly better fliers only when they were 16 days old. The flight ability of both species increased with age and in melon fly males and females developed at approximately the same rate; the flight ability of female oriental fruit flies developed earlier than that of the males. Among melon flies, 8-day-old maies and 9-day-old females reached earliest maximum weights and wingbeat frequencies. Generally, wingbeat frequencies of all 3 species increased with advancing age. Mediterranean fruit fly males and females at all ages recorded the highest mean wingbeat frequencies; next were both sexes of oriental fruit flies; melon flies had the lowest frequencies.

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