Lek Formation and Male-Male Competition in the Melon Fly, *Dacus cucurbitae* COQUILLET (Diptera: Tephritidae)¹

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The mating behavior of wild melon flies, *Dacus cucurbitae*, was observed under field conditions. Males congregated and engaged in wing vibration in the late afternoon on non-host plants such as *Bidens pilosa*, *Amaranthus lividus* and *Crassocephalum crepidioides*, which populated over bordering cucurbit fields. Males defended their calling sites from other males through wing vibration, fighting or mounting. The rate of mating success per male in relation to female encounters was extremely low (1: 61), suggesting that each female exerted "female choice." Judging from these results we conclude that males of the melon fly form leks.

INTRODUCTION

One of the essential prerequisites for successful application of the sterile insect technique to eradicate or control an insect pest is that mass-rearing and sterilization do not have adverse effects on mating ability of released insects. IWAHASHI et al. (1983) estimated the sexual competitiveness of sterile melon flies *Dacus cucurbitae*, under field conditions. The values of competitiveness was ca. 0.8 for sterile flies in the 5th to 10th generation from the beginning of mass-rearing, but decreased to ca. 0.2 in the 18th generation. They noted that such a serious reduction in competitiveness was not detected under laboratory conditions. SOEMORI et al. (1980) showed that males taken from a stock which was at about the 40th generation would mate with both mass-reared and wild females better than wild males in small cages, but the difference decreased when larger cages were used. The reason why this phenomenon occurred is unclear, but a possible explanation may be that some sort of changes might take place in mating behavior which would be well adapted to extremely high fly density under mass-rearing conditions. This change may have resulted in the assortative mating. To know whether such changes occurred or not we need detailed knowledge of mating behaviors of both wild and mass reared melon flies. Although some studies on the mating behavior have been conducted (KOBAYASHI et al., 1978; SUZUKI and KOYAMA, 1980, 1981), these were performed under artificial or semi-artificial conditions, using laboratory reared flies. Recently KUBA et al. (1984) reported on the mating behavior of the wild melon flies but their observations were made in a field cage, not in nature.

In this paper we report sites where the mating of wild melon flies under field con-

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ditions was observed and the sequence of encounter behaviors, especially with regard to lek formation and aggressive interactions between males.

MATERIALS AND METHODS

To determine where mating behavior occurred, we evaluated the relative abundance of melon flies on each of several plant species in three fields of cucurbit and on surrounding vegetation (Fig. 1) in the southern part of Okinawa Is. These observations were made within 3 min for each plant species patch in June, 1982 at 1730–1830, just before the time when mating begins. If no fly was seen additional 3 min survey by a sweep net was performed. When two or more flies were observed on a plant species we designated it as “Many.” When one fly was seen we termed it “Some.” When no fly was seen but some were collected by a sweep net, we designated it as “Few.” If there were no sign of fly, it was termed “None.” We found that three plant species harbored melon flies. Of these *Bidens pilosa* was the most convenient for observation of fly activities.

Observations of mating behavior were made on *B. pilosa* that were about 70 cm high for 6 days in July and 9 days in October, 1982. These were begun 1 hour before sunset and ceased when any detailed observations became impossible owing to darkness. When we found a calling male that was engaging in wing vibration on a bottom surface of leaf, we recorded all acts of the fly as long as it remained in view. When the calling male met another fly we recorded the sex of the latter, position of calling male relative to his counterpart (front, rear, other) and types of resultant behaviors. The same recordings were made when the calling male encountered a mated pair. In cases of aggressive encounters between males, the outcome, if one of the two retreated, was recorded. Recording of behaviors were conducted with a portable tape recorder (Sony TCS-350®).

RESULTS AND DISCUSSION

Relative abundance of flies on a host plant. *Momordica charantia*, and on each of 10 non-host species are represented in Fig. 1 by four categories. It is notable that fly density on *M. charantia* (numbered “1” in the figure) was not high in spite of the fact that it is one of the major host plants of the melon fly in Okinawa. This may partly be due to bad conditions for egg-laying when observations were made. In Okinawa most egg-laying activities of the melon fly are seen in the morning during warm seasons. The result, however, suggests that mating behaviors of this species does not occur on a host plant. Flies were abundant on *B. pilosa* (Compositae) (2), *Crassocephalum crepidioides* (Compositae) (3) and *Amaranthus lividus* (Amaranthaceae) (4). On these three plant species, especially *B. pilosa*, flies were seen on the bottom surface of leaves.

In late the afternoon, we saw many calling males on the bottom surface of leaves of *B. pilosa*. When there were two or more calling males nearby, each other, they appeared highly nervous. We frequently observed that several males within 15 cm or less of each other engaged in wing vibration simultaneously. Thus, we counted the calling males in space as follows: If we found a calling male we designated it as a “reference male” and counted all other calling males within ca. 15 cm of the reference male. The distance of 15 cm was partly for convenience of observation. However, it

Fig. 1. Study area. There are 3 cucurbit fields (ca. 10×20 m in area numbered "1"). Dark colored indicates the plants on which many flies were there, pale some, double line (dashed and dotted) few, and single line none. Observations were mainly made on *B. pilosa* numbered "2." 1. *Momoridica charantia* L. (Cucurbitaceae), 2. *Bidens pilosa* L. (Compositae), 3. *Crassocephalum crepidioides* BENTH (Compositae), 4. *Amaranthus lividus* L. (Amaranthaceae), 5. *Amaranthus retroflexus* L. (Amaranthaceae), 6. *Solanum alatum* MOENCH (Solanaceae), 7. *Miscanthus sinensis* ANDRES (Gramineae), 8. *Paspalum urvillei* STEUD (Gramineae), 9. *Leucaena lercoccephla* LAMK (Legminosae), 10. *Mimosa pudica* L. (Legminosae), 11. *Boehmeria nivea* L. (Urticaceae).

Table 1. Number of calling males discovered within ca. 15 cm from the reference calling male which had been found on a bottom surface of *B. pilosa* first

No. other calling males	No. observed cases
0	7
1	13
2	11
3	4
4	2
5	2
6	2
7	1
Total	42

was also considered to be a distance over which other individuals could perceive signals from the reference male. In 7 of the 42 observed cases, no other calling males could be seen within 15 cm of the reference male. But in the majority of cases (83%), each reference male had one or more (up to 7) other calling males nearby (Table 1).

Table 2 shows observed encounters of males with other males, females, or mating pairs and behaviors following the encounters. Here, encounter is defined as a meeting of flies in which there was (to the observer) discernible recognition by each fly of the other fly's presence, as evidenced by the flies' visual attentiveness or movement (PROKOPY et al., 1971). If a calling male encountered another male which also was engaged in wing vibration, each continued to vibrate the wings for a short time before engaging in additional actions. In 103 of 221 encounters, such males came to blows with mid and

Table 2. Observed encounters of males with other males, females or mating pairs and their outcomes on the bottom surface of leaves of *B. pilosa*

Male encounters with:	No. observed encounters	Resultant behaviour				
		No. contact	Fight	Fight and attempted mount	Attempted mount	Successful mating
Males	221	86	103	6	26	—
Females	61	53	0	0	7	1
Mating pairs	4	3	0	0	1	0

fore legs and thrust at each other with their heads. In 6 cases, a male fought for a few seconds, and then one male attempted to mount the other. In 26 cases, a calling male attempted to mount the other as soon as the counterpart approached him. All of these male to male interactions resulted in a decreased number of calling males in the observed space. By the time this decrease had occurred we frequently discovered one or two females within a few cm of the calling male. These females found near calling males are considered to be matured ones and to be attracted to calling males since in the field cage experiment (IWAHASHI, unpublished), we have observed that unmatured females never respond to wing vibrations of males.

In 8 of 61 encounters of males with females, the male attempted to mount. Only 1 male succeeded in mating. In this case, the male was located at the rear of the female at a distance of ca. 1 cm and continued wing vibration for 31 sec. As the female turned her head toward the male, the male approached her, leaped over her head and onto her abdomen. In the remaining 53 cases, females flew away without any physical contact, while males were engaged in wing vibration. These results indicate the rate of mating success per calling bout for each male to be extremely low, suggesting that each female exerted "female choice." In 3 cases, males approached to mating pairs and engaged in wing vibration, but soon they gave up to attempting to court such pairs.

It has been pointed out that attempted mounting between males in various insects is due to little or no ability of males to discriminate between the sexes prior to contact (e.g. MORGANTE et al., 1983). In the present study, however, a difference was discovered between the mounting of males and the mounting of females. When calling males encountered other flies, either of two distinct behavioral sequences occurred: (a) calling males ceased wing vibration instantaneously, and then the next actions followed; or (b) calling males engaged in wing vibration for a long period, usually several dozens of seconds or more, and then initiated one of the behaviors shown in Table 2. For convenience, we classified the former types as males engaged in wing vibration for less than 1 second and the latter types as engaging for more than 1 second (Table 3).

When calling males encountered other males, more than 95% (210 of 221) ceased wing vibration within 1 sec. This propensity to cease calling immediately after encounters with another male was especially evident when the calling male was located at the front of his counterpart. But when calling males encountered females, almost all the males (60 of 61) engaged in wing vibration for more than 1 sec. It is also noted that where counterparts of calling males were other males 94% of calling males were engaged in wing vibration at the front of counterpart males. However in the case of females as counterparts, only 29% of encounters were frontal. These results suggest

Table 3. Duration of wing vibration when calling males encountered males or females on the bottom surface of *B. pilosa*

Male encounters with	Position of male relation to counterpart	No. observed encounters	No. males engaged in wing vibration for	
			Less than 1 sec	More than 1 sec
Males	Front	207 (93.7) ^a	203 (91.8)	4 (1.8)
	Rear	9 (4.1)	5 (2.3)	4 (1.8)
	Other	5 (2.2)	2 (0.9)	3 (1.4)
	Total	221	210 (95.0)	11 (5.0)
Females	Front	18 (29.5)	1 (1.6)	17 (27.9)
	Rear	26 (42.6)	0	26 (42.6)
	Other	17 (27.9)	0	17 (27.9)
	Total	61	1 (1.6)	60 (98.4)

^a Numbers in parentheses indicate percent.

Table 4. Outcome of various types of behaviors resulting from encounters of males with males which occurred in the late afternoon on the bottom surface of leaves of *B. pilosa*

Type of behavior	Intruder won	Resident won	Unknown
Wing vibration	0	75	11
Fight	4	86	13
Fight and mount	0	4	2
Mount	0	10	16
Total	4 (2.2%)	175 (97.8%)	42

that males did discriminate between the sexes prior to physical contact, and they used the attempted mount against other males as "an escalated fighting behavior."

Table 4 shows the outcome of aggressive encounters between males. We designated the male that initiated wing vibration on a leaf as the "resident" and the counterpart that came there later as the "intruder." In 42 of 211 encounters, resulting outcomes were unclear, because (a) in some cases both males fell down together from the leaf, or (b) in other cases of attempted mounting, the sequences progressed so quickly that we could not decide the winner. In the unmistakable 179 cases, almost all intruders (175) were defeated. The exceptional 4 cases in which intruders won occurred only after fights such as head batting and "wrestling." It is notable that in 75 cases, residents won through the wing vibration only without any physical contact. In 32 cases, including 18 unknown ones, the competition was settled by attempted mounting.

KUBA et al. (1984) observed aggregations of calling melon fly males on a field caged non-host tree in the late afternoon and suggested such aggregations were leks. Lek formation in tephritid flies has been reported for *Dacus tryoni* (TYCHSEN, 1977), *Ceratitis capitata* (PROKOPY and HENDRICH, 1979; BURK and CALKINS, 1983), *Anastrepha fraterculus* (MORGANTE et al., 1983) and *A. suspensa* (BURK, 1983).

According to EMLEN and ORING (1977) a lek is defined as a communal display area where males congregate for the sole purpose of attracting and counting females and to which females come for mating. But thereafter, many authors have reviewed and defined the basic idea of lek more rigidly. Among them KIMSEY (1980) proposed a set of criteria for leks as follows:

1. Males aggregate and display at specific site for mating.
2. Males defend territories from conspecific males.
3. These territories do not contain food resources or oviposition sites.
4. The females have an opportunity to select their mate.

In the present study, males of the melon fly congregated and engaged in wing vibration on the non-host species of *B. pilosa* in the late afternoon, males defended their calling sites from other males through wing vibration, fighting or mounting, and female choice was suggested by the extremely low rate of mating success (1 of 61 male to female encounters). Thus, it can be concluded that males of the melon fly form leks in the late afternoon on the bottom surface of leaves of non-host plants situated around cucurbit fields.

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