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MATING BEHAVIOUR OF *SCHISTOPTERUMMOEBIUSI* BECKER (DIPTERA: TEPHRITIDAE)

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ABSTRACT

Mating behaviour of the tephritid, *Schistopterum moebiusi* Becker, including pre-mating trophallaxis, is described, discussed and compared with similar phenomena in other tephritids.

INTRODUCTION

Trophallaxis is an integral part of the mating behaviour of some fruit flies (Tephritidae). Various aspects of its role, particularly during pre-copulatory and post-copulatory phases of mating, were discussed previously (Freidberg, 1981). Herein, I describe and discuss another facet in the mating behaviour and associated trophallaxis of a fruit fly species, namely *Schistopterum moebiusi* Becker.

Schistopterum moebiusi is a small tephritid, about 2 mm long, is mainly black, with a mostly yellow head. It has a distinctive wing pattern that includes dark rays extending to the wing margin as well as brown spots in the mostly black proximal portion of the pattern. The generic name, *Schistoptenim*, describes the deep incision near the middle of the costal wing margin. The species occurs from South Africa to Israel, but has not been recorded from West Africa. Larvae, which were described by Efflatoun (1925), live in the flower heads *of Pluchea dioscoridis* (L.) DC. (Compositae). Munro (1955) also recorded *Ethula conyzoides* L. as a host. Observations on the mating behaviour of this fly species were made during the months of September and October on *P. dioscoridis* along the banks of the Yarkon River, in Tel Aviv, Israel. For some observations I used a magnifying glass. Photographs were taken in the field.

DESCRIPTION OF MATING BEHAVIOUR

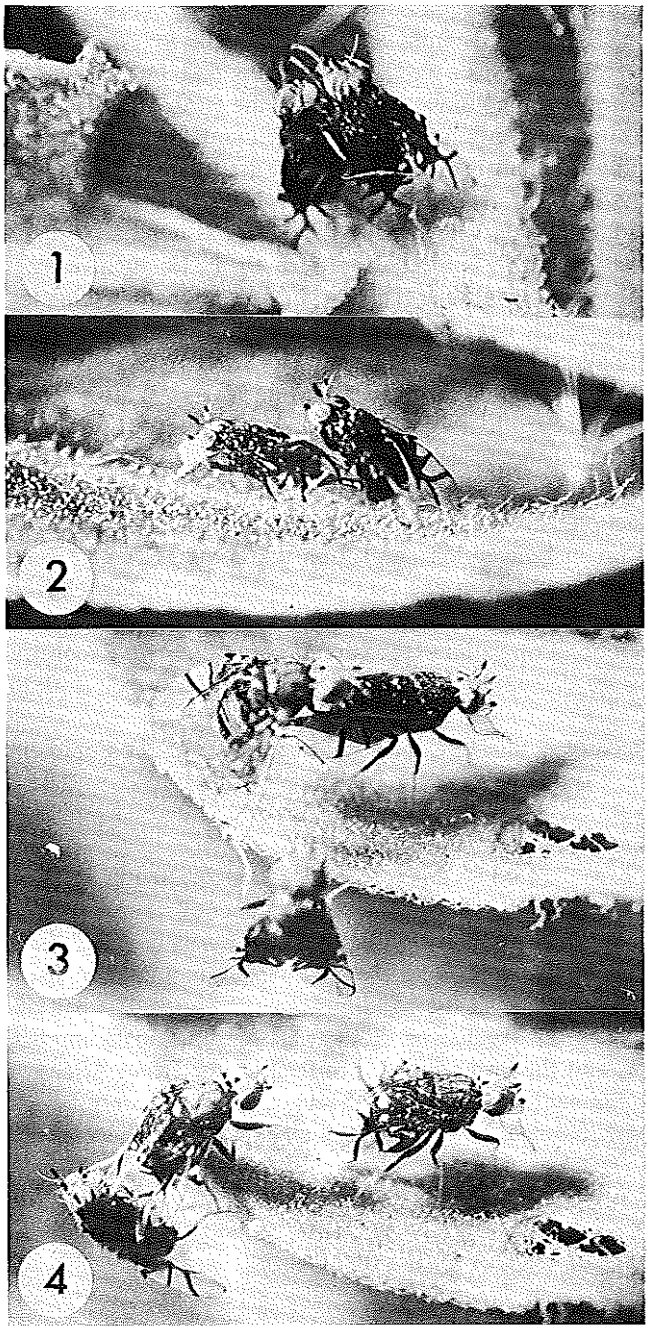
Courtship. In September and October mating activities take place mostly in the afternoon, from 1530 to 1730 (until 15 minutes after sunset). No activity was observed after dusk, even with artificial illumination. Males usually defend a territory, frequently standing on the upper side of a leaf just below an inflorescence. When another male intrudes the territory the male on guard runs toward the intruder, while scissoring rapidly with his wings. Usually this is sufficient to deter the intruder, and actual fights between males were rarely observed. During the rare fights the two rivals stand on

their hind legs with their venters touching (Fig. 1). When a female approaches, the guarding male meets her in a similar manner to that of meeting a male. An unreceptive female decamps by running or flying away, sometimes followed along several leaves by the male. In many cases the female is receptive and does not decamp. A receptive female remains on the same leaf, and the male continues his approach by scissoring and partially encircling the female several times clockwise and counter-clockwise. During this activity the female moves about, or remains stationary, scissoring and moving her wings slightly. This aspect of the courtship takes from 30 seconds to 2 minutes.

When a female stands motionless, the male extends his proboscis to the leaf surface and secretes from his labella a white, frothy material. This material is formed into a vertical pillar, with new material supplied to the top. In the last stage of secretion the male broadens the upper part of the pillar, so that its final form is like a hammer or a mushroom. The male then applies pressure to the pillar, tilting the structure to one side. The structure's final length is about 1 mm, and its white colour makes it conspicuous against the green background. Secretion lasts 10-50 seconds. During the secretion of the white froth the female faces the scene from a distance of usually less than 10 mm, mostly 1-2 mm. Sometimes she tries to approach the froth, but is stopped by scissoring activity of the male. A female will sometimes wait nearby, not facing the froth.

When secretion is finished, the male backs away a short distance. If the female is facing him, she immediately approaches, extrudes her proboscis and feeds on the froth. At the same time, the male continues his movement, and walking sideways he encircles the female and the froth. He then mounts the female from the rear, while she is feeding. If the female was not facing the male, or stood farther away, the male encircles her, and while scissoring, he orients the female toward the froth. In the latter case the female begins feeding, or the male first adds more froth on top of the pillar. If the female does not feed, the male may add froth a second or even a third time, until the female feeds or decamps. A female that feeds apparently extends her aculeus ("ovipositor"), which is grasped immediately by the male's clasper (9th tergum). The period from termination of secretion to establishment of genital contact lasts only a few seconds.

Copulation. Details of the copulation posture were difficult to observe, even with the aid of a magnifying glass. The female's body is more or less parallel to the substrate. Her wings form a "roof", with their costal margins dropped along the abdomen, and their trailing edges close together above the median line of the abdomen (Fig. 2). The antennae of the female form an angle of 45° above the body axis, with the aristae forming an additional angle of 45°. The aculeus is greatly extruded, possibly its whole length. The male's body forms an angle of about 45° with the female's body. His antennae and aristae form the same angles as those of the female. His hind legs touch the substrate, while his other legs grasp the female, although it is difficult to see exactly where they touch. It appears that the tarsi of the midlegs touch the apical part of the wings, and those of the forelegs touch their bases. At the beginning of copulation, sometimes also later, the male strokes the dorsum of the female's body with his forelegs.



Figs. 1-4 Behaviour of *Schistopterum moebiusi* Becker. 1. Males in combat on territory. 2. Copulation; the female is feeding on froth. 3. Copulation, while a second male is approaching. 4. The pair of fig. 3 withdrew, and the second male feeds on the froth.

Froth feeding and copulation sometimes proceed uninterrupted, until the female finishes the froth or several seconds thereafter. In this case copulation lasts 3-5 minutes.

If the male dismounts from the female shortly before she finishes feeding, he usually stays close to her, or moves nearby scissoring, but without trying to resume copulation. The female continues to feed on the froth until nothing is left (up to 1 more minute). In many instances the male dismounts while the female is still feeding, but behaves in a different manner. Two and a half to four minutes after beginning of copulation the male dismounts by a backwards movement, encircles the female and what is left of the froth, while facing them, and assumes a position in front of the female, so that the froth is located between them. He then resumes secretion and reconstructs the froth, while the female, who has stopped feeding, is facing him. The behaviour of the couple during froth reconstruction is similar to their behaviour during the initial formation of the froth. This includes attempts of feeding by the female and preventive actions by the male. In one case, however, a female was observed feeding from one side of the froth head, while the male was reconstructing it at the other side. After reconstruction the male mounts the female as described before, thus a "set" of sequential copulations results. A "set" is composed of a few alternating copulations and reconstructions. Each time the male fully reconstructs the froth, or even enlarges it beyond its original dimensions, an action that requires 10-45 seconds. In one case I observed 5 reconstructions in one "set" of copulations in the following sequence and periods (in minutes):

Courtship	Secretion	Copulation	Reconstruction I	Copulation	Reconstruction II
0:25	0:40	2:30	0:30	3:40	0:20

Copulation	Reconstruction III	Copulation	Reconstruction IV	Copulation
3:15	0:30	4:15	0:30	2:15

Reconstruction V	Copulation	Termination
0:45	4:45	Total 24:20 minutes.

This case was unusual for its total length and number of reconstructions.

As already stated, termination of copulation usually coincides with termination of feeding. Only in rare cases does the male remain mounted on the female after she has stopped feeding. One such case is illustrated in Figs. 3-4. A pair of flies was copulating, with the female feeding on froth, when another male approached them. The pair withdrew, and the intruder began to feed on the froth. After a few seconds the pair parted. Dismounting is always done by a smooth, barely noticeable, backward movement. After termination of copulation one mate or both leave the leaf by walking or flying.

DISCUSSION

The behaviour described here constitutes another example of mating trophallaxis, a phrase that was first used for the kind of trophallaxis shown by a tephritid, *Spathulina sicula* Loew (= *tristis* Rondani) (Freidberg 1981). "Mating trophallaxis" is presently defined as: "trophallaxis between mates, connected to copulation and taking place

TABLE 1. COMPARISON OF SOME ASPECTS OF COURTSHIP AND COPULATION BETWEEN FIVE SPECIES OF TEPHRITIDAE THAT UTILIZE "NUPTIAL GIFTS"

Species	*Stenopa vulnerata* (Loew)	*Icterica seriata* (Loew)	*Eutreta sparsa* (Wiedemann)	*Rioxa pornia* (Walker)	*Schistopterum moebiusi* Becker
Subfamily/tribe	Oedaspinae?	Tephritinae Xiphosiini	Tephritinae Ditrichini	Trypetinae	Schistopterinae
Reference	Novak & Foote 1975	Foote 1967	Stoltzfus & Foote 1965	Pritchard 1967	This article
Host and larval food	Compositae, stem gall	Compositae, flower head	Compositae, stem gall	Various fruits	Compositae, flower head
Field (1), Laboratory (2) observations	1, 2	1 (2)	1	2	1
Time of sexual activity	Early morning, late afternoon	Afternoon	?	Twilight	Mainly in the afternoon and evening
Normal site of froth	Leaves and stems	Leaves, under side	Leaves, upper side	(Cage)	Leaves, upper side
Shape of froth and height (mm)	Spherical or conical; small: 1-4, large: 5-8	Narrow (2-5)	Mostly conical (3-7)	Pyramidal (3 >)	Hammer or mushroom (1)
Number of froth mounds secreted before copulation	Usually 1, sometimes 1 large + 2-5 smaller	1	1	1	1
Froth secreted first (+) or courtship starts first (–)	+	+	+(?)	–	–
Number of breaks for additional secretions	0	0	0	1	0-5
Male mounts from in front (f) or from rear (r)	?	r	r	f	r
Proportion of froth eaten	?	small	small	1st mound, part of 2nd	All, or most
Termination of feeding and copulation simultaneous (+), not simultaneous (–)	+	+	+	+ or –	+ or –
Froth eaten by foreign elements (+)	?	?	+	?	+

shortly before, during or after copulation". In *S. sicula* the male's saliva is transferred to and eaten by the female immediately after copulation, hence it constitutes a case of post-mating trophallaxis. *Schistopterum moebiusi* exercises pre-mating trophallaxis. Pre-mating trophallaxis was described in four other tephritids (see Table 1 for references. What is common to all five species is that the sexually mature male secretes onto the substrate (normally on leaves of the host plant) a mound of material. This material, secreted through the labella, is frothy, viscous, sticky, and transluscent or white. When the female begins feeding on the froth, the male mounts her and copulation begins. In the following table some aspects of courtship and copulation within the five species are compared (Table 1).

While post-mating trophallaxis, as examplified by *S. sicula*, is evidently a manifestation of natural selection, pre-mating trophallaxis seems to be primarily or exclusively a manifestation of sexual selection. The male of *S. moebiusi* advertises himself as a fitting candidate for copulation by secreting small amounts of fragrant and/or tasty and/or nutritive material. This small amount of material is enlarged considerably by air bubbles, an easily obtainable component. Moreover, it should be stressed that there is no copulation without froth secretion. Preliminary observations show that sexual dimorphism exists in the salivary glands of *S. moebiusi*, a phenomenon associated with mating trophallaxis in the Tephritidae and Mecoptera (Freidberg, 1981; Pritchard, 1967; Thornhill, 1976). It seems that the froth secretion by males *S. moebiusi* originates in their salivary glands. Maturation of salivary glands in males of *S. sicula* roughly corresponds to maturation of their gonads (Freidberg, unpublished observations); it is likely that the same is true for *S. moebiusi*. Thus, froth provides the female with a means to select a sexually mature male. Some futile courtship scenes by immature males, in which no froth was secreted, were indeed observed. It is possible or even probable that the froth possesses further natural selective significance, such as having nutritive value. Its clear display gives the females an opportunity to assess its value and make their choice, which they do. The reconstructions of the froth, common in the mating of *S. moebiusi* (and *Rioxa pornia* (Walker) [Pritchard 1967]), support the assumption that the froth has natural selective advantage, in other words, why secrete more saliva, if already copulating? One possible answer to this question is that as a paternal investment in the progeny, the significance of the froth depends upon its quantity. There is, however, at least one more possibility to consider. Pritchard (1967) suggested that in *Rioxa pornia* the male produces a large amount of froth to keep the female immobile and ensure a complete sperm transfer. A second, larger mound is secreted after the female devoured the first, but before sperm transfer has been completed. In view of that suggestion it would be interesting to check the dynamics of sperm transfer in *S. moebiusi* with regard to the reconstructions of the froth.

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