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DO METHYL EUGENOL-FED MALES OF THE ORIENTAL FRUIT FLY (DIPTERA: TEPHRITIDAE) INDUCE FEMALE RE-MATING?

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ABSTRACT

Polyandry has been reported for various species of tephritid fruit flies, and efforts to explain this phenomenon have focused primarily on the respective roles of sperm stores and male accessory gland fluids. However, recent research on the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), demonstrated that female re-mating propensity was influenced by the "suitability" of available mates; preferred males were more likely to induce female re-mating than were less attractive males. The goal of this study was to determine whether male attractiveness similarly influenced female re-mating in the oriental fruit fly, *Bactrocera dorsalis* (Hendel). Females of this species are known to mate preferentially with males that previously ingested methyl eugenol (ME), a plant-borne compound whose metabolites are used in the synthesis of the male sex pheromone. Females were mated initially (with males denied ME), held isolated from males with access to oviposition substrate, and then offered ME-fed or non-ME-fed males at 1, 2, 3, or 6 weeks after the initial mating. Contrary to the Mediterranean fruit fly, there was no effect of male attractiveness (i.e., ME feeding status) on the re-mating tendency of *B. dorsalis* females. Also, time elapsed since the initial mating had no effect on the probability of female re-mating. When offered a choice of males, however, non-virgin females, like virgins, displayed a significant preference for ME-fed over non-ME-fed males.

Key Words: *Bactrocera dorsalis*, polyandry, mate selection, pheromone

RESUMEN

La poliandria ha sido reportado en varias especies de moscas tefritidas de la fruta y los esfuerzos hechos para explicar este fenómeno se han enfocado mayormente en los papeles respectivos de los almacenes de esperma y los fluidos de las glándulas accesorias del macho. Sin embargo, investigaciones recientes sobre la mosca mediterránea *(Ceratitis capitata* Wiedemann) de la fruta, han demostrado que la propensidad de las hembras para aparearse de nuevo fue influenciada por la idoneidad de los machos disponibles; fue mas posible para los machos preferidos el inducir a las hembras a aparearse de nuevo que los machos menos atractivos. La meta de este estudio fue el determinar en la mosca oriental de la fruta, *Bactrocera dorsalis* (Hendel) si los machos atractivos similarmente influenciaron a las hembras a aparearse de nuevo. Se sabe que las hembras de esta especie se aparean preferencialmente con machos que ingerieron eugenol metilo (EM), un compuesto producido de la planta cuyos metabolitos son usados en la síntesis de las feromonas sexuales del macho. Las hembras fueron apareadas inicialmente (con machos denegados de EM), mantenidas aisladas de los machos con aceso del sustrato para ovipositar y luego ofrecidas a machos alimentados con EM o sin EM a las 1, 2, 3 o 6 semanas después del apareamiento inicial. Al contrario de la mosca mediterránea de la fruta, no hubo efecto de los machos atractivos (alimentados con EM) sobre la tendencia de las hembras de *B. dorsalis* a aparearse de nuevo. Además, la cantidad de tiempo que pasaron después del apareamiento inicial no tuvo efecto sobre la probabilidad de las hembras a aparearse de nuevo. Cuando se ofrecio una opción de machos, sin embargo, las hembras no vírgenes, mostraron una preferencia significativa a los machos alimentados con EM que a los machos no alimentados con EM.

Several non-mutually exclusive hypotheses have been proposed for the widespread occurrence of polyandry in insects (Ridley 1988; Simmons 2001). Females may remate to (i) replace depleted sperm stores (sperm replenishment), (ii) acquire male-controlled resources (material benefits), (iii) replace sperm from a previous mate with sperm from a genetically superior partner (genetic benefits), (iv) minimize male harassment (convenience), or because (v) the propensity for female re-mating is a genetically correlated response to sexual selection on multiple mating by males (correlated evolution). Empirical support exists for all these hypotheses, with the possible exception of the final one involving the genetic link between multiple mating in the sexes (Simmons 2001).

Polyandry has been reported for various species of tephritid fruit flies, including representatives from the following genera: *Ceratitis* (Bonizzoni et al. 2002; Vera et al. 2003), *Bactrocera* (Tzanakakis et al. 1968; Ito & Yamagishi 1989; Song

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et al. 2007), *Anastrepha* (Sivinski & Heath 1988), *Toxotrypana* (Landolt 1994), and *Rhagoletis* (Opp & Prokopy 2000). Although widespread within the family, little work has been directed toward identifying the factor(s) promoting polyandry, and most of this has concerned only two species, the Mediterranean fruit fly (medfly), *C. capitata* (Wiedemann), and the Queensland fruit fly, *B. tryoni* (Froggatt). In the medfly, sperm replenishment and male accessory gland fluids both appear to influence female re-mating (Katiyar & Ramirez 1970; Nakagawa et al. 1971; Delrio & Cavalloro 1979; Jang 1995, 2002; Miyatake et al. 1999; Mossinson & Yuval 2003). In contrast, in the Queensland fruit fly, male accessory gland fluids play a major role in inhibiting female re-mating, whereas sperm stores appear to have little influence on female propensity to remate (Harmer et al. 2006; Radhakrishnan & Taylor 2007; see Kuba & Ito 1993 for similar results for the melon fly, *B. cucurbitae* (Coquillett)).

As evidenced by these studies, research on tephritids has focused exclusively on the effect of sperm supply on female re-mating or the role of male accessory fluids in inhibiting female re-mating. In lek-forming tephritids, including many *Ceratitis* and *Bactrocera* species, males do not control resources vital to females (Shelly & Whittier 1997). Consequently, it appears unlikely that females of these species mate multiply to acquire additional material resources. Furthermore, in lekking species, it appears unlikely that females remate to minimize male harassment, since courtship and copulation proceed only after female approach to stationary, signaling males (Shelly & Whittier 1997). Alternatively, the hypothesis that female tephritids remate to obtain sperm from a superior mate (i.e., to 'trade up', Halliday 1983) is conceivable but untested.

In a recent study, Shelly et al. (2004b) found that male attractiveness influenced female re-mating in the medfly. Previous work demonstrated that medfly females mate preferentially with males exposed to the aroma of certain plant-derived oils, such as orange oil (Shelly et al. 2004a) and ginger root oil (GRO; Shelly 2001), over non-exposed males. In assessing female re-mating propensity, Shelly et al. (2004b) found that non-virgin females were more likely to mate a second time if offered GRO-exposed males as opposed to non-exposed males. Whether this result indicates genetic trading up is unknown, because the adaptive basis of female preference for GRO-exposed males is unknown. Nonetheless, it does indicate that female re-mating behavior is flexible and may vary with the perceived quality of males available for repeat matings.

The goal of the present study was to determine whether male attractiveness similarly influenced re-mating by females of the oriental fruit fly, *B. dorsalis* (Hendel). Although field data are lacking, Shelly (2000a) found that *B. dorsalis* females have a fairly high incidence of re-mating in the laboratory. Over an 8-week period during which males were provided for one twilight (mating) period per week, approximately 50% of the 128 females observed re-mated, with most of these (87%) re-mating only once. Consistent with the aforementioned studies on other *Bactrocera* species, re-mating by *B. dorsalis* females was not obviously related to sperm depletion, since (i) the incidence of re-mating was independent of the length of time elapsed since the initial mating and (ii) egg production did not vary significantly before or after re-mating for most females.

Males of the oriental fruit fly are highly attracted to methyl eugenol (ME), a compound found in over 200 families of the plants (Tan & Nishida 1996). Males ingest this compound and use its metabolites to produce a long-range sex pheromone (Nishida et al. 1988). Several studies (Shelly & Dewire 1994; Tan & Nishida 1996) have demonstrated that ME consumption increases male mating success, apparently owing to the increased attractiveness of the male's pheromonal signal. Thus, as in the medfly, *B. dorsalis* females preferentially mate with males previously exposed to a particular chemical, thus allowing experimental manipulation of male attractiveness and subsequent evaluation of the effect of such manipulation on female re-mating propensity.

Materials and Methods

Study Insects

All flies used in the present study were from a laboratory colony started with 400-600 adults reared from mangos (*Mangifera indica* L.) collected in Waimanalo, Oahu. The colony was maintained in a screen cage (l:w:h, 1.2 × 0.6 × 0.6 m) and provided a mixture (3:1, wt:wt) of sugar (sucrose) and enzymatic yeast hydrolysate and water *ad libitum* and papayas (*Carica papaya* L.) for oviposition. Infested papayas were held over vermiculite, and the pupae were sifted from vermiculite 16-18 d later. Adults used in the mating trials were separated by sex within 48 h of eclosion, well before reaching sexual maturity at 15-18 d of age (TES, unpublished data), and held in screen-covered, 5-L plastic buckets; 100-125 individuals per bucket) with ample food and water. Flies were held at 24-28°C and 60-90% RH and received natural and artificial light under a 12:12 (L:D) photoperiod. When used in the study, the flies were 3-4 generations removed from the wild.

Female Re-mating

Mating activity in *B. dorsalis* is restricted to an approximately 1-h long period immediately preceding sunset (Roan et al. 1954; Arakaki et al.

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1984). Although males display vigorous wing-fanning (presumably to disperse the sex pheromone, Schultz & Bousch 1971; Kobayashi et al. 1978), little courtship is evident, and males jump on any approaching female. Mating pairs remain coupled through the night and break apart at sunrise.

To obtain initial matings, we placed approximately 50 males and 50 females (all 18-23 d-old virgins) in plexiglass cages ($30 \times 30 \times 40$ cm) in the afternoon (1400-1600 h). On a given day, 5-10 mating cages were established. Room lights were extinguished when flies were placed in the cages, consequently mating occurred under natural light. We removed unmated flies from the cages 3-4 h after sunset (using an aspirator under dim light) and left the mating pairs undisturbed in the cage through the night. The following morning we discarded the males and transferred the mated females to screen cages (30 cm cubes, 50-75 females per cage). Papayas were provided every other day (for 6-8 h) as an oviposition substrate (to mimic field conditions where females likely have multiple egg-laying opportunities) starting 2 d after the initial mating and continuing until the females were tested for re-mating either 1, 2, 3, or 6 weeks after the initial mating. We selected these intervals to monitor re-mating frequency soon after the initial mating (in possible response to low sperm transfer) as well as long after the initial mating (in possible response to sperm depletion through extensive oviposition). Ample food and water were provided and changed regularly.

To measure re-mating, we placed 10 mated females and 10 virgin males (19-29 d old) in plexiglass cages and scored matings in the same manner described above. In any given cage, males either had never been given access to ME or were fed ME the day before testing. To obtain ME-fed males, we applied 100 µL of ME to a cotton wick (held vertically by insertion through a hole in the lid of a plastic cup), which was then placed in a bucket holding 60-70 males. The chemical was introduced between 1000-1200 h and removed 1 h later. Feeding activity was not monitored, but in a previous study (Shelly 1997) over 90% of mature males fed on ME within a 1-h interval. For all combinations of post (initial)-mating interval and male treatment, re-matings were scored in 15 cages over 3-6 different days.

Female Mating Status and Mate Selection

As described below, the frequency of female re-mating varied independently of the ME feeding status of the available males. This finding suggested that, unlike virgin females (Shelly & Dewire 1994; Tan & Nishida 1996), non-virgin females may not discriminate among potential mates based on their ME status, and consequently we conducted a separate experiment to investigate this possibility.

Following the methods presented above, females were mated and held for testing 1 week later. On test days, we placed 1 non-virgin female, 1 ME-fed male, and 1 non-ME-fed male in transparent, 3.7-L plastic bottles 3-4 h before sunset and then scored the identity of mating males 2-4 h after sunset (males were marked 1 d prior to testing by placing a small dot of enamel paint on the thorax of chilled individuals). Following the same protocol, we also tested virgin females for discrimination between ME-fed and non-ME-fed males. On a given test day (n = 10 for mated females and n = 5 for virgin females, respectively), we set up 31-55 bottles with individual non-virgin females (for a total of 443 females tested) and 15-20 bottles with individual virgin females (for a total of 94 females tested).

Statistical Analysis

As neither the raw nor (log) transformed data was normally distributed, we assessed the impact of male ME 'status' (fed or non-fed) using Friedman's test, a nonparametric equivalent of the parametric 2-way analysis of variance (Daniel 1990), and treated time since the initial mating as the blocking variable. The mean numbers of re-matings observed for the different time by male status combinations were used in the analysis. In our analysis, weeks since the initial mating were the blocks, and the ME status of males presented for re-mating were the treatments. Following the Friedman test, we compared female re-mating frequency across time intervals with a Kruskal-Wallis test. In the mate choice experiment, we compared the observed mating frequencies for virgin and non-virgin females to that expected by chance (50% for each male type) using the normal approximation to the binomial. Analyses were performed with SigmaStat Statistical Software (Version 2.0). Means ± 1 SE are presented.

Results

With the effect of the blocking variable (i.e., weeks since initial mating) removed, we found no significant effect of male ME feeding status on female re-mating tendency (χ^2 = 0.24, df = 1, P = 0.65, Fig. 1). Using data pooled from both male types for each interval, we also found no significant variation in female re-mating frequency across the different time intervals (H = 4.1, df = 3, P = 0.26). Over all time intervals, the average number of females re-matings ranged only from 2.1-3.2 from a possible maximum of 10 when presented with ME-fed males and from 2.0-2.8 from a possible maximum of 10 when presented with ME-deprived males.

Consistent with previous work, virgin females showed a significant preference for ME-fed males, selecting them in 70% (35/50) of the total matings

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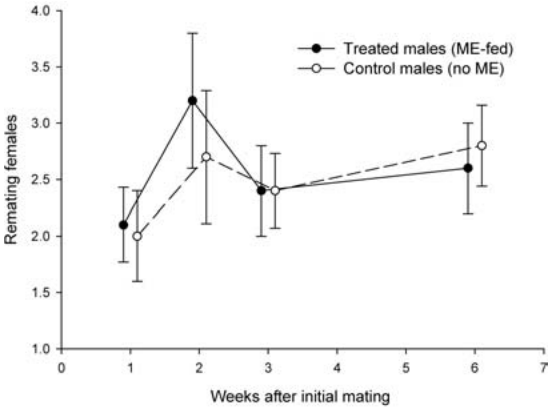


Fig. 1. Re-matings by *B. dorsalis* females presented with treated (ME-fed) or control (ME-deprived) males. Values represent mean numbers (±1 SE, n = 15 in all cases) of re-matings per cage (10 females per cage).

(Z = 2.61, P < 0.01). Non-virgin females likewise showed a significant preference for ME-fed males: 66% (34/53) of the re-mating females selected ME-fed males (Z = 2.0, P < 0.05). The overall re-mating frequency noted for non-virgins in this experiment (53/443 = 12%) was approximately half that observed in the preceding one (301/1200 = 25%). This difference in mating frequency may have reflected the differing fly densities used in the 2 experiments. Fly density (considering both sexes) was 3.03 flies/1000 cm^2 (20 flies/6600 cm^2) in the main experiment examining female re-mating propensity but only 1.31 flies/cm^2 (2 flies/1530 cm^2) in the mate choice test.

Discussion

Based on the data presented above, the re-mating frequency of *B. dorsalis* females was independent of the time elapsed since the first mating. This result is consistent with the aforementioned study (Shelly 2000a) that monitored re-mating and egg production for *B. dorsalis* females at weekly intervals over an 8-week period. As fruits were supplied periodically in both the present and the prior study, it seems likely that the number of eggs laid by individual females increased with the time available for oviposition (i.e., with time elapsed since the initial mating). If this assumption is valid, the time-independent likelihood of re-mating indicates that female receptivity is independent of egg deposition in the oriental fruit fly. This finding differs from those reported for several other tephritid species (Sivinski & Heath 1988; Landolt 1994). For example, working with the Caribbean fruit fly, *A. suspensa* (Loew), Sivinski and Heath (1988) found that 67% of females provided an oviposition substrate remated within 1 week of their initial mating compared to only 10% of females that were not provided an oviposition substrate. However, consistent with the present study, Chapman et al. (1998) reported no difference in re-mating frequency between normal (egg-laying) and irradiated (non-egg-laying) females of *C. capitata*. These differing results indicate that oviposition has a variable effect on female re-mating among tephritid species.

The data presented above also reveal that female re-mating was independent of the ME-mediated attractiveness of the males available for a second mating. This result was unexpected in light of (i) the earlier study on the Mediterranean fruit fly (Shelly et al. 2004b) showing that GRO-exposed males induced a higher level of female re-mating than non-exposed males, (ii) the repeated demonstration (Shelly & Dewire 1994; Shelly & Nishida 2004; Shelly et al. 2005, 2007) of the strong preference of virgin *B. dorsalis* females for ME-fed over ME-deprived males and (iii) the common observation from various taxa, including crickets (Bateman et al. 2001), spiders (Watson 1991), pseudoscorpions (Zeh & Zeh 2007), newts (Gabor & Halliday 1997), and guppies (Pitcher et al. 2003), that once-mated females display greater, not weaker, mate selectivity than virgin females.

Although methyl eugenol feeding had no effect on female re-mating frequency in no-choice tests, non-virgin females given a choice between ME-fed and ME-deprived males displayed a significant preference for ME-fed individuals. Taken together, these two findings indicate that, after a certain refractory period, a certain (time-independent) proportion of mated females are sexually receptive and, male type (with respect to methyl eugenol feeding) will not alter this proportion. However, when given a choice of male type, those females that are sexually receptive will generally select ME-fed males over ME-deprived males. While virgin and non-virgin *B. dorsalis* females show congruence in mate choice, the adaptive benefit of selecting ME-fed males remains unknown. As noted previously (Shelly 2000b), females do not appear to gain direct benefits (i.e., increased fecundity or longevity) by selecting ME-fed mates, raising the possibility that, by selecting ME-fed males, females may increase the probability of producing 'sexy sons', capable of locating ME and gaining copulations.

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