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EFFECT OF ADULT DIET ON SIGNALING ACTIVITY, MATE ATTRACTION,
AND MATING SUCCESS IN MALE MEDITERRANEAN FRUIT FLIES
(DIPTERA: TEPHRITIDAE)

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ABSTRACT

Field experiments were performed to examine the effect of adult diet on calling activity, female attraction, and mating success in male Mediterranean fruit flies, *Ceratitis capitata* (Wiedemann). In all tests, comparisons were drawn between males fed sugar only ("protein-deprived" males) and males fed a protein-sugar mixture ("protein-fed" males). In tests of long-distance attraction, aggregations consisting of protein-deprived males exclusively or protein-fed males exclusively were established in a coffee field, and females were released from a central release point. Protein-fed and protein-deprived males displayed similar calling levels, but approximately twice as many female sightings were recorded at groups of protein-fed males than at groups of protein-deprived males. A second test of female attraction compared single groups of protein-deprived and protein-fed males within the canopy of a field-caged host plant. As before, calling activity did not vary with diet, and in this case numbers of female sightings were also similar between aggregations of protein-fed vs. protein-deprived males. In mating trials conducted on field-caged host plants, protein-fed males achieved significantly more matings than protein-deprived males. These results are compared with other recent studies on the nutritional ecology of male Mediterranean fruit flies.

Key Words: medfly, *Ceratitis capitata*, adult diet, mate attraction, signaling

RESUMEN

Se llevaron a cabo experimentos de campos para examinar el efecto de la dieta de los adultos sobre la actividad de llamado, atracción de la hembra, y éxito de apareamiento en machos de la mosca del Mediterráneo, *Ceratitis capitata* (Wiedemann). En todas las pruebas se establecieron comparaciones entre machos alimentados solamente con azúcar (machos "privado de proteína") y machos alimentados con una mezcla de azúcar y proteína (machos "alimentados con proteínas"). En pruebas de atracción a largas distancias, grupos que consistían de machos privados de proteínas exclusivamente o de machos alimentados con proteínas exclusivamente fueron establecidos en un cultivo de café, y se liberaron hembras desde un punto central de liberación. Machos alimentados con proteínas y machos privados de proteínas desplegaron niveles de llamado similares, pero aproximadamente el doble de observaciones hacia los machos por parte de la hembra fueron registradas en los grupos de machos alimentados con proteínas comparados con el grupo de machos privados de proteínas. Una segunda prueba de atracción de las hembras comparó grupos individuales de machos privados de proteínas y grupos de machos alimentados con proteínas dentro del área foliar de la planta hospedera de la jaula en campo. Como se determinó anteriormente la actividad de llamado no varió con la dieta, y en este caso el número de observaciones hacia los machos por parte de las hembras fueron también similares entre los grupos de machos alimentados con proteínas vs. machos privados de proteínas. En las pruebas de apareamientos conducidas en plantas hospederas dentro de jaulas en el campo, los machos alimentados con proteínas lograron significativamente mayor número de apareamiento que los machos privados de proteínas. Estos resultados son comparados con otros estudios recientes sobre la ecología nutricional de los machos de la moscas del Mediterráneo.

In many insects, nutritional status may affect the ability of males to attract females and obtain matings. The association between nutrition and male reproductive behavior is manifest in 2 major ways. First, sexual activities, such as production of advertisement and courtship signals (Burk 1988,

Landolt & Sivinski 1992, Epsky & Heath 1993, Dronev 1996) and defense of calling sites or territories (Marden & Waage 1990, Plaistow & Siva-Jothy 1996, Hack 1997), are often energetically expensive, and male reproductive success may depend on the maintenance of sufficient fuel reserves

to adequately perform these behaviors. In addition to offsetting behavioral costs, males may use nutrients to synthesize material products needed for reproduction, i.e., pheromones (Edgar et al. 1974, Lofstedt et al. 1989, Nishida et al. 1997) or substances transferred during copulation, such as nuptial gifts (Gwynne 1990, Simmons et al. 1992) or sperm (Pitnick & Markow 1994).

In a series of provocative papers, Yuval and his colleagues (Warburg & Yuval 1996, 1997, Blay & Yuval 1997, Yuval et al. 1998, Field & Yuval 1999) investigated the effects of adult diet on male reproductive behavior in the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann. This species exhibits a lek mating system in which males defend individual leaves on host trees as mating territories and attract females to their perch via production of a sex pheromone (Prokopy & Hendrichs 1979, Arita & Kaneshiro 1989, Whittier et al. 1992). Yuval and his associates drew the following important conclusions: (a) in the field, lekking males were heavier and contained greater (mass-specific) amounts of sugar, protein, and protein than resting (non-lekking) males; (b) with the exception of sugar, nutrient levels declined through the day for field-collected, lekking males, suggesting a energetic cost of lekking; (c) under experimental dietary regimes, protein-fed males sustained longer bouts of pheromone-calling and courted more often than protein-deprived males; (d) in no-choice, laboratory trials, females mated more readily with protein-fed than protein-deprived males; and (e) females first mated to protein-deprived males were more likely to remate than females first mated to protein-fed males. Collectively, these results strongly suggest that adult diet has an important effect on the ability of *C. capitata* males to meet the energy costs associated with both courtship behavior and pheromone and ejaculate production.

The purpose of the present paper is to investigate further the effect of adult diet on the signaling behavior and mating success of *C. capitata* males. Three field experiments were conducted that compared protein-fed and protein-deprived males with respect to (1) calling level and female attraction between host-plants, (2) calling level and female attraction within the canopy of a single host plant, and (3) mating success under competitive (female choice) conditions.

MATERIALS AND METHODS

Female Attraction: between Host Plants

Because of the limited availability of wild individuals, the flies used in the between-plant, attraction trials were from a 6-year old strain mass-produced at the USDA-APHIS Fruit Fly Rearing Facility, Waimanalo, Oahu. This strain (known as "Maui-Med") originated from adults reared from

coffee (*Coffea arabica* L.) collected on Maui. Non-irradiated pupae were obtained 2 days prior to eclosion, and adults were separated within 24 h of emergence and held in plastic buckets covered with nylon screening (volume 5 liters; 50-60 flies per bucket). Males were separated into 2 dietary regimes: "protein-deprived" males were given only sugar (sucrose) plus water, and "protein-fed" males were given a 3:1 mixture (by volume) of sugar and protein hydrolysate plus water. All females were given the sugar-protein mixture plus water.

Trials were conducted within a 500-ha coffee field 8 km south of Haleiwa, Oahu (elevation 300 m). Prior detection efforts involving fruit collections as well as trimedlure-baited traps revealed that the wild population of *C. capitata* was very low in the study area. Rows contained approximately 5 plants per 10 m, and adjacent rows were separated by 2 m of bare ground. Coffee plants were 2.0-2.5 m tall and bore no fruit during the study.

During a given trial, we monitored male pheromone calling and female sightings for groups of protein-deprived vs. protein-fed males. Four aggregations (or leks) were established at individual coffee plants, with 2 plants containing protein-deprived males exclusively and 2 plants containing protein-fed males exclusively. Groups of 6 males (7-13 days old) were placed in transparent plastic cups (volume 400 ml) that were covered on both ends with wire mesh. Cups were hung horizontally with wire (i.e., with the long axis parallel to the ground), with strips of masking tape placed on the upper surface to provide shaded, "leaf-like" perch sites. A total of 4 cups was used per aggregation, i.e., each lek consisted of 24 males of a given dietary type. Cups on a given plant were placed in the same portion of the canopy (usually within 15 cm of one another) at 1.0-1.5 m above ground.

The 4 test plants were located in 2 rows separated by a central row that contained the plant at which females were released. The resulting spatial arrangement was a rectangle, with the test plants located at the corners and the release point located at the center. Dimensions of this rectangle were 20 m (distance between test plants in the same row) by 6 m (distance between test plants in different rows). Lek sites at diagonal positions were composed of the same male type (i.e., protein-deprived or protein-fed). Ten minutes following placement of the males (between 0815-0830 h), 400 females (8-14 days old) were released at the base of the designated release plant. Starting 10 min after the release of the females, we recorded the numbers of calling males and perching females at each aggregation at 10 min intervals over the next 90 min (i.e., a total of 10 observations per replicate). Females were counted if they perched directly on or within 15 cm of a cup. Because females were not marked, the number of female sightings represents a composite measure

that included both arrivals to and retention near a male aggregation. Trials were conducted under sunny or partly cloudy skies at air temperatures of 22-25°C. The same 4 coffee plants served as lek sites over all replicates, and for a given plant, the type of male present—protein-deprived vs. protein-fed—was alternated between successive trials. A total of 16 replicates was conducted with a minimum of 2 days separating successive replicates to allow female dispersal from the study area.

Female Attraction: within a Host Plant

Tests on within-plant, attraction were performed using wild flies reared from fruits of Jerusalem cherry (*Solanum pseudocapsicum* L.) collected in Hawaii Volcanoes National Park, Hawaii. Larval development proceeded *in situ*, and pupation occurred in vermiculite. Emerging wild adults were handled in the same manner described above, with males separated into protein-deprived or protein-fed groups.

Trials were conducted using a field-caged guava tree (*Psidium guajava* L.) at the University of Hawaii Agricultural Station, Waimanalo, Oahu. The tree was 2.4 m tall, and the canopy occupied most of the upper half of the screen-mesh tent (height—2.4 m; diameter—3 m). For each replicate, we placed 2 cups (same type as described above), 1 containing 5 protein-deprived males and 1 containing 5 protein-fed males, in the eastern part of the canopy. The cups, separated by a distance of 1 m, were placed at a height of 1.7 m in areas having similar leaf densities. When tested, males were 10-18 days old.

Cups were placed on the tree between 0830-0845 h, and 10 min later 30 unmarked females (12-19 days old) were released at the base of the tree. Starting 10 min after female release, we recorded the numbers of calling males and perching females (on or within 15 cm of a cup) for the 2 cups at 2.5 min intervals over the next 90 min (i.e., 37 observation per replicate). At the end of a replicate, females were captured and removed from the tent. All tests were conducted during conditions of full or nearly full sunlight. The cups were suspended in the same locations over all replicates, with the type of male present, protein-deprived vs. protein-fed, alternated between successive tests. A total of 12 replicates were conducted.

Mating Competitiveness

Flies used in the mating trials were reared directly from fruits of *S. pseudocapsicum* as described above or from a stock started with 400-500 wild adults (collected from *S. pseudocapsicum* as well) and maintained for 3 generations in the laboratory. Emerging adults were handled in the

same manner described above, with males separated into protein-deprived or protein-fed groups. For the purpose of identification, males of a given diet type were marked 1 day prior to testing by first cooling them for 2-3 min and then applying a small dot of enamel paint on the thorax. This procedure has no adverse effects, and flies resume normal activities within minutes of handling.

Trials were conducted at the aforementioned Agricultural Station using 2 field-caged guava trees similar to that described above. For each replicate, we placed 75 protein-fed males, 75 protein-deprived males, and 75 (protein-fed) females into a cage between 0800-0830 h, and mating pairs were collected over the next 5 h. When tested, males were 10-16 days old, and females were 12-18 days old. A total of 13 replicates was conducted.

Statistical Analyses

In both mate attraction experiments, male calling levels and female sightings for protein-deprived and protein-fed males were compared using the nonparametric Mann-Whitney test. Also, in both experiments, the relationship between male calling and female sightings among aggregations of a given diet type was described using simple linear regression. Significance of the regression was tested using ANOVA. Inter-dietary comparisons of regression lines (slopes and y-intercepts) were made using the Students t test.

For the mating trials, deviations from random mating were assessed in 3 ways. First, the sign test was performed over all replicates, testing whether the numbers of replicates in which protein-fed or protein-deprived males achieved the higher number of matings differed from that expected by chance (50% of the replicates for each male type). The binomial test was performed for individual replicates to compare the observed numbers of matings by protein-fed and protein-deprived males against those expected by chance (i.e., 50% of the matings by each male type). Third, the binomial test was run with data pooled over all replicates. The normal approximation (test statistic Z) to the binomial distribution was used for samples exceeding 25. All statistical procedures followed Zar (1996).

RESULTS

Female Attraction: between Host Plants

Protein-deprived and protein-fed males displayed similar levels of pheromone-calling. Within aggregations, an average of 7.2 (SD = 2.2) protein-fed males were pheromone-calling per observation compared to 7.0 (SD = 1.9) protein-deprived males (n = 32 for both groups; T = 1067.0; P > 0.05). In contrast, the numbers of female

sightings differed significantly between the 2 dietary types. For individual aggregations, the average total number of female sightings per replicate was 6.6 (SD = 3.9) for protein-fed males compared to only 3.6 (SD = 2.6) for protein-deprived males ($n = 32$ for both groups; $T = 1223.0$; $P < 0.02$).

For both diets, a significant positive relationship existed between female sightings and male calling level among aggregations (Fig. 1). Consistent with the above results, the slope observed for protein-fed males was greater than that found for protein-deprived males (1.7 vs. 1.3, respectively), although this difference was not significant ($t = 1.1$; $df = 60$; $P > 0.05$). Similarly, elevations did not differ significantly between the two diet types ($t = 0.2$; $df = 61$; $P > 0.05$).

Female Attraction: within a Host Plant

As in the previous experiment, the incidence of pheromone-calling was independent of male diet. For individual aggregations, 2.3 (SD = 0.8) protein-fed males were pheromone-calling per observation, on average, compared to 2.1 (SD = 0.8) protein-deprived males ($n = 12$ for both groups; $T = 140.5$; $P > 0.05$). Similarly, the average total number of female sightings at aggregations did not differ significantly between aggregations of protein-fed ($x = 38.7$; $SD = 13.8$) and protein-deprived ($x = 35.6$; $SD = 18.9$) males ($T = 144.0$; $P > 0.05$).

For both diets, a significant positive relationship existed between female sightings and male calling level among aggregations (Fig. 2). Regression lines did not differ significantly between pro-

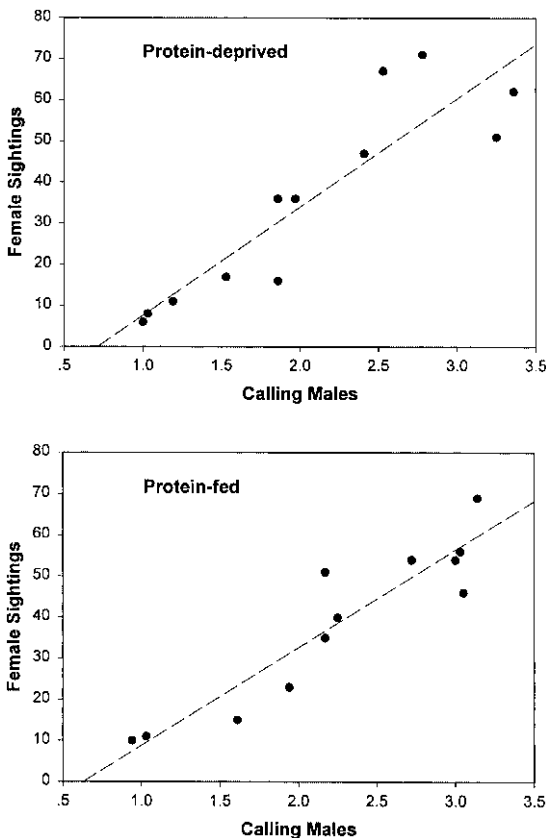


Fig. 1. Relationship between female sightings and male calling activity for protein-deprived and protein-fed males occurring on different host plants. Each point represents an individual aggregation; the ordinate represents total number of female sightings per replicate, and the abscissa represents the average number of calling males per observation for a given replicate. The regression equations were: protein-deprived males - $Y = (1.3)X - 5.7$ ($r^2 = 0.52$; $F = 31.6$; $df = 1, 30$; $P < 0.001$); protein-fed males - $Y = (1.7)X - 5.7$ ($r^2 = 0.60$; $F = 44.6$; $df = 1, 30$; $P < 0.001$).

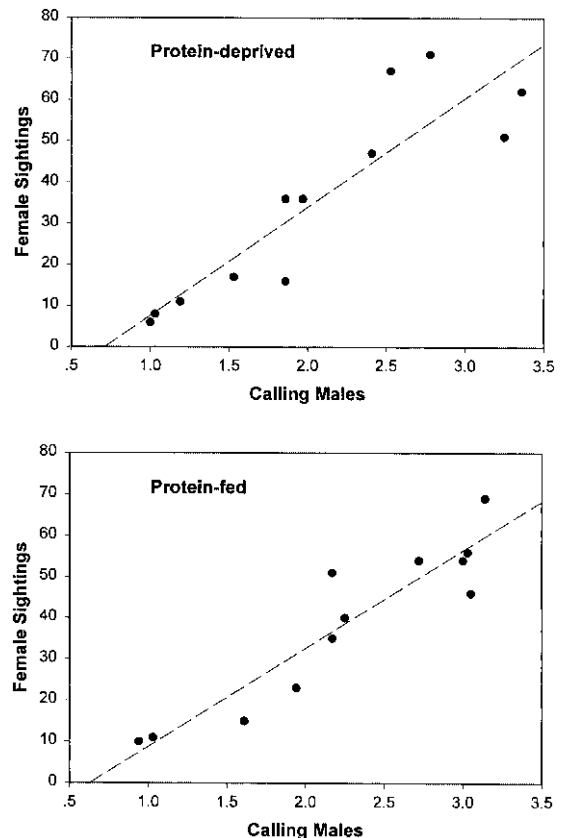


Fig. 2. Relationship between female sightings and male calling activity for protein-fed and protein-deprived males occurring on the same host plant. Each point represents an individual aggregation; the ordinate represents total number of female sightings per replicate, and the abscissa represents the average number of calling males per observation for a given replicate. The regression equations were: protein-fed males - $Y = (23.9)X - 15.1$ ($r^2 = 0.86$; $F = 63.8$; $df = 1, 8$; $P < 0.001$); protein-deprived males - $Y = (26.1)X - 18.1$ ($r^2 = 0.79$; $F = 38.3$; $df = 1, 8$; $P < 0.001$).

tein-fed and protein-deprived males in slope ($t = 0.4$; $df = 16$; $P > 0.05$) or y-intercept ($t = 0.1$; $df = 17$; $P > 0.05$).

Mating Competitiveness

An average of 24 matings (32% of the possible maximum; $SD = 6.1$; range = 16-41) was observed per replicate. The 3 analyses used to assess mating competitiveness yielded the same result: adult diet had a significant effect on male mating success. Protein-fed males obtained more matings than protein-deprived males in all 10 replicates for which a difference between male types was observed ($P < 0.001$; sign test; in 3 replicates the 2 male types had equal numbers of matings). Binomial tests on the individual replicates detected non-random mating in 4 of the 13 trials; in these cases, protein-fed males accounted for 71-83% of the matings ($P < 0.05$ in all instances; binomial test). Consistent with these results, a binomial test based on data from all replicates revealed a significant deviation from random mating, with protein-fed males achieving 60% (186/312) of all matings compared to 40% (126/312) for protein-deprived males ($Z = 3.4$; $P < 0.01$).

Although mating frequency varied with diet, the timing of mating activity was similar between protein-fed and protein-deprived males. Based on data from all replicates, we found no significant difference in the hourly distributions of matings for the 2 male types ($\chi^2 = 2.4$; $P > 0.05$). Over 50% of the matings occurred within the first 2 h of the tests for both protein-fed (110/186 = 59%) and protein-deprived (70/126 = 55%), and less than 10% of the matings were observed during the final hour for both types of males.

DISCUSSION

Previous studies on *C. capitata* males have demonstrated associations between diet and activity level, activity level and mating success, or among all 3 of these parameters. Warburg & Yuval (1996) found that protein-fed males expended more energy during courtship (i.e., courted more vigorously) than protein-deprived males, although they did not examine the relationship between courtship vigor and success. Conversely, Whittier et al. (1994) observed that mating frequency was positively associated with calling and courting frequency but did not examine the effects of adult diet on male activity. Prior to the present study, only Field & Yuval (1999) compared the activity level and mating success (or, more accurately, an index of mating success) of *C. capitata* males reared under differing dietary regimes. They reported that protein-fed *C. capitata* males exhibited longer calling bouts and more frequent courtships (the small number of observed matings precluded statistical analy-

sis) than protein-deprived males. Similar results have been reported for other Diptera. In *Drosophila grimshawii* Oldenberg, males maintained on a high protein diet displayed more vigorous courtship displays and obtained more matings than males fed a low protein diet (Droney 1996). Similarly, liver-fed males of the black blowfly, *Phormia regina* (Meigen), displayed a higher level of sexual activity (as indicated by attempted mountings) and inseminated more females than sugar-fed males (Stoffolano et al. 1995).

In the present study, diet-related differences in male calling activity were not evident in either the between- or within-plant, female attraction experiments. However, it is possible that this outcome reflected the short duration of our tests. For example, Field & Yuval (1999) reported diet-based, behavioral differences based on observations made over 7 h intervals, whereas we measured calling activity for periods of only 90 min. If calling involves substantial energy expenditure and if the presence of protein in the diet affects a male's ability to meet these costs, differences in calling level between protein-fed and protein-deprived males may increase with time and be evident only after sustained periods of activity. Although this possibility can not be ruled out, the finding that the temporal distributions of matings were similar between protein-fed and protein-deprived males strongly suggests that adult diet had a minor impact, if any, on the overall level of male sexual activity.

Despite the apparent similarity in activity levels, protein-fed males enjoyed a mating advantage over protein-deprived males. It is not known what factor(s) was responsible for this mating differential. The finding that females were sighted more frequently near protein-fed than protein-deprived males in the between-plant, attraction experiment indicates that diet affected the attractiveness of the pheromonal signal. Thus, the mating advantage of protein-fed males may have reflected directly their enhanced ability to attract potential mates to their territory. While plausible, the within-plant, attraction experiment failed to detect a diet-related difference in male attractiveness, suggesting that potential diet effects on signal quality may be manifest over large (>5 m) but not small (<2 m) distances. Alternatively, the differential mating success may have reflected differences in the courtship behavior of protein-fed and protein-deprived males. As noted above, adult diet affected the incidence of particular courtship displays in *Drosophila* males (Droney 1996), and a similar phenomenon may occur in *C. capitata* as well. Evaluation of this explanation requires detailed analysis of the videotaped courtship sequences of protein-fed and protein-deprived males.

Regardless of the underlying cause, the relationship reported here between adult diet and

mating success has important implications for the procedures used in the release of sterile males in suppression or eradication programs against the Mediterranean fruit fly. In ongoing programs, newly emerged sterile flies are typically held for several days prior to release and given only sugar and water for nutrition. Our data, along with those of Blay & Yuval (1997), suggest that the addition of a protein source to the holding cages might enhance the mating competitiveness of the sterile males. To examine this possibility, we are currently conducting experiments that compare the mating success of protein-fed vs. protein-deprived sterile males in competition with wild males.

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REFERENCES CITED

- ARITA, L. H., AND K. Y. KANESHIRO. 1989. Sexual selection and lek behavior in the Mediterranean fruit fly, *Ceratitidis capitata* (Diptera: Tephritidae). *Pacific Sci.* 43: 135-143.
- BLAY, S., AND B. YUVAL. 1997. Nutritional correlates of reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). *Anim. Behav.* 54: 59-66.
- BURK, T. 1988. Acoustic signals, arms races and the costs of honest signalling. *Florida Entomol.* 71: 400-409.
- DRONEY, D. C. 1996. Environmental influences on male courtship and implications for female choice in lekking Hawaiian *Drosophila*. *Anim. Behav.* 51: 821-830.
- EDGAR, J. A., C. C. J. CULVENOR, AND T. E. PLISKE. 1974. Coevolution of danaid butterflies with their host plants. *Nature* 250: 646-648.
- EPSKY, N. D., AND R. R. HEATH. 1993. Food availability and pheromone production of males of *Anastrepha suspensa* (Diptera: Tephritidae). *Environ. Entomol.* 22: 942-947.
- FIELD, S. A., AND B. YUVAL (In press). Sexual selection in medfly leks: the effect of nutritional status on male display endurance, and the correlates of female choice. *Behav. Ecol. Sociobiol.*
- GWYNNE, D. T. 1990. Testing parental investment and the control of sexual selection in katydids: the operational sex ratio. *Amer. Nat.* 136: 474-484.
- HACK, M. A. 1997. The energetic costs of fighting in the house cricket, *Acheta domesticus* L. *Behav. Ecol.* 8: 28-36.
- LANDOLT, P. J., AND J. SIVINSKI. 1992. Effects of time of day, adult food, and host fruit on incidence of calling by male Caribbean fruit flies (Diptera: Tephritidae). *Environ. Entomol.* 21: 382-387.
- LOFSTEDT, C., N. J. VICKERS, W. L. ROELOFS, AND T. C. BAKER. 1989. Diet related courtship success in the Oriental fruit moth, *Grapholita molesta* (Tortricidae). *Oikos* 55: 402-408.
- MARDEN, J. H., AND J. K. WAAGE. 1990. Escalated damselfly territorial contests are energetic wars of attrition. *Anim. Behav.* 39: 954-959.
- NISHIDA, R., T. E. SHELLY, AND K. Y. KANESHIRO. 1997. Acquisition of female attractive fragrance by males of the oriental fruit fly from a Hawaiian lei flower, *Fagraea berteriana*. *J. Chem. Ecol.* 23: 2275-2285.
- PITNICK, S., AND T. A. MARKOW. 1994. Male gametic strategies: sperm size, testes size, and the allocation of ejaculate among successive mates by the sperm-limited fly *Drosophila pachea* and its relatives. *Amer. Nat.* 143: 785-819.
- PLAISTOW, S., AND M. T. SIVA-JOTHY. 1996. Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proc. Roy Soc. London (B)* 263: 1233-1238.
- PROKOPY, R. J., AND J. HENDRICH. 1979. Mating behavior of *Ceratitidis capitata* on a field-caged host tree. *Ann. Entomol. Soc. Amer.* 72: 642-648.
- SIMMONS, L. W., R. J. TEALE, M. MAIER, R. J. STANDISH, W. J. BAILEY, AND P. C. WITHERS. 1992. Some costs of reproduction for male bushcrickets, *Requena verticalis* (Orthoptera: Tettigoniidae): allocating resources to mate attraction and nuptial feeding. *Behav. Ecol. Sociobiol.* 31: 57-62.
- STOFFOLANO, J. G., E. N. TOBIN, J. WILSON, AND C. M. YIN. 1995. Diet affects insemination and sexual activity in male *Phormia regina* (Diptera: Calliphoridae). *Ann. Entomol. Soc. America* 88: 240-246.
- WARBURG, M. S., AND B. YUVAL. 1996. Effects of diet and activity on lipid levels of adult Mediterranean fruit flies. *Physiol. Entomol.* 21: 151-158.
- WARBURG, M. S., AND B. YUVAL. 1997. Effects of energetic reserves on behavioral patterns of Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia (Berlin)* 112: 314-319.
- WHITTIER, T. S., K. Y. KANESHIRO, AND L. D. PRESCOTT. 1992. Mating behavior of Mediterranean fruit flies (Diptera: Tephritidae) in a natural environment. *Ann. Entomol. Soc. Amer.* 85: 214-218.
- WHITTIER, T. S., F. Y. NAM, T. E. SHELLY, AND K. Y. KANESHIRO. 1994. Male courtship success and female discrimination in the Mediterranean fruit fly (Diptera: Tephritidae). *J. Insect Behav.* 7: 159-170.
- YUVAL, B., R. KASPI, S. SHLOUSH, AND M. S. WARBURG. 1998. Nutritional reserves regulate male participation in Mediterranean fruit fly leks. *Ecol. Entomol.* 23: 211-215.
- ZAR, J. H. 1996. *Biostatistical analysis*. Prentice Hall, Upper Saddle River, NJ.