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EFFECTS OF POST-TENERAL NUTRITION ON REPRODUCTIVE SUCCESS OF MALE MEDITERRANEAN FRUIT FLIES (DIPTERA: TEPHRITIDAE)

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ABSTRACT

To realize their reproductive potential, male Mediterranean fruit flies must run a gauntlet of behavioral challenges during which they may be edged out by rivals, or fail the acid test of female choice. Milestones on this perilous road include: 1. showing up at a lek site, 2. emitting pheromone, 3. performing courtship, 4. Copulation, 5. sperm transfer and storage, 6. fertilization of eggs, 7. preventing or delaying female remating. In a number of recent studies focused on each of these steps we tested the hypothesis that post-teneral male nutrition affects male sexual performance. Both field and laboratory data indicate that protein nutrition increases a male's probability of emitting pheromone in a lek. Field cage data show that protein fed males are also more likely to engage in critical elements of close-range courtship, and evidence from several studies indicate that protein fed males are more likely to copulate than sugar-fed or starved flies. As to sperm transfer and storage, we find that the context of the experiment and the source of flies used affect the outcome, suggesting that diet alone cannot explain the variability in the probability of sperm being transferred, and in the amount of sperm transferred. To date we have not studied effects of male diet on fertilization. Nevertheless, we have shown that male diet significantly affects female receptivity: females whose first mate was protein-deprived, remate sooner than females whose first mate was protein-fed.

Key Words: *Ceratitis*, nutrition, sexual behavior, reproductive success, SIT

RESUMEN

Para realizar su potencial reproductivo, los machos de la mosca mediterránea deben aceptar el reto en cuanto a los desafíos de comportamiento durante los cuales ellos podrían ser eliminados por rivales, o fallar la prueba crítica de la selección de la hembra. Los puntos de referencia en este peligroso camino incluyen: 1. presencia en el lugar designado para el cortejo, 2. emisión de feromonas, 3. realización del cortejo, 4. copulación, 5. transferencia de esperma y almacenamiento, 6. fertilización de los huevos, 7. prevención o retraso del re-apareamiento de la hembra. En estudios recientes enfocados a cada uno de estos pasos, se probó la hipótesis de que la nutrición posterior a la muda en los machos afecta la actividad sexual del macho. Tanto la información del campo como la de laboratorio indican que la nutrición con proteínas aumenta la probabilidad del macho de emitir feromonas en el lugar del cortejo. La información de las jaulas de campo demuestran que los machos alimentados con proteínas también son más probables que se envuelvan en elementos críticos del cortejo a corta distancia, y evidencia proveniente de varios estudios indican que los machos alimentados con proteínas son más dados a copular que las moscas alimentadas con azúcar o no alimentadas. Con respecto a la transferencia de esperma y almacenamiento se ha conseguido que el contexto del experimento y la fuente de las moscas utilizadas afectan el resultado, sugiriendo que la dieta por sí sola no puede explicar la variabilidad en la probabilidad que el esperma se transfiera, y en la cantidad de esperma transferida. Hasta la fecha no hemos estudiado los efectos de la dieta del macho sobre la fertilización. No obstante, se ha demostrado que la dieta del macho afecta significativamente la receptividad de la hembra: las hembras cuyo primer apareamiento fue con machos privados de proteínas, se re-aparearon con mayor rapidez que la hembras cuyo primer apareamiento fue con machos alimentados con proteínas.

For male Mediterranean fruit flies, *Ceratitis capitata*, (Diptera: Tephritidae), as indeed for males in many insect species (Thornhill & Alcock 1983), the rewards of investing resources in sexual displays and courtship are not reaped equally by all investors (Whittier et al. 1994). The sterile insect technique (SIT) (Knipling 1955, Krafars 1998), is being used in many parts of the world to control medfly populations or prevent their establishment in new regions (Hendrichs et al. 1994, 1995, and references therein). As the success of

this technique hinges on the ability of released sterile males to copulate and inseminate females in the field, much of the applied research on the sexual biology of this insect is aimed at determining precisely what it is that makes a successful male, (Calkins 1984, Cayol et al. 1999, Shelly & Whittier 1996).

In insect species that acquire and store reproductive resources during the larval period (such as ephemeropterans, most trichopterans and many lepidopterans), male reproductive success

hinges greatly on how well they did as immatures. Thus it is common to find a correlation between male size and copulatory success in these species (Bisoondath & Wiklund 1997, Flecker et al. 1988.). Individuals that develop in sub-optimal environments become small adults and cannot do much to improve their lot. Conversely, the reproductive success of numerous other species hinges on their ability, as adults, to forage efficiently for various nutritional resources (see Droney & Hock 1998, Yuval et al. 1994). Adults in these species must decide when to forage for nutritional resources, when to invest time in reproduction, and when to desist altogether. These decisions are frequently triggered by physiological thresholds that dictate or regulate the expression of a discrete behavior. In these species the handicap of a poor larval environment may be later overcome by foraging successfully. Though the host in which larvae develop greatly affects adult qualities such as size, energetic reserves and fecundity (Hendrichs et al. 1991, Krainacker et al. 1987), the activity patterns of adult medflies in the field suggest that they belong to the latter group, as both males and females spend a considerable amount of time foraging for and feeding on various sources of carbohydrates and proteins (Hendrichs & Hendrichs 1990, Hendrichs et al. 1991, Warburg & Yuval 1997a, Warburg & Yuval 1997b, Yuval & Hendrichs 1999).

The mating system of the medfly, based on leks, is relatively complex, offering females many opportunities for choice (Shelly & Whittier 1997, Yuval & Hendrichs 1999). The sequence of events culminating in fertilization of a females eggs by the sperm of a particular male may be seen, from the males perspective, as an obstacle race, where the height of each obstacle is determined by nutritional thresholds, intra-sexual competition or female choice. Being able to overcome one such barrier, though a step in the right direction, does not guarantee success in the subsequent suite of challenges (see Eberhard 1996).

These hurdles can broadly be designated as follows: copulation, insemination and finally, fertilization. However, the more we learn about the medfly mating system, more specific milestones on the road to reproductive success can be identified. These are:

1. joining a lek
2. pheromone emission
3. performing courtship
4. copulation
5. sperm transfer and storage
6. fertilization of eggs
7. preventing or delaying female remating

We have investigated the relationship between post teneral nutrition of males and their success at most of these discrete steps. In the present paper, we briefly review our main findings on the subject.

LEK JOINING AND PHEROMONE EMISSION

The relationship between male nutritional status and participation in leks was studied both in the field and in field-cages.

Field Studies.

We studied lekking males on pitanga (*Eugenia uniflora*) trees located near Rehovot, in the central plain of Israel. We compared the nutritional status of males participating in leks to that of others resting nearby. Males were collected, their behavior (lekking or resting), recorded, and they were immediately chilled. Subsequently, biochemical analyses were performed to determine the levels of glycogen, sugar, lipids, and protein in each male. For full details of procedure, see Yuval et al. (1998). There were no significant size differences between resting and lekking males, indicating that size does not determine whether a male will join a lek. However, lekking males were significantly heavier than resting males, and this difference was reflected in the nutrients they contained. Males in both groups contained similar amounts of lipid, on average 21.06 $\mu\text{g}/\text{mg}$ for lekking males ($n = 183$) vs. 20.9 $\mu\text{g}/\text{mg}$ for resting males ($n = 148$). Similarly, glycogen did not vary between behavioral categories, 2.21 $\mu\text{g}/\text{mg}$ in lekking males vs. 2.43 in resting males. However, lekking males contained significantly more protein and sugar than resting males. Lekking males averaged 5.85 $\mu\text{g}/\text{mg}$ protein vs. 5.00 in resting males. Similarly, sugar in lekking males averaged 53.4 $\mu\text{g}/\text{mg}$ compared to 42.4 in resting males ($P = 0.01$). We concluded that leks are exclusive and that males must first forage successfully before they can join (Yuval et al. 1998).

Field Cage Experiments.

We tested the above conclusion in field cage experiments. We carried out two series of experiments in two field cages (1.85 \times 1.85 \times 1.80m, covered with a shade cloth on top), located on the campus of the Hebrew University in Rehovot. Citrus trees (*Citrus* sp.) with canopies of approximately 0.5m in diameter and 1.5 m in height, were placed inside the field cages as a lek site (Prokopy & Hendrichs 1979, Kaspi & Yuval 1999). Wild flies, reared from infested guava, were used in all experiments. After emergence, flies were segregated by sex, cloistered in 5-liter plastic containers, at densities of 60-80 per container, and were given one of two diet regimes: 'protein-fed' or 'sugar-fed'. Protein-fed flies had *ad libitum* access to water, dry sucrose and protein hydrolysate, sugar-fed flies had access to water and 20% sucrose solution.

When males were 9-10 days old, they were released in the field cage, and their propensity to lek and ability to copulate sexually mature virgin

females was monitored throughout the day of release. protein-fed males were more likely to emit pheromone in leks, and consequently, were more likely to copulate than sugar-fed males. Furthermore, protein-fed males tended to start calling earlier than their nutritionally deprived competitors. Though size was not related to initiation of lek behavior, large males were significantly more likely to copulate than small males. Amongst protein-fed males, large individuals tended to mate earlier than smaller ones (Kaspi et al. 2000). Independent experiments by other researchers, albeit conducted in small cages in the laboratory, found similar effects of male nutrition on pheromone emission (Papadopoulos et al. 1998). Recently, Shelly et al. (2002), determined in the field that leks of protein fed males are more attractive to females than leks of protein deprived males.

COURTSHIP

We analyzed the effect of nutrition on the various elements of courtship, by observing the behavior of lekking males towards virgin females on trees in a field cage. Within lek visits, the most frequently observed behavior was non-calling, while the most frequent mate-attraction behavior was calling. The only behavior to show a significant tendency to covary in frequency with diet was *court*, (defined as "orient toward a female and perform close-range courtship behavior" (Briceno et al. 1996)), which was more frequently performed by protein fed males (S. Field unpublished observations).

COPULATION

There is compelling evidence from several laboratory strains and from wild males that protein fed males are more likely to copulate. Flies of the long established "Vienna" strain copulated much more frequently (and faster) in the laboratory than did their sugar fed brethren (Blay & Yuval 1997), as did males of the much younger strain "Sade" (Taylor & Yuval 1999). Wild males that emerged in the laboratory and were tested for copulations in a field cage also succeeded significantly better than sugar fed males (see 1 & 2 above, Kaspi et al. 2000).

Copula duration is also affected by male diet (Field & Yuval 1999). However, this part of the sexual encounter comprises many conflicting and coinciding interests of both males and females, and deserves a more detailed analysis in the future (Taylor & Yuval 1999, Field et al. 1999).

SPERM TRANSFER & STORAGE

Probability of Sperm Transfer.

Not all copulations culminate in sperm storage by females (Seo et al. 1990). We conducted labora-

tory experiments with the "Sade" laboratory strain, in 5 liter cages. We found sperm in the spermathecae of 94% of 178 females who had copulated. Females were significantly less likely to store sperm of protein deprived males. Interestingly, effects of diet were limited to small males, and large males were comparatively unaffected (Taylor & Yuval 1999). However, when we dissected wild females who had copulated with wild males in a field cage, there was no evidence for a diet effect on sperm transfer (Taylor et al. 2000).

Number of Sperm Stored.

In the study of laboratory flies copulating in small cages, diet also significantly affected the amount of sperm stored. Females who copulated with protein-fed males stored more sperm in their spermathecae (on average, 3693 sperm cells) than did females who copulated with protein-deprived males (3037 on average; Taylor & Yuval 1999). When this study was repeated with wild males copulating with virgin females in a field cage, we found that the total number of sperm stored by females varied between testing days and increased with female size but was not influenced by male size or diet (Taylor et al. 2000). It appears that the context of the experiment and the source of flies used affect the outcome, suggesting that diet alone cannot explain the variability in the probability of sperm being transferred, and in the amount of sperm transferred.

FERTILIZATION

For a number of insect species, evidence is accumulating that when males of differing quality copulate with a female, this difference in quality is reflected in paternity patterns, irrespective of the copulation sequence. This may be the result of competition between males extended to the female reproductive tract (sperm competition), or of female ability to manipulate ejaculates and favor the sperm of a preferred male (Bisoondath & Wilkund 1997, LaMunyon & Eisner 1993, Eberhard 1996, Ward 1993). It is not known whether multiply mated medfly females will preferentially use the sperm of better nourished males over that of undernourished males. However, the non-random patterns of sperm allocation between the two spermathecae (Yuval et al., Taylor & Yuval 1999, Taylor et al. 2000) suggest that females may be able to exert some control over fertilization.

If females can control fertilization by manipulating ejaculates, then one way for males to preempt them (or avoid male-driven sperm competition), is to limit or postpone the receptivity of the females they copulate. As detailed below, the nutritional status of a female's first mate does affect her tendency to remate.

RENEWAL OF FEMALE RECEPTIVITY

We studied the effect of male diet on subsequent female receptivity by allowing virgin females to copulate with protein fed or protein deprived males (Blay & Yuval 1997). On the day following copulation, females were confined with a fresh set of virgin, protein fed males. Females whose first mate was protein deprived were significantly more likely to remate than females whose first mate was protein fed: 76% vs 61% ($n = 235$, $\chi^2 = 5.4$; $P < 0.05$). Furthermore, the latency to remating of females whose first mate was protein deprived was significantly shorter (Blay & Yuval 1997). We are still in the dark as to how this refractoriness is mediated. Recent studies with spermless males indicate that sperm has a short-term effect on female receptivity (Miyatake et al. 1999). The fact that protein-fed males are simultaneously superior at both inseminating (Taylor & Yuval 1999) and inducing non-receptivity in mates (Blay & Yuval 1997) points to an involvement of sperm or some associated quality. However, even poorly nourished males transfer an abundance of sperm to females, enough to fertilize most (if not all) of its eggs (Blay & Yuval 1999). Therefore additional factors associated with male nutrition, such as quality of accessory gland secretions (Jang 1995, Jang et al. 1998), weight or execution of copulatory courtship routines (Eberhard 1991), may influence female receptivity to further copulations.

MALE NUTRITION AND THE STERILE INSECT TECHNIQUE

Millions of sterile male medflies are released in SIT operations every week, in many locations throughout the world where the medfly is a pest or a threat. For SIT to succeed, these males must be able to join the leks of wild males or establish leks of their own, attract wild females, court, copulate and inseminate them, and inhibit them from remating for as long as possible. Managers of fly rearing facilities and program agencies as well as biologists at research institutions share a common interest in identifying male attributes and developing handling techniques that will contribute to the optimal performance of released males (Calkins 1984, Calkins et al. 1994, Cayol et al. 1999, FAO/IAEA 1998, McInnis et al. 1996, Shelly 1999, Shelly & Whittier 1996).

The significant effect of protein nutrition on the tendency of males to join leks, copulate and delay female remating suggests that adding protein to the diet of sterile males prior to their release will improve their performance in the field. To test this hypothesis, we examined how post-terneral nutrition during the first 4-8 days after emergence affects performance and copulatory success in leks of mass-reared sterile (*tsl* strain

Vienna 4/Tol-94) males (Kaspi & Yuval 2000). We found that males fed both protein and sugar were significantly more likely to emit pheromone in leks, and more likely to copulate than males fed only sugar. Sterile males, who had access to water and apples following four days feeding on protein and/or sugar were significantly more likely to copulate than their starved competitors who had access to water only. These results alone would encourage us to recommend a high protein diet for sterile males prior to release. However, we also found that after 24 hours of starvation, four day old protein-fed males suffered higher mortality than sugar-fed males (Kaspi & Yuval 2000). To date, there is no information on the foraging behavior of released males in the field. If they are capable of finding and exploiting sources of protein nutrition in the field, pre-release feeding on protein will not affect their survival and may greatly enhance their competitiveness. Conversely, if they are unable to forage efficiently, protein feeding prior to release may hasten their demise (see also Carey et al. 1998, Jacome et al. 1999). Thus more research is needed to determine the optimal diet that will balance sexual prowess and longevity of released sterile flies.

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REFERENCES CITED

- BISOONDATH, C. J. AND C. WILUND. 1997. Effect of male body size on sperm precedence in the polyandrous butterfly *Pieris napi* L. (Lepidoptera: Pieridae). *Behav. Ecol.* 8: 518-523.
- BLAY, S., AND B. YUVAL. 1997. Nutritional correlates to reproductive success of male Mediterranean fruit flies. *Anim. Behav.* 54: 59-66.
- BLAY S., AND B. YUVAL. 1999. Oviposition and fertility in the Mediterranean fruit fly (Diptera: Tephritidae): Effect of male and female body size and the availability of sperm. *Ann. Entomol. Soc. Amer.* 92: 278-284.
- BRICENO, R. D., D. RAMOS, AND W. G. EBERHARD. 1996. Courtship behavior of male *Ceratitidis capitata* (Diptera: Tephritidae) in captivity. *Florida. Entomol.* 79: 130-143.
- CALKINS, C. 1984. The importance of understanding fruit fly mating behavior in sterile male release programs (Diptera, Tephritidae). *Folia Entomol. Mexicana* 61: 205-213.
- CALKINS, C. O., K. BLOEM, S. BLOEM, AND D. L. CHAMBERS. 1994. Advances in measuring quality and assuring good field performance in mass reared fruit flies, pp. 85-96. *In* C. O. Calkins, W. Klassen and P. Liedo [eds.], *Fruit Flies and the Sterile Insect Technique*, CRC Press.

- CAREY, J. R., P. LIEDO, H. MULLER, J. WANG, AND J. VAUPEL. 1998. Dual modes of aging in Mediterranean fruit fly females. *Science* 281: 996-998.
- CAYOL, J. P., J. VILARDI, E. RIAL, AND M. T. VERA. 1999. New indices and method to measure the sexual compatibility and mating performance of *Ceratitidis capitata* (Diptera: Tephritidae) laboratory-reared strains under field cage conditions. *J. Econ. Entomol.* 92: 140-145.
- DRONEY, D. C. AND M. B. HOCK. 1998. Male sexual signals and female choice in *Drosophila grimshawi* (Diptera: Drosophilidae). *J. Insect. Behav.* 11: 59-71.
- EBERHARD, W. G. 1991. Copulatory courtship and cryptic female choice in insects. *Biol. Rev.* 66: 1-31.
- EBERHARD, W. G. 1996. Female control: sexual selection by cryptic female choice. Princeton: Princeton University Press. [FAO/IAEA] Food and Agriculture Organization of the United Nations and the International Atomic Energy 1998. Product quality control, irradiation and shipping procedures for mass-reared Tephritid fruit flies for sterile insect release programs, version 4. FAO/IAE, Vienna, Austria.
- FIELD, S. A., P. W. TAYLOR, AND B. YUVAL. 1999. Sources of variability in copula duration of Mediterranean fruit flies. *Entomol. Exp. Appl.* 92: 271-276.
- FIELD, S. A., AND B. YUVAL. 1999. Nutritional status affects copula duration in the Mediterranean fruit fly, *Ceratitidis capitata* (Insecta Tephritidae). *Ethol. Ecol. Evol.* 11: 61-70.
- FLECKER, A. S., J. D. ALLAN, AND N. L. MCCLINTOCK. 1988. Male body size and mating success in swarms of the mayfly *Epeorus longimanus*. *Holarc. Ecol.* 11: 280-285.
- HENDRICH, J., AND M. A. HENDRICH. 1990. Mediterranean fruit fly (Diptera: Tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and non-fruiting hosts and nonhosts. *Ann. Entomol. Soc. Amer.* 83: 632-641.
- HENDRICH, J., B. I. KATSOYANNOS, D. R. PAPA, AND R. J. PROKOPY. 1991. Sex differences in movement between natural feeding and mating sites and tradeoffs between food consumption, mating success and predator evasion in Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia* 86: 223-231.
- HENDRICH, J., G. FRANZ, AND P. RENDON. 1994. Use of sterile male-only releases as "biological pesticides" for control of Mediterranean fruit flies in commercial fruit production. *IOBC Bull.* 17: 212-224.
- HENDRICH, J., G. FRANZ, AND P. RENDON. 1995. Increased effectiveness and applicability of the sterile insect technique through male-only releases for control of Mediterranean fruit flies during fruiting seasons. *J. appl. Entomol.* 119: 371-377.
- JACOME, I., M. ALUJA, AND P. LIEDO. 1999. Impact of adult diet on demographic and population parameters of the topical fruit fly *Anastrepha serpentina* (Diptera: Tephritidae). *Bull. Entomol. Res.* 89: 165-175.
- JANG, E. B. 1995. Effect of mating and accessory gland injections on olfactory mediated behavior in the female Mediterranean fruit fly, *Ceratitidis capitata*. *J. Insect Physiol.* 41: 705-710.
- JANG, E. B., D. O. MCINNIS, D. R. LANCE, AND L. A. CARVALHO. 1998. Mating-induced changes in olfactory-mediated behavior of laboratory-reared normal, sterile, and wild female Mediterranean fruit flies (Diptera: Tephritidae) mated to conspecific males. *Ann. Entomol. Soc. Amer.* 91: 139-144.
- KASPI, R., AND B. YUVAL. 1999. Mediterranean Fruit Fly leks: factors affecting male location. *Funct. Ecol.* 13: 539-545.
- KASPI, R., P. W. TAYLOR, AND B. YUVAL. 2000. Diet and size influence sexual advertisement and copulatory success of males in Mediterranean fruit fly leks. *Ecol. Entomol.* 25: 279-284.
- KASPI, R., AND B. YUVAL. 2000. Post-teneral protein feeding improves sexual competitiveness but reduces longevity of mass reared sterile male Mediterranean fruit flies. *Ann. Entomol. Soc. Amer.* 93: 949-955.
- KNIPLING, E. F. 1955. Possibilities of insect control or eradication through the use of sexually sterile males. *J. Econ. Entomol.* 48: 459-462.
- KRAFSUR, E. S. 1998. Sterile insect technique for suppressing and eradicating insect population: 55 years and counting. *J. Ag. Entomol.* 15: 303-317.
- KRAINACKER, D. A., J. R. CAREY, AND R. I. VARGAS. 1987. Effect of larval host on life history traits of the Mediterranean fruit fly, *Ceratitidis capitata*. *Oecologia* 73: 583-590.
- LAMUNYON, C., AND T. EISNER. 1993. Postcopulatory sexual selection in an arctiid moth (*Utetheisa ornatrix*). *Proc. Natl. Acad. Sci.* 90: 4689-4692.
- MCINNIS, D. O., D. R. LANCE, AND C. G. JACKSON. 1996. Behavioral resistance to the sterile insect technique by Mediterranean fruit fly (Diptera: Tephritidae) in hawaii. *Ann. Entomol. soc. Amer.* 89: 739-744.
- MİYATAKE, T., T. CHAPMAN, AND L. PARTRIDGE. 1999. Mating-induced inhibition of remating in female Mediterranean fruit flies *Ceratitidis capitata*. *J. Insect. Physiol.* 45: 1021-1028.
- PAPADOPOULOS, N. T., B. I. KATSOYANNOS, N. A. KOULOUSSIS, A. P. ECONOMOPOULOS, AND J. R. CAREY. 1998. Effect of adult age, food, and time of day on sexual calling incidence of wild and mass-reared *Ceratitidis capitata* males. *Entomol. Exp. Appl.* 89: 175-182.
- 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.
- SEO, S. T., R. I. VARGAS, J. E. GILMORE, R. S. KURASHIMA, AND M. S. FUJIMOTO. 1990. Sperm transfer in normal and gamma-irradiated, laboratory-reared Mediterranean fruit flies (Diptera: Tephritidae). *J. Econ. Entomol.* 83: 1949-1953.
- SHELLY, T. E. 1999. Trimedlure and the mating competitiveness of irradiated male Mediterranean fruit flies (Diptera: Tephritidae). *Environ. Entomol.* 28: 780-786.
- SHELLY, T. E., AND T. S. WHITTIER. 1996. Mating competitiveness of sterile male Mediterranean fruit flies (Diptera: Tephritidae) in male-only releases. *Ann. Entomol. Soc. Amer.* 89: 754-758.
- SHELLY, T. E., AND T. S. WHITTIER. 1997. Lek behavior of Insects, pp. 273-292. In J. C. Choe and B. J. Crespi [eds.] *Mating systems in insects and arachnids*, Cambridge: Cambridge University Press.
- SHELLY, T. E., S. S. KENNELLY, AND D. O. MCINNIS. 2002. Effect of adult diet on signaling activity, mate attraction, and mating success in male Mediterranean fruit flies (Diptera: Tephritidae). *Florida Entomol.* 85: 150-155.
- TAYLOR, P. W., AND B. YUVAL. 1999. Postcopulatory sexual selection in Mediterranean fruit flies: advantages for large and protein-fed males. *Anim. Behav.* 58: 247-254.

- TAYLOR, P. W., R. KASPI, AND B. YUVAL. 2000. copula duration and sperm storage in Mediterranean fruit flies from a wild population. *Physiol. Entomol.* 25: 94-99.
- THORNHILL, R., AND J. ALCOCK. 1983. *The evolution of insect mating systems.* Cambridge: Harvard University Press.
- WARBURG, M. S., AND B. YUVAL. 1997a. Circadian patterns of feeding and reproductive activities of Mediterranean fruit flies (Diptera: Tephritidae) on various hosts in Israel. *Ann. Entomol. Soc. Amer.* 90: 487-495.
- WARBURG, M. S., AND B. YUVAL. 1997b. Effects of energetic reserves on behavioral patterns of Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia* 112: 314-319.
- WARD, P. I. 1993. Females influence sperm storage and use in the yellow dung fly *Scathophaga stercoraria* (L.) *Behav. Ecol. sociobiol.* 32: 313-319.
- 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., S. BLAY, AND R. KASPI. 1996. Sperm transfer and storage in the Mediterranean fruit fly. *Ann. Entomol. Soc. Amer.* 89: 486-492.
- YUVAL, B. AND J. HENDRICH. 2000. Behavior of flies in the genus *Ceratitis* (Dacinae: Ceratidini), pp. 429-456. *In* M. Aluja and A. Norrbom [eds.] *Fruit Flies (Tephritidae): phylogeny and evolution of behavior.* Boca Raton: CRC Press.
- YUVAL, B., M. HOLLIDAY HANSON, AND R. K. WAHINO. 1994. Energy budget of swarming male mosquitoes. *Ecol. Entomol.* 19: 74-78.
- YUVAL, B., R. KASPI, S. SHLOUSH, AND M. WARBURG. 1998. Nutritional reserves regulate male participation in Mediterranean fruit fly leks. *Ecol. Entomol.* 23: 211-215.