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Anastrepha striata (Diptera: Tephritidae) Females That Mate with Virgin Males Live Longer

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ABSTRACT The consequences for females copulating with males suffering from sperm and accessory gland product depletion have rarely been investigated, especially in the context of male food shortage. In *Anastrepha striata* (Schiner), mating success is highly skewed, with some males copulating many times and others not at all. Because males transmit substances to females through labelum-to-labelum contact before copulation, mating could be especially costly to males fed a low-quality diet, and females that copulate with these males could suffer a fitness cost. To test this, we evaluated the reproduction and longevity of females that mated with males fed a high- or low-quality diet according to mating order (i.e., whether the female was the first or subsequent mate of a particular male). Contrary to predictions of sperm depletion, female fecundity and fertility did not vary according to mating order and were not influenced by male adult diet. However, longevity was significantly greater for females that were the first to copulate with a virgin male compared with females that subsequently mated with the same male (nonvirgin). Copula duration did not vary with mating order but was longer in the case of males fed a low-quality diet. We discuss the role that trophallaxis or accessory gland products may have in modulating female longevity.

KEY WORDS mating behavior, sperm depletion, longevity, trophallaxis, *Anastrepha striata*

THE COSTS FOR FEMALES THAT copulate with males suffering from sperm and/or accessory gland product (AGP) depletion are still poorly understood (Wedell et al. 2002), especially in the context of adult nutrition. Multiple mating can be costly to both females and males (Arnqvist and Nilsson 2000, Cordero 2000). For example, in the blowfly *Lucilia cuprina* (Wiedemann) and the lekking sandfly *Lutzomyia longipalpis* (Lutz & Neiva), females mated to successful, but sperm-depleted males, suffer from low fertility (Smith et al. 1990, Jones 2001). In species that exhibit trophallaxis, where there is an exchange of substances before mating, repeated copulations may be especially costly to both sexes. In the firefly *Photinus ignitus* Fall, male nuptial gift production declined with successive matings and limited male mating success (Cratsley et al. 2003).

Additionally, the ejaculate itself can be nutritious to females and aid in reproduction (Markow and Ankney 1984, Pitnick et al. 1991, Cordero 1996) or survival. For example, in the Caribbean fruit fly, *Anastrepha suspensa* (Loew), males transfer substances to females during copulation and a small amount has been detected in unfertilized eggs (Sivinski and Smittle 1987). Also, in the cricket *Gryllus lineaticeps* Stal, female life span increases due to male ejaculates (Wagner et al. 2001, Wagner and Harper 2003). Importantly, males

can become depleted of AGPs as well as of spermatozooids with successive copulations (Simmons 2001). Moreover, male dietary stress may further limit the amount of substances that females receive either through nuptial gifts (Boggs 1995) or through the ejaculate and these in turn may affect female reproduction or longevity. For example, various proteins have been found in the AGPs of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and a large amount of these substances becomes depleted only 30 min after initiation of the copula (Marchini et al. 2003). It is likely that an adequate adult diet is necessary for the synthesis of these proteins.

Here, we chose *Anastrepha striata* Schiner as a likely candidate to exhibit a shortage of substances transferred through trophallaxis and/or sperm and AGP depletion. *A. striata* is an oligophagous tephritid species (Norrbom et al. 1999), infesting mostly fruit of trees within the genus *Psidium* (Myrtaceae) (Aluja et al. 2000a). Males wing fan, releasing a sexual pheromone, either alone or in leks from the underside of leaves of host or nonhost trees (Aluja et al. 1993). Once a female approaches a calling male, she initiates a series of circular movements around the male, who stands motionless with its proboscis extended. Labelum-to-labelum contact ensues, with transfer of materials from the male to the female (trophallaxis) (Aluja et al. 1993, 2000b). There are, on average, 13.3 ± 1.9 (mean \pm SE) copulation attempts before a

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successful copulation begins (Aluja et al. 1993). Some males may copulate several times, whereas others do not copulate at all. Copulations last 29.2 ± 2.3 min. Previously, it has been shown that male diet can have an important effect on *A. striata* mating competitiveness (Aluja et al. 2001).

We tested the effect of male mating history on the fecundity (number of eggs laid), fertility (proportion of eggs hatched), daily oviposition rate (number of eggs laid divided by the time over which females laid eggs), time until sperm depletion (number of days in which females laid fertile eggs), and longevity of singly mated *A. striata* females according to the recent sexual experience and adult diet of their mates. We predicted that these female life-history parameters would decrease with mating order and that this would be more apparent for females that had mated with males fed a low-quality diet. Furthermore, because males engage in trophallaxis with females, we predicted a negative effect on these female parameters with increasing mating number. As it may take males time to replenish sperm and AGPs, we also predicted that copula duration would increase with mating order and that the interval between copulations as well as copula duration would be longer for males fed a low-quality diet.

Materials and Methods

Pupae were obtained from infested guavas, *Psidium guajava* L., from the state of Nayarit, Mexico. Only pupae weighing 10–20 mg were used to reduce possible effects of size on fly performance. When adults emerged from the pupae, they were separated by sex into Plexiglas cages (30 by 30 by 30 cm), and males were fed either a high-quality diet (3:1 mixture of dry sucrose and hydrolyzed protein, respectively) offered ad libitum or a low-quality diet (dry sucrose [no protein] offered on a restricted basis (i.e., only every third day) (Aluja et al. 2001). All females were fed on a high-quality diet offered ad libitum. At day 11 of age, all surviving adults were individually marked on the pronotum with a dot of color paint (Politec, Distribuidora Rodin S. A. de C.V. Mexico, Tlahuac, Mexico D.F.).

When adults reached 12 d of age, males fed on high- or low-quality diets were individually placed in a Plexiglas observation cage with five females (i.e., one male of either type with five females in a cage). A total of 14 individual males (seven fed on a high-quality diet and seven fed on a low-quality diet) were observed from 11:00 a.m. to 6:30 p.m. for 24 consecutive days. To provide individuals with some vegetation cover, small branches from citrus trees placed inside a glass bottle with water were put in the cage. Cotton balls soaked with water were also provided. All copulations and their durations were registered. At the end of each day, males were removed from the observation cage and placed in a separate one with their respective diet regime. In the case of males fed on a poor quality diet (dry sucrose [no protein] offered on a restricted basis (i.e., only every third day), the latter meant that on certain days during the observation period, some

males were placed in cages containing water but no food. Females were left in the observation cage and were provided with sucrose plus protein ad libitum. The next day, before observations began, males were placed again in the observation cage without food. Males that failed to copulate within 2 d or died were replaced (nine males fed on a high-quality diet and seven fed on a low-quality diet). Female age at mating varied from 13 to 33 d (19, 15, 22, median, lower, and upper quartile, respectively). Females were not replaced with virgins once they mated. Cages were rotated every day around the table on which observations took place.

At the end of each copulation, females were captured, released into plastic containers (13 by 13 by 25 cm) and labeled according to their mating order. In each container, an agar sphere (Bacteriological Agar, BD Bioxon, Becton Dickinson de Mexico, Cuatitlán Izcalli, Edo. de Mex., Mexico) measuring 3.0 cm in diameter, colored with green food dye (McCormick-Herdez S. A. de C.V., San Luis Potosí, San Luis Potosí, Mexico) and wrapped in Parafilm "M" (American National Can, Chicago, IL), was used as oviposition substrate (Boller 1968). We added an artificially flavored guava drink (Be-Light de Fresqui Bon, Dulco S.A. de C.V., Cuatitlán Izcalli, Edo. de México, Mexico) to agar spheres to make them more attractive to *A. striata* females (M.A., unpublished data). Spheres were hung from the ceiling of cages with a paper clip. Agar spheres were dissected and changed daily. Eggs removed from spheres were placed in petri dishes with dark cloth on top of humid cotton. These chambers were placed in a room at $30 \pm 1^\circ\text{C}$ and 73% RH. Egg eclosion was recorded 6 d later. Egg number, egg eclosion, and longevity were recorded for all females. In total, we monitored 51 females until they died (up to 184 d).

All data were transformed to ranks (Conover and Iman 1981). Reproductive parameters, such as fertility and fecundity, were analyzed separately from female life span. A multiple analysis of covariance (MANCOVA) was performed with fecundity and fertility as dependent variables; male diet and mating order as independent variables; and copula duration, days between copulations, and female age at mating as covariables. Two-way analyses of variance (ANOVAs) were performed on daily oviposition rate and time until sperm depletion by using male diet and female mating order as independent variables. One-way ANOVAs were performed on total lifetime fecundity and on daily oviposition rate (number of eggs laid each day divided by the total fecundity) of females that had copulated with a virgin or nonvirgin male. A stepwise linear regression model was run for female longevity with copula duration, days between copulations, male diet, female age at mating and whether the female had copulated with a virgin or previously mated male (nonvirgin) as independent variables. To explore the possibility that females copulating with virgin males were more sexually receptive (a potential signal of good health or vigor) than females copulating with nonvirgin males, we analyzed the number of days that

females were exposed to males in cages before they copulated and whether they had copulated with a virgin or nonvirgin male by means of a one-way ANOVA. To explore the relationship between fecundity and longevity, linear regressions were run on fecundity and female longevity for females mating with virgin or nonvirgin males. Lifetime female fecundity between females that copulated with virgin or nonvirgin males was analyzed by means of a one-way ANOVA. Copula duration for the first three copulations of all males and the interval between matings (i.e., days elapsed between the first and second copulation and the second and third copulation) were analyzed each by a two-way, repeated measures ANOVA by using male diet and mating order as independent variables. All statistical analyses were performed using Statistica software (StatSoft 1999).

Results

Although we predicted a decrease in fecundity and fertility with higher mating order (i.e., first, second, third, etc., to copulate with a male), we found no significant effect in these variables according to male diet or mating order, even when considering copula duration, time elapsed between copulations, and female age at mating as covariates in the analysis (MANCOVA: $R = 0.28$; $df = 2, 37$; $P = 0.76$ diet; $R = 0.54$; $df = 8, 74$; $P = 0.82$ mating order; and $R = 0.85$; $df = 8, 74$; $P = 0.60$ diet \times mating order).

Mating order and male diet had no effect on either oviposition rate (two-way ANOVA: $F = 0.09$; $df = 1, 38$; $P = 0.93$ diet; $F = 0.87$; $df = 4, 38$; $P = 0.49$ mating order; and $F = 0.91$; $df = 4, 38$; $P = 0.47$ diet \times mating order) or the number of days females laid fertile eggs (a proxy for sperm depletion) (two-way ANOVA: $F = 0.19$; $df = 1, 39$; $P = 0.67$ diet; $F = 2.03$; $df = 4, 39$; $P = 0.11$ mating order; and $F = 0.46$; $df = 4, 39$; $P = 0.76$ diet \times mating order).

When comparing females that copulated with virgin or nonvirgin males, we found no significant differences in total lifetime fecundity (one-way ANOVA: $F = 0.74$; $df = 1, 49$; $P = 0.40$) or in daily oviposition rate ($F = 3.68$; $df = 1, 256$; $P = 0.056$).

The stepwise regression model for female longevity revealed that neither female age at mating, male diet, copula duration, or days elapsed between copulations had a significant effect. Rather, female longevity was significantly associated with male sexual experience (virgin versus nonvirgin) (linear regression: $\beta = 0.33$, $r^2 = 0.11$; $F = 6.06$; $df = 1, 49$; $P = 0.017$). Females that copulated with a virgin male lived significantly longer than females that subsequently copulated with these same males (Fig. 1). Females that mated with virgin males lived a median of 107 d (89 and 116, lower and upper quartile, respectively) ($n = 13$). In contrast, females that subsequently mated to these males lived a median 75 d (47 and 101, lower and upper quartile, respectively) ($n = 38$).

Importantly, we found no statistically significant difference when comparing the number of days it took

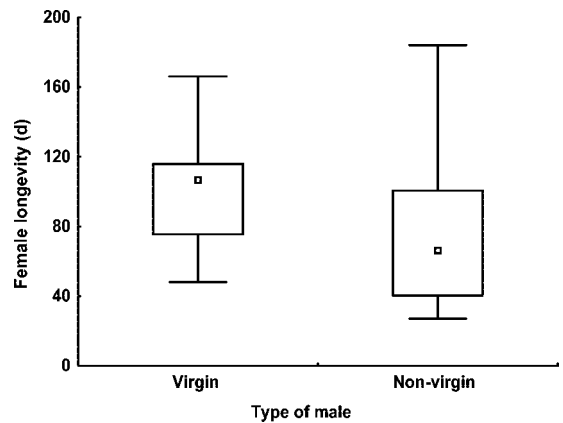


Fig. 1. Longevity of *A. striata* females that copulated with males when they were virgin or with males that had previous mating experience (nonvirgin). Whiskers represent range, boxes represent quartiles, and small squares represent medians ($F = 5.69$; $df = 1, 49$; $P = 0.021$).

females to copulate with virgin or nonvirgin males (one-way ANOVA: $F = 1.60$; $df = 4, 46$; $P = 0.19$). Some females that were the second, third, or fourth to copulate with a male in some cages, actually copulated sooner than the first females in other cages. That is, the variance in days that first females (i.e., ones copulating with a virgin male) took to copulate was comparable to the variance in days that subsequent females took to copulate (i.e., female sexual receptivity did not seem to play a role in determining which females mated with virgin males).

Lifetime fecundity was positively, but weakly, correlated with life span (linear regression: $r^2 = 0.11$; $F = 6.13$; $df = 1, 49$; $P = 0.02$). To elucidate the effect of male mating history on the relationship between female longevity and lifetime fecundity, we analyzed these variables separately for females mating with virgin or nonvirgin males. A positive association was found between lifetime fecundity and longevity for females copulating with nonvirgin males (linear regression: $r^2 = 0.17$; $F = 7.22$; $df = 1, 36$; $P = 0.011$), but no association was found for females copulating with virgin males (linear regression: $r^2 = 0.01$; $F = 0.17$; $df = 1, 11$; $P = 0.69$) (Fig. 2).

Copula duration was significantly influenced by male diet but not mating order (two-way repeated measures ANOVA: $F = 11.73$; $df = 1, 11$; $P = 0.006$ diet; $F = 0.58$; $df = 2, 22$; $P = 0.566$ order; and $F = 1.43$; $df = 2, 22$; $P = 0.259$ diet \times order). Males fed a high-quality diet had significantly shorter copulations than males fed a low-quality diet (Fig. 3). Days elapsed between copulations were not different according to mating order or between diets (two-way repeated measures ANOVA: $F = 0.64$; $df = 1, 11$; $P = 0.439$ diet; $F = 0.26$; $df = 1, 11$; $P = 0.619$ order; and $F = 0.152$; $df = 1, 11$; $P = 0.903$ diet \times order). Male mating intervals varied from 0 to 8 d (median 1 d, 1 and 3, lower and upper quartiles, respectively).

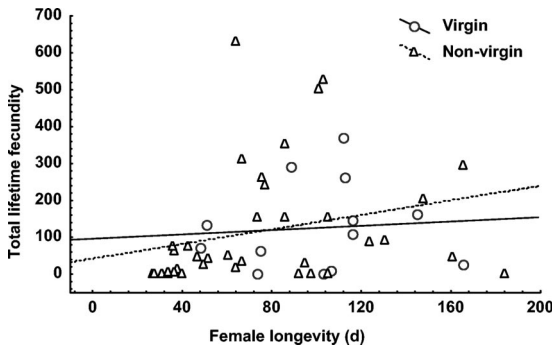


Fig. 2. Relationship between longevity and lifetime egg production (fecundity) for *A. striata* females copulating with virgin or nonvirgin mated males. Females copulating with virgin males: circles and continuous line, $r^2 = 0.01$; $F = 0.17$; $df = 1, 11$; $P = 0.69$; and females copulating with nonvirgin males: triangles and dotted line, $r^2 = 0.17$; $F = 7.22$; $df = 1, 36$; $P = 0.011$.

Discussion

The median longevity of females that copulated with virgin males was 32 d greater than the median longevity of females copulating with nonvirgin males. This increase in life span benefits both males and females, because females will have more time to find hosts.

Male nutrient donations in the form of materials transferred before or during the copulation have been shown to affect female life span in insects (Arnqvist and Nilsson 2000). Specifically, seminal fluids and sperm have been shown to positively affect female life-span in *G. lineaticeps* (Wagner et al. 2001, Wagner and Harper 2003). Virgin males may have more resources available to transfer to females, and these resources may decrease in volume with subsequent matings. Thus, females copulating with males depleted of materials transferred in the ejaculate or depleted of materials transferred through trophallaxis may suffer a decrease in longevity as was probably the case here



Fig. 3. Copula duration for *A. striata* males fed a high quality diet (sucrose plus protein ad libitum), or a low-quality diet (sucrose every third day). Differences between treatments are statistically significant ($F = 11.73$; $df = 1, 11$; $P = 0.006$). Whiskers represent range, boxes represent quartiles, and small squares represent medians.

with *A. striata* females. However, the nutritional value of materials transferred through trophallaxis or through the ejaculate is unknown in this species. In *C. capitata*, AGPs seem to be proteinaceous in nature (Jang 1995, Marchini et al. 2003), but they may not necessarily be nutritious for the female (Cordero 1995).

Alternatively, a longer life span for females copulating with virgin males may be due to them being the most sexually receptive to mating, generally healthier and predisposed to a longer life. Although we cannot discard the latter two possibilities, females that copulated with virgin males were not the most sexually receptive, as there were no differences between the amount of days females took to copulate with a male when he was virgin or nonvirgin. Thus, we believe that in this study, a longer life span for females can indeed be attributed to them copulating with a virgin male as is the case with *C. capitata* (Whittier and Kaneshiro 1991).

Although we do not know for certain whether *A. striata* females prefer virgin over nonvirgin males, it is likely that this is the case. Females are very choosy when mating, and the elaborate precopulatory courtship exhibited by males may allow females to select between virgin and nonvirgin mates. There are ≈ 13 male mating attempts before an actual copulation takes place (Aluja et al. 1993). Females frequently reject males, and some females do not copulate at all in the laboratory. Mate choice for a virgin male may be especially important in this species as most females seem to be monandrous (M.A. et al., unpublished data). However, this issue warrants further investigation particularly in light of the fact that in *C. capitata* Shelly and Whittier (1993) have shown that females do not prefer virgin over nonvirgin males, even though females benefit from an increase in fecundity and longevity when copulating with virgin males (Whittier and Kaneshiro 1991).

Male adult diet did not affect female longevity or any reproductive parameters. This suggests that wild *A. striata* males transfer similar amounts of sperm regardless of male diet. In contrast, female *C. capitata* store more sperm when copulating with a protein-fed male (Taylor and Yuval 1999). Repeated mating demands energetic expenses. Here, males fed a low-quality diet (i.e., fed sucrose every third day) had longer copulations than males fed a high-quality diet. Similarly, protein-deprived mass-reared *C. capitata* males have longer copulations than protein-fed males (Blay and Yuval 1997, Taylor and Yuval 1999, Field and Yuval 1999). However, for wild males inclusion of protein into the diet had no effect on copula duration (Taylor et al. 2000, Shelly and Kennelly 2002). In contrast, Aluja et al. (2001) report that *A. striata* males ingesting protein have longer copulations than males fed sucrose plus bird feces (*Turdus grayi* Bonaparte) or fed an open fruit (a high sugar-low protein diet). Furthermore, these authors found that males fed sucrose ad libitum did not copulate. These differences can be explained by the fact that, in our study, males faced no intraspecific competition, whereas in Aluja et

al. (2001) that was not the case. Males fed a low-quality diet may take longer to transmit ejaculates to females and may only be able to do so when not in competition with other males. Males have been seen to climb on top of copulating pairs, which may interfere with the copulation. Thus, males fed a low-quality diet may have shorter copulations when competing with other males, but the latter needs to be investigated in future studies.

Faced with limited resources, males may maintain either constant nuptial gift size or constant intervals between successive matings (Cratsley et al. 2003). Intervals between copulations for *A. striata* were not constant, varying from 0 to 8 d, and were unaffected by male diet. Mating order had no effect on copula duration. That is, males maintained constant copula durations with different females, which suggests that previous sexual experience does not influence copula duration and that males can control to some extent the length of the copula.

In conclusion, male mating history affects female longevity in *A. striata*. At lek sites, virgin and mated males may be found simultaneously and the elaborate precopulatory courtship by males may provide females with information regarding the previous sexual experience of a potential mate. However, as noted, female choice for virgin or nonvirgin males still needs to be determined in this species. Additional studies also are needed to determine whether it is substances transferred through labelum-to-labelum contacts or whether AGPs are responsible for increasing *A. striata* female life span. If indeed males transfer nutritious materials, mating repeatedly should result in fitness benefits for females.

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References Cited

- Aluja, M., I. Jácome, A. Birke, N. Lozada, and G. Quintero. 1993. Basic patterns of behavior in wild *Anastrepha striata* (Diptera: Tephritidae) flies under field-cage conditions. *Ann. Entomol. Soc. Am.* 86: 776–793.
- Aluja, M., J. Piñero, M. López, C. Ruiz, A. Zúñiga, E. Piedra, F. Díaz-Fleischer, and J. Sivinski. 2000a. New host plant and distribution records in Mexico for *Anastrepha* spp., *Toxotrypana curvicauda* Gerstaecker, *Rhagoletis zoqui* Bush, *Rhagoletis* sp., and *Hexachaeta* sp. (Diptera: Tephritidae). *Proc. Entomol. Soc. Wash.* 102: 802–815.
- Aluja, M., J. Piñero, I. Jácome, F. Díaz-Fleischer, and J. Sivinski. 2000b. Behavior of flies in the genus *Anastrepha* (Trypetinae: Toxotrypanini), pp. 375–408. *In* M. Aluja and A. L. Norrbom (eds.), *Fruit flies (Tephritidae): phylogeny and evolution of behavior*, CRC, Boca Raton, FL.
- Aluja, M., I. Jácome, and R. Macías-Ordóñez. 2001. Effect of adult nutrition on male sexual performance in four tropical fruit fly species of the genus *Anastrepha* (Diptera: Tephritidae). *J. Insect Behav.* 14: 759–775.
- Arnqvist, G., and T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav.* 60: 145–164.
- Blay, S., and B. Yuval. 1997. Nutritional correlates of reproductive success of male Mediterranean fruit flies (Diptera: Tephritidae). *Anim. Behav.* 54: 59–66.
- Boggs, C. L. 1995. Male nuptial gifts: phenotypic consequences and evolutionary implications, pp. 215–242. *In* S. R. Leather and R. J. Hardie (eds.), *Insect reproduction*, CRC, Boca Raton, FL.
- Boller, E. F. 1968. An artificial eggging device for the European cherry fruit fly *Rhagoletis cerasi*. *J. Econ. Entomol.* 61: 850–852.
- Conover, W. J., and L. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Stat.* 35: 124–132.
- Cordero, C. 1995. Ejaculate substances that affect female insect reproductive physiology and behavior: honest or arbitrary traits? *J. Theor. Biol.* 174: 453–461.
- Cordero, C. 1996. On the evolutionary origin of nuptial seminal gifts in insects. *J. Insect Behav.* 9: 969–974.
- Cordero, C. 2000. Trade-off between fitness components in males of the polygynous butterfly *Callophrys xami* (Lycaenidae): the effect of multiple mating on longevity. *Behav. Ecol. Sociobiol.* 48: 458–462.
- Cratsley, C. K., J. A. Rooney, and S. M. Lewis. 2003. Limits to nuptial gift production by male fire flies *Photinus ignitus*. *J. Insect Behav.* 16: 361–370.
- Field, S. A., and B. Yuval. 1999. Nutritional status affects copula duration in the Mediterranean fruit fly, *Ceratitis capitata* (Insecta: Tephritidae). *Ethol. Ecol. Evol.* 11: 61–70.
- Jang, E. B. 1995. Effects of mating and accessory gland injections on olfactory-mediated behavior in the female Mediterranean fruit fly, *Ceratitis capitata*. *J. Insect Physiol.* 41: 705–710.
- Jones, T. M. 2001. A potential cost of monandry in the lekking sandfly *Lutzomyia longipalpis*. *J. Insect Behav.* 14: 385–399.
- Marchini, D., G. Del Bene, L. Cappelli, and R. Dallai. 2003. Ultrastructure of the male reproductive accessory glands in the medfly *Ceratitis capitata* (Diptera: Tephritidae) and preliminary characterization of their secretions. *Arthropod Struct. Dev.* 31: 313–327.
- Markow, T. A., and P. F. Ankney. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. *Science (Wash. DC)* 224: 302–303.
- Norrbom, A. L., L. E. Carroll, F. C. Thompson, I. M. White, and A. Freidberg. 1999. Systematic database of names, pp. 65–251. *In* F. C. Thompson (ed.), *Fruit fly expert identification system and systematic information database*. Myia (1998) 9, vii + 524 pp. & Diptera Data Dissemination Disk (CD-ROM) (1998) 1.
- Pitnick, S., T. A. Markow, and M. F. Riedy. 1991. Transfer of ejaculate and incorporation of male-derived substances by females in the Nanoptera species group (Diptera: Drosophilidae). *Evolution* 45: 774–780.

- Shelly, T. E., and T. S. Whittier. 1993. Effect of sexual experience on the mating success of males of the Mediterranean fruit fly, *Ceratitidis capitata* Wiedemann (Diptera: Tephritidae). *Proc. Hawaiian Entomol. Soc.* 32: 91–94.
- Shelly, T. E., and S. Kennelly. 2002. Influence of male diet on male mating success and longevity and female remating in the Mediterranean fruit fly (Diptera: Tephritidae) under laboratory conditions. *Fla. Entomol.* 85: 572–579.
- Simmons, L. W. 2001. Sperm competition and its evolutionary consequences in the insects. Princeton University Press, Princeton, NJ.
- Sivinski, J., and B. Smittle. 1987. Male transfer of materials to mates in the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). *Fla. Entomol.* 70: 233–238.
- Smith, P. H., C. Gillott, L. B. Browne, and A.C.M. Van Gerwen. 1990. The mating-induced refractoriness of *Lucilia curpina* females: manipulating the male contribution. *Physiol. Entomol.* 15: 469–481.
- StatSoft. 1999. Statistica for Windows. Computer program manual, version 5.1. StatSoft, Inc. Tulsa, OK.
- 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.
- Wagner, W. E., R. J. Kelley, K. R. Tucker, and C. J. Harper. 2001. Females receive a life-span benefit from male ejaculates in a field cricket. *Evolution* 55: 994–1001.
- Wagner, W. E., and Harper, C. J. 2003. Female life span and fertility are increased by the ejaculates of preferred males. *Evolution* 57: 2054–2066.
- Wedell, N., M.J.G. Gage, and G. A. Parker. 2002. Sperm competition, male prudence and sperm-limited females. *Trends Evol. Ecol.* 17: 313–320.
- Whittier, T. S., and K. Y. Kaneshiro. 1991. Male mating success and female fitness in the Mediterranean fruit fly (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 84: 608–611.

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