

Attraction of Naïve and Fruit-Experienced Mexican Fruit Flies to Mangoes and Grapefruits in Wind-Tunnel Bioassays

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ABSTRACT

Wild strain, mated, female Mexican fruit flies, *Anastrepha ludens* (Loew), with no prior experience with fruit (naïve), were attracted to grapefruits (*Citrus paradisi*) but not to mangoes (*Mangifera indica*) in wind tunnel experiments. Oviposition experience with either fruit prior to testing increased attraction to both fruits but more so to the experienced fruit. Oviposition propensity was greater on grapefruits than on mangoes and was not affected by prior fruit experience. Oviposition propensity on mangoes was no greater than on plastic yellow balls. Responses of laboratory females were similar to those of wild females except that responses were generally higher. Wild strain, sexually mature, naïve males were attracted to grapefruits but not mangoes and fruit experience had little effect. Laboratory males were attracted to both fruit types, and experience with either fruit type increased attraction to mangoes.

Additional Index Words: *Anastrepha ludens*, *Diptera*, *Tephritidae*, *citrus*.

The Mexican fruit fly, *Anastrepha ludens*, is a polyphagous frugivorous insect that is known to utilize over 30 host fruits in nature (Norrbon & Kim 1988). Recent work testing attraction and oviposition by Mexican fruit flies to grapefruit, *Citrus paradisi*, sweet oranges, *Citrus sinensis*, and fruits of the yellow chapote, *Casimiroa greggii*, showed that gravid wild-strain females without prior exposure to fruit (naïve) were not attracted to these fruits any more than to plastic yellow fruit models (Robacker & Fraser 2002a, 2002b, 2003). However, all three fruits were attractive to females that had previous exposure to them in cages. Naïve laboratory-strain females were attracted slightly to these fruits compared with fruit models but also became more responsive to the fruits following exposure to them. Our interpretation of these data was that laboratory colonization selected for an opportunistic fly that was more capable than wild flies of responding to general fruit stimuli. All together, the results demonstrated that females learned to respond to fruit they had experienced, and suggest that attraction to specific fruits in nature is weak until females have ovipositional experience with them. Although it is not known how generally Tephritidae need exposure to fruit before they will be attracted to it, it is accepted that exposure to a particular fruit type not only increases acceptance of that fruit in future encounters, but also decreases acceptance of fruit other than the experienced one (Fletcher & Prokopy 1991).

The mango, *Mangifera indica*, is another important host of the Mexican fruit fly. Like grapefruits and oranges, mangoes are not native hosts, having originated in Asia. Unlike grapefruits and oranges that are preferred hosts of this fly wherever they are grown, mangoes are preferred hosts only in certain areas of Mexico. Baker et al. (1944) reported that mangoes are more heavily infested than citrus in higher-elevation central Mexico but are only slightly attacked in lower-elevation northeastern Mexico where entire grapefruit crops could be lost to infestation. Reasons for the different preferences in different parts of Mexico are not clear, but were not due to mango varietal differences according to Baker et

al. (1944). There is some indication that competition with *A. obliqua* Macquart for mangoes (Aluja et al. 2000), and different habitat preferences of *A. ludens* and *A. obliqua* based on elevation (Baker et al. 1944, *A. obliqua* as *A. mombinpraeoptans* Sein), may account for some of the geographic differences in mango utilization by the Mexican fruit fly.

The objectives of this work were to determine attractiveness of mangoes to naïve and mango-experienced and grapefruit-experienced males and gravid females of the Mexican fruit fly, and to evaluate acceptance of mangoes for oviposition. Attractiveness (upwind movements toward fruit and landing on fruit) and acceptance (oviposition behavior) of grapefruit and yellow plastic balls, already studied in previous work (Robacker & Fraser 2001, 2002a), were measured as controls. Laboratory-strain and wild-strain Mexican fruit flies were tested in separate experiments.

MATERIALS AND METHODS

Insect Rearing and Handling. Laboratory flies were obtained from a culture at our facility in Weslaco, TX. Laboratory stock originated from 2,000 pupae collected from yellow chapote fruit from the Montemorelos area of Nuevo Leon in northeastern Mexico in 1997. This culture had been maintained on artificial diet for approximately 56 generations at the time of our work. Eggs were collected after oviposition into red xanthan-gum gel covered with parafilm. No fruit or fruit extract was used in rearing of the laboratory culture. Wild flies were obtained from grapefruits, sour oranges, *Citrus aurantium*, and yellow chapote, *Casimiroa greggii*, collected in Nuevo Leon. Field infestation of mangoes in Nuevo Leon generally is low compared with infestation of grapefruits, sour oranges, and yellow chapote fruits.

Adults of both strains were held in Plexiglas cages (20.5 x 20.5 x 20.5 cm) with screened tops containing a diet mixture of

sugar and yeast hydrolysate, with water supplied separately. One third of the cages was supplied with a grapefruit and another third with a mango starting 1 or 2 days after eclosion. Grapefruits were variety Rio Red and were obtained in orchards near the station in Weslaco, TX. Various varieties of mangoes were used depending upon availability. Mangoes were obtained from a local market after importation from Mexico. Neither grapefruits nor mangoes had been sprayed with pesticides at any time. Laboratory conditions where test flies were housed were $22 \pm 2^\circ\text{C}$ and $50 \pm 20\%$ relative humidity with a photophase of 0630 to 1930 h provided by fluorescent lights.

Experimental Procedure. Bioassays were conducted in a Plexiglas wind tunnel with the dimensions of $0.3 \times 0.3 \times 1.2$ m. Each end of the wind tunnel was screened to allow airflow. The downwind end contained a baffle system to create a uniform airflow through the chamber. Air was pulled through the chamber at 0.4 m/sec by an exhaust fan connected to the downwind end. Air exiting the chamber was directed into an exhaust hose and removed to the outdoors. The top of the chamber had two circular openings (12.8 cm diameter) with Plexiglas covers, located at each end of the chamber, to allow easy access to the chamber's interior. A 75 W "soft white" light bulb (General Electric Co., Cleveland, OH) in a reflecting lamp was positioned 17 cm above the downwind end of the chamber. The purpose of this light was to minimize flying into the upwind end of the chamber that was not orientation to the fruit sample. Bioassays were conducted in the same laboratory where adult flies were held in cages with fruit, however, the wind tunnel and cartons with flies to be tested were kept on the other side of the laboratory from cages containing fruit. In addition to the direct exhaust from the wind tunnel, this room contains inlet and outlet vents to bring new air into the room from outdoors and remove air from the room to the outdoors. Complete air replacement occurred eight times per hour.

Wild strain and laboratory strain flies were used in experiments at ages 19-30 and 18-27 days post eclosion, respectively. This age range was based on observations of sexual maturation, mating, and oviposition behavior by both strains of flies in holding cages containing grapefruit and on previous results (Robacker & Fraser 2001, 2002a, 2002b). Flies to be used in bioassays were transferred into cylindrical paper cartons (473 ml), approximately 12 of each sex per carton, 24 h prior to testing. Cartons were not provided with food or fruit so flies had been starved for 24 hours when trials were conducted. Previous research demonstrated that 24 h of food deprivation enhanced attraction of Mexican fruit flies to grapefruits and did not affect oviposition propensity compared with non-starved flies (Robacker & Fraser 2001). Cartons were sprayed with water several hours before trials were conducted.

Grapefruits used in bioassays were ripe, Rio Red variety grapefruits like those described above. A circular piece of the rind and pulp measuring 2.5 cm in diameter was removed from both grapefruits and mangoes so that volatiles from both the peel and pulp were present in the aroma. This was done because previous research showed that grapefruits wounded in this way were more attractive than undamaged fruits to oviposition-ready females (Robacker & Fraser 2002a). Grapefruits and mangoes were washed with water before each trial to remove any chemicals left by flies in the previous trial.

To conduct a trial, a grapefruit or mango was suspended

on a chicken-wire platform from the opening in the upwind end of the chamber, and one carton of flies was placed under the downwind opening. Flies were allowed 5 min to leave the carton and respond to the fruit, and then were removed from the chamber. We recorded upwind movement if flies passed a point 2/3 of the distance from the release carton to the fruit, landing if flies either landed on or walked onto the fruit, and oviposition attempts on grapefruits and mangoes. Upwind movements and landings were considered measures of attraction and oviposition attempts were considered as a measure of the first stage of acceptance. Actual egg deposition, the final acceptance of the fruit, was not measured. Bioassays were limited to 5 min to reduce accidental upwind movements and landings due to random movements of non-responding flies.

Two experiments were conducted, one with laboratory flies and one with wild flies. Each replication of each experiment was conducted as a series of nine trials, each testing one of three fly types (naïve, grapefruit-experienced, mango-experienced) with one of three fruit types (grapefruit, mango, yellow plastic ball), in random order. Each fruit was used for all three trials of one replication of the experiment, then discarded. Yellow plastic balls (8 cm diam.) used as fruit-model controls were described previously (Robacker 1992). Experiments were conducted between 1000 and 1630 h. In previous experiments, time of the day between 0900 and 1700 h did not affect attraction to host fruit and oviposition behavior (Robacker & Fraser 2001).

Statistical Analyses. All behaviors except oviposition propensity were tested by analysis of variance using SuperANOVA (Abacus Concepts, 1989). Proportions of flies that moved upwind, landed on the fruit, or attempted oviposition, were transformed by arcsin of the square root before statistical analyses. Proportions of 0 were replaced with $1/4n$ before transformation (Snedecor & Cochran 1967). Effects of fruit type, experience, and their interactions were calculated for each fly behavior by factorial ANOVA. Additional analyses were performed to determine the overall treatment effect for the nine fruit type by experience treatments. Means separations for these nine treatments were conducted using Fisher's protected least significant difference method (Snedecor & Cochran 1967). Separate analyses were conducted for males and females. Oviposition propensity (percentage of females that attempted oviposition after landing on a fruit) was analyzed by Chi-square tests (Snedecor & Cochran 1967).

RESULTS

Wild Females. Results are shown in Table 1. Statistics for LSD comparisons in Table 1 are: upwind movement - $F = 7.4$, $df = 8,72$, $P < 0.0001$; landings - $F = 11.5$, $df = 8,72$, $P < 0.0001$; and oviposition attempts - $F = 8.9$, $df = 8,72$, $P < 0.0001$. Means comparisons in Table 1 show that more naïve females landed on grapefruits than on yellow balls. Otherwise, attraction and oviposition responses of naïve females to fruit were not greater than to yellow balls. Generally, however, females responded to fruit more than to yellow balls. This trend was examined in analyses of test-fruit effects, summed over experience treatments. Statistics for these test-fruit effects are: upwind movement - $F = 10.8$, $df = 2,72$, $P < 0.0001$; landings - $F = 25.3$, $df = 2,72$, $P <$

Table 1. Percentages of Mexican fruit flies, with or without fruit experience, attracted to and attempting oviposition in mangoes or grapefruits in a wind tunnel: wild strain females.

Test fruit: Experience	Moved Upwind ¹	Landed on Fruit ¹	Attempted to Oviposit on Fruit ¹	Oviposition Propensity on Fruit ²
Yellow ball:				
Naïve	9.2 a	0.8 a	0.0 a	0.0(1)
Grapefruit exp	20.1 bcd	0.8 a	0.0 a	0.0(1)
Mango exp	12.5 ab	1.7 a	0.0 a	0.0(2)
Grapefruit:				
Naïve	15.2 abc	9.2 bc	2.5 a	27.3(11)
Grapefruit exp	34.3 ef	28.5 d	13.5 b	47.1(34)
Mango exp	31.1 def	15.1 c	10.1 b	66.7(18)
Mango:				
Naïve	13.3 ab	3.3 ab	0.0 a	0.0(4)
Grapefruit exp	26.4 cde	14.4 c	0.0 a	0.0(17)
Mango exp	39.8 f	27.3 d	3.3 a	12.5(32)

¹Values are mean percentages of females responding out of the total females in the trial. n = 10 trials each test fruit/experience group; 11.9 females/trial. Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

²Values are percentages of females to attempt oviposition out of the number (n) of females that landed on the fruit/ball.

0.0001; and oviposition attempts - $F = 24.3$, $df = 2,72$, $P < 0.0001$. Fisher's protected LSD (not shown) indicated that females responded more to either fruit than to yellow balls, except that attempted ovipositions did not differ between mangoes and yellow balls. Oviposition propensity (tendency to attempt oviposition given that a landing occurred) was greater on grapefruits than on mangoes ($\chi = 16.6$, $df = 1$, $P < 0.001$), summed over experience treatments.

More females experienced with either fruit moved upwind toward and landed on both fruit types, than did naïve females, as shown by most means comparisons in Table 1. Also, more females experienced with grapefruits landed on grapefruits than on mangoes and more females experienced with mangoes landed on mangoes than on grapefruits. Finally, females experienced with either fruit type also had more attempted ovipositions on grapefruits, but not significantly higher oviposition propensities, than did naïve females. Fruit experience did not enhance oviposition behavior on mangoes.

Laboratory Females. Results are shown in Table 2. Statistics for LSD comparisons in Table 2 are: upwind movement - $F = 23.3$, $df = 8,168$, $P < 0.0001$; landings - $F = 33.3$, $df = 8,168$, $P < 0.0001$; and oviposition attempts - $F = 15.7$, $df = 8,168$, $P < 0.0001$. Means comparisons in Table 2 show that both naïve females and females experienced with fruit responded more to either fruit than to yellow balls. Oviposition propensity was greater on grapefruits than yellow balls ($c = 4.7$, $df = 1$, $P < 0.05$), summed over experience treatments, but did not differ between mangoes and yellow balls. Also, oviposition propensity by naïve females did not differ on fruits and yellow balls.

Upwind movement and landing responses on grapefruits

vs. mangoes, did not differ in most means comparisons. However, more females experienced with either fruit attempted oviposition on grapefruits than on mangoes. Also, oviposition propensity was greater on grapefruits than on mangoes ($\chi = 8.1$, $df = 1$, $P < 0.01$), summed over experience treatments.

Females experienced with either fruit responded more to grapefruit than did naïve females (LSD comparisons in Table 2). Females with mango experience responded more to mangoes than did naïve females, but experience with grapefruit generally did not enhance responses of females to mangoes. Experience with fruit did not affect attraction to, or oviposition behavior on, yellow balls. Experience with grapefruits enhanced attraction to grapefruits more so than to mangoes and experience with mangoes enhanced attraction to mangoes more so than to grapefruits. This was demonstrated by significant test-fruit type by experience-fruit type interactions for both upwind movements ($F = 4.3$; $df = 1,63$; $P < 0.05$) and landings ($F = 4.7$; $df = 1,63$; $P < 0.05$) in ANOVA's using reduced models with data for yellow balls and naïve females removed. Experience with fruit did not affect oviposition propensity on fruit or yellow balls.

Wild Males. Results are shown in Table 3. Statistics for LSD comparisons in Table 3 are: upwind movement - $F = 1.2$, $df = 8,72$, $P = 0.29$; and landings - $F = 4.0$, $df = 8,72$, $P < 0.001$. Neither fruit type nor fruit experience affected upwind movements. More males landed on grapefruits than on mangoes or yellow balls as indicated by most means comparisons. Fruit experience had little affect on attraction except that wild males with grapefruit experience landed on grapefruit more often than did those with mango experience.

Table 2. Percentages of Mexican fruit flies, with or without fruit experience, attracted to and attempting oviposition in mangoes or grapefruits in a wind tunnel: laboratory females.

Test fruit: Experience	Moved Upwind ¹	Landed on Fruit ¹	Attempted to Oviposit on Fruit ¹	Oviposition Propensity on Fruit ²
Yellow ball:				
Naïve	15.7 a	2.0 a	0.8 a	40.0(5)
Grapefruit exp	15.0 a	2.7 a	0.0 a	0.0(7)
Mango exp	12.4 a	2.8 a	0.5 a	14.3(7)
Grapefruit:				
Naïve	27.8 b	16.7 b	8.7 bc	52.4(42)
Grapefruit exp	51.8 d	39.3 e	19.2 d	49.5(101)
Mango exp	41.2 c	32.3 de	18.0 d	56.1(82)
Mango:				
Naïve	30.5 b	20.2 bc	5.2 b	25.5(51)
Grapefruit exp	42.3 cd	26.8 cd	4.1 ab	40.0(25)
Mango exp	44.3 cd	31.4 de	11.3 c	35.0(80)

¹Values are mean percentages of females responding out of the total females in the trial. n = 22 trials each test fruit/experience group; 11.7 females/trial. Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

²Values are percentages of females to attempt oviposition out of the number (n) of females that landed on the fruit/ball.

Laboratory Males. Results are shown in Table 3. Statistics for LSD comparisons in Table 3 are: upwind movement - $F = 5.8$, $df = 8,168$, $P < 0.0001$; and landings - $F = 13.9$, $df = 8,168$, $P < 0.0001$. More males were attracted to fruit than to yellow balls as indicated by most means comparisons in Table 3. Responses to grapefruits and mangoes generally did not differ. Fruit experience had little effect on attraction to grapefruits. However, experience with either fruit generally increased responses to mangoes.

DISCUSSION

Results were similar to those reported previously for responses of female Mexican fruit flies to grapefruits, oranges, and yellow chapote fruits (Robacker & Fraser 2002a, 2002b, 2003). In each case, the fruits were not very attractive to naïve wild females. Also, attraction increased if females had previous experience with the fruits. Responses of naïve laboratory females were greater than those of naïve wild females and also increased with fruit exposure. Increased attraction to fruits following exposure to them has been reported for numerous fruit fly species (Cooley et al. 1986, Prokopy et al. 1990a, 1990b, 1991, 1993, Fletcher & Prokopy 1991).

Although similar to previous data, results differed in some ways. In the current work, attraction of naïve wild female Mexican fruit flies to grapefruits was significantly greater than to plastic yellow balls. In previous studies, attraction of naïve wild females to grapefruits and oranges was not significantly greater than to plastic yellow balls. Attraction to mangoes by naïve wild females was not greater than attraction to plastic yellow balls. Also, oviposition propensity on mangoes was significantly lower than on

grapefruits. In previous work, no differences in oviposition propensity were found in comparisons of grapefruits with either oranges or yellow chapote fruits. Because grapefruits, oranges and chapote fruits are Rutaceae and mangoes are Anacardiaceae, the possibility is suggested that Mexican fruit flies prefer citrus over at least some other families of plants for oviposition. Alternatively, because flies used in this work originated from Nuevo Leon where field infestation of grapefruits is usually higher than that of mangoes (Baker et al. 1944), it is possible that these flies constitute a host race that prefers grapefruits over mangoes. It would be interesting to conduct additional studies using flies from central Mexico where infestations of mangoes often are quite high (Baker et al. 1944) to determine if those flies would prefer mangoes over grapefruits.

Another possible explanation for the large difference in oviposition attempts on grapefruits vs. mangoes is that fruit acceptability in trials two and three may have been affected differently for mangoes and grapefruits by prior oviposition into fruits during the first trial of each replication. However, linear regression of the number of oviposition attempts on the order of testing accounted for less than 1% of the variance in oviposition attempts for both grapefruits and mangoes with either wild or laboratory females. Thus, there is no indication that either fruit type was changing in acceptability during the three trials of each replication.

As in our previous study comparing attraction to grapefruits and oranges (Robacker & Fraser 2003), experience with either grapefruit or mangoes influenced attraction to the other fruit, a phenomenon termed cross induction (Jaenike 1983). This was evident as increased upwind movements toward and/or landings on grapefruits following experience with mangoes, and mangoes following experience with grapefruits. Experience with either fruit

Table 3. Percentages of Mexican fruit flies, with or without fruit experience, attracted to mangoes or grapefruits in a wind tunnel: males.

Test fruit: Experience	Wild Strain		Laboratory Strain	
	Moved Upwind	Landed on Fruit	Moved Upwind	Landed on Fruit
Yellow ball:				
Naive	5.1 a	0.0 a	11.8 ab	1.9 a
Grapefruit exp	6.7 a	0.0 a	8.8 a	0.8 a
Mango exp	3.3 a	0.0 a	11.7 ab	1.5 a
Grapefruit:				
Naive	9.6 a	5.3 bc	19.5 c	10.9 bc
Grapefruit exp	12.5 a	8.3 c	22.9 cd	16.9 cd
Mango exp	4.5 a	1.8 ab	21.7 c	16.1 bcd
Mango:				
Naive	5.8 a	0.8 a	17.1 bc	9.7 b
Grapefruit exp	9.9 a	0.9 ab	22.2 c	16.5 cd
Mango exp	9.3 a	2.6 ab	30.3 d	22.0 d

Values are mean percentages of males responding out of the total males in the trial. Wild strain: n = 10 trials each test fruit/experience group; 11.7 males/trial. Laboratory strain: n = 22 trials each group; 11.5 males/trial. Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

did not decrease attraction to the other fruit as had been reported for several other species of fruit flies (Cooley et al. 1986, Papaj & Prokopy 1986, Prokopy et al. 1986, Fletcher & Prokopy 1991).

Results of this work were also similar to those of our previous studies regarding attraction of males to host fruits (Robacker & Fraser 2002a, 2002b, 2003). This includes generally less attraction than females and generally greater responses by laboratory males than wild males. The current study differs in that attraction of males to grapefruits was greater than in previous work both for wild and laboratory flies. Results are in line with those of published work for males of other fruit flies (Prokopy et al. 1973, Fein et al. 1982, Reissig et al. 1982, Prokopy et al. 1989, Nigg et al. 1994, Prokopy & Vargas 1996, Katsoyannos et al. 1997, Cornelius et al. 2000).

Including this work, we have now conducted studies of host-fruit attraction by mature males and gravid females of the Mexican fruit fly to grapefruits, oranges, yellow chapotes, and mangoes. Similar results in all these studies, as discussed above, suggest several general conclusions. Wild flies with no previous host experience are only weakly attracted to these fruits. Laboratory flies respond at higher rates than wild flies, suggesting genetic selection for opportunism due to laboratory constraints. Although attraction of naïve laboratory and wild flies was not great, some attraction did occur. This indicates that flies without prior oviposition experience search for fruit stimuli of a very general nature, a behavior that results in finding host fruit about which they learn characteristics specific to the experienced fruit.

Exposure to host fruits increases attraction to those and similar hosts. These results indicate that learning plays an important role in host selection. It seems plausible that naïve females searching for general fruit stimuli learn characteristics (size, color, chemicals) of whatever host fruit they encounter first, resulting in directed search for this host as long as they continue to have success finding it. While other possibilities cannot be discarded and fine tuning of these hypotheses may be needed, this

model of the host foraging behavior of this polyphagous fly is well supported by our data.

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LITERATURE CITED

- Abacus Concepts. 1989. *SuperANOVA*. Abacus Concepts, Inc., Berkeley, CA.
- Aluja, M., J. Pinero, I. Jacome, F. Diaz-Fletcher, and J. Sivinski. 2000. Behavior of flies in the genus *Anastrepha* (Trypetinae: Toxotrypanini), pp. 375-406 In M. Aluja and A. L. Norrbom (eds.). *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*. CRC, Boca Raton.
- Baker, A. C., W. E. Stone, C. C. Plummer, and M. McPhail. 1944. A Review of Studies on the Mexican Fruitfly and Related Mexican Species. USDA Miscellaneous Publication 531.
- Cooley, S. S., R. J. Prokopy, P. T. McDonald, and T. T. Y. Wong. 1986. Learning in oviposition site selection by *Ceratitis capitata* flies. *Entomol. Exp. Appl.* 40:47-51.
- Cornelius, M. L., J. J. Duan, and R. H. Messing. 2000. Volatile host fruit odors as attractants for the Oriental fruit fly (Diptera: Tephritidae). *J. Econ. Entomol.* 93:93-100.
- Fein, B. L., W. H. Reissig, and W. L. Roelofs. 1982. Identification of apple volatiles attractive to the apple maggot, *Rhagoletis pomonella*. *J. Chem. Ecol.* 8:1473-1487.

- Fletcher, B. S. and R. J. Prokopy. 1991. Host location and oviposition in tephritid fruit flies, pp. 139-171 *In* W. J. Bailey and J. Ridsdill-Smith (eds.). *Reproductive Behaviour of Insects: Individuals and Populations*. Chapman & Hall, New York.
- Jaenike, J. 1983. Induction of host preference in *Drosophila melanogaster*. *Oecologia* 58:320-325.
- Katsoyannos, B. I., N. A. Kouloussis, and N. T. Papadopoulos. 1997. Response of *Ceratitidis capitata* to citrus chemicals under semi-natural conditions. *Entomol Exp. Appl.* 82:181-188.
- Nigg, H. N., L. L. Mallory, S. E. Simpson, S. B. Callahan, J. P. Toth, S. Fraser, M. Klim, S. Nagy, J. L. Nation, and J. A. Attaway. 1994. Caribbean fruit fly, *Anastrepha suspensa* (Loew), attraction to host fruit and host kairomones. *J. Chem. Ecol.* 20:727-743.
- Norrbom, A. L. and K. C. Kim. 1988. *A List of the Reported Host Plants of the Species of Anastrepha (Diptera: Tephritidae)*. USDA-APHIS-PPQ, APHIS 81-52.
- Papaj, D. R. and R. J. Prokopy. 1986. Phytochemical basis of learning in *Rhagoletis pomonella* and other herbivorous insects. *J. Chem. Ecol.* 12:1125-1143.
- Prokopy, R. J. and R. I. Vargas. 1996. Attraction of *Ceratitidis capitata* (Diptera: Tephritidae) flies to odor of coffee fruit. *J. Chem. Ecol.* 22:807-820.
- Prokopy, R. J., S. S. Cooley, and S. B. Opp. 1989. Prior experience influences the fruit residence of male apple maggot flies, *Rhagoletis pomonella*. *J. Insect Behav.* 2:39-48.
- Prokopy, R. J., S. S. Cooley, and D. R. Papaj. 1993. How well can relative specialist *Rhagoletis* flies learn to discriminate fruit for oviposition? *J. Insect Behav.* 6:167-176.
- Prokopy, R. J., R. A. I. Drew, B. N. E. Sabine, A. C. Lloyd, and E. Hamacek. 1991. Effect of physiological and experiential state of *Bactrocera tryoni* flies on intra-tree foraging behavior for food (bacteria) and host fruit. *Oecologia* 87:394-400.
- Prokopy, R. J., T. A. Green, and R. I. Vargas. 1990a. *Dacus dorsalis* flies can learn to find and accept host fruit. *J. Insect Behav.* 3:663-672.
- Prokopy, R. J., T. A. Green, T. T. Y. Wong, and D. O. McInnis. 1990b. Influence of experience on acceptance of artificial oviposition substrates in *Ceratitidis capitata* (Wiedemann). *Proc. Hawaiian Entomol. Soc.* 30:91-95.
- Prokopy, R. J., V. Moericke, and G. L. Bush. 1973. Attraction of apple maggot flies to odor of apples. *Environ. Entomol.* 2:743-749.
- Prokopy, R. J., D. R. Papaj, S. S. Cooley, and C. Kallet. 1986. On the nature of learning in oviposition site acceptance by apple maggot flies. *Anim. Behav.* 34:98-107.
- Reissig, W. H., B. L. Fein, and W. L. Roelofs. 1982. Field tests of synthetic apple volatiles as apple maggot (Diptera: Tephritidae) attractants. *Environ. Entomol.* 11:1294-1298.
- Robacker, D. C. 1992. Effects of shape and size of colored traps on attractiveness to irradiated, laboratory-strain Mexican fruit flies (Diptera: Tephritidae). *Florida Entomol.* 75:230-241.
- Robacker, D. C. and I. Fraser. 2001. Effects of food deprivation on attraction of Mexican fruit flies (Diptera: Tephritidae) to grapefruit in a wind tunnel. *Ann. Entomol. Soc. Am.* 94:954-958.
- Robacker, D. C. and I. Fraser. 2002a. Attraction of Mexican fruit flies (Diptera: Tephritidae) to grapefruit: Enhancement by mechanical wounding of and experience with grapefruit. *J. Insect Behav.* 15:399-413.
- Robacker, D. C. and I. Fraser. 2002b. Do Mexican fruit flies (Diptera: Tephritidae) prefer grapefruit to yellow chapote, a native host? *Florida Entomol.* 85:481-487.
- Robacker, D. C. and I. Fraser. 2003. Relative attractiveness of oranges and grapefruits to Mexican fruit flies (Diptera: Tephritidae) in a wind tunnel. *J. Entomol. Sci.* 38:566-575.
- Snedecor, G. W. and W. G. Cochran. 1967. *Statistical methods*. The Iowa State University, Ames, IA.