DO MEXICAN FRUIT FLIES (DIPTERA: TEPHRITIDAE) PREFER GRAPEFRUIT TO YELLOW CHAPOTE, A NATIVE HOST?

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DO MEXICAN FRUIT FLIES (DIPTERA: TEPHRITIDAE)
PREFER GRAPEFRUIT TO YELLOW CHAPOTE, A NATIVE HOST?

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ABSTRACT

Wild strain, mated, female Mexican fruit flies, *Anastrepha ludens* (Loew), with no prior experience with fruit (naïve), were not attracted to and did not attempt oviposition in yellow chapote (*Sargentia greggii*) fruit more so than grapefruit (*Citrus paradisi*) in wind tunnel experiments. Naïve, mated laboratory strain females preferred grapefruit. Prior experience with chapote increased attraction of both laboratory and wild strains to chapote. More naïve than chapote-experienced females of both strains attempted to oviposit on the sides of the wind tunnel. Naïve laboratory strain males were more attracted to grapefruit than chapote. Naïve wild males and chapote-experienced wild and laboratory males did not prefer either fruit.

Key Words: *Anastrepha ludens*, fruit fly, grapefruit, yellow chapote, attraction, oviposition, experience

RESUMEN

Las hembras apareadas de raza silvestre de la mosca mexicana de las frutas,*Anastrepha ludens* (Loew), con no experiencia anterior con frutas (ingenuas), no fueron atraídas a y no trataron ovopositar más en la fruta de chapote amarillo (*Sargentia greggii*) que en toronjas (*Citrus paradisi*) en experimentos de túnel de viento. Las hembras ingenuas de la raza apareada en el laboratorio preferieron las toronjas. La experiencia anterior con chapote aumentó la atracción de la raza del laboratorio y de la raza silvestre hacia el chapote. Más hembras ingenuas que hembras con experiencia con chapote de ambas razas trataron a ovopositar en los lados del túnel de viento. Los machos ingenuos de la raza del laboratorio fueron atraídos más hacia las toronjas que al chapote. Los machos ingenuos silvestres y los machos con experiencia con chapote de la raza silvestre y del laboratorio no preferieron cualquiera de las frutas.

The Mexican fruit fly, *Anastrepha ludens* (Loew), is a polyphagous pest of citrus, mango, and other fruits in Mexico and Central America (Norbom & Kim 1988) and a perennial inhabitant of the citrus growing areas of south Texas. Although the original range of the fly is not completely understood, it is widely agreed that the montane regions of northeastern Mexico represent at least part of the native range and that a large citrus tree that grows in these mountains and valleys is among the fly’s native hosts (Baker et al. 1944). This tree, *Sargentia greggii*, produces small oblong yellow-green fruit (typical fruit 2.5-3.0 cm long and 1.2-1.6 cm diam.) that give it its common name, the yellow chapote (Plummer et al. 1941). Unlike grapefruit, *Citrus paradisi*, in which larvae feed on the fleshy pulp, early instar larvae feed on the still-soft seed in immature chapote fruit before moving into the flesh (Plummer et al. 1941). Field workers searching for the fly in its native habitat know to look for stands of these trees growing along streams in mountain canyons where adults can be found on the wing and larvae in fallen fruit during the fruiting season. Although not reminiscent of typical commercial citrus in that the fruit contains relatively little flesh and a large stone and has only a weak non-citrus-like aroma, it obviously is among the favored hosts of this fly.

Among commercial citrus, indications are that grapefruit is the preferred host of this fly based on high infestations in grapefruit orchards compared with those of other citrus (Baker et al. 1944). In laboratory wind-tunnel experiments, naïve (no previous experience with fruit), laboratory-strain, oviposition-ready female Mexican fruit flies were attracted to grapefruits mechanically wounded to enhance release of peel and pulp volatiles (Robacker & Fraser 2002). Surprisingly, naïve, wild-strain, oviposition-ready female Mexican fruit flies were not attracted to grapefruit in those experiments. We interpreted these results to mean that wild flies did not recognize grapefruit as a host because it is not a native species, whereas lab flies, due to selection pressures from laboratory colonization, were more opportunistic, facilitating response to general fruit stimuli. However, wild females that had prior experience with grapefruit were attracted to the fruit in that work. This suggested that wild fly populations were able to adapt by learning to search for grapefruit.
In retrospect, it did not seem unreasonable that wild female Mexican fruit flies would not respond instinctively to grapefruit, a species introduced to the new world. However, we hypothesized that attraction of wild flies to chapote fruit would not require learning. This made sense because chapote trees are large and the fruit inconspicuous, both visually and aromatically (as judged by human olfaction), so that finding the fruit by random searching seemed less likely than searching by innate visual and olfactory recognition programs.

In the present work, we wanted to test the hypothesis that Mexican fruit flies instinctively respond to chapote fruit. Our approach was to compare responses of naive flies to chapote fruit with responses to grapefruit in no-choice situations. Responses to grapefruit were studied previously (Robacker & Fraser 2002) and were re-examined here only for comparison with chapote. We also wanted to investigate effects of experience with chapote fruit on subsequent responses to chapote and grapefruit. Two experiments were conducted in a wind tunnel to evaluate responses of laboratory and wild-strain Mexican fruit flies.

**MATERIALS AND METHODS**

Insects, 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 has been maintained on artificial diet for approximately 50 generations. Eggs are collected after oviposition into red gel covered with parafilm. No fruit or fruit extract is used in rearing. Laboratory and wild-strain Mexican fruit flies to grapefruits and did not affect oviposition propensity compared with non-starved flies (Robacker & Fraser 2001, 2002). 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. Cups were not provided with food so flies had been starved for 24 h 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). Cups were sprayed with water several hours before trials were conducted.

Grapefruits used in bioassays were ripe, Rio Red variety grapefruits from an orchard located near the station in Weslaco, TX. A circular piece of the rind and pulp measuring 2.5 cm in diameter was removed from grapefruits 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 2002). Chapote fruits used in bioassays were picked from trees and ranged from small and green to full size and yellow green depending on season and location where fruit were found. Small green fruit were used whenever available because Plummer et al. (1941) indicated that field collections of green, half-grown fruits were more heavily infested than mature fruits with Mexican fruit fly larvae. Because of the small size of the chapote fruits, a group of 7 fruits was used together as the attractant source. One chapote fruit was cut in half to increase emission of volatiles. The exposed...
wounded area of the two chapote fruit halves was roughly equal to that of a wounded grapefruit. Grapefruits and chapote fruits 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 group of chapote fruit was suspended in a chicken-wire basket (with standard window screening on the bottom when chapote fruit were tested) from the opening in the upwind end of the chamber, and one cup of flies was placed under the downwind opening. Flies were allowed 5 min to leave the cup and respond to the fruit, and then were removed from the chamber. We recorded upwind movement if flies passed a point \( \frac{3}{4} \) of the distance from the release cup to the fruit, landing if flies either landed on or walked onto the fruit, oviposition into grapefruits and chapotes, and attempts to oviposit onto the plexiglass walls of the bioassay chamber. Bioassays were limited to 5 min to reduce accidental upwind movements and landings due to random movements of non-responding flies. Experiments were conducted in series of four treatments tested in random order: chapote-experienced flies offered a grapefruit, chapote-experienced flies offered chapote fruit, naive flies offered a grapefruit and naive flies offered chapote fruit. Experiments were conducted between 1100 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 Super-ANOVA (Abacus Concepts, 1989). Proportions of flies that moved upwind, landed on the fruit, attempted oviposition on fruit or the walls of the wind tunnel, were transformed by arcsin of the square root (Snedecor & Cochran 1967) before statistical analyses. Proportions of 0 were replaced with \( \frac{1}{4n} \) before transformation. Effects of fruit type, experience, and their interactions were calculated for each fly behavior. Additional analyses were performed to determine the overall treatment effect for the 4 fruit type by experience treatments. Separate analyses were conducted for males and females. Means separations were conducted using Fisher’s protected least significant difference method (Snedecor & Cochran 1967). Oviposition propensity (percentage of females that attempted oviposition after landing on a fruit) was analyzed by Chi-square tests (Snedecor & Cochran 1967).

RESULTS

Results for wild females are shown in Table 1. Upwind movements, landings, and oviposition behavior by naïve females in response to chapote fruit vs. grapefruit did not differ. More chapote-experienced females moved upwind toward chapote \( (F = 7.6; \text{df} = 3.75; P < 0.001) \) compared with responses of naïve females to chapote, naïve females to grapefruit and chapote-experienced females to grapefruit. More chapote-experienced females than naïve females landed on either chapote or grapefruit \( (F = 3.2; \text{df} = 3.75; P < 0.05) \). There were no differences in total attempted ovipositions on either fruit type by either naïve or chapote-experienced females. Oviposition propensity also did not differ significantly for the various treatments based on a Chi-square test of single classifications with equal expectations. Chapote-experienced females (summed over fruit types) attempted to oviposit on the sides of the wind tun-

| Table 1. Percentages of Mexican Fruit Flies With or Without Prior Experience With Chapote Fruit Attracted to and Attempting Oviposition in Grapefruit or Chapote Fruit in a Wind Tunnel: Wild Strain Females.* |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Test fruit: experience          | Moved upwind    | Landed on fruit | Attempted to oviposit on fruit | Oviposition propensity on fruit | Attempted to oviposit on wind tunnel |
| Grapefruit:                     |                 |                 |                              |                               |                               |
| Naive                           | 10.4 a          | 3.6 a           | 0.7 a                        | 18.2                          | 2.6 a                        |
| Chapote-experienced             | 13.9 a          | 5.1 ab          | 0.6 a                        | 13.3                          | 0.6 a                        |
| Chapote:                        |                 |                 |                              |                               |                               |
| Naive                           | 11.6 a          | 3.5 a           | 0.3 a                        | 11.1                          | 2.3 a                        |
| Chapote-experienced             | 23.4 b          | 10.2 b          | 3.3 a                        | 32.3                          | 1.0 a                        |

*Means followed by different letters in the same column are significantly different at the 5% level by Fisher’s protected LSD.

Values are mean percentages of females responding out of the total females in the trial. \( n = 26 \) trials each test fruit/experience group; 11.7 females/trial.

Values are percentages of females responding out of females that landed on the fruit. Grapefruit, naïve: \( n = 11 \) females landed; Grapefruit, chapote-experienced: 15; Chapote, naïve: 9; Chapote, chapote-experienced: 31. No significant differences were found by Chi-square test of single classifications with equal expectations.
nel less than naïve females, as indicated by a significant experience effect by ANOVA ($F = 4.1; df = 3.75; P < 0.05$).

Results for laboratory females are shown in Table 2. More naïve females landed on ($F = 13.1; df = 3.69; P < 0.0001$) and attempted oviposition in ($F = 9.6; df = 3.69; P < 0.0001$) grapefruit than chapote. Also, oviposition propensity of naïve females was higher on grapefruit than on chapote ($\chi^2 = 4.0; df = 1, P < 0.05$). More females experienced with chapote than naïve females landed on and attempted oviposition in chapote. Conversely, more naïve females than chapote-experienced ones (summed over fruit types) attempted oviposition on the sides of the wind tunnel ($F = 11.6; df = 1.69; P < 0.01$). Oviposition propensity was not significantly affected by experience. Also, experience with chapote had little effect on any of the responses to grapefruit. However, interaction of fruit type with experience was significant for total oviposition attempts ($F = 5.5; df = 1.69; P < 0.05$). This effect occurred because experience with chapote increased oviposition in chapote but decreased oviposition in grapefruit.

Results for males are shown in Table 3. More wild strain males, summed over experience treatments, moved upwind toward chapote than grapefruit ($F = 4.1; df = 1.75; P < 0.05$) (Table 3). More naïve laboratory strain males landed on grapefruit than on chapote fruit ($F = 3.1; df = 3.69; P < 0.05$). Also, summed over experience treatments, more laboratory males landed on grapefruit than on chapote ($F = 7.9; df = 1.69; P < 0.01$). Experience with chapote fruit had no significant effects on responses of either strain to either fruit; however, a general trend of higher responses by chapote-experienced flies occurred. The experience effect was borderline significant for landings bywild males ($F = 3.8; df = 1.75; P = 0.05$).

### Table 2. Percentages of Mexican fruit flies with or without prior experience with chapote fruit attempted to and attempting oviposition in grapefruit or chapote fruit in a wind tunnel: laboratory females.

| Test fruit: experience | Moved upwind | Landed on fruit | Attempted to oviposit on fruit | Oviposition propensity on fruit | Attempted to oviposit on wind tunnel |
|------------------------|--------------|----------------|-------------------------------|--------------------------------|----------------------------------|
| Grapefruit:            |              |                |                               |                                |                                  |
| Naive                  | 35.5 a       | 20.8 c         | 10.5 c                        | 50.8 b                         | 8.6 c                            |
| Chapote-experienced    | 32.4 a       | 21.3 c         | 7.9 bc                        | 37.3                           | 2.2 a                            |
| Chapote:               |              |                |                               |                                |                                  |
| Naive                  | 28.0 a       | 5.1 a          | 1.1 a                         | 21.4 a                         | 7.4 bc                           |
| Chapote-experienced    | 27.6 a       | 11.4 b         | 4.3 b                         | 37.5                           | 2.8 ab                           |

*Means followed by different letters in the same column are significantly different at the 5% level by Fisher's protected LSD.

*Values are mean percentages of females responding out of the total females in the trial. n = 24 trials each test fruit/experience group; 11.6 females/trial.

*Values are percentages of females responding out of females that landed on the fruit. Grapefruit, naïve: n = 59 females landed; Grapefruit, chapote-experienced: 59; Chapote, naïve: 14; Chapote, chapote-experienced: 32. Means for response by naïve females to grapefruit vs. chapote were significantly different by Chi-square test of proportions in 2 independent samples. No significant differences among the 4 means were found by Chi-square test of single classifications with equal expectations.

**DISCUSSION**

Wild strain male and female Mexican fruit flies that had no prior experience with chapote fruit did not exhibit more attraction to or oviposition behavior on chapote, a native host, than grapefruit, an introduced host of this species (Tables 1 and 3). Robacker and Fraser (2002) showed that naïve wild flies were not attracted to grapefruit compared with a plastic yellow ball indicating that they did not respond instinctively to grapefruit as a host. Combining previous results with those from the current work suggests that wild flies also do not instinctively respond to chapote as a host.

Although it is widely accepted that fruit flies are attracted to their host fruit for oviposition (Fletcher & Prokopy 1991; Jang & Light 1996), most demonstrations have used laboratory flies or wild flies with host experience. Some studies that demonstrated host attraction by wild, naïve female tephritids are Averill et al. (1988) with apple maggot, Rhagoletis pomonella, Landolt and Reed (1990) with papaya fruit fly, Toxotrypana curvicauda, Prokopy et al. (1990a) with the oriental fruit fly, Bactrocera dorsalis, and Prokopy and Vargas (1996) and Katsoyannos et al. (1997) with the Mediterranean fruit fly, Ceratitis capitata. We know of no published research showing that wild-strain female fruit flies are not attracted to their natural host material. Such studies usually are regarded as experimental failures rather than demonstrations of actual biological phenomena.

Attraction of naïve, wild male fruit flies to host fruit volatiles has rarely been demonstrated. Katsoyannos et al. (1997) showed that wild, naïve male Mediterranean fruit flies are attracted to volatiles from oranges. Another example is attraction of semi-wild (reared on apples for ca. 32...
generations) males to apple volatiles (Fein et al.
1982). Also with apple maggot, Prokopy et al.
(1989) showed that naive, wild males spent more
time on fruit when released onto hawthorn than
on apple, suggesting preferential response to a
native host.

Naive laboratory A. ludens were more at-
tracted to and females attempted oviposition
more often in grapefruit than chapote (Tables 2
and 3). Robacker and Fraser (2001, 2002) demon-
strated that grapefruits were much more attrac-
tive than yellow balls to naive laboratory females.
The differential in landings on grapefruits (with
pulp wounds like those used in the current work)
vs. yellow balls was 20 to 1 for 1-d starved females
(Robacker & Fraser 2001) compared with 4 to 1
for grapefruit vs. chapote in the current study.
This suggests that chapote should be 5× more attrac-
tive than a yellow ball to naive, hungry, labo-
ratory females, but this was not tested. Attraction
of males to grapefruit could not be demonstrated
in previous work unless they were starved for 2
days prior to testing (Robacker & Fraser 2001).
However, given the greater attraction of naive
laboratory males to grapefruit than to chapote in
the current work, the indication is that grapefruit
is also attractive to males starved for 1 d.

Attempts to prove attraction of naive, labora-
tory-strain male fruit flies to native host fruit
have been few. Successful demonstrations include
attraction to volatiles of fermented chapote fruit
by Mexican fruit flies (Robacker et al. 1990), at-
traction to various fruit extracts by Caribbean
fruit flies, A. suspensa (Nigg et al. 1994), and at-
traction to coffee fruit by Mediterranean fruit
flies (Prokopy & Vargas 1996). Possibly, at least
some of these cases as well as those involving wild
males may represent non-specific responses to
fruit odors by flies motivated by hunger rather
than host attraction.

Previous experiments have indicated that
naive laboratory-strain Mexican fruit flies
(starved or food satiated) are attracted to grape-
fruit but naïve wild flies (food satiated) are not
(Robacker & Fraser 2001, 2002). Experiments
presented here indicate that attraction of naive
laboratory females (starved for 1 d) to chapote is
much weaker than to grapefruit. Apparently,
unknown selective pressure that resulted in attrac-
tion to grapefruit but not chapote was imposed
during laboratory rearing. As stated in the meth-
ods, no fruit or fruit extract is used at any point in
the rearing procedure. A red gel in flat circular
containers is used to collect eggs, but even if this
was perceived by flies as a supernormal visual
fruit stimulus, data from Robacker and Fraser
(2002) indicate that visual stimuli from grape-
fruit are not important compared with the fruit
volatiles. As in our earlier work, we again assert
that laboratory flies are more opportunistic than
wild flies. As such, the stronger (by human olfac-
tion) although unfamiliar aroma of grapefruit
may provide a good general fruit stimulus com-
pared with the weaker aroma of chapote.

Experience with chapote increased attraction
to and oviposition behavior on chapote by wild and
laboratory strain females compared with inexperi-
enced females (Tables 1 and 2). Previously we
showed increased responses to grapefruit by wild
and laboratory females experienced with grape-
fruit (Robacker & Fraser 2002). These results were
expected based on numerous papers that have
demonstrated increased attraction to and usage of
fruits following exposure to those fruits in Medi-
terranean fruit fly and several species of Rhagoletis
and Bactrocera (Cooley et al. 1986, Prokopy et
al. 1990a,b, 1991, 1993, Fletcher & Prokopy 1991,
Averill et al. 1996). Experience with chapote had
little effect on responses to grapefruit. Many stud-
ies have shown that experience with one fruit de-
creases responses to novel fruit types (Cooley et
al. 1986, Papaj & Prokopy 1986, Prokopy et al. 1986,
Fletcher & Prokopy 1991).

Propensity of both wild and laboratory females
to attempt oviposition on the sides of the wind tun-
ner was greatly reduced if flies had previous expe-

| Test fruit: experience | Wild strain | Laboratory strain |
|------------------------|-------------|-------------------|
|                        | Moved upwind | Landed on fruit | Moved upwind | Landed on fruit |
| Grapefruit:            |             |                   |             |                |
| Naive                  | 5.5 a        | 1.6 a             | 16.2 a       | 8.4 b          |
| Chapote-experienced    | 7.0 a        | 3.6 a             | 18.1 a       | 7.6 b          |
| Chapote:               |             |                   |             |                |
| Naive                  | 7.9 a        | 1.0 a             | 15.9 a       | 2.1 a          |
| Chapote-experienced    | 9.4 a        | 2.3 a             | 18.1 a       | 4.4 ab         |

Values are mean percentages of males responding out of the total males in the trial. Wild strain: n = 26 trials each test fruit/experience group; 11.8
males/trial. Laboratory strain: n = 24 trials each group; 11.2 males/trial. Means followed by different letters in the same column are significantly different
at the 5% level by Fisher’s protected LSD.
rience with chapote. We obtained the same result previously for Mexican fruit flies experienced with grapefruit (Robacker & Fraser 2002). The reason for this effect is unknown but could be related to higher egg load of naive flies or learning from fruit experience. A similar effect was found by Prokopy et al. (1990b) in which acceptance of plastic oviposition spheres by Mediterranean fruit flies decreased for flies experienced with host fruit.

Effects of experience with chapote on responses by males were relatively small. The trend was that experience increased attraction to chapote. Previously we showed that experience with grapefruit increased attraction of laboratory males to grapefruit, although the effects were smaller than for experienced females (Robacker & Fraser 2002). Also, Prokopy et al. (1989) showed that experience with apple or hawthorn fruit increased preference by apple maggot males for the experienced fruit. In addition, Sivinski (1990) and Henneman and Papaj (1999) provided evidence that male fruit flies may learn to associate host fruit with females if they are given experience with host fruit while females are present on the fruit. However, Prokopy et al. (1989) found no additional effect from experience with females on fruit beyond preference gained by experience with the fruit by itself. Thus, experience with fruit generally increases attraction of male fruit flies to that fruit, but the reasons are unclear.

Grapefruit and chapote differ greatly in color, size and odor. Our experiments were not designed to determine how important each of these characteristics was in attractiveness of the 2 fruit types to the flies. Data from earlier work indicated that odor was very important in attraction of both naive and experienced flies to grapefruit, but no assessment of visual stimuli was possible (Robacker & Fraser 2002). Both visual and chemical characteristics of host fruit are known to play roles in innate and learned attraction of fruit flies to the fruit (Papaj & Prokopy 1986, Prokopy et al. 1990a, Fletcher & Prokopy 1991, Prokopy et al. 1994, Henneman & Papaj 1999).

Our data indicate that chapote fruit is not preferred to grapefruit by either wild or laboratory strain Mexican fruit flies. A potentially critical factor that may have influenced our results is the maturity level of the chapote fruit. Plummer et al. (1941) presented data that showed that adult Mexican fruit flies were present in chapote stands only during a short period when trees were in bloom and setting fruit, then populations declined rapidly as fruits matured. Taken together with data that showed that larvae feed in the seed before it hardens during fruit maturation, it has been inferred that oviposition-ready females are most attracted to chapote fruit only during fruit set and early stages of maturation. In our work, we used only chapote fruit picked off of trees and attempted to obtain fruit from each of several lo-
cations as soon as possible after set. However, it is possible that our fruit was already beyond its most attractive stage by the time we used it in bioassays. In this regard, it is interesting that no ovipositions occurred during the first month (out of 4 months) of testing when fruits were very small and green. This suggests that another possible problem may be changes in the attractive quality of fruit as soon as it is picked from trees. Thus, it may be necessary to investigate the attractiveness of early stage chapote fruit in the field by observing ovipositing females on chapote trees. A more practical approach would be to study fruit fly behavior on field-caged trees from bloom to fruit drop. Perhaps such an investigation would show that the flies are not attracted to even the earliest fruit so much as they are attracted to the flowers and then remain on the trees to oviposit on the small fruit, not because it is attractive but because it is the only fruit present.

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