Influence of Previous Experience with Host Plant Foliage on Behavior of Mediterranean Fruit Fly Females

RONALD J. PROKOPY[1], MARTIN ALUJA[1], DANIEL R. PAPAJ[1], BERNARD D. ROITBERG[2] AND TIM T. Y. WONG[3]

ABSTRACT

Consistent with the findings of a previous study, foliage-naive gravid females of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), when released onto the foliage of non-fruiting host plants in a field cage, spent more time on the foliage of citrus than of tomato plants of comparable size. We found here that 3 days of previous experience with the foliage of citrus or tomato plants did not detectably alter the nature of this response pattern. This suggests that prior experience of medfly females with plant foliage (in contrast to prior experience with plant fruit) is probably of negligible biological significance. We also found that the response pattern of medfly females of a strain cultured in the laboratory for more than 300 generations was qualitatively similar to but quantitatively different from the response pattern of wild medflies.

Previous studies revealed that inexperienced (naive) gravid female Mediterranean fruit flies (medflies), *Ceratitis capitata* (Wiedemann), of wild origin released onto the foliage of non-fruiting host and non-host plants remained longer on the foliage of certain host plants (e.g. citrus) than on the foliage of other host plants (e.g. tomato) or non-host plants (e.g. pine) (Prokopy et al. 1986). Other studies have shown that after wild-origin medfly females arrive on host fruit, their propensity to accept (bore into) or reject that fruit prior to egg deposition can be modified by previous ovipositional experience with that or another fruit species, and hence involves learning (Cooley et al. 1986). Medfly females from a colony cultured in the laboratory under artificial conditions for more than 300 generations also have been found capable of such learning of host fruit characters after alighting on fruit, although to a lesser degree than wild females (McDonald 1986, Papaj et al. 1987).

To date, there has been no investigation of ways in which previous experience on a host plant, prior to alighting on a fruit, might influence medfly behavior. In this study, we asked whether the length of time gravid medfly females of wild and laboratory-colony origin remained on the foliage of non-fruiting citrus and tomato plants was influenced by previous

[1]Department of Entomology, University of Massachusetts, Amherst, Massachusetts 01003, USA.
[2]Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6, CANADA.
[3]Tropical Fruit and Vegetable Research Laboratory, Agricultural Research Service, USDA, ARS, Honolulu, Hawaii 96804, USA.

experience with the foliage of these plants. We assumed that residence time on a plant was a reasonable index of fly search effort within a plant.

MATERIALS AND METHODS

The wild medflies originated from larvae that infested field-collected fruit of unsprayed loquats, *Eriobotryia japonica*, taken from the Kula area of the island of Maui in Hawaii. The lab-cultured medflies had been reared for more than 300 continuous generations using artificial oviposition devices and artificial larval media described in detail in Tanaka et al. (1969). Upon eclosion, females of like origin were held together with males in cages supplied with food (yeast hydrolysate and sucrose) and water under laboratory conditions (temperature ca. 25°C, relative humidity ca. 40%, daylength ca. 13 hours).

When mature (at 12-15 days), 16 female and 4 male wild-origin flies were transferred into each of 9 exposure cages (30 × 30 × 30 cm) placed next to a partly-shaded window in the laboratory. Three of the exposure cages contained a potted citrus plant, *Citrus lima* (Rutaceae), each ca. 26 cm in canopy diameter and each bearing ca. 90 leaves of a mean area of ca. 17 cm^2/leaf. Three contained a potted tomato plant, *Lycopersicon esculentum* (Solanaceae), each ca. 26 cm in canopy diameter and each bearing ca. 49 leaves of a mean area of 14 cm^2/leaf. Each plant was washed gently but thoroughly with water before use and was arranged so that the pot was beneath the floor of the exposure cage. The remaining 3 exposure cages contained no plants (i.e. the flies remained foliage-naive). All 9 cages were provided with food (of above type) and water. To encourage fly visitation of the plant foliage, 3 water-rinsed host kumquat fruit, *Fortunella japonica* (Rutaceae), each 20 mm diam and punctured 4 times with an insect pin (to facilitate ovipositor penetration), were hung by wire near the center of the canopy of each caged plant (or from the ceiling of cages without plants) to serve as oviposition sites. These fruit were replaced with fresh specimens after 2 days. The same protocol was used with mature (6-10 day old) lab-cultured flies.

All tests were conducted in two 3.5 × 3.5 × 3 m clear-nylon-screen field cages on the grounds of the USDA Tropical Fruit and Vegetable Research Laboratory in Honolulu. Water-washed test plants were positioned 1 m above ground near the center of each cage. Each of the 2 citrus test plants (1/cage) was 35 cm in canopy diameter and bore ca. 107 leaves of a mean area of 23 cm^2/leaf. Each of the 2 tomato test plants likewise was ca. 35 cm in canopy diameter but bore ca. 180 leaves of a mean area of 16 cm^2/leaf. All test plants were without fruit. All tests occurred on the 4th day after flies were introduced into the exposure cages. For testing, a female was taken from an exposure cage and allowed to oviposit in a kumquat fruit affixed to a dissecting probe and held within the plant canopy (the exposure plants, but not kumquat fruit, were allowed to remain in the exposure cages throughout the day of testing). Immediately after completion of ovipositor dragging that followed oviposition, the female was transferred gently onto a

leaf at the lower center of the canopy. We adopted this procedure to standardize as much as possible the physiological state of released females. To ensure uniformity of procedure, females were always released onto the same leaf. Using a stopwatch or a portable computer, we monitored the duration of time the female spent on a test plant until it left the plant or 15 min. elapsed (only 7 of 174 wild flies tested and 6 of 192 lab flies tested reached the 15 min. limit). After completion of testing on a citrus or tomato plant, the female was placed into an empty 30 × 30 × 30 cm cage for 30-50 min., after which it was tested on a plant of the opposite type. At the end of testing on the 2nd plant, all females were offered a kumquat fruit. Those that did not attempt oviposition into such fruit were considered as not having been in a physiological state conducive to oviposition site foraging and were excluded from data analysis (= less than 2% of all flies assayed). To minimize experimental error, we alternated fly exposure and test plant treatments in a carefully controlled systematic fashion. Tests of lab- and wild-origin flies were conducted in March and May (1986), respectively.

For comparing treatment mean values, we used the Mann-Whitney U test (Sokol and Rohlf 1981). We chose this non-parametric statistical procedure because we felt our data did not fulfill the required assumptions of an approach involving analysis of variance.

RESULTS

For wild medflies, there were no significant differences among citrus-exposed, tomato-exposed or foliage-naive females in time spent on citrus test plants (Table 1). Likewise, there were no significant differences among wild females of these 3 exposure treatments in time spent on tomato test plants. For each exposure treatment, wild females, spent significantly more time on citrus than on tomato test plants.

TABLE 1. Mean duration (seconds) of residence of medfly females (released individually) on the foliage of a non-fruiting host citrus or tomato test plant after 3 days of exposure to the foliage of one of these plant types, or when foliage-naive.

Exp.	Fly Origin	Exposed For 3 Days To	No. Assayed	Mean (± S.E.) Time on Test Plants*	
				Citrus	Tomato
1	Wild	Citrus	30	206(±45)a_1	57(±15)a_2
		Tomato	29	256(±53)a_1	58(±13)a_2
		Foliage-Naive	28	208(±53)a_1	55(±13)a_2
2	Lab-cultured	Citrus	32	224(±32)a_1	146(±38)ab_2
		Tomato	32	285(±46)a_1	172(±28)a_2
		Foliage-Naive	32	142(±32)b_1	87(±21)b_2

*Values in each column (row) in each experiment followed by the same letter (number) are not significantly different at the 0.01 level.

For lab-cultured medflies, there was no significant difference between citrus-exposed and tomato-exposed females in duration of stay on citrus test plants nor any significant difference between females of these 2 exposure treatments in duration of stay on tomato test plants (Table 1). However, foliage-naive lab-cultured females spent significantly less time on citrus test plants than did either citrus-exposed or tomato-exposed females, and significantly less time on tomato plants than tomato-exposed females. For each exposure treatment, lab-cultured females remained significantly longer on citrus than on tomato test plants.

The fact that during the 3-day plant-exposure period, an average of 496(±130), 404(±148), and 525(±201), eggs per exposure cage was laid in kumquat fruit by citrus-exposed, tomato-exposed and foliage-naive wild medflies and an average of 1659(±536), 1713(±211), and 1717(±251) eggs per exposure cage was laid by citrus-exposed, tomato-exposed and naive lab-cultured females suggests that females probably had considerable contact with the plant foliage surrounding the kumquat fruit in each exposure cage treatment.

DISCUSSION

Our results are consistent with an earlier report (Prokopy et al. 1986) that foliage-naive, gravid wild-origin medfly females spend more time on the foliage of non-fruiting citrus than on the foliage of non-fuiting tomato host plants of comparable size (ca. 1.6 and 3.9 times longer on citrus than tomato in Prokopy et al. (1986) compared with 3.7 times longer on citrus than tomato here). Our findings indicate that a 3-day period of lab-cage experience on the foliage of citrus or tomato plants (each provided with citrus fruit in which many eggs were laid) did not detectably alter the degree of this greater response of wild-origin medflies to the foliage of non-fruiting citrus compared with non-fruiting tomato plants. This stands in marked contrast to effects of a 3-day period of lab-cage exposure of wild-origin medflies to different species of host fruit, wherein the degree to which fruit of a given species are accepted or rejected for oviposition after alighting is significantly influenced by previous egglaying experience with fruit of that or another species (Cooley et al. 1986, Papaj et al. 1987).

Several differences in various plant-foraging and fruit-acceptance behavior traits have been found between medflies of wild origin from the Kula area of Hawaii and medflies from the laboratory culture used here (Prokopy et al. 1984, Papaj et al. 1987, Prokopy et al., unpub. data). In this study, citrus-exposed, tomato-exposed, and naive lab-cultured medflies, just like their wild counterparts, spent more time on citrus test plants than on tomato test plants. Qualitatively, therefore, the response pattern was similar for both types of flies. Quantitatively, however, the response pattern was different. Thus, for all 3 fly exposure treatments, the degree to which wild flies discriminated between citrus and tomato test plants was considerably greater than the degree to which lab-cultured flies discriminated between these test plant types.

There exist 3 aspects of this study which could affect the relevance of our findings to medfly behavior in nature. First, we recognize these experiments might have been confounded by allowing flies the possibility of associating citrus fruit (kumquat) with citrus foliage in one exposure treatment but not allowing them the possibility of associating like fruit and foliage type in the other exposure treatment. If such confounding were to have been important, however, we would have expected a difference between citrus-exposed wild females and foliage-naive wild females in response to citrus plants. This did not occur. Second, flies were exposed to and tested on rather small plants under confined conditions. Possibly fly exposure to larger citrus or tomato plants (or to other sorts of host plants less "offensive" to flies than tomato) under completely natural conditions would in fact give rise to a detectable effect of previous experience with plant foliage on fly residence time on a plant. Conducting experiments of this sort under completely natural conditions is exceptionally challenging, however. Third, the plants on which the flies were tested had no fruit. Possibly some index of fly foraging behavior other than plant residence time (e.g. fruit finding or oviposition rate levels) might be influenced by previous experience with plant foliage.

These caveats notwithstanding, our findings suggest that the biological significance (if any) of previous experience of medfly females with host foliage is probably negligible compared with the biological significance of previous experience with host fruit. This also appears to be the case in the apple maggot fly, *Rhagoletis pomenella* (Walsh) (Papaj and Prokopy, in review).

ACKNOWLEDGMENTS

We thank Jon Nishimoto for assistance and Julia Connelly for typing the manuscript. This study was supported by the Science and Education Administration of the U.S.D.A. under grant 8603158 from the Competitive Research Grants Office, and by Massachusetts Agricultural Experiment Station Project 604.

REFERENCES CITED

Cooley, S.S., R.J. Prokopy, P.T. McDonald, and **T.T.Y. Wong. 1986.** Learning in oviposition site selection by *Ceratitis capitata* flies. Ent. Exp. Appl. 40:47-51.

McDonald, P.T. 1986. Influence of prior egg-laying experience on choice of host fruits for oviposition by the Mediterranean fruit fly, *Ceratitis capitata*. Proc. Hawaii. Entomol. Soc. 27:121-124.

Papaj, D.R., R.J. Prokopy, P.T. McDonald, and **T.T.Y. Wong. 1987.** Differences in learning between wild and laboratory *Ceratitis capitata* flies. Ent. Exp. Appl. 45:65-72.

Prokopy, R.J., P.T. McDonald, and **T.T.Y. Wong. 1984.** Inter-population variation among *Ceratitis capitata* flies in host acceptance pattern. Ent. Exp. Appl. 35:65-69.

Prokopy, R.J., D.R. Papaj, and **T.T.Y. Wong. 1986.** Fruit-foraging behavior of Mediterranean fruit fly females on host and non-host plants. Florida Entomol. 69:651-657.

Sokol, R.R. and **F.J. Rohlf. 1981.** Biometry (2nd ed). W.H. Freeman, New York. 859p.

Tanaka, N., L.F. Steiner, K. Ohinata, and **R. Okamoto. 1969.** Low-cost larval rearing medium for mass-production of Oriental and Mediterranean fruit flies. J. Econ. Ent. 62:967-968.