Foraging Behavior of Laboratory Cultured Mediterranean Fruit Flies on Field-Caged Host Trees

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ABSTRACT

We examined the intra-tree foraging behavior of mature, individually-released, laboratory-cultured (for more than 300 generations) Mediterranean fruit fly females, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), on field-caged potted host trees bearing different densities or qualities of host fruit (kumquats) and compared 27 behavioral traits with those of wild-origin females examined earlier under the same conditions. Responses of the lab-cultured females were generally qualitatively similar to but quantitatively different from responses of the wild females.

The quality of laboratory-cultured tephritid flies is an important concern of all those who employ such insects in experimental studies or in programs involving release of sterile adults for fly management (Chambers 1975, 1977, Boller and Chambers 1977a, b, Meats et al. 1987). Owing to its worldwide economic importance and use against it of the sterile insect release method as a principal means of population suppression, the Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), has received more attention in terms of performance capabilities of laboratory-reared individuals than any other tephritid. For most traits measured, flies cultured in various laboratories for varying numbers of generations have been found to perform differently than wild individuals under comparable conditions (e.g. Leppla et al. 1983, Chambers et al. 1983, Boller and Calkins 1984, McInnis et al. 1985, Robinson et al. 1986, Prokopy et al. 1978, 1984, Papaj et al. 1987).

Recently, we examined the intra-tree foraging behavior of mature individually-released, wild-origin medfly females on field-caged host trees bearing different densities or qualities of host fruit (Prokopy et al. 1987). Here, we report on the intra-tree foraging behavior of mature laboratory-cultured medfly females evaluated under essentially the same experimental conditions as the wild-origin individuals.

MATERIALS AND METHODS

All lab-cultured medflies originated from a colony that had been in continuous culture for more than 300 generations at the USDA, ARS, Tropical Fruit and Vegetable Research Laboratory in Honolulu. Upon eclosion, females were held together with males in cages supplied with food (yeast

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hydrolysate and sucrose) and water (but no fruit) under laboratory conditions (25°C, 80% RH, 13h natural daylength).

All tests were conducted in March 1987, using an identical experimental setup as described for studies conducted in March 1986, by Prokopy et al. (1987). The same non-fruiting citrus trees, plastic-tarpaulin field cages, and test sites were used in 1987 as in 1986 for studies of wild-origin females.

The experimental treatments and procedures were identical with those of Prokopy et al. (1987). Thus, we positioned either 0, 3 or 12 non-infested 20-cm-diameter kumquat fruit on each tree, or 12 kumquat fruit infested with medfly eggs and covered by medflies with marking pheromone deposited during ovipositor dragging on the fruit surface after egglaying. As in Prokopy et al. (1987), pheromone-marked egg-infested kumquats were prepared by exposing each of them during the preceding 18h (3 PM-9 AM) to 12 mature females of laboratory colony origin.

For testing, a single mature female (7-10 days old) was selected at random from a laboratory cage and, following oviposition and marking pheromone deposition on a kumquat fruit attached to a dissecting probe, was transferred gently onto a leaf at the lower center of the tree canopy. Using a stopwatch and tape recorder, we monitored the location and duration of the same fly behaviors using the same protocol as Prokopy et al. (1987). None of the 102 lab-cultured females assayed remained on a tree for the entire duration of the allotted test period (60 min.). Only 6 failed to attempt oviposition into a kumquat fruit offered immediately after testing, and thus were considered as having been in a physiological state non-conducive to oviposition site foraging, and were excluded from data analysis.

Temperature at tree center during tests ranged from 25-32°C. In Prokopy et al. (1987), temperature during tests ranged from 25-36°C but was found to explain only a very minor part of the variation in foraging behavior among flies within treatments. As in Prokopy et al. (1987), we erected a clear-plastic wind barrier around part of each field cage to maintain calm conditions within the cage.

To be consistent with Prokopy et al. (1987), for comparing treatment median values (24 females per treatment), we used a median test (Siegel 1956) at the 0.05 level. Analysis based on median rather than mean values was judged to be the more appropriate approach given the 60-minute limit on duration of the test period. For comparing proportions of treatment females exhibiting a response, we used a G-test at the 0.05 level (Sokal and Rohlf 1981). To facilitate comparisons, we present in Tables 1 and 2 not only the data collected here on the performance of lab-cultured females but also corresponding data presented earlier in Prokopy et al. (1987) on the performance of wild females.

RESULTS

Like wild females, lab-cultured females foraging in trees harboring non-infested fruit tended to spend more total time, more time moving, and

more time resting on a tree as fruit density increased (Table 1). However, in nearly every case, the amount of time spent by lab-cultured females on a tree before leaving was only about half that of wild females. For lab-cultured females, Giving-up-time (GUT) remained virtually constant across trees harboring different fruit density levels, whereas for wild females, GUT decreased with increasing fruit density and was always greater in value than for lab-cultured females (GUT equals time since the last oviposition — either in the fruit from which the fly was initially released or in a fruit encountered while foraging — until departure from the tree). As with wild females, in lab-cultured females there was no consistent pattern among the 3 fruit density levels in number of leaves visited and total time, time moving, or time resting on foliage.

Like wild females, lab-cultured females on trees with 12 fruit spent significantly more total time on fruit, visited significantly more fruit, and attempted egglaying a significantly greater number of times than females on

TABLE 1. Behavior of lab-cultured *C. capitata* females on host trees harboring varying densities or qualities of kumquat fruit (N = 24 flies/treatment; median values are given)[a]. Data in parentheses represent values for wild-origin females taken from Prokopy et al. 1987. All time values are given in seconds.

Parameter	0 fruit	3 non-infested fruit	12 non-infested fruit	12 infested fruit
Entire tree				
Total time	125c(220c)	468b(987ab)	804a(1497a)	645ab(600b)
Time moving	54c(33b)	76bc(112a)	131ab(268a)	145a(197a)
Time resting	83a(126c)	152a(286ab)	162a(422a)	164a(221bc)
GUT	125a(220ab)	115a(167ab)	123a(135b)	182a(240a)
Foliage				
No. leaves visited	3b(3a)	4b(4a)	3b(5a)	8a(4a)
Total time	125a(221a)	148a(223a)	130a(208a)	203a(144a)
Time moving	54a(35a)	54a(42a)	53a(44a)	70a(38a)
Time resting	83a(119a)	64a(157a)	71a(136a)	91a(123a)
Fruit				
No. fruit visited	—	1c (1b)	2b(4a)	3a(5a)
No. oviposition attempts	—	1b(5bc)	3a(10a)	2b(1c)
No. ovipositor draggings	—	1b(2a)	2a(3a)	1b(0b)
Total time[b]	—	229b(663b)	557a(1353a)	339ab(300b)
Total time/fruit visit[c]	—	519a(1061a)	753a(1353a)	486a(359b)
Time moving/fruit visit[c]	—	40b(69a)	80a(31b)	90a(34b)
Time resting/fruit visit[c]	—	55a(148a)	52a(61b)	42a(14c)
Time ovipositing/attempt	—	122a(53a)	80a(47a)	91ab(20b)
Time dragging/bout	—	68a(70a)	64a(66a)	71a(38b)
Time from end of dragging to departure from that fruit	—	13a(56a)	19a(49a)	18a(44a)

[a]Values followed by the same letter within a row are not significantly different at the 0.05 level.
[b]Median values based on all females tested, including those which did not visit any fruit.
[c]Median values based on only those females which visited a fruit.

trees with 3 fruit (Table 1). In each case, however, the values for lab-cultured females were only about half (or less than half) the values for wild females. As with wild females, on a per-fruit-visit basis, in lab-cultured females there were no significant differences between these 2 treatments in total time, time ovipositing or dragging the ovipositor following oviposition, or time since completion of ovipositor dragging until departure from a fruit. For each treatment, values for time ovipositing per attempt were about twice as great for lab-cultured as for wild females, possibly reflecting a greater number of eggs deposited per clutch. Values for time dragging the ovipositor following egglaying were about the same for both types of flies, while for each treatment, values for total time spent on fruit per visit and time from end of ovipositor dragging until departure from a fruit were half or less for lab-cultured compared with wild flies.

Like wild females, a significantly smaller proportion of lab-cultured females discovered fruit at the 3- than at the 12-density level of non-infested fruit (Table 2). However, for wild females a significantly greater proportion of total visits at the 3- than at the 12-density level resulted in an oviposition attempt and ovipositor dragging, whereas corresponding values for lab-cultured females did not decline with increasing fruit density and were in all cases almost identical with values for wild females at the 3-fruit density level. For both these density levels and for both types of flies, the proportion of first visits to a fruit that culminated in an oviposition attempt or ovipositor dragging bout was much greater than that for subsequent visits to the same fruit.

While wild medflies on trees with 12 infested (pheromone-marked) fruit spent significantly less total time, spent significantly less time resting, and exhibited a significantly longer GUT than flies on trees with 12 non-infested fruit, there were no such significant differences manifested by lab-cultured medflies (Table 1). There were no significant differences between these 2 treatments for either type of fly in total time, time moving, or time resting on foliage. Both types of flies on trees with 12 pheromone-marked fruit attempted oviposition and engaged in ovipositor dragging a significantly fewer number of times than flies on trees with 12 non-infested fruit. However, the magnitude of these differences was far greater in wild than in lab-cultured flies. Wild flies in trees with 12 pheromone-marked fruit spent significantly less total time on fruit, less total time and less time resting per fruit visit, less time ovipositing per attempt, and less time dragging the ovipositor per dragging bout than wild flies on trees with 12 non-infested fruit. In contrast, lab-cultured flies exhibited no such differences.

In the case of both lab-cultured and wild medflies, there was no difference in proportion of females discovering 12 non-infested or 12 pheromone-marked fruit (Table 2). Also, for both types of flies, a significantly smaller proportion of first visits as well as total visits to pheromone-marked fruit resulted in an oviposition attempt or ovipositor dragging bout than first visits or total visits to non-infested fruit. Among the latter comparisons, all values for lab-cultured females were greater than for wild females, particularly so for pheromone-marked fruit.

TABLE 2. Behavior of lab-cultured *C. capitata* females on host trees harboring varying densities or qualities of kumquat fruit (% values are given)[a]. Data in parentheses represent values for wild-origin females taken from Prokopy et al. 1987.

Parameter	3 non-infested fruit		12 non-infested fruit		12 infested fruit	
	N	%	N	%	N	%
Flies discovering a fruit	24	54b(67b)	24	88a(96a)	24	79ab(88ab)
Oviposition attempts						
Total visits to fruit resulting in oviposition attempts	24	67a(72a)	45	64a(47b)	100	30b(27c)
First visit to fruit resulting in oviposition attempts	14	93a(91a)	32	84a(76a)	47	51b(32b)
Self-marked fruit receiving oviposition attempt on re-visits	9	22a(25a)	10	30a(17a)	25	8a(18a)
Non-self-marked fruit receiving oviposition attempt on re-visits	1	100a(50a)	3	0a(29a)	28	14a(23a)
Ovipositor dragging						
Total visits to fruit resulting in ovipositor dragging	24	67a(66a)	45	64a(36b)	100	25b(8c)
First visits to fruit resulting in ovipositor dragging	14	93a(82a)	32	78a(55b)	47	45b(10c)
Self-marked fruit receiving ovipositor dragging on re-visit	9	22ab(25a)	10	30a(10a)	25	4b(9a)
Non-self-marked fruit receiving ovipositor dragging on re-visit	1	100a(50a)	3	0a(18a)	28	11a(6a)

[a]See Table 1.

DISCUSSION

In previous experiments involving comparison of fruit-acceptance behavior of wild medfly females with medfly females that originated from the same laboratory colony tested here, it was found that (a) lab-cultured females produced an equivalent quality and quantity of host-marking pheromone but were unresponsive to such pheromone (Prokopy et al. 1978), (b) lab-cultured females exhibited greater propensity to attempt oviposition in large fruit (Prokopy et al. 1984), and (c) lab-cultured females were less capable of learning and remembering host fruit characters (Papaj et al. 1987).

In this study, the qualitative nature of the response of lab-cultured females to 3 levels of host fruit density on potted host trees and 2 sorts of

host fruit quality was, in most respects, similar to that of wild females. In other words, for most parameters measured, the order in which treatment values ranked for a given parameter was usually the same for both types of flies. To illustrate, of the 43 treatment value comparisons in Tables 1 and 2 that involved a significant difference in response by wild flies, the order in which the values ranked within a comparison was the same for both types of flies in 35 of the comparisons (= 81%).

On the other hand, the degree of discrimination between varying densities and qualities of fruit exhibited by the lab-cultured flies was often considerably less than that exhibited by wild flies, indicating quantitative differences in various intra-tree foraging behavior traits. To illustrate, of the 35 aforementioned comparisons in which the order of values ranked the same for wild and lab-cultured flies, the mean difference between values was 302% in the case of wild flies but only 109% in the case of lab-cultured flies. The magnitude of value differences between fly types was especially great in regard to non-infested versus infested fruit.

Precisely why lab-cultured females were unresponsive to host marking pheromone in Prokopy et al. (1978) but exhibited some degree of responsiveness in this study (albeit at a low level compared with wild flies) is unknown. At least 4 factors could be involved: (a) the amount of pheromone deposited on marked test fruit was much greater in this study; (b) the physiological state of flies assayed in this study could have rendered them more sensitive to pheromone; (c) conduct of the assays on host trees in field cages in this study could have allowed flies to discriminate between marked and unmarked fruit to a greater degree than in the lab-cage assays of Prokopy et al. (1978), as is true for *Rhagoletis pomonella* (Walsh) flies (Averill and Prokopy 1987); and (d) other infested-fruit-associated, oviposition-deterring cues besides host marking pheromone (such as cues from eggs — Papaj et al., unpub. data) almost surely played a role here, whereas in Prokopy et al. (1978) they were absent.

In conclusion, this study revealed that responses of lab-cultured females (from a colony maintained for more than 300 generations in Hawaii) to varying densities and qualities of host fruit on potted trees were generally qualitatively similar to, but generally quantitatively different from, responses of wild-origin females. Because both types of flies were maintained and tested under virtually identical experimental conditions, we conclude that these quantitative differences may have resulted from artificial selection during the more than 300 generations in culture.

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