Effect of Food Deprivation on the Foraging Behavior of *Rhagoletis pomonella* (Diptera: Tephritidae) Females for Food and Host Hawthorn Fruit[1]

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ABSTRACT The behavior of released mature female apple maggot flies, *Rhagoletis pomonella* (Walsh), deprived of all food for 18-24 h was compared with that of females that had continuous access to food. Assays were carried out on individual field-caged host trees that contained *Crataegus mollis* host hawthorn fruit and/or vials of sucrose and enzymatic yeast hydrolysate as food, and in open-field patches of host trees that contained hawthorn fruit and/or food. Two hypotheses were evaluated: (1) food-deprived flies would be in a physiological state that would compromise their ability to find food and oviposition sites, and (2) food deprivation would generate a "sense of malaise" or impending death leading to "dumping" eggs in unusually large numbers at the earliest opportunity. Except for a greater proportion of food-deprived than non-deprived females finding or being observed at food, the behavior of food-deprived and non-deprived females did not differ significantly. Neither of the hypotheses was supported by the data.

KEY WORDS *Rhagoletis pomonella*, foraging, physiological state, shortage of food.

An insect foraging for an essential resource may adjust its searching activities and resource use pattern in response to any number or combination of variables that occur in the environment or the insect itself (Miller and Stricker 1984). In recent years, a growing amount of information on the foraging behavior of tephritid fruit flies has been obtained (Prokopy and Roitberg 1989). There is little information for tephritids, however, on how the physiological state of females (particularly in regard to feeding status) affects foraging and acceptance of fruit for oviposition.

For *Rhagoletis pomonella* (Walsh), the principal adult sources of food in nature are insect honeydew, bird feces, and unidentified substances (possibly microorganisms), all of which are found predominantly on foliage (Neilson 1971, Hendrichs and Prokopy 1990). Frequent or heavy rainfall could wash away adult food, thus creating a temporary shortage. Laboratory tests have shown that nearly half of *R. pomonella* adults perish if deprived of food for two consecutive days but suffer no above-normal mortality after one day of food deprivation (Prokopy et al., unpublished data).

Here, two hypotheses were evaluated concerning the effects of food shortage on *R. pomonella* adults. Deprivation of food for 18-24 h would (1) compromise fly ability to find food and oviposition sites, and (2) generate a "sense of malaise" or impending death that would result in laying or "dumping" eggs in unusually large numbers at the earliest opportunity.

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Materials and Methods

All assayed flies originated from puparia formed in 1988 by larvae that infested apples collected from unsprayed trees near Amherst, MA. The puparia were kept at 3°C for ca. 7 months, after which they were incubated at 25°C until eclosion. Adults of both sexes were subsequently maintained together in laboratory cages with food (sucrose and enzymatic yeast hydrolysate, 4:1) and water at 25°C, 60% RH, and a photophase of 18h. Females used in all tests were 14-19 days old (mature), presumably mated, and without previous exposure to fruit or other oviposition substrates. About 18-24h prior to testing, females were divided into two groups. One group (non-deprived) had continuous free access to sucrose, enzymatic yeast hydrolysate and water. The other group (food-deprived) had access only to water.

Fruit used in all tests were hawthorns (*Crataegus mollis*), the native larval host of *R. pomonella*. Because fresh hawthorns were not available during the testing period (June to early August), hawthorns picked the previous year and kept in cold storage were used. All fruit were rinsed before use.

Field cage assays evaluated food and fruit finding and acceptance responses of non-deprived and food-deprived females. A potted non-fruiting hawthorn tree ca. 1m in canopy diameter was enclosed in each of two cylindrical nylon screen field cages (3m tall × 3m diam). A blue plastic tarpaulin above each cage protected the tree from direct sunlight and rainfall. Each tree was rinsed thoroughly before testing to remove existing food. In tests, each tree received either 15 hawthorns and 15 vials of food, 15 hawthorns and no vials of food, or no hawthorns and 15 vials of food. The hawthorns and food vials were suspended by wire from the branches and distributed evenly throughout the canopy. The food vials were 2-DRAM glass vials that were filled with an aqueous mixture of sucrose and enzymatic yeast hydrolysate (4:1) and contained a cotton wick extending 1 cm above the vial. A small moist triangle of paper was used to transfer each test female from its holding cage to the upper surface of a designated release leaf near the lower center of the tree. *R. pomonella* females foraging within host trees typically engage in a series of short upward flights while they explore the canopy. Each female was allowed a maximum of 10 min on the release leaf. Those staying longer were not included in the data. A female leaving the release leaf within 10 min was then allowed 10 min to forage within the canopy. Those which alighted on a fruit or food vial were allowed to remain there up to 5 min, during which we observed whether the female bored with her ovipositor into the fruit or extended her proboscis to feed. A trial consisted of tracking a single female and was terminated after the first visit to a fruit or a food vial, or after the female left the tree canopy or remained 10 min without visiting a fruit or food vial. All trials were conducted between 0900 and 1500h. Treatments were alternated in a systematic fashion to minimize effects of variation in temperature, humidity, and time of day. Forty females were released per treatment.

Open field assays evaluated food and fruit foraging behavior of nondeprived and food-deprived females in four small patches of hawthorn trees in a large open grass field (ca. 240 × 240m). The methodology was similar to that of Averill and Prokopy (1992). Each of the patches consisted of five potted non-fruiting

hawthorn trees: one central tree and four equidistant surrounding trees, whose canopies were ca. 1m from the canopy of the central tree. Canopies of all trees were ca. 1m diam. The five-tree patches were located in a square, with patches ca. 80m apart. All trees were rinsed thoroughly before use. The minimum distance between any patch and the nearest foliage (other than grass) was ca. 80m. One day before testing, and before dividing flies into non-deprived and food-deprived groups, each female was allowed to fly ca. 50 cm in the laboratory to insure it was flight worthy (i.e., wings were not injured). It was then marked on the dorsum of the thorax with colored liquid paper (Opp and Prokopy 1987). This permitted coding of the four groups that corresponded to the four patches of trees that comprised a replicate.

Between 0800 and 0830h on each test day, 20 females were gently transferred individually from a holding cage (using a triangle of moist paper) onto interior foliage of the center tree of each of the four patches. The center tree contained no fruit or vials of food. Each of the four surrounding trees contained the same treatment: 10 hawthorn fruit, or 10 hawthorn fruit plus five vials of food. The fruit and food vials were distributed evenly among the tree canopy. If food was not present on the center tree of a patch, flies deprived of food for 18-24h would not have immediate access to food. The ability of a fly to move from the center tree and forage for food and fruit on surrounding trees while still in a food-deprived state could therefore be assessed. Hourly from 0900 to 1300h, each tree in each patch was examined thoroughly for the presence of flies and the type of occupied structure. At 1400h, all hawthorns were removed and brought to the laboratory, where numbers of eggs were counted. Sticky red spheres were hung in each tree at the end of a trial to capture remaining flies. There were four replicates per treatment and at least two days between the end of one replicate and the start of the next.

Results

Field Cage Assays. There were no significant differences in proportions of food-deprived (98-100%) versus non-deprived (90-95%) females leaving the release leaf on the caged trees, irrespective of fruit/food presence or absence (Table 1). There were no significant differences in proportions of food-deprived (30-45%) versus non-deprived (40-48%) females that alighted on a fruit, with or without food vials present in the trees. Nor were there any significant differences in proportions of alighting food-deprived and non-deprived females that bored into fruit (67-75 versus 69-84%, respectively). Non-deprived females that found a hawthorn on trees having both fruit and food took significantly longer to do so than food-deprived females or than either type of female on trees with fruit but no food. Significantly greater proportions of food-deprived (35-43%) than non-deprived (8-10%) females alighted on a food vial. All such alighting females fed on the cotton wick of the vial after arrival. Food-deprived females that found a food vial on trees having both fruit and food did so significantly faster than non-deprived females or than either type of female on trees with food but no fruit.

Table 1. Behavior of non-deprived and food-deprived (for 18-24h) *R. pomonella* females released individually onto a field-caged potted tree on which 15 hawthorn fruit and/or 15 vials of food were hung. No. females released per treatment = 40.*

Fruit	Food	Female Status	% females that left release leaf	% females that found a fruit	% females that found a food vial	% finders that bored into a fruit	% finders that fed on a food vial	% females that left tree without finding a fruit or food vial
Yes	Yes	Non-Dep	95 a	40 a (230"a)	10 b (209"a)	69 a	100 a	13 b
		Food-dep	98 a	30 a (84" b)	35 a (23" b)	75 a	100 a	13 b
Yes	No	Non-Dep	90 a	48 a (146" b)	–	84 a	–	13 b
		Food-dep	98 a	45 a (126" b)	–	67 a	–	25 ab
No	Yes	Non-dep	95 a	–	8 b (168" a)	–	100 a	45 a
		Food-dep	100 a	–	43 a (141"a)	–	100 a	20 b

* Values in the same column followed by the same letter are not significantly different according to G tests involving paired comparisons at the 0.05 level. Values in ( ) indicate mean time in search from moment a female left release leaf until it alighted on a fruit or food vial; values in the same column followed by the same letter are not significantly different according to Mann Whitney U tests at the 0.05 level.

Open Field Assays. During the first census period of fly location (0900 h), there were no significant differences in overall mean proportions of released food-deprived (49-51%) versus released non-deprived (45-53%) females observed in tree patches, with or without food (Table 2). For both types of females, however, there was a slight numerical tendency toward greater presence in patches with food. There were no significant differences among food-deprived versus non-deprived females in proportions observed on the central tree on which females were released (35-44 vs. 40-44%) or in proportions observed on leaves and branches (13-19 vs. 17-22%) or fruit (29-43 vs. 34-36%) on the four trees surrounding the central tree in each patch. A significantly greater proportion of food-deprived than non-deprived females (17 vs. 7%) was observed on food vials.

Over all five census periods of fly location (0900-1300h) in the open field assay, there were no significant differences in overall mean proportions of released food-deprived (33-38%) versus released non-deprived (34-39%) females observed in tree patches, with or without food (Table 3). For both types of females, there was a slight numerical tendency toward greater presence in patches with food. There were no significant differences among food-deprived versus non-deprived females in proportions observed on the central tree on which females were released (14-20 vs. 17-29%) or in proportions observed on leaves and branches (29-30 vs. 24-34%) or fruit (43-51 vs. 38-50%) on the four trees surrounding the central tree in each patch.

The number of eggs laid in hawthorns over the ca. 6h test period by food-deprived females was virtually identical in patches with food versus patches without food (means of 2.48 vs. 2.45 eggs per released female). This was no greater than the number laid by non-deprived females in patches without food (2.56 eggs per released female). Non-deprived females laid ca. 30% more eggs (mean of 3.34 per released female) in patches with food than without food, but the difference was not significant. The probability is very high that nearly all eggs deposited in each patch originated from females released in that patch. Of the total of 591 sightings of females over all census periods over all patch types, 574 (97%) involved females that had been released in the patch in which they were sighted (indicated by color code on the dorsum). Of the 17 sightings not in this category, eight involved non-released wild females that evidently had immigrated into a patch from some distance away. The other nine (six non-deprived, three food-deprived) involved females that had been released in a different patch. Among these nine females, two-thirds of each fly type originated from patches without food and two-thirds of each fly type was found in patches with food.

Discussion

Several lines of evidence from this study do not support the first hypothesis that deprivation of food for 18-24h would compromise the ability of *R. pomonella* adults to find food and fruit resources. First, in field cage assays, the proportion of food-deprived females that left the leaf on which they were released and the proportion that found a hawthorn fruit or food vial was no less than the proportion of non-deprived females that did so. In fact, significantly more food-deprived than non-deprived females found a food vial. Second, in field cage

Table 2. Observations at 0900h of non-deprived and food-deprived (for 18-24h) *R. pomonella* females released on a central potted hawthorn tree (without fruit or food) surrounded at 1 m distance by 4 other potted hawthorn trees ((each with 10 hawthorn fruit and each with or without 5 vials of food) in a large open field. No. females released per treatment per replicate = 20. No. replicates per treatment = 4.*

Fruit	Food	Female Status	Mean proportion of females per replicate observed in tree patch at 0900h census	% of all observed females on			
				central release tree	Surrounding 4 trees		
					leaves & branches	fruit	food vials
Yes	Yes	Non-Dep	53 a	40 a	17 a	36 a	7 a
		Food-dep	51 a	35 a	19 a	29 a	17 b
Yes	No	Non-Dep	45 a	44 a	22 a	34 a	–
		Food-dep	49 a	44 a	13 a	43 a	–

* Values in the same column followed by the same letter are not significantly different at the 0.05 level according to ANOVA and Duncan's multiple range test. For the ANOVA, values for the actual numbers of flies (not proportions) were used.

Table 3. Observations over 5 hourly census periods (0900-1300h) of non-deprived and food-deprived (for 18-24h) *R. pomonella* females released on a central potted hawthorn tree (without fruit or food) surrounded at 1 m distance by 4 other potted hawthorn trees ((each with 10 hawthorn fruit and each with or without 5 vials of food) in a large open field. No. females released per treatment per replicate = 20. No. replicates per treatment = 4.*

Fruit	Food	Female Status	Mean proportion of females per replicate observed in tree patch over all 5 census periods†	% of all observed females on				Mean no. eggs laid in fruit per female released.
				central release tree	Surrounding 4 trees			
					leaves & branches	fruit	food vials	
Yes	Yes	Non-Dep	39 a	17 a	24 a	50 a	10 a	3.34 a
		Food-dep	38 a	14 a	30 a	43 a	13 a	2.48 a
Yes	No	Non-Dep	34 a	29 a	34 a	38 a	–	2.56 a
		Food-dep	33 a	20 a	29 a	51 a	–	2.45 a

* See Footnote of Table 2.

† Proportions were determined as follows: [maximum possible no. females observable during each census period (20) × no. census periods (5) × no. replicates (4)] - [actual no. females observed during each census period × no. census periods × no. replicates].

assays, food-deprived females tended to find both hawthorn fruit and food vials more quickly than non-deprived females. Third, in open field assays, food-deprived females were just as prone to move away from the central release tree without food or fruit resources and were just as likely to be found on food vials or hawthorn fruit on surrounding trees in the patch as were non-deprived females.

Likewise, the data do not support the second hypothesis that deprivation of food for 18-24h would generate a "sense of malaise" or impending death, causing *R. pomonella* flies to "dump" or lay abnormally large numbers of eggs. Both field cage and open field assays failed to demonstrate that food-deprived females exhibit greater propensity than non-deprived females to oviposit in hawthorn fruit.

Although a food deprivation period of 18-24h was of sufficient length to affect significantly the arrival of *R. pomonella* on food vials, one could argue that a longer period might be necessary before effects on fruit foraging and oviposition behavior become apparent. If this were true, then ovipositional effects must manifest themselves quite suddenly rather than gradually. A significant proportion of *R. pomonella* flies perish when deprived of food for 24-36h (Prokopy et al, unpublished data).

Averill and Prokopy (1992) studied the behavior of non-deprived *R. pomonella* females in patches of hawthorn trees very similar to those constructed here. They found that after several hours, a significantly greater proportion of females released in patches that contained *C. mollis* hawthorn fruit plus vials of food remained in the patch (and were observed on fruit) than was the case among females released in patches that contained *C. mollis* fruit without food vials. The fruit in patches with food received 39% more eggs than fruit in patches without food. Similar trends (although not significant) occurred in this study. Non-deprived females laid 30% more eggs in patches with food than in patches without food. The only substantial difference between the two studies involved the nature of the central tree in each five-tree patch. In Averill and Prokopy (1992), the central tree contained the same amount of food and/or fruit as the four surrounding trees. Here, the central tree contained no food or fruit, for reasons given earlier. In contrast to the behavior of non-deprived females in Averill and Prokopy (1992) and in this study, food-deprived females in this study exhibited no tendency to be present more often on *C. mollis* hawthorn fruit or to lay more eggs in fruit in tree patches that contained both fruit and food compared with patches that contained no food.

Effects of a shortage of oviposition sites on the foraging and ovipositional behavior of several different insects have been examined in some depth (Bell 1990, Courtney and Kibota 1990). To the best of our knowledge, this is the first reported study of effects of food shortage on the oviposition-site foraging and egglaying behavior of an insect. The lack of a significant observed influence of 18-24 h food shortage on fruit finding and oviposition rate in *R. pomonella* could be interpreted as lack of strong selection pressure molding the physiology and behavior of *R. pomonella* flies toward greater ovipositional propensity when under stress from failure to find food. Even though the presumption has been made here that periodic food shortage could occur in nature as a consequence of heavy rainfall washing away food, food shortage may occur too infrequently in nature to constitute selection pressure sufficiently strong to alter fruit foraging behavior. Alternatively, other factors may continually override shortage of food in shaping fly fruit foraging behavior.

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References Cited

Averill, A. L. and R. J. Prokopy. 1992. Foraging of *Rhagoletis pomonella* for interactive food and fruit resources. Entomol. Exp. Appl. (in press).

Bell, W. J. 1990. Searching behavior patterns in insects. Ann. Rev. Entomol. 35: 447-467.

Courtney, S. P. and T. T. Kibota. 1990. Mother doesn't know best: selection of hosts by ovipositing insects, pp. 161-188. *In:* E.A. Bernays (ed.), Insect/Plant Interactions, CRC Press, Vol. 2. Boca Raton, FL.

Hendrichs, J. and R. J. Prokopy. 1990. Where do apple maggot flies find food in nature? Mass. Fruit Notes 55(3): 1-3.

Miller, J. R. and R. L. Strickler. 1984. Finding and accepting host plants, pp. 128-157. *In*: W. J. Bell and R. T. Cardé, (eds.), Chemical Ecology of Insects. Sinauer Press, Sunderland, Mass.

Neilson, W. T. A. 1971. Dispersal studies of a natural population of apple maggots. J. Econ. Entomol. 64: 648-653.

Opp, S.B. and R. J. Prokopy. 1987. Seasonal changes in resightings of marked, wild *Rhagoletis pomonella* flies in nature. Fla. Entomol. 70: 449-457.

Prokopy, R. J. and B. D. Roitberg. 1989. Fruit fly foraging behavior, pp. 293-306. *In:* A.S. Robinson and G. Hooper (eds.), Fruit Flies, Their Biology, Natural Enemies and Control. Elsevier, Amsterdam.