

## **Prior Experience Influences the Fruit Residence of Male Apple Maggot Flies, *Rhagoletis pomonella***

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*Male apple maggot flies spend considerable time residing on individual host fruit as territories on which they force-copulate arriving females in search of oviposition sites. Here, we present evidence from investigations in nature and the laboratory that shows the propensity of males to reside on a hawthorn or apple fruit as a territory is significantly modifiable through prior experience with fruit and, hence, involves learning. Previous studies revealed that after a female apple maggot fly, *Rhagoletis pomonella*, arrived on a host hawthorn or apple fruit, its propensity to accept or reject that fruit for egg-laying was similarly modifiable through prior fruit-exposure experience and also involved learning. We discuss how host fruit learning in males and females, in concert with genetic-based differences in host fruit residence and acceptance behavior between populations of flies originating from hawthorn and apple, could give rise to a reduction in gene flow between populations of flies on these two host types.*

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**KEY WORDS:** learning; experience; male territoriality; host race formation; *Rhagoletis*.

### **INTRODUCTION**

Recent books (e.g., Mackintosh, 1983; Marler and Terrace, 1984; Staddon, 1984) and reviews (Papaj and Rausher, 1983; Domjan and Galef, 1983; Shettleworth, 1984; Kamil and Roitblat, 1985) provide abundant evidence of the importance of learning (considered here to be a change in behavior with experience) in the resource foraging behavior of a wide variety of invertebrate and vertebrate animals. In herbivorous insects, adult or nymphal exposure to a par-

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ticular food type has been found to affect subsequent choice of plants for feeding (Phillips, 1977; Cassidy, 1978; Rowell-Rahier, 1984; Blaney and Simmonds, 1985; Lewis, 1986), choice of where to forage for food (Bernays and Wrubel, 1985), and propensity to respond to host-plant odor (Visser and Thiery, 1986). Similarly, female exposure to a particular plant type for egg-laying has been shown to influence female propensity to accept that or other plant types for oviposition in butterflies (Papaj and Rausher, 1983; Stanton, 1984; Papaj, 1986; Traynier, 1986), tortoise beetles (Rausher, 1983), and *Rhagoletis* (Prokopy *et al.*, 1982, 1986; Papaj and Prokopy, 1986) and *Ceratitis* (Cooley *et al.*, 1986) fruit flies.

Notably lacking among studies on herbivorous insects is attention to the possible role of learning in the foraging behavior of males for potential mates. Indeed, except for investigations of learning in mate-finding by *Itopectis* parasitic wasps (Robacker *et al.*, 1976) and of conditioned courtship behavior in *Drosophila* males (e.g., Tompkins *et al.*, 1983), this aspect of learning in resource foraging behavior has been largely ignored for insects in general.

Male insects usually concentrate their mate-foraging efforts at one of four possible locales: zones where females emerge, areas in which females forage for food, places at which females oviposit, or distinctive topographical features serving as rendezvous sites (Parker, 1978; Thornhill and Alcock, 1983). In some species, males actively compete with one another for possession of territory at such locales. As discussed in a recent review by Kaufmann (1983), the concept of territory, although fraught with ambiguity, consists of both spatial and temporal components in which an individual or group maintains priority of access to some critical resource through social interactions with other individuals or groups. Such territories may be unstable, however, as has been demonstrated by Courtney and Anderson (1986) for cases in which the density of males at an encounter site and the cost of male movement are low.

In the apple maggot fly, *Rhagoletis pomonella* (Walsh), mating is initiated exclusively on host plants where egg-laying by females occurs (Prokopy *et al.*, 1971). Such plants may include the original native host, hawthorn (*Crataegus*), or introduced plants such as apple (*Malus*), which *R. pomonella* acquired as a host some time within the past two centuries (Bush, 1966). Early in the fruiting season, when most *R. pomonella* females are virgin, sexual encounters occur largely on host-plant foliage (Smith and Prokopy, 1980). There, the males court prospective mates from a frontal position. With the onset of oviposition, however, sexual encounters cease to occur on foliage and take place almost exclusively at the site of egg-laying, the host fruit (Prokopy *et al.*, 1971; Smith and Prokopy, 1980). During the time of peak mating, males in one study (Prokopy and Bush, 1973) were found to spend 89% of their time residing on and patrolling fruit, although the average time spent per fruit visit may vary from only a few minutes to over a half-hour. When a male alights on a fruit already occupied

by another male, it usually will elicit the attention of the resident male. Some form of agonistic behavior is likely to ensue, often resulting in one of the two males leaving the fruit (Prokopy and Bush, 1973). When a female arrives on a fruit occupied by a male or on a nearby fruit within the visual range of a male, the male is alerted by the movements made by the female during preoviposition, egg-deposition, or postoviposition behavior. In most cases, the male approaches the female from the rear and attempts forced copulation with the female (Prokopy and Bush, 1973; Smith and Prokopy, 1980). Such forced copulation is highly advantageous to the male, because the great majority of eggs laid during the next week or two is fertilized with sperm of the last male achieving copulation (Opp and Prokopy, unpublished data). Therefore, in our opinion, an individual fruit occupied and defended by a male *R. pomonella* for even a few minutes constitutes a true territory in that it provides a male priority of access to mating opportunities with arriving females.

Previous studies have revealed that after a female *R. pomonella* fly has arrived on a host hawthorn or apple fruit, its propensity to accept (bore into) or reject that fruit prior to egg deposition is modifiable according to the degree of prior ovipositional experience with that or another fruit type (Prokopy *et al.*, 1982, 1986; Papaj and Prokopy, 1986). Here, we asked whether the propensity of a male *R. pomonella* to reside on a hawthorn or apple fruit as a territory (measured as duration of fruit residence) was similarly modifiable according to the nature of prior experience with fruit and whether fruit residence might influence mating success.

## MATERIALS AND METHODS

For the field tests, we examined responses of wild males found on unsprayed *Crataegus mollis* hawthorn trees or on sympatric (1.6 km away) Red Delicious apple trees in Amherst, Massachusetts. On each tree type, tests were conducted in 1986 midway between the time of the first appearance of the flies on the trees (mid-June, apples; mid-July, hawthorns) and their disappearance (mid-September, apples; mid-October, hawthorns). We believe that this allowed the males (which apparently live 3–5 weeks in nature) to have gained appreciable fruit exposure and mating experience. Test males were selected at random by pointing blindly to a spot in the tree canopy and surveying carefully the foliage and fruit in the vicinity of the spot until a noncopulating male was sighted. Moving slowly and using a leaf placed gently beneath the foretarsi of the male, we transferred the male to a water-rinsed, noninfested *C. mollis* or Red Delicious fruit at the end of a hand-held probe. All *C. mollis* fruit were circa 18 mm in diameter, picked in 1985, and held in cold storage until use. All Red Delicious apples were circa 48 mm in diameter and picked in 1986. Each male was allowed to spend up to 5 min on the initial fruit offered. Following that or following

earlier departure from the fruit, the male was allowed to rest on a leaf for circa 1 min before it was offered a fruit of the second type. As long as our movements were slow, the males seemed unaffected by this transfer procedure. Each test male was removed permanently from the tree following assay. The order in which fruit were presented was reversed for the next male tested.

For the laboratory tests, all flies originated from puparia formed by larvae that infested mixed varieties of apple fruit collected from unsprayed trees in Amherst. Flies were maintained from eclosion onward in  $20 \times 20 \times 20$ -cm aluminum screen/Plexiglas cages at either five males per cage (Experiment 1) or five males plus five females per cage (Experiment 2). Each cage was supplied with food (sucrose and enzymatic yeast hydrolysate) and water and was kept at  $25^{\circ}\text{C}$  and 70% relative humidity (RH) under an 18-h photoperiod. All cages were devoid of fruit from Day 1 to Day 12. In Experiment 1, from Day 13 (by which time most individuals of both sexes are reproductively mature) until Day 16, clean uninfested fruit were suspended by wire from the ceiling of cages as follows: one-third of the cages each received five *C. mollis* fruit (circa 18 mm in diameter), one-third each received one Red Delicious apple (circa 65 mm in diameter), and one-third received no fruit (these males were termed naive). The same three-treatment protocol was followed for Experiment 2. In both experiments, on Day 16, males were removed individually from the treatment cages and transferred in small plastic cups to an empty cage. There, each male was allowed to rest 5 min before it was offered (allowed to walk or fly onto) a clean, uninfested *C. mollis* or Red Delicious apple fruit. The male was allowed to remain on the fruit until it departed or until 30 min had elapsed. Following this, the male was allowed to rest 5 min and was then offered a fruit of the opposite type. The order in which fruit were presented was reversed for the next male tested. In Experiment 2, from Day 18 to Day 21, all males that had been exposed to *C. mollis* fruit from Day 13 to Day 16 were exposed to Red Delicious apples, while all males that had been exposed to Red Delicious apples from Day 13 to Day 16 were exposed to *C. mollis* fruit. Naive males remained naive. The females in all three treatments were replaced with new, 18-day-old naive females. Males were tested on Day 21 in the same manner as on Day 16.

To affirm the contribution of male residence on fruit to mating success, we conducted tests under seminatural conditions in a  $3 \times 3 \times 3$ -m Saran screen field cage. In this cage, we placed a single, potted, nonfruiting hawthorn tree (*Crataegus* sp.) having a canopy width and height of 1.3 m each. On the day of field-cage testing, 30 *C. mollis* fruit, as described previously, were suspended by wire from the branches of the tree in 10 clusters of 3 fruit each, evenly spaced throughout the tree. All flies originated as larvae from unsprayed trees in Amherst and were maintained in the laboratory as described previously, with the exception that males and females were held in separate cages from eclosion. On Day 12, females were prepared for testing by division into three groups: unmated (virgin) females, females allowed one mating, and females

allowed unlimited (multiple) matings over the course of 2 days. Previous studies had shown that mating status significantly affected female propensity to oviposit, with greater numbers of matings resulting in increased oviposition (Opp and Prokopy, 1986). To prepare males for testing on Day 12, five *C. mollis* fruit were hung in the aluminum screen/Plexiglas cages housing virgin males to allow males to become experienced with fruit. On Day 15, 10 to 30 virgin, fruit-experienced males were released onto the hawthorn tree in the field cage and were allowed to acclimate for 30 min before testing. Each test commenced upon release of a single female fly of known mating status onto a lower leaf of the tree. The female was visually followed and was allowed to remain on the tree until she mated or until 30 min had elapsed. Locations of the initiation of all copulations were recorded.

## RESULTS

In the field experiment, males from hawthorn trees resided significantly longer on hawthorn than on apple fruit, whereas males from apple trees resided significantly longer on apple than on hawthorn fruit (Table I). Males from each tree type resided for about the same length of time on hawthorn fruit (no significant difference), but males from hawthorn trees resided for far less time on apples than did males from apple trees.

In the laboratory test where males were caged without females (Experiment 1), males exposed to hawthorn fruit and naive males resided significantly longer on hawthorn fruit than on apples (Table II). On the other hand, males exposed to apples resided about the same length of time (no significant difference) on each fruit type. There were no significant differences among males of the three exposure treatments in response to hawthorn fruit, but males exposed to hawthorn fruit resided for far less time on apples than males exposed to apples, with naive males being intermediate.

In the laboratory experiment where males were caged with females (Exper-

**Table I.** Propensity of *R. pomonella* Males on *Crataegus mollis* Hawthorn or Red Delicious Apple Trees in Nature to Establish Residence on *C. mollis* Hawthorn or Red Delicious Apple Fruit.

Males on trees of	N	Median duration (s) of male residence on fruit of <sup>a</sup>	
		Hawthorn	Apple
Hawthorn	41	62a <sub>1</sub>	16b <sub>2</sub>
Apple	41	85b <sub>1</sub>	276a <sub>1</sub>

<sup>a</sup> Values in each row (column) followed by the same letter (number) are not significantly different at the 0.01 level according to a Mann-Whitney *U* test.

**Table II.** Propensity of *R. pomonella* Males in Laboratory Cages to Establish Residence on *Crataegus mollis* Hawthorn or Red Delicious Apple Fruit After Having Been Caged Alone (Experiment 1) or with Females (Experiment 2) and Exposed to Fruit of One or the Other Type for 3 days or When Naive (No Previous Exposure to Any Fruit)<sup>a</sup>

Expt.	Males exposed to fruit of	N	Median duration (s) of male residence on fruit of <sup>b</sup>	
			Hawthorn	Apple
1	Hawthorn	58	425 <sub>a1</sub>	17 <sub>b2</sub>
	Apple	59	114 <sub>a1</sub>	121 <sub>a1</sub>
	No fruit	58	238 <sub>a1</sub>	38 <sub>b1,2</sub>
2a	Hawthorn	53	490 <sub>a1,2</sub>	8 <sub>b2</sub>
	Apple	51	155 <sub>a2</sub>	110 <sub>a1</sub>
	No fruit	50	428 <sub>a1</sub>	18 <sub>b1,2</sub>
2b	Was apple, now hawthorn	47	815 <sub>a1</sub>	8 <sub>b3</sub>
	Was hawthorn, now apple	48	330 <sub>a1</sub>	61 <sub>b1</sub>
	Remained no fruit	48	500 <sub>a1</sub>	36 <sub>b2</sub>

<sup>a</sup>Experiment 2a, males exposed to fruit of designated type on Days 13–16; Experiment 2b, males exposed to fruit of opposite type on Days 18–21.

<sup>b</sup>Values in each experiment in each row (column) followed by the same letter (number) are not significantly different at the 0.01 level according to a Mann-Whitney *U* test.

iment 2a), the pattern of results was essentially the same as in Experiment 1 (Table II). In Experiment 2b (Table II), males that had been exposed to hawthorn fruit in Experiment 2a and had spent a significantly shorter time on apples than males that had been exposed to apples in Experiment 1a now, after having been subsequently exposed to apples for 3 days, spent a significantly longer time on apples than males originally exposed to apples and subsequently exposed to hawthorn fruit. This result demonstrates the changeability of male response to fruit type according to fruit-exposure regime.

In the field-cage experiment, the great majority (97%) of all matings was initiated on fruit, regardless of female mating status (Table III). Only two mat-

**Table III.** Site of Initiation of Mating by *R. pomonella* on a Field-Caged Hawthorn Tree in Which 30 *Crataegus mollis* Fruit Were Hung.

Female mating status	N	Site of initiation of mating	
		Leaf	Fruit
Virgin	52	1	17
Mated once	51	1	25
Multiply mated	53	0	14
Total		2	56
Percentage of matings		3.4	96.6

ings were initiated by males on leaves, including a mating with a virgin female and a mating with a female mated once.

## DISCUSSION

The combined results of the field assays, in which males spent a significantly longer time on fruit characteristic of the tree on which they were found than on unfamiliar fruit, is suggestive, but does not prove, that male behavior on fruit is modified by prior experience. Additional data presented elsewhere (Prokopy *et al.*, 1988) reveal a significant larval-host-origin effect that undoubtedly contributed in part to the difference between males on hawthorn and males on apple trees in residence time on hawthorn and apple fruit. The magnitude of the larval-origin effect is considerably less than the magnitude of the tree-of-male-residence effect found in this study, however. The combined results of the laboratory assays, in which males exhibited a significant change in residence time on hawthorn or apple fruit according to prior fruit experience, do constitute convincing evidence that males are able to learn characters of fruit on which they establish territories. Whether the fruit characters learned by males are both chemical and physical, as is the case for *R. pomonella* females (Papaj and Prokopy, 1986), remains to be determined. It should be pointed out that, similar to the behavior of *R. pomonella* females in certain laboratory tests (Prokopy and Papaj, unpublished), males in the laboratory tests conducted here never spent a significantly longer time on fruit of apple than on fruit of the native host, hawthorn. Perhaps a period of fruit exposure longer than 3 days (as almost surely would have occurred on the apple trees in nature) is required to elicit a significantly lesser tendency to reside on the native host.

Prokopy *et al.* (1986) showed in two experiments that female *R. pomonella* learned to reject unfamiliar fruit and in a third experiment that females learned both to reject unfamiliar fruit and to accept familiar fruit. The fact that the response level of naive *R. pomonella* males to hawthorn and apple fruit in both laboratory experiments here was consistently intermediate between that of hawthorn- and that of apple-exposed males suggests, under the criteria of Prokopy *et al.* (1986), that males, like females, may learn both to "reject" unfamiliar fruit and to "accept" familiar fruit.

At the conclusion of the first laboratory experiment, we hypothesized that providing females together with host fruit in the exposure cages might enhance the effect of fruit exposure on the subsequent response of males to fruit. In other words, we hypothesized that initiation of copulation with females on fruit in cages [which previously we observed to occur frequently (Prokopy *et al.*, 1971) and presume occurred here] might constitute a form of "reward" to males and further augment the effect of training males to a particular fruit type. The close correspondence, in both experiments, of values for residence time on test fruit does not lend support to this hypothesis, however. Possibly fruit characters

alone, or residence on a particular fruit type in the presence of other males, provide sufficient stimuli to effect learning of fruit type by males.

We do not yet know what the adaptive value (if any) might be to male *R. pomonella* of learning characters of host fruit on which territories are established and copulation is initiated. Because we have shown that under seminatural conditions the majority of matings, regardless of female mating status, occurs on host fruit, we are assuming that males that have been or are able to learn host-fruit properties are more fit in terms of acquiring territories and mates (and hence favored by natural selection) than males that have been unable or are not able to learn such properties. Prior to addressing in future research this question of the fitness value of learning host-fruit properties, we plan to examine in greater depth the territorial behavior of males on fruit. We especially would like (a) to determine whether certain individual fruit on a tree might constitute a critical resource for males (i.e., might be particularly favored by females), (b) to manipulate densities and distributions of males, females, and fruit so as to alter the degree of social interaction among flies, and (c) to assess directly the degree to which male residence time on fruit is associated with the ability of males to compete for favored fruit against other males and to acquire mates.

The only other invertebrate group of which we are aware in which mating is confined to the host plant and the response of both females and males to host-plant characters is modified through prior host-plant experience is hummingbird flower mites (Ascidae). Through an elegant series of studies, Colwell (1985) found that such mites spend most of their lives in the inflorescences of hummingbird-pollinated plants, where they feed on nectar and pollen, mate, and reproduce. The mites move between inflorescences by "stowing away" in the nostrils of hummingbirds. Colwell (1985) postulates that gene flow between mites on the ancestral host-plant species and an incipient colony on a novel host plant depends on such factors as founder effects on genetically specified host preference traits and the effectiveness of rapid host-plant learning. Colwell believes that such factors predispose hummingbird flower mites to form host races and speciate sympatrically.

Whether some populations of *R. pomonella* on hawthorn and apple trees have already formed host races sympatrically or are now in the process of doing so is a subject of much debate (Bush, 1975; Futuyama and Meyer, 1980; Jaenike, 1981; Paterson, 1981; Diehl and Bush, 1984; Futuyama and Peterson, 1985). If *R. pomonella* males and females utilize host plants under which they emerge or other host plants of that same type for mating or oviposition, and if, as appears to be the case in at least some populations (Prokopy *et al.*, 1988), there is a significant (although not strong) genetic basis for such a tendency, then the additional influences of prior host-fruit experience effects on male propensity to defend fruit as a territory and female propensity to oviposit could act



in concert with genetic-based effects so as to give rise to some degree of reduction in gene flow between populations on different host types. Further research must be conducted to determine the validity of this scenario and whether *R. pomonella* is, in fact, undergoing host-race formation under sympatric conditions.

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