CAN OVIPOSITING *RHAGOLETIS POMONELLA* FEMALES (DIPTERA: TEPHRITIDAE) LEARN TO DISCRIMINATE AMONG DIFFERENT RIPENESS STAGES OF THE SAME HOST BIOTYPE?

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ABSTRACT

Previously, we found that after a female apple maggot fly, *Rhagoletis pomonella* (Walsh), alights on a host apple or hawthorn fruit, its propensity to accept (bore into) or reject that fruit prior to egg deposition may depend on the species as well as the cultivar of fruit with which it had prior egglaying experience. Here, we asked whether *R. pomonella* females are able to learn characters associated with different ripeness stages of a single biotype of apple or hawthorn fruit. Combined results of laboratory, field cage, and field tests revealed little evidence of a significant effect of previous experience with conspecific fruit of different ripeness stages (manifest as green versus red fruit) on fruit acceptability.

RESUMEN

Previamente, encontramos que después que larvas de la mosca de la manzana, *Rhagoletis pomonella* (Walsh), se posa en la manzana hospedera o en la fruta de 'hawthorn', la propensidad de aceptar (perforar) o rechazar esa fruta antes de poner huevos, pudiera depender de la especie así como de la fruta del cultivo sobre la cual tenía experience previa en poner sus huevos. Aquí, nos preguntamos si hembras de *R. pomonella* son capazes de aprender caracteres asociados con diferentes grados de madurez de una variedad de manzana o de fruta de 'hawthorn'. Resultados combinados de laboratorio, con jaulas en el campo y pruebas de campo, revelaron muy poca evidencia de un efecto significante de previas experiencias con frutas co-específicas en diferentes estados de madurez (manifestados verde contra fruta roja) en la aceptacíon de la fruta.

The apple maggot fly (AMF), *Rhagoletis pomonella* (Walsh), is an oligophagous insect that oviposits and develops in fruit of several Rosaceae hosts, including hawthorn (*Crataegus*) (the native host) and apple (*Malus*) (an introduced host). Earlier, we found that after a female AMF alights on a hawthorn or apple fruit, its propensity to accept (bore into) or reject that fruit prior to deposition of an egg in the fruit flesh can be altered by previous egglaying experience with one or the other fruit speies, and hence involves learning (Prokopy et al. 1982, 1986, Papaj & Prokopy 1986). Recently, we showed that AMF females also are able to learn characteristics of three different apple biotypes (the cultivars Early McIntosh, Red Delicious, and Golden Delicious) (Prokopy & Papaj 1988). The effect of fruit biotype-learning is not as strong as the effect of fruit species-learning.

Here, we asked whether AMF females are able to learn characters associated with different ripeness stages of a single biotype of apple or hawthorn fruit.

Materials and Methods

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, Mass. Both sexes were maintained together from eclosion in 30 x 30 x 30 cm Plexiglas/screen cages (35-90 females and 7-18 males/cage, according to the experiment). Each cage was supplied with food (sucrose and enzymatic yeast hydrolysate) and water and was kept at 25° C and 60% RH under an 18h photoperiod. All cages were devoid of fruit from Day 1 to Day 14.

On Day 15, by which time females were mature, each cage in Exp. 1 and 2 received either 12 "green" Early McIntosh apples (picked in early July, when the first ovipositing females were seen on these trees), 12 "red" early McIntosh apples (picked in late July, when the fruit were ripe and beginning to drop), or a mixture of 12 green and 12 red apples of these types. All apples were ca. 38 mm diam. Each cage in Exp. 3, 4a, and 4b recived either 26 green *C. mollis* hawthorn fruit (picked in mid-August, when the first ovipositing females were seen on these trees), 26 red *C. mollis* fruit (picked in mid-September, when the fruit were ripe and beginning to drop), or a mixture of 26 green and 26 red *C. mollis* fruit of these types. All hawthorn fruit were ca. 16-18 mm diam. In all experiments, fruit were replaced with fresh specimens of the same type on Day 17. All fruit were stored at 3° C until use.

On Day 19, females were removed individually from the fruit-exposure cages and were transferred in small plastic cups to empty cages for testing (the fruit in the exposure cages were allowed to remain there the entire day). Each female was permitted to rest 3 min before it was offered (allowed to walk or hop onto), in random succession, representatives of each type of fruit to which flies in that experiment had been exposed. A female was allowed to remain on the fruit until it accepted the fruit (attempted to bore) or rejected the fruit (left without attempting to bore or remained 5 min without acceptance). Females were allowed to rest 3 min between fruit offerings. From Day 20 to Day 23, all females in Exp. 4a that had been exposed to green hawthorns from Day 15 to Day 19 were exposed to red hawthorns, while all those that had been exposed to red hawthorns from Day 15 to Day 19 were exposed to green hawthorns. These females were tested on Day 24.

For the field cage tests, flies were of the same host origin and were maintained until Day 14 in the same way as in the laboratory tests. On Day 15, ca. 70 females and 20 males were transferred into each of 2 clear-nylon-screen exposure cages (1x1x2m) placed outdoors and protected from direct sunlight by an opaque tarpaulin. A single non-fruiting potted apple tree, provided with fly food and water, was placed in each cage. On one tree we hung 36 green *C. mollis* fruit picked the previous day (in mid-August). On the other tree, we hung 36 red *C. mollis* fruit picked in mid-September the previous year and stored at 3° C until use. All fruit were 16-18 mm diam. They were replaced with fresh specimens on Day 17.

On Day 19, while in the process of boring into fruit of the same type to which they had been exposed, females were transferred individually onto a leaf of a non-fruiting potted apple tree in a nearby 3.5 x 3.5 x 3m test cage. Either 12 green or 12 red hawthorn test fruit of the types used in the exposure cages were placed ca. 20cm from the transfer leaf. Females alighting on a test fruit were assessed for acceptance or rejection of the fruit in the same manner as in the laboratory tests. Following acceptance or rejection of a green or red test fruit, the female was transferred to an empty 30x30x30 cm cage for 3 min, after which it was released onto a leaf (on the opposite side of the test cage tree) surrounded by 12 test fruit of the opposite color.

The field tests were carried out in late July on Early McIntosh trees and mid-September on *C. mollis* trees. Test females were selected at random by the observer

pointing blindly to a spot in the tree canopy and surveying carefully the fruit in the vicinity of the spot until a female was sighted on a fruit. Moving slowly and using a moistened leaf placed gently beneath the foretarsi, we transferred each female to one of 3 fruit types affixed at the end of a hand-held probe. For flies on the Early McIntosh trees, the 3 fruit types were: green Early McIntosh apples ca. 46 mm diam, picked in early July from the trees on which the tests were conducted and stored at 3° C until use; red Early McIntosh apples ca. 48 mm diam, picked from the test trees just before testing (late July); and red *C. mollis* fruit ca. 18 mm diam, picked in mid-September the previous year and stored at 3° C until use. For flies on the *C. mollis* trees, the 3 fruit types were: green *C. mollis* fruit ca. 16mm diam, picked from the test trees in mid-August and stored at 3° C until use; red *C. mollis* fruit ca. 18 mm diam, picked from the test trees just before testing (mid-September); and red Early McIntosh apples ca. 47 mm diam., picked in late July and stored at 3° C until use.

For field testing, each female was allowed to spend up to 5 min on each fruit offered. In only 4 of 150 fruit offerings on apple trees and in 0 of 192 fruit offerings on hawthorn trees did a female actually spend the allotted 5 min. After recording whether the female accepted or rejected the first fruit, we allowed her to rest on a leaf ca. 15-30 sec before offering a fruit of another type. So long as our movements were slow, females seemed largely unaffected by these procedures. The order in which fruit types were presented was randomized. Females which flew away before transfer to each of the 3 fruit types were excluded from data analysis. Each female was removed from the tree following assay.

Results

In laboratory Expts 1 and 2, the propensity of females to accept green or red Early McIntosh apples was not affected significantly by prior exposure for 3 days to green or red apples or to a mixture of these fruit types (Table 1). Similarly, in laboratory Expts. 3, 4a, and 4b, the tendency of females to accept green or red hawthorn fruit was, almost without exception, not affected significantly by previous experience over 3 days with green or red hawthorns or a mixture of these fruit types (Table 1). The only exception involved significantly greater acceptance of red hawthorns than green hawthorns by females exposed to red hawthorns in Expt. 4a.

In the field cage experiment, prior exposure of females for 3 days to green or red hawthorns on potted trees had no signifiant effect on subsequent propensity of females to accept green or red hawthorns on the test tree (Table 2).

In the field experiment, females on Early McIntosh trees (the fruit of which were red) accepted green and red Early McIntosh apples with equal propensity but significantly rejected red hawthorns (Table 3). Females on hawthorn trees (the fruit of which were red) accepted green and red hawthorns about equally (no significant difference) but significantly rejected red Early McIntosh apples (Table 3).

Discussion

R. pomonella females foraging for oviposition sites within a host tree are likely to encounter, in the course of a single day, fruit of varying ripeness stages and hence fruit of varying degrees of acceptability for egglaying (Averill & Prokopy 1989). For our tests, we chose to expose flies and assess fly response to fruit of 2 quite different ripeness stages: fruit picked early in the fly oviposition season (designated as green fruit) and fruit picked toward the end of the fly oviposition season (designated as red fruit). The results of the laboratory experiments indicate that conspecific green and red fruit (apple or hawthorn) were about equally acceptable to females previously exposed

TABLE 1. PROPENSITY OF *R. POMONELLA* FEMALES EXPOSED IN LABORATORY CAGES FOR 3 DAYS TO GREEN OR RED EARLY MCINTOSH APPLE OR *C. MOLLIS* HAWTHORN FRUIT TO ACCEPT FRUIT OF THESE TYPES FOR OVIPOSITION.

Experiment	exposed to	N	% accepting test fruit of [a]	
			Green apples	*Red apples*
1	Green apples	30	$30a_1$	$37a_1$
	Red apples	29	$31a_1$	$34a_1$
2	Green apples	56	$39a_1$	$46a_1$
	Red apples	59	$29a_1$	$41a_1$
	Mixture (50:50) of green and red apples	51	$45a_1$	$55a_1$
			Green hawthorns	*Red hawthorns*
3	Green hawthorns	41	$63a_1$	$56a_1$
	Red hawthorns	41	$61a_1$	$71a_1$
4a	Green hawthorns	87	$76a_1$	$82a_1$
	Red hawthorns	82	$65b_1$	$82a_1$
	Mixture (50:50) of green and red hawthorns	84	$73a_1$	$73a_1$
4b[b]	Green hawthorns, then red hawthorns	72	$68a_1$	$68a_1$
	Red hawthorns, then green hawthorns	80	$82a_1$	$78a_1$
	Mixture (50:50) of green and red hawthorns	72	$68a_1$	$78a_1$

[a]Values in each row (column) in each experiment followed by the same letter (numerical subscript) are not significantly different at the 0.05 level according to G tests with Yate's correction for continuity.

[b]The same individuals exposed to green hawthorns, red hawthorns, or a mixture of green and red hawthorns in Expt. 4a were exposed to the opposite fruit type for 3 days.

to a mixture of green and red fruit. In these as well as in the field cage and field experiments, there was little evidence of a significant effect of prior experience with conspecific green or red fruit on acceptability of these fruit types. In contrast, there was strong evidence from the field experiments of a significant negative effect of prior experience with fruit of one species on acceptability of fruit of the other species. The

TABLE 2. PROPENSITY OF *R. POMONELLA* FEMALES EXPOSED IN FIELD CAGES FOR 3 DAYS TO GREEN OR RED *C. MOLLIS* HAWTHORN FRUIT ON POTTED TREES TO ACCEPT FRUIT OF THESE TYPES FOR OVIPOSITION.

	% accepting test fruit of [a]			
exposed to	(N)[b]	Green hawthorns	(N)[b]	Red hawthorns
Green hawthorns	(22)	$91a_1$	(24)	$88a_1$
Red hawthorns	(25)	$76a_1$	(24)	$88a_1$

[a]Values in each row (column) followed by the same letter (numerical subscript) are not significantly different at the 0.05 level according to G tests with Yate's correction for continuity.

[b]In all, 26 females from each of the 2 field exposure cages were released onto the test tree. N represents the number of females alighting on test fruit.

TABLE 3. PROPENSITY OF *R. POMONELLA* FEMALES ON RED-FRUIT-BEARING EARLY MCINTOSH APPLE OR *C. MOLLIS* HAWTHORN REES IN NATURE TO ACCEPT GREEN OR RED FRUIT OF THESE TYPES FOR OVIPOSITION.

		% accepting test fruit of[a]			
on trees of	N	Green apples	Red apples	Green hawthorns	Red hawthorns
Apple	50	58a	60a	—	12b
Hawthorn	64	—	0b	9a	12a

[a]Values in each row followed by the same letter are not significantly different at the 0.05 level according to G tests with Yate's correction for continuity.

level of acceptance of test green or red McIntosh apples (58 and 60%) by females on McIntosh trees in the field was comparable to that (60% for red McIntosh) by females in a study conducted in a previous year on these same McIntosh trees (Prokopy & Papaj 1988). For reasons unknown, however, the level of acceptance of test green and red hawthorn fruit (9 and 12%) by females on hawthorn trees was much lower than that (60% for red hawthorn) by females in a study conducted in a previous year on these same hawthorn trees (Prokopy & Papaj 1988).

Previously, we found that ovipositing *R. pomonella* females are capable of learning to reject novel host fruit species of unfamiliar size or chemistry (Papaj & Prokopy 1986) as well as novel host fruit biotypes of unfamiliar chemistry (Prokopy & Papaj 1988). Here, the size and shape of conspecific green and red fruit were essentially the same. Our findings suggest that color of host fruit is not an important stimulus involved in fly learning to accept or reject fruit after alighting. They also suggest that chemical distinctions among different ripeness stages of fruit of the same biotype (Carle et al. 1987) are too few or too unapparent to engender a manifest degree of fly learning. If it should turn out through future work that *R. pomonella* flies are in fact able to learn to accept or reject fruit of different ripeness stages borne by the same tree or different trees of the same biotype, it appears from the experiments reported here that the effect on host use pattern would be minor indeed compared with fly ability to learn to accept or reject fruit of different species or biotypes.

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A NON-MIGRATORY, NON-DIAPAUSING POPULATION OF THE MONARCH BUTTERFLY, *DANAS PLEXIPPUS* (LEPIDOPTERA: DANAIDAE), IN BERMUDA

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ABSTRACT

A non-migratory, non-diapausing population of the monarch butterfly, *Danadus plexippus* L. (Lepidoptera: Danaidae), became established on Bermuda after the precolonial cedar/palmetto forest was opened up by settlers. As part of the Bermuda Department of Agriculture and Fisheries Monarch Conservation Project, 703 monarchs were tagged to gather information on their distribution and movements. One hundred sixty-nine recoveries were made, 96% at the same site at which the butterfly was first captured. Twenty-three individuals were recaptured two or more times. Adult resident monarchs in Bermuda live about 3 to 4 weeks in summer, but up to 13 weeks in winter. They tend to remain near or return continually to a few large milkweed patches. Males spend more time at these sites than females.

RESUMEN

Una población no-migratoria y no en diapausa de la mariposa monarca, *Danaus plexippus* L. (Lepidoptera: Danaidae), se estableció en las Bermudas después que un bosque precolonial de cedros y palmetos fue abierto por colonizadores. Como parte del Proyecto de Conservació de la Mariposa Monarca del Departamento de Agricultura y de Pesca de las Bermudas, 703 monarcas se marcaron para obtener información sobre su distribución y movimientos. Se recobraron 109, 96% en el mismo lugar donde se capturaron por primera vez. Se recapturaron 23 individuos dos o más veces. Monarcas adultos residentes de las Bermudas viven de 3 a 4 semanas en el verano, pero hasta 13 semanas en el invierno. Ellas tienden a mantenerse cerca o retornan continuamente a varias áreas grandes con plantas de 'milkweed'. Los machos pasan más tiempo en estos lugares que las hembras.

Bermuda is a small cluster of islands 1040 km east-southeast of Cape Hatteras, North Carolina, USA. Seven main islands, now connected by bridges, form a fishhook-shaped cluster 35 km long and 1.5 km or less in width. Total land area is only 54 km^2 with a maximum elevation of 74 m. The Gulf Stream passes near Bermuda and moderates the climate; temperatures rarely exceed 33° C or fall below 5° C. Rainfall averages 1420 mm annually and is distributed fairly evely throughout the year.