ALIGHTMENT OF APPLE MAGGOT FLIES ON FRUIT MIMICS IN RELATION TO CONTRAST AGAINST BACKGROUND

RONALD J. PROKOPY
Department of Entomology
University of Massachusetts
Amherst, MA 01003

ABSTRACT

I evaluated an hypothesis, developed from earlier studies, that apple maggot flies, *Rhagoletis pomonella* (Walsh), within a tree should be better able to find fruit of any color when looking outward or upward rather than inward or downward. Artificial fruit mimics were created by covering all or half of 6-cm-diam rubber spheres with red or green artist pigments whose reflectance spectra closely matched those of natural red or green fruit. Numbers of flies alighting on such mimics placed in apple trees revealed that response was (a) greater to red than green pigment, irrespective of pattern of pigment distribution, (b) greater to bi-colored mimics whose red half faced downward as opposed to upward, and (c) no different to bi-colored mimics whose red half faced inward compared with outward. Possible explanations for partial but not full support of the hypothesis are discussed.

RESUMEN

Yo evalué una hipótesis, desarrollada de estudios previos, que las moscas de *Rhagoletis pomonella* (Walsh) deben de encontrar frutas de cualquier color cuando miran dentro de un árbol hacia afuera, más que hacia dentro o abajo. Se crearon frutas artificiales cubriendo toda o la mitad de esferas de goma con pigmentos de artistas rojos o verdes, cuyo espectro de reflección es muy parecido al color natural de frutas rojas o verde. El número de moscas posándose en las imitaciones colocadas en árboles de manzana, reveló que la reacción (a) fue mayor hacia el pigmento rojo que hacia el verde, independiente del patrón de distribución del pigmento, (b) fue mayor hacia la imitación bicolor en el cual la mitad roja miraba hacia abajo que cuando miraba hacia arriba, y (c) no fue diferente a la imitación bicolor en el cual la mitad roja miraba hacia dentro comparada con la que miraba hacia afuera. Se discuten posibles explicaciones que apoyan parcial pero no totalmente esta hipótesis.

Fruit of hawthorn, apple, and other host trees are sites of mating and oviposition activities in apple maggot flies, *Rhagoletis pomonella* (Walsh) (Prokopy et al. 1971, 1972). Flies of each sex detect individual fruit within host trees principally or exclusively by vision, responding positively to such characters as fruit shape, size, and color (Prokopy 1968, 1977, Aluja and Prokopy, unpub. data). Using artificially pigmented fruit whose reflectance properties very closely mimicked those of natural fruit, Owens and Prokopy (1986) found that irrespective of hue (i.e. dominant wavelength of reflected light), alightment of *R. pomonella* females and males on fruit mimics increased successively with decreasing total reflectance intensity between 350-600 nm (i.e. the visual sensitivity spectrum of *R. pomonella* (Owens 1982)). This was true even when the natural fruit on the tree were green and relatively high in reflectance intensity, suggesting that attractiveness differences could not be explained solely by mimic resemblance to natural fruit. The combined evidence from that study and earlier studies (Prokopy

1968, Owens and Prokopy 1984) led Owens and Prokopy (1986) to conclude that apple maggot flies use intensity contrasts to detect fruit within trees.

Two mechanisms in concert were proposed by Owens and Prokopy (1986) as conferring detectability of fruit by apple maggot flies on the basis of contrast of fruit against background.

The first hypothesized mechanism involves the physiology of fly vision. *R. pomonella* has maximum visual sensitivity in the spectral region of peak emission of energy from skylight (below 520 nm) and peak reflectance of energy from foliage (520-580 nm) but minimum visual sensitivity to energy reflected from red-colored (ripe) fruit (above 580 nm) (Owens 1982). Such visual receptor properties confer maximum intensity contrast between red fruit and energy emitted from skylight or energy reflected from or transmitted through foliage, rendering red fruit the most readily detectable color of fruit in all situations.

The second hypothesized mechanism involves the behavior of fruit-foraging flies. Assessment of fruit and background reflectance properties (Owens and Prokopy 1984, 1986) reveals that intensity of contrast between fruit (of any color) and background is likely to be greatest for a fly viewing fruit (which is opaque) against a background of skylight or light transmitted through foliage. Such a view would be optimal from a position within the tree looking outward, or from below a fruit looking upward. From this vantage point, a fruit, irrespective of ripeness stage, would appear dark against a bright background. Extensive observation of the movements of *R. pomonella* has in fact revealed that a considerably greater degree of discovery of red fruit (as determined by degree of head movement of stationary flies) occurs when flies are across from or beneath red fruit rather than above red fruit (Roitberg 1985.)

The experiments reported here were aimed at providing further information on the second (behaviorally-based) hypothesized mechanism of fruit discovery by *R. pomonella* flies.

Materials and Methods

Artificially-pigmented fruit mimics were created by covering all or half of solid-rubber spheres (6 cm diam) with one of the following pigments (Winsor-Newton, London): (a) artist oil Cadmium Red (designated as red), or (b) artist oil Winsor Green (1.5%) mixed with artist oil Cadmium Yellow (98.5%) (designated as green). The spectral reflectance curves of these artificially-pigmented red or green fruit mimics are given in Owens and Prokopy (1986). They approximate closely the curves of natural red or green hawthorn or apple fruit (Owens and Prokopy 1986). All fruit mimics were coated thinly with Tangletrap (Tangletrap, Grand Rapids, Mich.) to capture alighting flies. Previous studies have shown that a thin coating of Tangletrap has no more than a very slight effect on the reflectance spectra of artificially pigmented surfaces (Prokopy 1968).

The mimics were hung by wire in abandoned Early MacIntosh apple trees that harbored a substantial population of mating and ovipositing *R. pomonella* flies and bore a moderate crop of ripening fruit. The fruit were 4-6 cm diam and were about half red (outward facing surface), half green (inward facing surface) in color at the time these experiments were conducted (July 15-19, 1985). The canopy of each of the 3 trees used was ca. 7 m tall x ca. 9 m diam. Only the outer one-fourth of the canopy bore fruit. The fruit mimics were positioned ca. 1 m inward from the canopy perimeter (i.e. about midway between the outer and inner limits of the fruit bearing surface) and ca. 2 m above ground. An area free of branches, foliage, and fruit was created ca. 10 cm around each mimic to permit unobscured vision. There was a minimum distance of 1 m between mimics.

The following 3 experiments were conducted, each involving a comparison of 2 types of fruit mimics: (a) entire surface of mimic green vs. entire surface red; (b) inward-facing half of mimic green, outward-facing half red vs. inward-facing half of mimic red, outward-facing half green; and (c) downward-facing half of mimic green, upward-facing half red vs. downward-facing half of mimic red, upward-facing half green. Each of the 2 mimics per experiment remained in position for 15 min (a longer time would have depleted the fly population too extensively), after which flies were removed and positions were reversed. In all, there were 9 pairs of positions per experiment (i.e. 18 replicates of each treatment). The same positions were used across all 3 experiments.

After each pair of replicates was completed, light intensity at each position was measured by holding the photosensitive element of a Gossen Panlux light meter next to a mimic and pointing it directly inward (toward the tree trunk), directly outward, directly upward, and directly downward. It is recognized that a photometer which furnishes measurements in lux rather than in microwatts/cm/sec can provide no more than a crude estimate of the amount of light energy perceptible by an insect. This is so because such a photometer is equipped with filters to match the human eye sensitivity spectrum, thereby rendering the photometer somewhat insensitive to spectral areas of high insect sensitivity (eg. energy below 500 nm). Nonetheless, owing to lack of availability of a more appropriate instrument, it was believed that even a crude estimate of light distribution was better than none. Following light intensity measurement, the number of real apples within 30 cm of each position was counted.

All data were submitted to Wilcoxin's signed rank test (0.05 level) (Steel and Torrie 1960) for analysis.

Results

Among fruit mimics that were entirely of the same color, significantly more males, numerically (though not significantly) more females, and significantly more total flies alighted on red mimics than on green ones (Table 1, Exp. 1). Among bi-colored fruit mimics, there were no significant differences in numbers of males, females, or total flies alighting on mimics whose inward facing half was green (outer half red) and whose inward facing half was red (outer half green) (Table 1, Exp. 2). However, significantly more males, numerically (though not significantly) more females, and significantly more total flies alighted on mimics whose downward facing half was red (upper half green) than whose upward facing half was red (downward half green) (Table 1, Exp. 3).

For each experiment, the percent of flies alighting on the inward vs. outward, or the downward vs. upward facing half of each fruit mimic type is given in Table 2. Among mimics that were entirely green or entirely red, there were no significant differences between opposite sectors in numbers of alighting flies. Among bi-colored mimics, significantly more males, numerically (though not always significantly) more females, and significantly more total flies alighted on red sectors than on green ones, irrespective of sector orientation.

Mean light intensity was significantly greater when facing directly outward from mimic positions than directly inward (means of 48,000 vs. 14,300 lux) and when facing directly upward from mimic positions than directly downward (means of 74,800 vs. 16,900 lux). Finally, there were no significant differences among sectors around a mimic position in mean number of real apples located within 30 cm of a position: upward, inward sectors = 3.1 apples; downward, inward sectors = 2.4 apples; upward, outward sectors = 4.2 apples; and downward, outward sectors = 3.2 apples.

TABLE 1. TOTAL NUMBERS OF *R. POMONELLA* FLIES ALIGHTING ON FRUIT-MIMICING SPHERES WHOSE SURFACES WERE ENTIRELY- OR HALF-COVERED WITH RED (R) OR GREEN (G) ARTIST PIGMENT. EIGHTEEN REPLICATES PER TREATMENT.

		Total no. alighting		
Exp.	Treatment	Males[1]	Females	Total
1	G entire	14b	15a	29b
	R entire	66a	24a	90a
2	G inward, R outward	48a	21a	69a
	R inward, G outward	54a	22a	76a
3	G downward, R upward	26b	17a	43b
	R downward, G upward	59a	23a	82a

[1]Any values in each column in each experiment followed by the same letter are not significantly different.

DISCUSSION

In the Introduction, it was hypothesized that the physiology of apple maggot fly vision in concert with fly behavior should confer greatest ability on flies to detect and respond to fruit within a tree from positions looking outward or upward. The results of this study support this hypothesis in part but not in entirety. Thus, the combined data on numbers of individuals alighting on fruit mimics indicate that apple maggot flies, particularly males, are (a) more positively responsive to red than green pigment on a fruit mimic, irrespective of pattern of pigment distribution, (b) more positively responsive to a bi-colored (red-green) fruit mimic when the red portion is facing downward rather than upward, and (c) no more responsive to a bi-colored (red-green) fruit mimic when the red portion is facing inward compared with outward.

The greater intensity of light measured when the photosensitive element of the light meter was oriented upward or outward compared with downward or inward from fruit mimic positions suggests that the background may have been brighter for a fly looking upward or outward than downward or inward toward a mimic. The lack of positional difference in numbers of real fruit within 30 cm of the fruit mimics (i.e. within the distance at which 6-cm fruit are likely to be seen by an apple maggot fly (Roitberg 1985)), rules out potential bias that could have affected the locale at which flies accumulated prior to flight toward a fruit mimic.

One can do no more than speculate as to why apple maggot flies were more responsive to bi-colored mimics whose red portion faced downward than to those whose red portion faced upward, but were not more responsive to bi-colored mimics whose red portion faced inward compared with those whose red portion faced outward. Possibly ommatidia in the upper region of the fly's eye are endowed, as a group, with greater ability to detect dark objects, such as fruit, against a brighter background than are ommatidia in the central or lower regions of the eye. If there were indeed differential sensitivity among regions of the eye to large dark objects, such differences might have arisen over evolutionary time primarily as a mechanism of rapid detection of approaching predators (eg. birds) and not primarily as a mechanism of fruit detection. An additional explanation for the experimental results might lie in the fact that outward facing (i.e. sunlight facing) portions of fruit turn red before inward facing portions. Perhaps such a fruit ripening pattern has constituted, over evolutionary time, little selection pressure on flies for detecting red portions of fruit from positions within a tree looking outward. Whichever, *R. pomonella* is not the only tephritid fly that responds positively

TABLE 2. PERCENT OF *R. POMONELLA* FLIES ALIGHTING ON INWARD (IN) VERSUS OUTWARD (OUT) OR DOWNWARD (DOWN) VERSUS UPWARD (UP) FACING HALVES OF RED (R) OR GREEN (G) PIGMENTED FRUIT MIMICING SPHERES.

			Percent of flies alighting					
			Males		Females		Total	
Exp.	Treatment	Comparison	In	Down	In	Down	In	Down
1	G entire	G in vs. G out	50	—	73	—	62	—
		G down vs. G up	—	57	—	33	—	45
	R entire	R in vs. R out	53	—	54	—	53	—
		R down vs. R up	—	45	—	50	—	47
2	G in, R out	R out vs. G in	29[a]	—	43	—	33[a]	—
	R in, G out	R in vs. G out	70[a]	—	86[a]	—	75[a]	—
3	G down, R up	R up vs. G down	—	23[a]	—	41	—	30[a]
	R down, G up	R down vs. G up	—	75[a]	—	83[a]	—	77[a]

[a]Significant difference between the 2 members of a comparison.

to resource stimuli that are overhead. Black cherry fruit flies, *R. fausta* (Osten-Sacken), forage for food (nectar from extra-floral nectaries on host foliage) by making short flights to a succession of leaves above them, followed eventually by a long flight downward, from whence the upward movement process resumes (Prokopy 1975).

Further tests are needed to determine whether the pattern of *R. pomonella* fly response to bi-colored fruit mimics observed here is characteristic of fly response on other host plant types, and is subject to influence by atmospheric conditions, ripeness stage of fruit, degree of prior fruit experience of flies, and distance of a mimic from the nearest fruit or foliage. Along these lines, it would be particularly useful eventually to be able to separate color factors that affect fly detection of a fruit from a distance from color factors that affect fly alightment on a particular fruit sector once a fruit has been detected and approached. This will require detailed examination of flight paths of fruit-approaching flies.

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