

## ***Dacus dorsalis* Flies Can Learn to Find and Accept Host Fruit**

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Mature oriental fruit fly females, *Dacus dorsalis*, from a population cultured on host fruit in the laboratory for one generation responded positively to visual and olfactory stimuli of individual natural kumquat (*Fortunella japonica*) and apple (*Malus pumila*) host fruit or models of these fruit hung from branches of potted trees in field enclosures. When females were exposed for 3 days to natural kumquats or apples on trees and subsequently released individually onto trees harboring one or the other of these fruit types, a significantly greater proportion of those exposed to kumquats than those exposed to apples or those not exposed to any fruit visited kumquats. Females exposed to kumquats for at least 3 days followed by at least 3 days of exposure to apples retained ability to find kumquats. Compared with females exposed to apples for 3 days or with naive females, females exposed to kumquats for 3 days exhibited no less ability to find apples but did significantly refrain from accepting apples for oviposition. A final test was conducted in which females were exposed to natural kumquats or apples for 3 days and tested for response to inanimate models of either the same color and size as natural kumquats (orange, 20-mm diameter) or apples (green, 75-mm diameter) or models of the same color but opposite size. Results suggest that fruit size is the principal character learned and used in finding kumquats, which apparently are somewhat inconspicuous to an inexperienced foraging *D. dorsalis* female.

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**KEY WORDS:** *Dacus dorsalis*; learning; foraging; oviposition.

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## INTRODUCTION

There is evidence that several herbivorous insects (Papaj and Prokopy, 1989), insect parasitoids (van Alphen and Vet, 1986), and saprophagous insects (Jaenike, 1988) are capable of learning to find important resources. Among tephritid flies, to date only the Mediterranean fruit fly, *Ceratitidis capitata* (Wiedemann), has been shown to be able to learn to find an essential resource. To illustrate, a greater proportion of medfly females visited species of host fruit with which the females had become familiar through prior visitation and oviposition than fruit of host species with which they were unfamiliar (Prokopy *et al.*, 1989a).

Here, we first asked whether females of the oriental fruit fly, *Dacus dorsalis* Hendel, used fruit visual or odor cues (or both) to find host kumquat fruit (*Fortunella japonica*) or host apple fruit (*Malus pumila*) hung on potted trees in field cages. Compared with females of *Rhagoletis*, *Anastrepha*, and *Ceratitidis* tephritid flies, *D. dorsalis* females seem less able to bore through the skin of on-tree host fruit with the ovipositor (personal observation). Rather, *D. dorsalis* females often use preexisting punctures made by other tephritids or wounds made by birds or other agents for access to the fruit flesh, where the eggs are deposited. Thus, in contrast to the situation with *R. pomonella* (Walsh) females, which in most circumstances use solely fruit visual stimuli to find individual fruit within a tree (Prokopy, 1968; Aluja, 1989), we hypothesized that *D. dorsalis* females might respond positively to odor as well as visual properties of individual fruit, particularly freshly punctured fruit.

We next asked whether the propensity of *D. dorsalis* females to alight on kumquats or apples was influenced by previous experience with these fruit. After detecting such an effect, we asked, finally, what sorts of host fruit cues modified subsequent female responses to these fruit.

## MATERIALS AND METHODS

Parent adults of all *D. dorsalis* flies used here were reared from infested fruit of tropical almond (*Terminalia catappa*) collected in nature in Kauai. They were maintained under insectary conditions at the Tropical Fruit and Vegetable Research Laboratory in Honolulu and were allowed to oviposit in fruit of papaya (*Carica papaya*), the immediate source of flies for our studies. After eclosion, the flies were maintained in laboratory cages containing food (sucrose and yeast hydrolysate) and water (but no fruit) until sexually mature (29–33 days old), at which time they were employed in tests.

For each experiment, about 80 female and 20 male mature *D. dosalis* flies were transferred into each of two or three clear nylon-screen exposure cages (1 m long  $\times$  1 m wide  $\times$  2 m tall) placed outdoors. The top of each cage was covered with a partly opaque tarpaulin to exclude direct sunlight and rainfall.

A single small nonfruiting potted host guava tree (*Psidium guava*) was placed 1 m above ground in the center of each cage. Each tree was about 65 cm in canopy diameter and 60 cm tall and bore about 140 leaves. Before use, the foliage and stems of each tree were rinsed with water. On each tree we hung water vials with cotton wicks and, as a source of ample food, strips of filter paper dipped in an aqueous slurry of yeast hydrolysate and sucrose, dried before use.

In experiment 1, designed to compare female response to fruit visual versus fruit odor stimuli, we hung on one caged tree four orange-colored, water-rinsed kumquats (20-mm diameter) purchased from a local supermarket and four wooden models of kumquats (20-mm diameter) coated with a mixture of Winsor and Newton (London) artist pigments [titanium white 244SL series 2 (32.4%), cadmium yellow 222 SL series 4 (64.8%), and cadmium red 219 SL series 4 (3.8%)] to mimic the reflectance of the kumquats (Fig. 1). On a second caged tree, we hung two green-colored water-rinsed “Granny Smith” apples (75-mm diameter) purchased from a local supermarket and two plastic models of apples (75-mm diameter) coated with a mixture of Winsor and Newton pigments [mars black 248 series 2 (1.2%), winsor green 170 SL series 2 (1.5%), titanium white 244 SL series 2 (32.9%), and cadmium yellow 222 SL series 4 (64.4%)] to mimic the reflectance of the apples (Fig. 1). Measurements of diffuse reflectance from surfaces of guava leaves, kumquat and apple fruit, and fruit mimics were made with a Shimadzu UV-210 spectrophotometer equipped with an integrating sphere (Bausch and Lomb Inc.). The natural fruit received no punctures other than the two holes made during attachment of wire for hanging. These

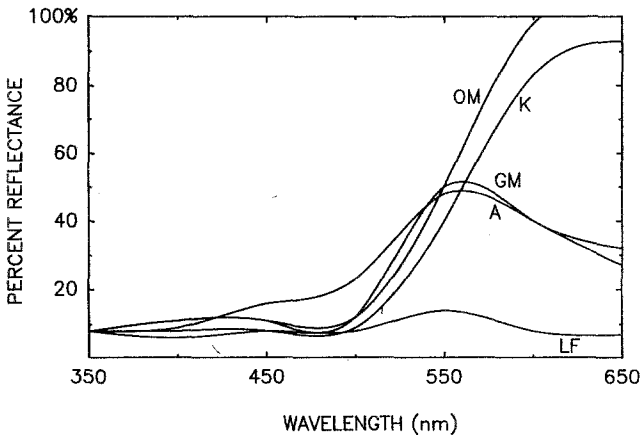


Fig. 1. Spectral reflectance of guava leaves (LF), natural kumquats (K), natural Granny Smith Apples (A), orange models of kumquats (OM), and green models of apples (GM).

were sealed with paraffin wax. The models dried about 2 weeks before use and, when used, emitted no odor detectable by the human nose. As evidence that pigments applied to the models did not affect fly behavior adversely, in preliminary tests we observed no unusual patterns of behavior (e.g., excessive preening) of flies that alighted on models. Fruit and models were positioned about 15 cm apart. Positions were reversed after each trial. We counted the number of flies alighting on natural fruit and models over the 5-min duration of each trial, transferring each alighting fly to the cage wall within seconds after alighting. There were 10 trials per experiment.

In Experiment 2, we compared the tendency of *D. dorsalis* females to alight on punctured versus nonpunctured natural kumquats or apples. The design was similar to the first experiment. Each punctured fruit received 10 holes (0.3 mm in diameter  $\times$  2 mm deep) with a dissecting probe just before the start of a trial. In the nonpunctured fruit, the two wire-attachment holes were sealed with paraffin.

Experiments 3–5 were aimed at evaluating the influence of previous experience with fruit on propensity to alight on natural fruit of a familiar versus an unfamiliar type or on fruit models. For experiments 3 and 5, on Day 1 we hung on one caged tree 18 kumquats, each punctured twice with a dissecting probe to facilitate entry of the ovipositor into the flesh, and on a second caged tree, four Granny Smith apples, each punctured nine times. In both cages, fruit were spaced evenly among the branches. In a third cage in Experiment 3, no fruit were hung on the tree to maintain flies in a naive condition. Early on Day 3, fruit in the first two cages were replaced with fresh specimens of the same type and number. On Day 4 (a test day), half of the fruit were removed from each cage at 9 AM to circumvent overdepletion of female egg load while still providing a moderate level of available fruit. Removed fruit were returned to the cages at 4 PM but taken away again at 9 AM on Day 5 (also a test day). For Experiment 4, from Day 6 to Day 8, all flies that had been exposed to kumquats from Day 1 to Days 3–5 in Experiment 3 were exposed to Granny Smith apples, while all that had been exposed to Granny Smith apples from Day 1 to Days 3–5 in Experiment 3 were exposed to kumquats. Females in Experiment 4 were tested again on Days 9 and 10.

On test days, females were assayed for propensity to alight upon and bore into natural fruit or inanimate models of fruit. Tests were conducted in cylindrical (3.5 m in diameter  $\times$  3.5 m tall) clear nylon-screen field cages. Each cage contained a single nonfruiting guava test tree having a size and leaf number equivalent to those of trees in the exposure cages. Each test tree was water-rinsed before use. In Experiments 3 and 4, we hung either 12 evenly spaced kumquats or 3 evenly spaced Granny Smith apples on each tree. Just before testing a female, each fruit was punctured as in Experiment 2. In Experiment 5, test fruit consisted of 12 orange-pigmented or 12 green-pigmented 20-mm-

diameter wooden spheres or of 3 orange-pigmented or 3 green-pigmented 75-mm-diameter plastic spheres hung on a test tree. The pigments were the same as those in Experiment 1. Inclusion in Experiment 5 of different colored models of the same size in a balanced experimental approach was for the purpose of assessing the effect of fruit color versus size on female ability to find fruit.

For testing females in Experiments 3–5, a fruit of the same type to which a female had been exposed was attached to a dissecting probe and held in the canopy of an exposure tree until a female alighted on it and commenced boring. For females in Experiment 3 that were naive, we alternated using a kumquat and an apple. During boring, the female and fruit were moved gently to the test cage, where the foretarsi of the still-boring female were nudged onto the upper surface of a leaf at the lower center of the plant canopy. After boring, the females walked readily onto the leaf surface. We adopted this procedure to standardize as much as possible the physiological state of released females. To ensure uniformity of procedure, females were always released onto the same leaf of a test tree. Females that did not leave the release leaf within 5 min were disqualified.

We monitored the duration of time each female spent on the test tree since leaving the release leaf until she visited a fruit, she left the tree without visiting a fruit, or 10 min elapsed without her visiting a fruit. The latter females were considered nonfinders. If a female in Experiments 3 and 4 alighted on a fruit, we monitored whether she bored or left the fruit without boring. Each female was tested twice (in Experiment 3, once against each of the two natural fruit types; in Experiment 4, once against each of the two natural fruit types; in Experiment 5, once against two of the four fruit model types), with 20 min of rest in an empty laboratory cage between tests. The advantages and disadvantages of restricting assessment of the response of an individual to a single treatment type versus assessing its response to a series of treatment types are discussed by Kamil (1988). We chose the later approach (though in modified form for Experiment 5). To minimize experimental error, we alternated fly exposure and test fruit treatments in a carefully controlled systematic fashion. All tests were conducted in March 1989.

## RESULTS

There were significantly more alightings by *D. dorsalis* females on non-punctured natural kumquats than on orange wooden models of kumquats [means of 2.1 vs 0.7;  $P \leq 0.01$ , Wilcoxon matched-pairs signed-ranks test (Siegel, 1956)]. Likewise, there were significantly more alightings on nonpunctured natural apples than on green plastic models of apples (6.2 vs 2.7;  $P \leq 0.01$ , Wilcoxon test). Punctured fruit received more visits than nonpunctured fruit. Thus, there were significantly more visits to punctured kumquats than to non-

punctured kumquats (4.1 vs 2.2;  $P \leq 0.01$ , Wilcoxon test) and significantly more visits to punctured apples than to nonpunctured apples (12.8 vs 9.2;  $P \leq 0.01$ , Wilcoxon test).

As shown in Experiment 3 (Table I), significantly more *D. dorsalis* females exposed for 3 days to kumquats (76%) than to apples (28%) or to no fruit (32%) alighted on kumquats. There were no significant differences among females in these three fruit exposure regimes in the proportion alighting on apples (64, 76, and 64%, respectively). Although there was a tendency for kumquats to be found faster by kumquat-exposed than by apple-exposed or naive females, the difference was not significant. Nor were there any significant differences among females of these three exposure regimes in time from release on a test tree to alighting on an apple. Finally, 100% of kumquat-exposed, 86% of apple-exposed, and 100% of naive females arriving on kumquats accepted kumquats for oviposition (no significant differences). In contrast, significantly fewer kumquat-exposed (44%) than apple exposed (89%) or naive (88%) females arriving on apples accepted apples for oviposition.

In Experiment 4 (Table I), the proportion of females finding kumquats or apples and the mean time from female release to alighting on a kumquat or an apple were no different among females that had been exposed to kumquats for 3–5 days in Experiment 3 and then to apples for 3–5 days in Experiment 4 or females that had been exposed to apples for 3–5 days in Experiment 3 and then to kumquats for 3–5 days in Experiment 4. While kumquat-alighting females from both of these exposure histories accepted kumquats about equally for oviposition (93 and 100%, respectively), a significantly greater proportion of the former (88%) than the latter (46%) that alighted on apples accepted apples for oviposition.

In Experiment 5 (Table 1), we found that significantly more females exposed for 3 days to kumquats (58%) than to apples (17%) alighted on orange wooden models of kumquats. Although a greater proportion of females exposed for 3 days to kumquats (63%) than to apples (42%) alighted on green, kumquat-size wooden models, the difference was not significant. Nor were there any significant differences among females exposed for 3 days to kumquats or apples in proportion alighting on green plastic models of apples (46 vs 63%, respectively) or orange, apple-sized plastic models (58 vs 63%, respectively). We applied a logistic regression analysis to these data (BMDPLR) (Dixon, 1985), which indicated that color had no significant effect on our results. Therefore, we collapsed the data over color to look at the effect of prior exposure on fly response to model size alone. This analysis indicated that significantly more apple-exposed flies alighted on large models than on small models (63 vs 29%, respectively;  $\chi^2 = 10.74$ ,  $P \leq 0.001$ ). Numbers of kumquat-exposed flies alighting on large versus small models were not significantly different (52 vs 60%, respectively;  $\chi^2 = 0.677$ ,  $P \leq 0.41$ ).

**Table 1.** Following 3 Days of Exposure to Natural Kumquats (KT), Apples (AP), or No Fruit (NO), Percentage of Assayed *D. dorsalis* Females Arriving on Natural (NAT) Test Fruit or Fruit Models (MDL) Under Single-Choice Test Conditions. Time from Release Until Arrival, and Percentage of Arriving Females Accepting Test Fruit for Oviposition

Expt No.	Females exposed to	Pretest experience		Test results											
		Approx. total No. eggs laid in fruit during 3-day exposure period	N <sup>c</sup>	% females arriving on test fruit <sup>b</sup>				Mean time from release to arrival on fruit (s) <sup>b</sup>				% arriving females accepting test fruit <sup>b</sup>			
				NAT	KT	NAT	AP	NAT	KT	NAT	AP	NAT	KT	NAT	AP
3	KT	2500	25	76a	64a	191a	195a	100a	44b						
	AP	1400	25	28b	76a	267a	171a	86ab	89a						
	NO	—	25	32b	64a	266a	171a	100a	88a						
4 <sup>c</sup>	KT, then AP	1200	22	68a	73a	247a	182a	93a	88a						
	AP, then KT	1500	22	59a	59a	215a	151a	100a	46b						
5 <sup>d</sup>	KT	1000	24	58a	46a	135ab	75b	—	—						
		1500	24	17b	63a	133ab	75b	—	—						
	AP	MDL	MDL	MDL	MDL	MDL	MDL	MDL	MDL	MDL					
		SM	GRN	LG	ORG	SM	GRN	SM	GRN	SM	GRN				
	KT	1000	24	63a	58a	159a	175a	—	—						
		1500	24	42ab	63a	130ab	175a	—	—						

<sup>a</sup>Number of females released on test tree.  
<sup>b</sup>Values in each experiment followed by the same letter are not significantly different at the 0.05 level according to G tests (for percentage arrivers or acceptors) or Mann-Whitney U tests (for time to arrival).  
<sup>c</sup>Females exposed for 3–5 days to KT and then for 3–5 days to AP or females exposed for 3–5 days to AP and then for 3–5 days to KT.  
<sup>d</sup>Models were the same color and size as natural kumquats (MDL KT) or natural apples (MDL AP) or the same size and opposite color as natural kumquats (MDL SM GRN) or the same size and opposite color as natural apples (MDL LG ORG).

## DISCUSSION

Our findings reveal that *D. dorsalis* females respond positively to visual stimuli of inanimate models of individual kumquats and apples within host trees. Response is greater when fruit visual stimuli exist in combination with fruit odor stimuli (as in unpunctured natural fruit) and greater still when natural fruit are freshly punctured. These findings confirm our hypothesis that *D. dorsalis* females, favoring preexisting punctures when ovipositing in on-tree fruit, use both fruit visual and fruit odor stimuli as cues in finding individual fruit in a host tree. Although *D. dorsalis* females do refrain from ovipositing in punctures containing conspecific or heterospecific larvae, they do not refrain from laying eggs in uninfested punctures or punctures containing only eggs (Prokopy *et al.*, 1989b).

Our experiments further reveal that the propensity of *D. dorsalis* females to alight on natural kumquats in host trees is affected significantly by the nature of their prior experience with kumquats. Thus, a higher proportion of females familiar with kumquats than females familiar with apples or females unfamiliar with fruit visited natural kumquats. Possibly kumquats are somewhat inconspicuous in appearance to females lacking prior experience finding kumquats. Once such experience has been obtained, however, apparently it is not quickly forgotten. Thus, females exposed to kumquats for 3–5 days and subsequently exposed not to kumquats but to apples for 3–5 days found kumquats as readily as females having very recent exposure to kumquats. In contrast to the experience-dependent propensity of females to alight on kumquats, prior experience with kumquat or apple fruit played no significant role in female propensity to alight on apples. A significantly greater proportion of naive females visited apples than kumquats (64 vs 32%), suggesting that apples may be more conspicuous than kumquats.

In our final experiment, where females were exposed to natural kumquats or apples but tested for propensity to alight on inanimate models that were essentially either the same color and size as natural kumquats or apples or of the same color but opposite size, females responded to those models mimicking natural fruit in the same pattern as to natural fruit. The only difference was that the proportion of females finding inanimate models was somewhat less across all model types, possibly owing to the absence of fruit odor from the models. The logistic regression analysis of the combined data for response to models similar in size and color to natural fruit and similar in color but opposite in size strongly suggests that among fruit visual stimuli, it is largely the small fruit size rather than orange fruit color that renders kumquat fruit somewhat inconspicuous to inexperienced foraging *D. dorsalis* females. Odor of kumquat fruit also may have been learned by kumquat-exposed females, but our experimental design did not permit assessment of this possibility.

Recent studies of *C. capitata* flies suggest that fruit size likewise is a principal character learned by fruit-seeking females during within-tree search, with



fruit color and odor apparently being of lesser or no importance (Prokopy *et al.*, 1989a). Among other phytophagous insects, host experience enhances upwind response to host-plant odor in *Leptinotarsa* beetles (Visser and Thiery, 1986), *Schistocerca* nymphs (Lee *et al.*, 1987), and *Bruchophagus* seed chalcids (Kamm, 1989). Color and/or light intensity cues are learned by *Heliconius* and *Pieris* butterflies in finding nectar sources or egg-laying sites (Swihart and Swihart, 1970; Traynier, 1987; Lewis and Lipani, 1990) and by *Melanoplus* grasshopper nymphs in finding food (Bernays and Wrubel, 1985). Ovipositing *Battus* butterflies find suitable hosts sometimes by learning the shape of host leaves (Rausher, 1978; Papaj, 1986a) and sometimes by learning visual cues associated with terminal leaf buds of hosts (Papaj, 1986b).

In addition to learning to find apparently somewhat inconspicuous kumquats, *D. dorsalis* females learned to accept host fruit for oviposition after alighting on it. Here, however, our data show that females accepted natural kumquats equally well, irrespective of type of prior experience with fruit. But females accepted natural apples significantly more often when naive or when their most recent ovipositional experience was with apples rather than kumquats. Additional laboratory tests confirmed the significance of this pattern (Prokopy *et al.*, unpublished data). Besides *D. dorsalis*, females of *R. pomonella*, *C. capitata*, and *D. tryoni* (Froggatt) likewise are capable of learning to accept fruit for egg laying (Prokopy and Fletcher, 1987; Prokopy and Papaj, 1988; Papaj *et al.*, 1989).

Ultimately, we would like to determine whether tephritid flies such as *D. dorsalis* and *C. capitata* form a true search image when foraging for fruit in a host tree. As discussed by Guilford and Dawkins (1987), this is a somewhat daunting challenge. We would need to demonstrate that increased ability to detect inconspicuous fruit with experience would interfere with ability to detect conspicuous fruit and that enhanced ability to detect one type of inconspicuous fruit would not enhance ability to detect other equally inconspicuous fruit types of different appearance.

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