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Cross-Induction of Fruit Acceptance by the Medfly *Ceratitis capitata:* The Role of Fruit Size and Chemistry

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Groups of female Mediterranean fruit flies, Ceratitis capitata *(Wiedemann), were exposed for several days to one of three host fruit species. Oviposition-site acceptance behavior was subsequently assayed on five fruit species. Females accepted most often the fruit to which they were exposed. Females exposed to a small fruit, mock orange, accepted other fruit species less often as the size of the fruit increased; females exposed to a large fruit, sweet orange, accepted other fruit species more often as the size of the fruit increased. This tendency for experience with one host fruit species to alter differentially behavioral responses to alternative host fruit species has been defined as cross-induction. In contrast, females exposed to a medium fruit, kumquat, were not cross-induced: females accepted the medium fruit very often and rejected all other fruit species to approximately the same degree regardless of size. When females were exposed to small, medium, or large fruit and tested on spherical wax fruit models of a variety of sizes, patterns similar to those with real fruit were observed. Whereas naive females generally accepted a given model as frequently as real fruit of a similar size, experienced females generally accepted models much less frequently than real fruit. In a final experiment, females were exposed to different fruits and tested on spherical wax models treated with fruit chemicals. Experienced females generally accepted fruit-treated spheres more often than untreated spheres. In addition, females usually accepted most often models treated with chemicals from the fruit to which they were exposed. Two hypotheses about the mechanism by which experience alters fruit acceptance—*

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termed the "sliding template" and "closing window" hypotheses—are presented. Results of fruit and model acceptance by naive and experienced females support the latter hypothesis.

KEY WORDS: host preference; experience; learning; oviposition behavior; Mediterranean fruit fly; *Ceratitis capitata;* host chemistry.

INTRODUCTION

Cross-induction of host preference is defined as the tendency for experience with a host species by feeding or ovipositing insects to alter behavioral responses to different alternative host species in different ways (Jaenike, 1983). Jaenike, for example, found that female *Drosophila* flies exposed to onion medium exhibited an increase in propensity to oviposit in a second medium, apple, but a decrease in propensity to oviposit in a third medium, tomato, relative to flies exposed to yet a fourth medium, grape. An important implication of this result is that the consequences of experience for host use by a generalist cannot be predicted reliably from assays employing a limited number of host species.

Because experimental subjects were usually exposed to and tested on just two host species, cross-induction has gone largely undetected in previous insect learning studies (Jaenike, 1983; Papaj and Prokopy, 1986) including our own investigations on the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Tephritidae) (Cooley *et al.*, 1986; Papaj *et al.*, 1987). In this study, we describe cross-induction of fruit acceptance by ovipositing Mediterranean fruit flies (medfly). In doing so, we elucidate the fruit stimuli toward which responses are altered by experience. Finally, we examine two hypotheses—termed the "sliding template" and "closing window" hypotheses—concerning the mechanism by which experience alters acceptance of different fruit species.

MATERIALS AND METHODS

Wild medflies were reared from infested loquat (*Eriobotrya japonica;* Rosaceae) collected in Kula, Maui, Hawaii. Males and females were held together at about 25°C, 60% RH, and 13:11 L:D in cages supplied with food (yeast hydrolysate and sucrose) and water.

Effect of Experience on Fruit Acceptance

Flies were separated into 4 cages (25 females and 5 males/cage) between 2 and 4 days after females were reproductively mature [12–14 days postemergence for wild medfly (Wong and Nakahara, 1978)]. The exposure regime was similar to that reported by Papaj *et al.* (1987) and Cooley *et al.* (1986). On Day

1, a single navel sweet orange, *Citrus sinensis* (Rutaceae) (85 ± 5-mm diameter), was introduced into Cage 1. The sweet orange had been punctured with a dissecting needle about 25 times to facilitate oviposition through the thick skin and into the fruit flesh. At the same time, 10 kumquats, *Fortunella japonica* (Rutaceae) (24 ± 3-mm diameter), were hung by wire from the top of Cage 2. Each kumquat was punctured four times with a dissecting needle. Finally 20 freshly picked mock oranges, *Murraya paniculata* (Rutaceae) (8 ± 2-mm diameter), were hung from the top of Cage 3. Each mock orange had been punctured twice with a dissecting needle. Cage 4 contained no fruit. Flies in the latter cage had no opportunity to oviposit into fruit or artificial oviposition devices. Midway through Day 2, fruits in Cages 1–3 were replaced with fresh specimens.

On Day 4, all females in each exposure treatment were tested for propensity to attempt to oviposit into each of five fruits: sweet orange, Valencia orange (*Citrus sinensis;* Rutaceae) (62 ± 2-mm diameter), kumquat, coffee (*Coffea arabica;* Rubiaceae) (13 ± 3-mm diameter), and mock orange. These fruits were chosen to reflect a range of sizes, because fruit size is known to be important in acceptance of oviposition sites by naive tephritid flies (Prokopy and Boller, 1971; Katsoyannos and Pittara, 1983; Papaj and Prokopy, 1986). Flies were removed from the exposure cage, introduced individually into a test cage, and tested 5 min later. An uninfested test fruit that had been washed in water, warmed to room temperature, and punctured with a dissecting needle was then placed in the cage. The female hopped or walked onto a test fruit. It was removed from the fruit when it either accepted the fruit (attempted to bore into the fruit with its ovipositor) or rejected the fruit (left without attempting to bore or remained on the fruit for 5 min without boring). The fly was tested 5 min later on the next fruit species. The order of test fruit presentation was alternated so that each test fruit species was presented first an equal number of times within each exposure treatment. Oviposition into test fruit was prevented by removing a female that attempted to bore before the ovipositor was extended into the fruit. Oviposition was prevented because oviposition into a test fruit represented an opportunity to learn that would have affected subsequent tests. In contrast, the fruit acceptance of females that have been exposed to fruit but that did not oviposit does not seem to change (Papaj, unpublished data).

Effect of Experience on Acceptance of Fruit Models of Different Sizes

This experiment was similar to the first except that, due to problems of fruit availability, mandarin orange, *Citrus reticulata* (Rutaceae) (70-mm diameter), was substituted for sweet orange and calamondin, *Citrus mitis* (Rutaceae) (25-mm diameter), was substituted for kumquat. In addition, females were tested not on real fruit but on artificial fruit models in the form of wax-coated spheres of five different diameters: 6, 11, 24, 54, and 80 mm. The spheres were prepared by coating plastic and clay spheres with ceresin wax dyed red. Ceresin wax in the form of hollow hemispheres is known to elicit relatively high rates of oviposition by tephritid flies (Prokopy and Bush, 1973; Katsoyannos and Pittara, 1983). Exposure and testing procedures were identical to those described above.

Effect of Experience on Acceptance of Chemically Treated Fruit Models

In the third set of experiments, experienced and naive females were tested on wax spherical fruit models treated with surface fruit chemicals. Wax spheres were treated with fruit chemicals using the procedure described by Papaj and Prokopy (1986). Parafilm (American Can Co.) was stretched and wrapped around individual fruit or groups of fruits. The parafilm was left on the fruits for 2 days at room temperature. The parafilm was then removed and applied to wax spheres of each size category. The surface originally in contact with the surface of the fruit was always placed in contact with the surface of the fruit model. It was removed from the wax spheres after 2 h and the spheres were used immediately in testing over a 4-h period. Each day, freshly treated spheres were used in testing.

In one assay, females were exposed to sweet orange, kumquat, or no fruit and tested on large (80-mm-diameter) and medium (21-mm-diameter) wax spheres treated with sweet orange-wrapped, kumquat-wrapped, or blank Parafilm. In another assay, females were exposed to sweet orange, mock orange, or no fruit and tested on large and small (8-mm-diameter) spheres treated with sweet orange-wrapped, mock orange-wrapped, or blank Parafilm. Testing procedures were identical to those described above.

All statistical analyses were performed using SAS statistical routines for personal computers (SAS Institute, 1985) or Statgraphics statistical routines (STSC Corp., 1986).

RESULTS

Effect of Experience on Acceptance of Real Fruit

The overall pattern of acceptance of fruit of different sizes by experienced female medflies depended on the fruit to which they were exposed (Figs. 1A–C). An analysis of covariance indicated that the linear relationship between fruit size and fruit acceptance depended on the fruit to which females were exposed [ANCOVA; fruit size × fruit exposure effect, $F(2,9) = 6.58$, $P < 0.05$]. In both sweet orange and mock orange treatments, experience altered differentially acceptance of different fruits, reflecting cross-induction of preference. Females

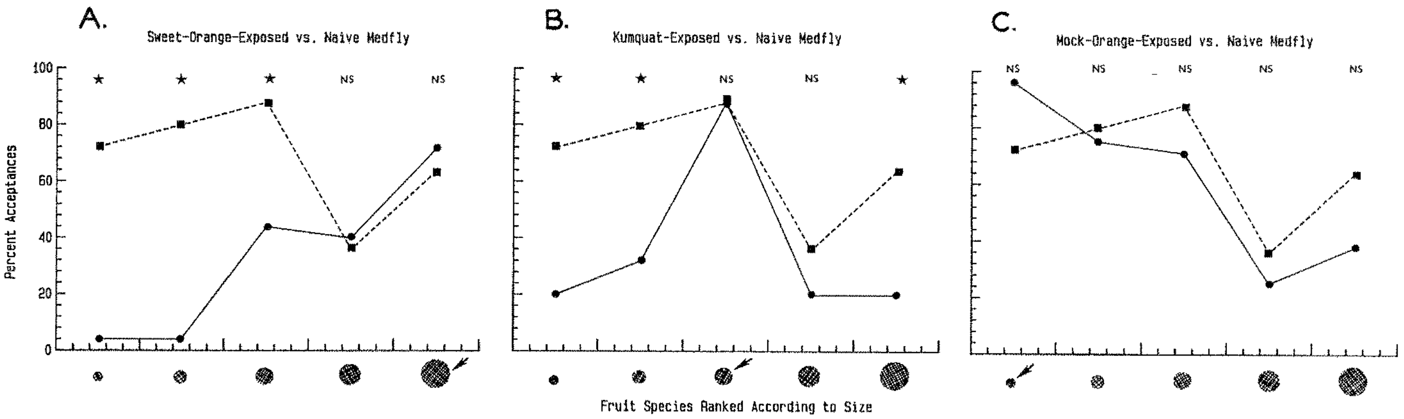

Fig. 1. Acceptance of fruit of different sizes by naive female medflies (dashed line) and female medflies exposed previously to host fruit (solid line). Fruit types in order of increasing size are mock orange, coffee, kumquat, Valencia orange, and sweet orange. Stars indicate significant differences between naive and experienced flies according to a two-way χ^2 test with Yates correction at an alpha level of 0.01 to correct for experiment-wise error rate. NS indicates no significant difference. Arrows point to the fruit to which females were exposed: (A) sweet orange, (B) kumquat, and (C) mock orange.

exposed to large sweet orange, for example, were progressively more likely to accept fruit as the ranked size of test fruit increased [Fig. 1A; simple regression, $F(1,3) = 21.7$, $P < 0.02$]. Females exposed to small mock orange, in contrast, were progressively less likely to accept fruit as the ranked size of the test fruit increased [Fig. 1C; simple regression, $F(1,3) = 15.3$, $P < 0.03$]. In contrast to sweet orange-exposed and mock orange-exposed individuals, females exposed to kumquats were very likely to accept kumquats but exhibited an almost identically low acceptance of each of the other four fruits [Fig. 1B; simple regression, $F(1,3) = 0.01$, $P > 0.9$], reflecting the absence of a linear relationship between fruit acceptance and fruit size and a corresponding absence of cross-induction.

Experience with a fruit of a particular size generally reduced a female's propensity to accept fruit of other sizes, relative to females with no fruit experience at all (i.e., naive females). The magnitude of the reduction was usually proportional to the difference in size between the exposure and the test fruit. Sweet orange-exposed females, for example, were as likely to accept sweet orange and the next smaller fruit, Valencia orange, as were naive females but were much less likely to accept the three smallest fruits than were naive females (Fig. 1A). A three-way *G* test between fruit acceptance (accept vs reject) and fruit exposure (sweet orange vs kumquat vs mock orange) and test fruit species (all five test fruit species) indicated that differences in acceptance of different fruit species depended on the fruit species to which females were exposed (fruit acceptance × fruit exposure × test fruit interaction, $G = 38.64$, df = 4, $P < 0.0001$). Similarly, kumquat-exposed females were as likely to accept kumquat and the next larger fruit, Valencia orange, as were naive females, but were less likely to accept the other three fruits than were naive females (Fig. 1B). The overall pattern was not, however, significant (three-way *G* test, fruit acceptance × fruit exposure × test fruit interaction, $G = 7.02$, df = 4, $P > 0.1$). Mock orange-exposed females, in contrast, exhibited a more complex pattern, accepting mock orange slightly (although not significantly) more frequently than did naive females and accepting all other fruit slightly less frequently than did naive females (Fig. 1C). The overall pattern was highly significant (three-way *G* test, fruit acceptance × fruit exposure × test fruit interaction, $G = 11.05$, df = 4, $P < 0.05$). The greatest reduction in acceptance by mock orange-exposed females relative to naive females was associated with sweet orange, the fruit most different in size from mock orange.

Effect of Experience on Acceptance of Fruit Models of Different Sizes

Naive females responded to artificial fruit models approximately as they did to real fruit (Fig. 2) with one notable exception: acceptance of the smallest wax sphere was markedly less than acceptance of the smallest real fruit (*G* test, $P < 0.05$).

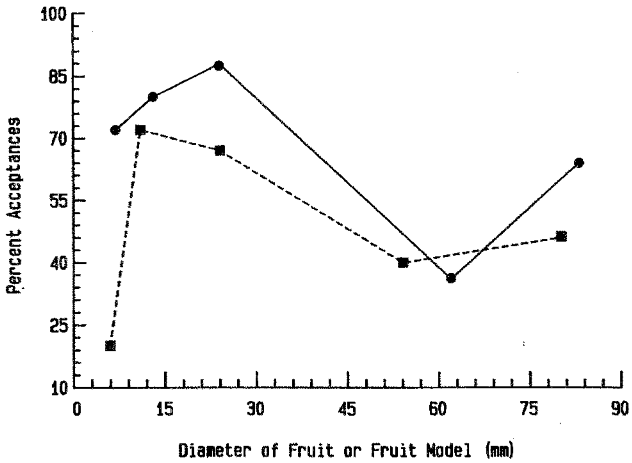

Fig. 2. Acceptance of real fruit (solid line) or wax spheres (dashed line) of different diameters by naive female medflies.

Although the relationship between acceptance of wax spheres and sphere size by experienced females depended only marginally on the fruit to which they were exposed [Figs. 3A–C; ANCOVA; fruit size × fruit exposure effect, $F(2,9) = 2.92$, $P > 0.05$], results with wax spheres tended to affirm results with real fruit. Mandarin orange-exposed females, like their sweet orange-exposed counterparts on real fruit, were generally more likely to accept spheres as the size of the sphere increased (Fig. 3A). Nevertheless, mandarin orange-exposed females accepted most frequently a sphere that was considerably smaller than mandarin orange. Like their kumquat-exposed counterparts on real fruit, calamondin-exposed females were most likely to accept the sphere most similar in size to calamondin and rejected all other spheres to approximately the same extent (Fig. 3B). Finally, mock orange-exposed females, like their counterparts on real fruit, were generally less likely to accept spheres as the size of the sphere increased (Fig. 3C). Nevertheless, the sphere closest in size to mock orange was accepted considerably less frequently than the next larger sphere.

Effect of Experience on Acceptance of Chemically Treated Models

Overall, mandarin orange-exposed and calamondin-exposed females attempted oviposition into artificial fruit models much less frequently than did naive females (Figs. 3A and B), suggesting that some cue to which these females became sensitive with experience was lacking in the models. Assays with Parafilm-treated models suggest that this cue was chemical in nature. Females generally accepted wax spheres treated with fruit chemicals more often than untreated spheres of the same size (Tables I and II). This tendency was most

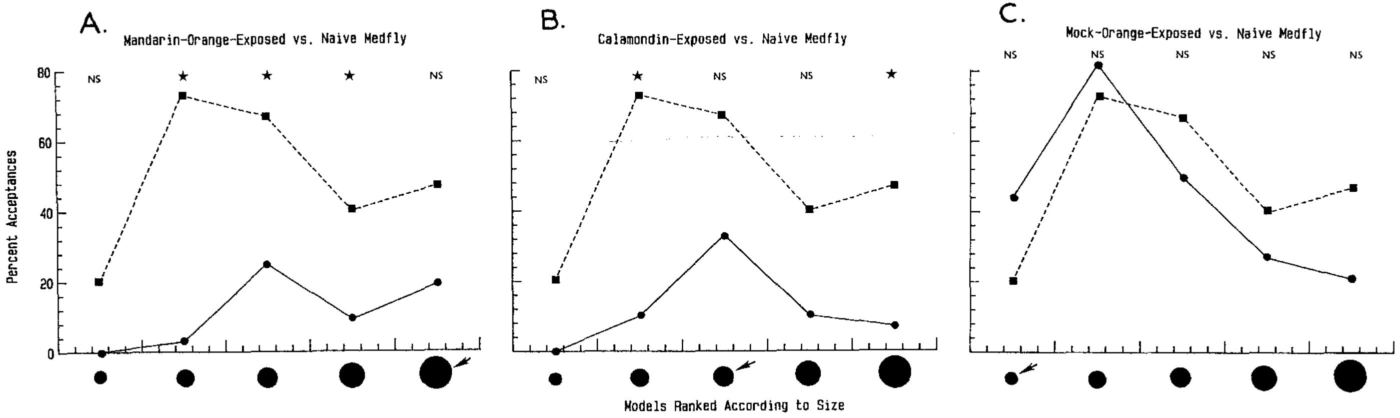

Fig. 3. Acceptance of wax spheres of different sizes by naive medflies (dashed line) and medflies previously exposed to host fruit (solid line). Sphere diameters (mm) in order of increasing size are 7, 11, 24, 54, and 80. Stars indicate significant differences between naive and experienced flies according to a two-way χ^2 test with Yates correction at an alpha level of 0.01 to correct for experiment-wise error rate. NS indicates no significant difference. Arrows point to the model closest in size to the fruit to which females were exposed. The fruits were (A) mandarin orange, (B) calomondin, and (C) mock orange.

Table I. Percent Acceptance of Parafilm-Treated Wax Spheres of Different Sizes by Females Exposed to Sweet Orange and Kumquat

		% females accepting sphere of diameter[a]					
		80 mm Parafilm treatment			21 mm Parafilm treatment		
Fruit exposure		Sweet orange	Kumquat	Blank	Sweet orange	Kumquat	Blank
Sweet orange	*N*	37	37	37	37	37	37
	%	38 ac_1	22 ac_1	3 b_1	46 c_1	41 cd_1	22 ac_1
Kumquat	*N*	39	39	39	39	39	39
	%	31 ac_1	41 a_1	31 ac_2	72 b_1	85 b_2	69 bc_2

[a] Values in rows followed by the same letter are not significantly different according to a Yates-corrected χ^2 test at the 0.01 level (to correct for experiment-wise error rate). Values in columns followed by the same number are not significant according to the same criterion.

striking for sweet orange-exposed females tested on large spheres and mock orange-exposed females tested on small spheres. Logistic regression analysis (SAS Institute, 1985) was used to distinguish the effects of fruit experience (sweet orange vs kumquat in the first assay, sweet orange vs mock orange in the second assay) on acceptance responses to sphere size (80-mm vs 21-mm diameter in the first assay, 80-mm vs 8-mm diameter in the second assay) or to Parafilm treatment (sweet orange vs kumquat in the first assay, sweet orange vs mock orange in the second assay).

Table II. Percent Acceptance of Parafilm-Treated Wax Spheres of Different Sizes by Females Exposed to Sweet Orange and Mock Orange.

		% females accepting sphere of diameter[a]					
		80 mm Parafilm treatment			8 mm Parafilm treatment		
Fruit exposure		Sweet orange	Mock orange	Blank	Sweet orange	Mock orange	Blank
Sweet orange	*N*	30	14	22	30	14	16
	%	30 a_1	0 a_1	5 a_1	3 a_1	0 a_1	0 a_1
Mock orange	*N*	30	15	22	30	15	22
	%	20 a_1	7 a_1	14 a_1	53 b_2	80 b_2	45 ab_2

[a] Percentages in rows followed by the same letter are not significantly different according to a Yates-corrected χ^2 test at the 0.01 level (to correct for experiment-wise error rate). Percentages in columns followed by the same number are not significant according to the same criterion.

In the first assay, the overall effect of experience on acceptance depended on both the size of the sphere (Table I; logistic regression, fruit exposure × sphere size effect, $\chi^2 = 5.48$, df = 1, $P < 0.02$) and the type of Parafilm with which the sphere was treated (logistic regression, fruit exposure × Parafilm treatment effect, $\chi^2 = 7.85$, df = 1, $P < 0.02$). Sweet orange-exposed females were more likely to accept a sweet orange-treated sphere than either a kumquat-treated or a blank sphere. Kumquat-exposed females were also slightly more likely to accept a kumquat-treated sphere of a given size than either a sweet orange-treated or a blank sphere.

In the second assay, the effect of experience on acceptance again depended significantly on the size of the sphere (Table II; logistic regression, fruit exposure × sphere size effect, $\chi^2 = 13.49$, df = 1, $P < 0.0002$). Females exposed to sweet orange were more likely to accept a large than a small sphere; females exposed to mock orange were more likely to accept a small than a large sphere. In contrast to the first assay, the effect of experience on acceptance did not depend significantly on the type of Parafilm with which the sphere was treated (Table II; logistic regression, fruit exposure × Parafilm treatment effect, $\chi^2 = 3.47$, df = 2, $P > 0.10$). Nevertheless, sweet orange-exposed females were more likely to accept a sweet orange-treated sphere than either a mock orange-treated or a blank sphere. Similarly, mock orange-exposed females were more likely to accept a mock orange-treated small sphere than either a sweet orange-treated or a blank small sphere.

DISCUSSION

Previous studies on the specialized tephritid fruit fly, the apple maggot fly (*Rhagoletis pomonella*), established that prior adult experience alters fruit acceptance at least in part by modifying responses to fruit size and chemistry (Papaj and Prokopy, 1986, 1987). The present study extends this finding to the medfly, a generalist tephritid attacking over 250 host species. In some cases the effects of experience on medfly response to fruit size and to fruit chemistry acted independently (Table I; logistic regression, fruit exposure × Parafilm treatment × sphere size effect, $\chi^2 = 1.27$, df = 2, $P > 0.5$), a result paralleled in learning by apple maggot flies (Papaj and Prokopy, 1986). Sometimes, however, the effect of experience on response to fruit size depended on fruit chemistry. In the absence of fruit chemicals, for example, mock orange-exposed females commonly rejected the small mock orange-sized wax sphere (Fig. 3C). The application of mock-orange chemicals to the surface of the sphere raised acceptance of the model to a level comparable to that of the actual fruit (Table II, Fig. 1C). Possibly, the chemical(s) suppressed flight [which is the most common negative response to the blank 8-mm model (Papaj, unpublished data)] and, by doing so, enhanced the likelihood of ovipositor boring. Regardless of the actual mechanism, the finding that physical and chemical stimuli interact during learning of host-selection behavior complements the growing body of evidence that physical and chemical stimuli interact during the host-selection behavioral sequence itself (Harris and Miller, 1982; Prokopy *et al.*, 1987).

While both sets of stimuli were involved in learning, only physical stimuli associated with fruit size were shown unambiguously by our results to account for cross-induction of fruit acceptance. With respect to fruit size, at least two hypotheses concerning the mechanism by which experience alters fruit acceptance by the medfly can be erected: (1) there is an internal template of fruit sizes which are accepted to differing degrees, a template which slides to favor acceptance of the fruit with which females are experienced; and (2) there is a window of fruit sizes which are accepted to differing degrees, a window which closes to favor acceptance of the fruit with which females are experienced. These alternative hypotheses are summarized graphically in Fig. 4.

If the "sliding template" hypothesis was valid, plots of fruit acceptance vs fruit size for experienced flies should take the same form as that for naive flies (shown in Figs. 1A–C) but should be shifted in one direction or another along the fruit size axis (Fig. 4A). For sweet orange-exposed females, the plot for naive flies should be shifted right so that peak acceptance occurs on sweet orange. For mock orange-exposed females, the plot should be shifted left so that peak acceptance occurs on mock orange. Since peak acceptance for naive flies occurs on kumquat, the plot for kumquat-exposed flies should be identical

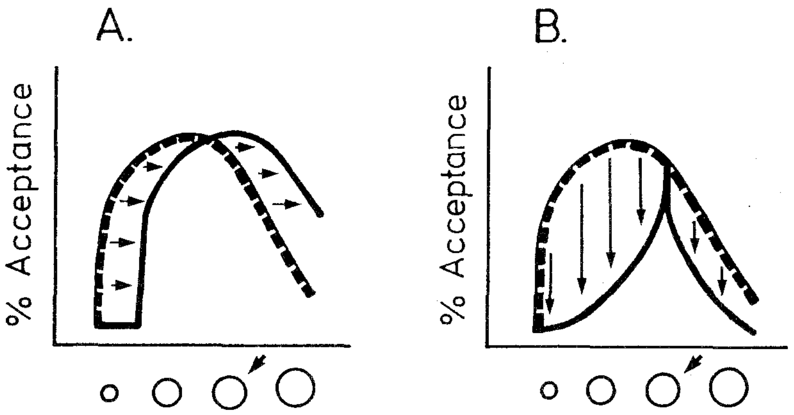

Fig. 4. (A) sliding template hypothesis. Experience shifts the acceptance curve in the direction indicated by arrows so that peak acceptance corresponds to the fruit with which females are experienced. (B) Closing window hypothesis. Experience shifts acceptance of all fruit except the one with which females are experienced in the direction indicated by the arrows. Circles on abscissa represent fruit size increasing continuously. Arrow on abscissa points to the fruit with which females are experienced. Dashed line represents fruit acceptance curve for naive females; solid line represents fruit acceptance curve after experience.

to that of naive flies. Clearly, the plots for neither sweet orange-exposed nor mock orange-exposed females were simple phase shifts of the plot for naive females (Figs. 1A–C). Nor was the plot for kumquat-exposed females identical to that for naive females (Fig. 1B).

Rather, the acceptance of the fruit to which females were exposed remained largely the same as that for naive females and the acceptability of fruit other than those to which females were exposed was diminished. In other words, a window of fruit acceptance contracted with experience as proposed by the "closing window" hypothesis (Fig. 4B). This effect was most obvious when flies were exposed to kumquat, the fruit of intermediate size. When flies were exposed to sweet orange or mock orange—fruits of extreme size—acceptance of the other fruits diminished according to their position along the size continuum. In other words, the window closed but "leaked" acceptance of fruit similar in size to the fruit with which females were experienced.

This pattern of "leakiness" in which responses to different fruit species were affected differently by previous adult experience is, by definition, cross-induction of preference. For kumquat-exposed females, the window of acceptance was not "leaky" and admitted only kumquat. Since they rejected all other fruit species approximately equally (Fig. 1B), there was little, if any, cross-induction for kumquat-exposed females. For mock orange-exposed and sweet orange-exposed females that rejected alternative fruit species according to their similarity in size to the exposure fruit, cross-induction was striking. Cross-induction for these females could essentially be quantified as the slope of the regression of fruit acceptance on fruit size (Figs. 1A–C).

In our study, naive females were not permitted to oviposit. These females therefore differed from experienced females both in the degree of prior exposure to fruit and in the number of eggs they had laid prior to testing. In experiments with apple maggot flies, Prokopy *et al.* (1987) found that naive females behaved similarly to females that had the opportunity to oviposit but that had been experienced with more than one fruit species (so-called "untrained" females). Both groups showed essentially the same deviation in fruit acceptance from females experienced with a single fruit species. For that reason alone, differences between naive females and females experienced with a single host fruit species can probably be ascribed to differences in fruit experience and not to differences in egg load.

In addition, even if the absolute preference of naive females differed from that of experienced females in part because of differences in egg load, this would not account for the pattern of differences between naive flies and flies that were exposed to different fruit species. Differences in egg load between naive and experienced females may alter the absolute amount by which the fruit acceptance window appears to close with each kind of fruit experience but would not make the closing window hypothesis more tenable than the sliding template hypothesis.

The function of cross-induction (indeed, of learning itself) in medfly foraging is currently unclear. It is difficult to imagine, however, an adaptive reason for females to reject fruits according to their similarity in size to the fruit with which they are accustomed. It is perhaps more plausible to suppose that this pattern reflects a constraint built into an herbivore's host recognition system and that cross-induction has little, if any, adaptive value. In short, an experienced ovipositing insect might accept different host species to differing degrees, not because these differences in response necessarily benefit its progeny or increase its rate of oviposition, but simply because the insect cannot distinguish between the host species with which it has prior experience and alternative species that are similar in appearance (e.g., size). Whether or not it is adaptively significant, though, cross-induction of preference should have an impact on the extent to which experienced insects use alternative species as these become available over space or time (Jaenike, 1983). For the Mediterranean fruit fly, this impact will remain ambiguous until learning under field conditions is rigorously investigated.

ACKNOWLEDGMENTS

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