The Role of Experience in Plant Foraging by the Aphid Parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae)

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Experiments were conducted to test the hypothesis that plant learning by a relative plant-specialist parasitoid wasp should influence the probability of orienting to plant odors (plant finding) and the duration of searching on a plant after landing (plant examining). The insect tested was Diaeretiella rapae *M'Intosh (Hymenoptera: Aphidiidae), a parasitoid wasp that usually attacks aphids on cruciferous plants, but occasionally on other plants. Laboratory experiments using collard as the cruciferous plant and potato as the novel plant demonstrated that postemergence (adult) plant experience affected plant examining only on the less preferred plant, potato, and was reversible and relatively long-term (that is, lasted > 2 days). Postemergence experience with potato did not increase orientation to potato odor in a wind tunnel, but postemergence experience with collard resulted in a trend of increased likelihood of flying to collard odor. Preemergence treatments affected plant finding but not plant examining.*

KEY WORDS: parasitoid; plant foraging; habitat selection; experience; learning; *Diaeretiella rapae;* Hymenoptera; Aphidiidae

INTRODUCTION

Learning (modifications of behavior that are relatively long-term and reversible) has been demonstrated at different stages of host foraging for numerous species

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of phytophagous (reviewed by Papaj and Prokopy, 1989) and entomophagous insects (reviewed by Arthur, 1981; Vinson, 1981). Much of this work has addressed learning behavior involved in host finding and examining (*sensu* Miller and Strickler, 1984). For parasitoids, the stage immediately preceding host finding has been called host habitat or host community *location* (Vinson, 1976, 1981, 1984). However, for parasitoids of herbivorous insects, after a foraging female alights on a plant she may still examine the site for hosts for a variable length of time. We call the suite of behaviors following physical contact with such a site, but prior to encountering a host or host kairomone, microhabitat or plant *examining*. Following Singer (1986) we avoid restricting the commonly used term *acceptance* to this stage of foraging behavior in recognition of the fact that *both* plant finding and plant examining may involve perception and acceptance of sensory information. The purpose of the work reported here was to determine if previous experience with plants can influence either component of plant foraging—finding or examining—by a parasitoid wasp.

We studied the solitary endoparasitoid of aphids, *Diaeretiella rapae* M'Intosh (Hymenoptera: Aphidiidae). This wasp usually attacks aphids on cruciferous plants, which it is thought to find by responding to mustard oils (Read *et al.*, 1970; but see Sheehan and Shelton, 1989). *Diaeretiella* is virtually the sole primary parasitoid attacking cabbage aphid on crucifers (Hafez, 1961; Nemec and Starý, 1984), but it also commonly attacks other aphid species on crucifers (Pimentel, 1961; Root and Gowan, 1978; Horn, 1984). However, the wasp is also reported sporadically from 30 different species of aphids infesting plants in more than a dozen plant families (Mackauer and Starý, 1967; Nemec and Starý, 1984). This distribution suggests that *D. rapae* is a crucifer specialist, but not entirely so. The ability to learn plant characteristics could facilitate the utilization of alternative hosts where or when crucifers are scarce.

As a relative plant specialist *D. rapae* is a good candidate for assessing the importance of learning in parasitoids. Previous studies on parasitoids of herbivorous insects have demonstrated learning in plant finding by plant generalists (Arthur, 1966; Vinson *et al.*, 1977; Wardle and Borden, 1985, 1986; Drost *et al.*, 1986, Lewis and Tumlinson, 1988). Furthermore, most workers believe that learning capacity should be better developed in generalist than in specialist foragers (Arthur, 1971; Cornell, 1976; Waage, 1979; Glasser, 1984; Vet and Opzeeland, 1984). Implicit in this belief is the untested assumption that specialists trade off behavioral flexibility for increased searching efficiency. Demonstration of learning in foraging by plant specialist parasitoids would indicate that diet specialization need not preclude behavioral flexibility and that learning is more widespread than currently believed.

MATERIALS AND METHODS

Insects and Plants

Female *D. rapae* (5th–25th generation from wasps originally collected from cabbage aphid on cabbage near Geneva, New York) were used in all experiments. Stock cultures of wasps were reared continuously in cabbage aphid (*Brevicoryne brassicae*), the preferred host (Hafez, 1961), on collard (*Brassica oleraceae acephala* cv. Vates). Stock wasps were then allowed to parasitize green peach aphid (*Myzus persicae*), a common alternative host on both crucifers and potatoes (Shands *et al.*, 1965; Horn, 1984). Wasps were reared in green peach aphid either on collard for 1–2 generations or on potato (*Solanum tuberosum* cv. Green Mountain) for 1 or for 15–20 generations before use in experiments.

Plant Finding Assay

To test the effect of experience on plant finding we flew wasps singly in a no-choice wind tunnel assay. A 51-cm floor fan pushed air at 50 cm/min through a 60 × 60 × 200-cm glass and Plexiglas chamber. A darkened upwind section was separated from the test section by an organdy screen that reduced turbulence and also hid the odor source from parasitoids. The test section was the downwind 80 cm of the chamber. Strips of black tape at 20-cm intervals on the floor were used to provide visual reference for flying wasps. Six 40-W Sylvania Daylight fluorescent bulbs suspended above the chamber shone through diffusing paper to provide 30 lux of light at release height. At the chamber exit, air from the central portion of the tunnel was vented from the room.

We designed this assay to distinguish pre- from postemergence treatment effects in response to plant odor. Prior to emergence from the mummified aphid wasps spend 1–2 days as teneral adults (Hafez, 1961), so preemergence effects may occur during the teneral adult stage or earlier. We varied pre- and postemergence plant experience by removing mummified aphids from collard and potato plants and allowing wasps to emerge in conditioning cages on either the same or on the other type of plant, thereby creating four treatments. Conditioning cages contained potted aphid-infested plants and were placed in semicontrolled environment chambers (19–22°C; 40–70% relative humidity; 16:8 L:D cycle) only with other plants of the same type (collard or potato).

We allowed wasps (<2 days old) to walk on a leaf and oviposit in green peach aphids for 2 min before releasing them in the wind tunnel. This practice resulted in calmer behavior upon release and increased the likelihood of ori-

enting in the odor plume (cf. Drost *et al.*, 1988). We released wasps from a vial positioned on a platform in the odor plume of a single collard or potato leaf (approximately 300-cm^2 leaf surface area). This test leaf was the same type as the leaf on which the wasps had just previously oviposited. Immediately prior to releasing the wasp, the test leaf was scored 10 times with a 0.5-cm-diameter leather punch to release leaf volatiles and placed upwind of the organdy screen with a piece of green netting 5 cm in diameter attached to it. Wasps did not fly upwind to the green netting in the absence of leaf ordor, but the presence of green increased the number of flights to the front screen (W. Sheehan, unpublished data). Wasps that alighted on or within 10 cm of the green netting within 5 min after leaving the release vial were considered to have reached the target; if they did not, wasps were given a second opportunity after 60 s. We tested the responses of 20 wasps from each of the four conditioning treatments to collard odor and 20 from each to potato odor. Proportions of wasps reaching the target were analyzed by chi-square multiway contingency tests. All responses were used to test the null hypothesis that the pattern of responses to collard odor was independent of the pattern of responses to potato odor. Responses to each odor source were then tested separately, with a continuity correction. Since there is only one degree of freedom for such tests, significance must be interpreted conservatively.

Plant Examining Assay

To see if plant experience affected acceptance of the plant during examining we measured searching times of wasps on collard and potato. Experiments were performed and conditioning cages were held in the aforementioned environment chambers. Wasps were reared in green peach aphids on collard or potato and transferred as mummies to leaves placed in 30 × 30 × 38-cm Plexiglas cages where the adults emerged. These conditioning cages contained plants (10 cut leaves in vials) and green peach aphids, except for two treatments in which wasps were exposed to collard leaves alone (see Fig. 4), and naive treatments, in which wasps were exposed to neither plants nor aphids. Food for adult wasps was provided by streaking the cage tops with a 40% honey solution. Except where precluded by the nature of the treatment only wasps <2 days old that were actively searching leaves (walking while antennating the leaf surface) in conditioning cages were used in experiments. Wasps for all experiments were collected by aspirating them gently into cotton padded glass vials.

In all tests we released wasps individually onto single, uninfested collard or potato leaves, which were changed after two to four trials. Test leaves had not been infested with aphids and therefore were not contaminated with honey-

dew, which acts as a kairomone for *D. rapae* (Ayal, 1987; W. Sheehan, unpublished data). In initial tests comparing pre- versus postemergence effects we released wasps directly onto leaves and observed them for 5 min or until they flew off the leaf (preliminary observations showed that wasps almost never returned to the leaf within 5 min). The assay was subsequently modified so that wasps were allowed to fly onto the leaf from the rim of a transfer vial held 3 cm below the leaf. We used a Radio Shack TRS-80 Model 100 computer programmed as an event recorder to record time spent actively searching, cleaning, and resting on the leaf. Wasps were observed for 10 min or until they left the leaf; those that failed to establish (spent < 10 s) on a leaf were given a second trial.

Pre- Versus Postemergence Effects. The same protocol of switching mummies used in the plant finding assay was followed in testing for pre- versus postemergence treatment effects on plant examining. We also tested naive wasps, that is, wasps exposed to neither plants nor aphids after emergence. Naive wasps were reared as larvae either in cabbage aphids on collard (for 15–20 generations at the time of testing), in green peach aphids on collard (for 1–2 generations), or in green peach aphids on potato (for 1 or for 15–20 generations). Data were analyzed by ANOVA and, where necessary, unequal variance *t* tests.

Effects of Postemergence Experience. In the remaining experiments we tested only the effect of postemergence experience on plant examining behavior since preemergence treatment did not affect searching time. All wasps emerged from green peach aphid mummies that had been transferred from collard to plants in conditioning cages. Conditioning cage treatments included aphid-infested potato, aphid-infested collard, and collard alone. The effect of wasp age on plant examining behavior was determined on both collard and potato. Wasps in two age classes (0–2 and 2–4 days) were tested on collard; these and a 4- to 6-day-age class were tested on potato. Data were analyzed by ANOVA.

Memory Effect on Potato. In the following two experiments we tested wasps only on potato leaves since searching times were similar on collard, regardless of plant or aphid experience. To test duration of modification of plant examining behavior (memory effect) we allowed adult wasps to experience aphid-infested collards or potatoes for 1–2 days and then isolated them from both stimuli for 4, 24, 48, or 72 h before testing. Individual wasps were not retested. Searching times of these wasps were compared with those of wasps (0–2 days old) tested immediately after initial conditioning (that is, isolated for 0 h). Data were analyzed by linear regression methods.

Reversibility Effect on Potato. To test reversibility of postalighting acceptance behavior we allowed wasps to experience aphid-infested plants of one type for 1–2 days before switching them to aphid-infested plants of the other

type for 1, 4, 24, 48, or 72 h before testing. As in the memory experiment above, we compared searching times with those of untreated wasps (0–2 days old, not switched to the other plant) and we did not retest individuals. Log transformed pre- and posttreatment means were analyzed by ANOVA.

RESULTS

Plant Finding

The pattern of responses by wasps to collard odor in the wind tunnel was independent of the pattern of responses to potato odor ($P > 0.35$; Fig. 1). When flown to collard odor both pre- and postemergence experience treatments appeared to affect the proportion of wasps reaching the target (Fig. 1, left). Wasps reared on collard flew significantly more often to collard than those reared on potato ($P < 0.006$). Furthermore, there is a trend toward a postemergence effect: slightly more wasps that experienced collard after emergence flew to collard odor than did wasps that experienced potato after emergence (19 versus 16 wasps; $P < 0.14$). In contrast to collard odor, potato odor stimulated fewer flights by wasps in all treatments (Fig. 1, right). In these trials the only suggestion of a treatment effect was of a preemergence effect, and wasps reared on potato as larvae flew to potato odor *less* often than collard-reared wasps ($P <$
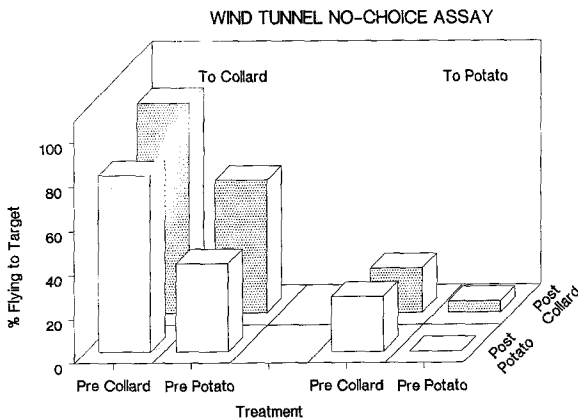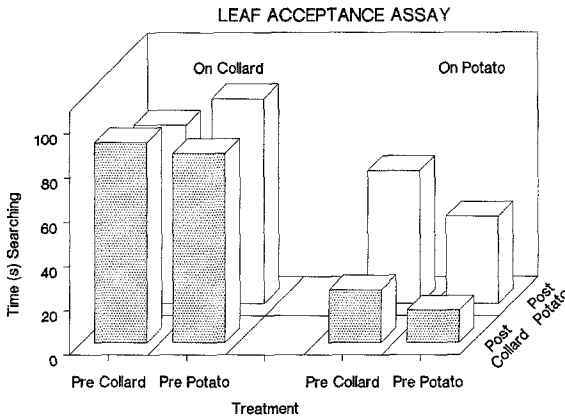

Fig. 1. Percentages of wasps that flew to collard and potato odor as a function of pre- and postemergence treatment. Pre, preemergence plant (experienced by larval, pupal, and teneral adult wasp stages); post, postemergence plant. $N = 20$ wasps for each treatment combination (=bar).

0.01). None of the wasps reared on potato as both larvae and adults flew to potato odor.

Plant Examining

Pre- Versus Postemergence Effects. Overall, searching time was significantly higher on collard for wasps in all treatments ($P < 0.0001$; Fig. 2). Wasps that experienced collard after emergence searched collard 4.5 times (68.6 ± 14.2 s) longer than they searched potato, while wasps that experienced potato after emergence searched collard 1.7 times (36.1 ± 15 s) longer than they searched potato. When released onto collard leaves, neither pre- nor postemergence plant treatments had an effect on searching time ($P > 0.84$ and $P > 0.93$, respectively; Fig. 2, left). However, when released onto potato, wasps that experienced potato after emergence searched potato 2.6 times (60.7 ± 12.0 s) longer than wasps that experienced collard after emergence (Fig. 2, right). Preemergence treatment had no effect on searching time on potato ($P > 0.22$).

Naive wasps searched collard longer than potato in all treatments ($P < 0.0001$; Table I). Searching times on potato for naive wasps reared as larvae in cabbage aphid on collard were similar ($P > 0.90$) to those reared in green peach aphid on collard. However, there was considerably *less* ($P < 0.01$) searching by naive wasps reared as larvae for one generation in green peach aphids on potato. After 15–20 generations on potato, searching times had

Fig. 2. Mean searching times (s) on collard and potato as a function of pre- and postemergence treatment. Pre, preemergence plant (experienced by larval, pupal, and teneral adult wasp stages); post, postemergence plant. $N = 18$–21 wasps tested in each treatment combination (=bar).

Table I. Searching and Cleaning Times on Potato and Collard for Naive Wasps[a]

Treatment				Time on potato (s)					Time on collard (s)			
Plant	Aphid	Generation	N	Search	SE	Clean	SE	N	Search	SE	Clean	SE
Collard	CA	Stock	20	55.5	19.7	141.0	33.5	—	—	—	—	—
Collard	GPA	1–2	54	50.6	9.3	117.6	23.6	8	350.6	49.5	203.5	50.6
Potato	GPA	1	64	24.0	3.9	100.9	20.7	4	133.0	48.8	181.7	119.6
Potato	GPA	15–20	57	55.2	12.5	99.8	21.0	10	240.3	65.0	254.5	57.2

[a]Wasps did not experience plants or aphids after emergence from mummies. CA, cabbage aphid; GPA, green peach aphid; N, sample size; SE = 1 standard error.

increased significantly ($P < 0.005$) and were not different ($P > 0.90$) from naive collard-reared wasps.

Effects of Postemergence Experience. Results similar to those above were found in the modified assay in which only postemergence experience was tested and wasps were allowed to fly onto the leaf (compare the four right-hand points in Fig. 3 with the four "Pre Collard" bars in Fig. 2). Again, potato-experienced wasps searched potato longer (3.2 times, or 93.0 $\pm$ 34.8 s; $P < 0.05$) than collard-experienced wasps and there was no difference between treatments in searching times on collard ($P > 0.56$). Compared with plant experience alone ("Collard Only" in Fig. 3), oviposition experience on collard neither increased searching time on collard ($P > 0.48$) nor decreased searching time on potato ($P > 0.60$). In fact, there was a slight trend in the opposite direction in both cases. The major difference between initial and modified plant examining assay results is that in the latter, potato-experienced wasps tended to spend more (but not significantly more), rather than less, time searching potato than collard. Notably, in both assays potato-experienced adults tested on potato showed the most variation in searching time among all treatments.

Wasp age had no effect on searching time of collard-experienced wasps when released onto potato ($P > 0.81$) and no effect on potato-experienced wasps less than 4 days old ($P > 0.68$; Fig. 4A). Only for the oldest age class was there a significant decline in searching time ($P < 0.01$). When released onto collard there was again no significant decrease in searching time for potato-experienced wasps up to 4 days ($P > 0.71$; Fig. 4B). However there was a
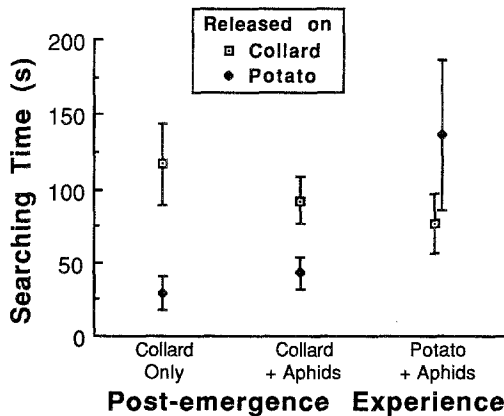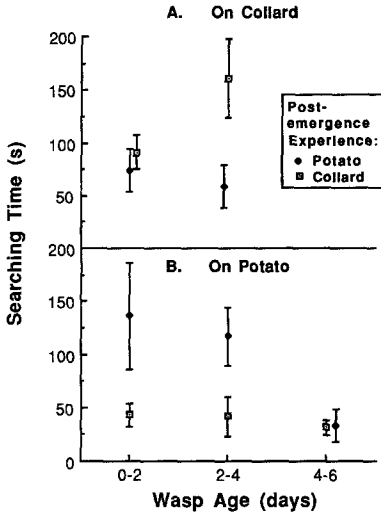

Fig. 3. Mean searching times (s $\pm$ SE) on collard and potato as a function of postemergence adult experience. Wasps were confined for 1–2 days with collard only, with aphid-infested collard, or with aphid-infested potato. $N =$ 13–26 wasps tested in each treatment.

Fig. 4. Mean searching time (s ± SE) as a function of age (time from emergence from mummy) and postemergence plant experience. Conditioning plants were aphid-infested. All wasp larvae were reared in green peach aphid on collard. $N = 13–23$ wasps tested in each treatment. (A) Searching time on collard. (B) Searching time on potato.

trend toward *increased* searching time by older collard-experienced wasps ($P > 0.06$).

Memory Effect on Potato. Wasps isolated from potato searched potato longer than wasps isolated from collard, as shown by the significantly different intercepts of the fitted linear regressions in Fig. 5 ($P < 0.005$). Although there was a suggestion of a negative slope for potato-experienced wasps, the slopes were not significantly different from zero for either potato or collard-experienced wasps ($P > 0.29$ and $P > 0.23$, respectively). Thus the effects of potato conditioning on searching time lasted for at least 2 days.

Reversibility Effect on Potato. Wasps switched from potato to collard searched potato less than wasps that only experienced potato ($P < 0.05$; Fig. 6A). The effect of potato experience appeared to be forgotten after 1 day in the presence of collard. On the other hand, when switched from collard to potato, wasps searched potato longer than wasps that experienced collard alone ($P < 0.004$; Fig. 6B). The effect lasted for at least 2 days.

DISCUSSION

Previous experience with plants most clearly affected plant examining by postemergent-conditioned *D. rapae*. Postemergence experience with potato as compared with collard resulted in a longer examining time on potato but did not affect examining time on collard (Figs. 2 and 3). On the other hand, post-emergence experience with collard resulted in a trend (nonsignificant) toward
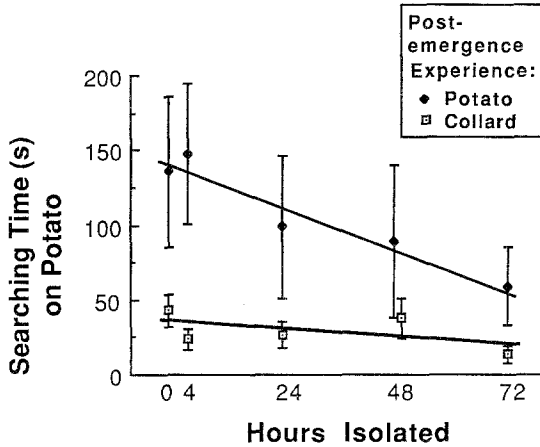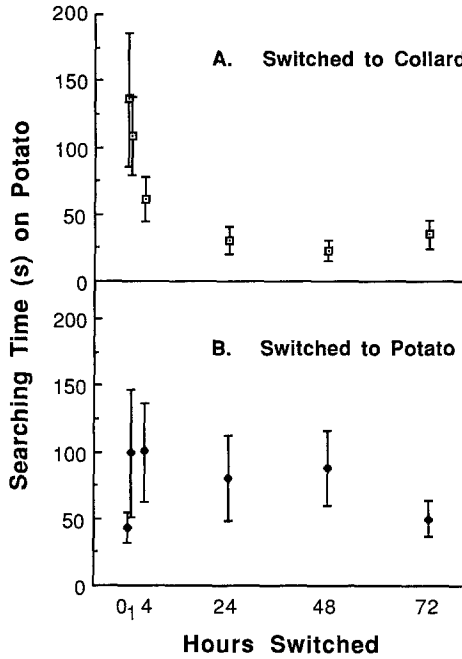
Fig. 5. Memory of plant acceptance. Mean searching times (s ± SE) on potato are shown for wasps confined with aphid-infested potatoes (♦) or collards (□) for 1–2 days and then either tested directly (0 h) or isolated from both plants and aphids for 4–72 h before testing. Individual wasps were not retested. For potato-experienced wasps, $Y = 141.5 - 1.20$ (± 1.13) h. For collard-experienced wasps, $Y = 35.2 - 0.21$ (± 0.17) h. $N = 10$–20 wasps tested in each treatment, except the 72-h potato treatment, in which only two wasps were tested.

increased likelihood of flying to collard odor (Fig. 2). Our experiments with naive wasps (Table I) are consistent with the implication from distribution records (Nemec and Starý, 1984) that crucifers are intrinsically preferred by *D. rapae*. Therefore experience with a less acceptable plant, such as potato, may increase the likelihood of searching a similar plant if one is reencountered. But it *may* also reduce the likelihood of flying to the more acceptable plant, a crucifer.

The term learning applies to behavior that is both relatively long-term and reversible (Papaj and Prokopy 1989). Modification of plant examining behavior by *D. rapae* qualifies on both counts. Effects of conditioning to potato persisted for >2 days after isolation when wasps were tested on potato (Fig. 5). Confining wasps with potato after collard resulted in wasps searching potato longer, and conversely holding wasps on collard after potato caused a decrease in searching time on potato (Fig. 6). Furthermore, the effects persisted, suggesting that recent experience is remembered and overrides earlier experience, at least in determining acceptance of a novel plant such as potato. Age effects were necessarily confounded in these experiments (compare Figs. 4B, 5, and 6). If age could be factored out, persistence of potato postalighting acceptance behav-

Fig. 6. Reversibility of plant acceptance. Mean searching time (s $\pm$ SE) on potato for wasps switched from potato to collard (A) or from collard to potato (B). Wasps were confined with potato or collard for 1–2 days and then either tested directly (0 h) or confined with the other plant for 1–72 h before testing. All plants were aphid-infested; individual wasps were not retested. $N = 10$–20 wasps tested in each treatment, except 72-h treatments, in which five and seven wasps were tested.

ior might continue even longer. Searching times of older wasps were the same or shorter than those of young wasps, except for collard experienced wasps searching collard, where older wasps searched longer (Fig 4A).

As Vet and Opzeeland (1984) found for parasitoids of *Drosophila*, and as other workers have found for herbivorous and saprophagous insects (for example, Jaenike, 1983), it was the response to the less preferred habitat that showed the most variation. Thus potato experience increased searching time on potato but collard experience did not increase searching time on collard (Fig. 3). Furthermore when wasps were tested on potato, searching times were more variable for potato-experienced than for collard-experienced wasps, even after adjusting for higher means (Figs. 5 and 6). In contrast, the similarity of searching times on collard, independent of plant or aphid experience (Fig. 3), suggests the exis-

tence of intrinsically determined giving up times (Pyke, 1984) on the preferred plant.

The role of oviposition in postalighting plant acceptance learning is unclear from these experiments. Oviposition experience on collard had no effect on acceptance of collard or potato (Fig. 3), but if collard is intrinsically preferred we should not expect such an effect. Unfortunately a test of the effect of oviposition on conditioning to potato could not be attempted because wasps confined with uninfested potato leaves spent most of their time on the cage ceiling; such a treatment would not be comparable to one using infested potatoes. It may seem logical *a priori* that habitat learning should be dependent on successful oviposition, at least for parasitoids that seek plants before hosts. However, Vet (1983) found that experiencing a novel habitat without hosts was sufficient to induce habitat preference in *Leptopilina clavipes*, although oviposition greatly strengthened the response. Studying short-term experience effects, Drost *et al.* (1986) demonstrated that neither oviposition nor plant experience, separately, increased oriented wind tunnel flight by *Microplitis croceipes* to an infested plant; only experience with host feces or with the host–plant complex did. Perhaps analogously, Thorpe and Jones (1937) were able to condition *Venturia canescens* to the order of a new host without oviposition.

Our data suggest a significant preemergence effect on plant finding (orientation to plant odors). However, the effect could be due (1) to "larval conditioning" (that is, conditioning carried over from the larval to the adult stage), (2) to adult conditioning to traces of the larval environment encountered by teneral adult wasps prior to emergence from the mummy, or (3) to artificial selection (unintended selection for wasp performance on a particular plant as a consequence of differential survival or reproduction on that plant). There are several claims for larval conditioning in the parasitoid literature (Thorpe and Jones, 1937; Vinson *et al.* 1977; Vet, 1983) but these studies have generally found stronger effects of adult conditioning. Furthermore most of these studies have not adequately controlled for artificial selection (Papaj and Rausher, 1983). We cannot rule out the possibility that traces of the larval environment were contacted by teneral adult wasps. Recent experiments with *Microplitis demolitor*, a plant generalist parasitoid of *Heliothis* larvae (Lepidoptera: Noctuidae), suggest that factors in the host pupal case that are derived from the larval environment but experienced by the teneral adult may be important in habitat conditioning (Hérard *et al.*, 1988). These results support the thesis proposed by Corbet (1985) that it is impossible rigorously to distinguish larval conditioning from postlarval effects in holometabolous insects.

In our experiments variation in preemergence treatment effects on plant finding probably had an important genetic component. Artificial selection for potato acceptance was minimized by using first-generation wasps reared on aphids on potato. However naive adults from this treatment searched potato *less*

than their collard-reared parents (Table I). Intense adverse selection on wasps when initially transferred to potato seems to be the most likely explanation. There was, moreover, an increase in searching time on potato by naive wasps after 15–20 generations on potato (Table I), possibly suggesting subsequent selection for potato acceptance. Although sample sizes were limited, the latter group of naive wasps appeared to search collard longer as well; the reason is unknown.

These findings have several implications for the way we view parasitoid host selection. (1) By thinking in terms of host habitat finding, and not of host habitat examining, we may be overlooking important components of the host selection process that occur after a host plant is found. Elsewhere (Sheehan and Shelton, 1989), we reported that *D. rapae* leaving rates decreased in larger patches of crucifers, but we were unable to demonstrate an effect of patch size on finding rates. The distinction between finding and examining is analogous to the distinction between prealightment and postalightment behaviors of ovipositing butterflies. Similar to our findings, the results of several butterfly oviposition studies have shown that prealightment and postalightment preferences for plants can differ (reviewed by Singer, 1986). The importance of examining learning at different levels of foraging behavior has been stressed for herbivorous insects by Papaj (Papaj and Rausher, 1983; Papaj and Prokopy, 1986). (2) The assumption that specialist insects should not be good learners needs to be examined critically. In our study, plant examining, and possibly plant finding, behaviors were found to be modifiable by experience. (3) Ignorance of the nature and importance of plant experience may account for some of the failures of biological control releases. For example, Shands *et al.* (1975) noticed that *D. rapae* emerged frequently from green peach aphids infesting greenhouse potatoes but less often from the same aphids infesting field potatoes in Maine. Supposing that control by this wasp could be augmented in field potatoes, they embarked on a massive release program. However they reared the wasp in aphids on Chinese cabbage. After releasing >100,000 *D. rapae* only 2 mummies yielding the wasp were found, and those were in control plots. It is possible, although evidence is lacking, that exposing wasps to potato before release would have improved their performance.

Why should *D. rapae* learn to accept alternative plants? Most crucifers are relatively ephemeral. The ability to exploit hosts on other plants may enable wasps, which are active throughout the growing season (Hafez, 1961; Starý, 1970), to survive in the absence of crucifers. Thus learning may help wasps utilize locally abundant hosts (compare Jaenike, 1982; Rausher, 1985). Also, wasps can disperse as larvae in alate aphids (Hafez, 1961). Learning to accept the plants such wasps emerge on may increase fitness in a diverse environment, where the risk of not finding cruciferous plants to search may be high. Jaenike (1982, 1988) and Rausher (1984) discussed how such behavioral plasticity can

facilitate the spread of adaptive alleles in local populations. Perhaps learning is most advantageous to *D. rapae* in diverse environments where crucifers are relaively rare and is of less importance in simplified environments, such as in agricultural monocultures.

ACKNOWLEDGMENTS

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