Postemergence Learning in the Insect Parasitoid, *Cotesia congregata* (Say) (Hymenoptera: Braconidae)

K. M. Kester[1,2] and P. Barbosa[1]

Exposing newly emerged females of Cotesia congregata *(Say) to wild cherry, an inherently unattractive plant, and their host larvae at 0–4 h after adult emergence induced a positive searching response to wild cherry and an inhibited response to cabbage, an attractive plant. Inherent responses were not affected when females were exposed to their hosts at 0–12 h and to cherry at 8–12 h after emergence. The induced response to cherry was constant until its disappearance at 6–7 days; inhibition of the response to cabbage was released at 4–5 days after emergence. Postemergence exposure to cherry and parasitoid cocoons induced similar but weaker searching responses. Induced searching responses exhibit features of associative learning and receptor modification. In addition to its presumed role in foraging, postemergence experience with plants may encourage assortative mating of* C. congregata *within suitable host habitats and, thus, facilitate local adaptations to specific plants.*

INTRODUCTION

Exposure to environmental cues associated with the host habitat following emergence, i.e., early adult or postemergence experience, has been demonstrated to induce changes in behavioral responses to hosts or host-habitat features in phytophagous, frugivorous, saprophagous, and entomophagous insects.

---

[1] Department of Entomology, 1300 Symons Hall, University of Maryland, College Park, Maryland 20742.
[2] To whom correspondence should be addressed.

For example, early adult experience induces changes in orientation and ovipositional responses to hosts in frugivorous and saprophagous insects (Prokopy *et al.*, 1982; Jaenike, 1982, 1983, 1988; Hoffman, 1988). Likewise, postemergence experience in insect parasitoids affects components of foraging behavior such as orientation to host habitats (Vet, 1983; Hérard *et al.*, 1988; Kaas *et al.*, 1990), searching responses to plants (Sheehan and Shelton, 1989), and ovipositional responses to host-habitat features (Wardle and Borden, 1985). The potential for inducing such behavioral responses may be greatest during the period immediately following adult emergence, as reported for *Exeristes roborator* (Wardle and Borden, 1985). In this parasitic icheumonid, newly emerged adults conditioned to hosts in an artificial habitat for 10 days showed stronger ovipositional responses to the artificial habitat compared to those conditioned at 5 or 10 days after emergence for the same amount of time.

Induction of host-habitat preferences through early adult experience has been hypothesized to increase the likelihood of assortative mating, enhance potential linkage of adult behavioral preferences and progeny survival, and thus, lead to genetic subdivisions within heterogeneous populations of phytophagous, frugivorous, or saprophagous insects (Bush, 1969; Jaenike, 1982, 1988; Smith, 1987; Papaj and Prokopy, 1988). Alternatively, early adult experience has been hypothesized as a mechanism for the development of new host associations in the absence of evolutionary changes within insect populations (Corbet, 1985). It is with respect to the latter hypothesis that postemergence experience has been most often considered in insect parasitoids, although preimaginal conditioning has been hypothesized to facilitate sympatric speciation in *Nasonia vitripennis* (Smith and Cornell, 1979).

As noted by Corbet (1985), Jaenike (1988), and others, earlier reports and hypotheses regarding the effects of preimaginal conditioning may be more correctly attributable to the effects of postemergence experience, due to the confounding of these in most systems studied. For example, host-habitat orientation in the braconid, *Microplitis demolitor*, is affected by early adult experience with host-habitat cues present in the pupal case of its host (Hérard *et al.*, 1988). Since the host-habitat cues were available during larval development of the parasitoid, preimaginal conditioning may have been assumed if potential effects of preemergent and postemergent experience had not been differentiated in this study.

Cotesia congregata (Say) (Hymenoptera: Braconidae) is a gregarious larval endoparasitoid of *Manduca sexta* (L.) (Lepidoptera: Sphingidae) and other sphingids. Typically, larvae of *M. sexta* (and other sphingids) rest in an inverted position along the midvein of a single leaf (on large-leafed plants such as tobacco) or on leaf stems (on small-leafed plants such as tomato). Upon completion of their larval development, parasitoids egress from their host larva and spin cocoons. Most parasitoid cocoons remain attached to the host larva and

detached cocoons are often trapped in plant cervices, e.g., the base of leaf stems, or on sticky leaf surfaces. We have observed that immediately following emergence from their cocoons, females of *C. congregata* engage in active examination of the plant on which they emerge. This behavior consists of walking with continuous antennal palpation of upper leaf surfaces and has been observed in parasitoids that have developed in hosts which have previously fed on the same plant or on artificial diet. Typically, females examine the upper surface of the most proximate leaf relative to the position of their host larva. Male parasitoids typically emerge before their female siblings and also aggregate on the upper leaf surfaces, where they engage in courtship displays involving a characteristic rapid "fanning" of their wings. Although males may be attracted to plants, too, they may also be attracted to sex pheromones emitted by their female siblings since wing fanning is observed even in the absence of plants. Both sexes occasionally hover around the plant, often alighting to resume examination, courtship, and mating behaviors. Newly emerged females often walk and occasionally drag their ovipositors along the cuticle of their hosts immediately after emerging from their cocoons. However, they do not show a full ovipositional response to appropriately aged unparasitized host larvae for at least the first day following emergence.

On the basis of our observations, we hypothesized that plant examination by preovipositional females would induce a searching response to the examined plant. Further, we hypothesized that exposure to plants immediately following adult emergence was critical for induction of this response. Here we present evidence to support both of these hypotheses. Also, on the basis of the results of related work, we offer hypotheses regarding the nature and potential ecological function of this learning response in *C. congregata*.

MATERIALS AND METHODS

Insects and Plants

Parasitoids used in the experiments described below were from our stock laboratory colony. Originally established in 1983, this colony has been invigorated on several occasions with parasitoids collected from *M. sexta* on tobacco and has been continuously maintained on *M. sexta*, fed on a semisynthetic (wheat germ) diet. Parasitoids used in this experiment were reared as described by Barbsoa *et al.* (1991) except that host larvae were fed on a modified version of the BioServ hornworm diet (Kemper, unpublished), and unless noted otherwise, parasitoid cocoons were not detached from their host larvae. Other than that provided experimentally, parasitoids had no experience with plants.

Wild cherry leaves were randomly collected from three trees on the University of Maryland campus, College Park, MD, and held in water (about 1 h)

before being used for exposure treatments or searching assays. Cabbage leaves were removed from one of three greenhouse plants and handled in a similar manner. Cabbage plants and wild cherry leaves were free of apparent disease or insect damage. Cabbage was cultivated without pesticides.

Searching Assay

Females were held individually in a 1-dram glass vial with cork stopper for 2–5 min prior to testing. To control for possible leaf area responses, a single 0.8-cm (diameter) disk of either wild cherry or cabbage was introduced into the vial for 2 min. Total time spent searching within this time period was recorded for each female. "Searching" was defined as active antennal palpation on any area of the leaf disk. Females were tested only once. Assays were conducted during daylight hours at $30 \pm 1°C$ and $68 \pm 6\%$ RH.

Experiment 1: Effect of Time Period of Postemergence Exposure on Induction of Searching Responses

This experiment simulates the observed behavior of newly emerged females of *C. congregata* to test our hypothesis that exposure to a specific plant in the presence of the caterpillar host induces a positive searching response to this plant when such plant exposure occurs immediately after adult emergence. Newly emerged *C. congregata* were exposed to torn leaves of wild cherry in the presence of the host larvae from which they emerged (their "caterpillar hosts") for a 4-h period immediately following emergence of the first females within each of two to four cohorts or 8 h later. The two to four cohorts in the later treatment group remained in contact with their caterpillar hosts from emergence and throughout the period they were exposed to wild cherry. A control group, consisting of two to four cohorts exposed only to their caterpillar hosts, was established at the same time.

Parasitoids were retained within clear (150-ml) plastic cups during the 4-h exposure period (one cohort per cup). The 4-h exposure period ensured a minimal exposure of 30 min with leaves and/or host for parasitoids emerging over a 2- to 3.5-h period within a single cohort. After the 4-h exposure period had elapsed, cups were introduced into plastic holding cages with lids opened and left ajar to permit more extended exposure. However, all but one or two parasitoids left the cups as soon as lids were removed. In an effort to control for potential effects due to the time elapsed from last exposure to assay of searching responses, cups were not removed until 24 h after exposure treatments were initiated. Searching assays were conducted 24 h after the cups were removed. Thus, total direct exposure time of parasitoids to plant material was 4 h, total possible exposure time was 24 h, and time elapsed between the last

possible exposure and the initiation of searching assays was 24 ± 1 h for each treatment group. The experiment was replicated three times.

Two days after adult emergence, we assayed the searching responses of 5–10 individual females, from each of the three treatment groups, to either wild cherry or cabbage. Wild cherry, a food plant of several alternate host species of *C. congregata*, was selected because, without prior experience with this plant, naive females of *C. congregata* are only weakly attracted to it, as indicated in a related study (Kester and Barbosa, in preparation). Although there are no recorded host species of *C. congregata* feeding on cruciferous plants, cabbage (and other conspecifics) elicits the strongest searching response of all plants we have tested and therefore serves as a reliable positive control in searching assays.

This experiment was designed as a three-way analysis of variance (ANOVA) to test for main and interactive effects of experimental replication (3), time of initial exposure to wild cherry (0–4 h, 8–12 h, or no exposure to wild cherry), and plant species (wild cherry or cabbage) on searching time (n = 126). Data were transformed by SQRT (searching time + 0.5) to correct for normality of residuals and analyzed using SAS GLM (SAS Institute, 1985). Means comparisons were made using the PDIFF function and a Boneferroni's method for adjusting the level of significance (P = 0.5/number of comparisons).

Experiment 2: Effect of Type of Postemergence Exposure on Induction of Searching Responses

This experiment tests the individual and combined effects of postemergence exposure to host and plant on the induction and inhibition of searching responses identified in the first experiment. Treatment groups consisted of two or three cohorts each of *C. congregata*, which were exposed to either (1) the caterpillar hosts from which they emerged, (2) wild cherry leaves, (3) both caterpillar hosts and wild cherry leaves, or (4) neither host nor plant (cocoons were removed from host larvae about 4 h before emergence of adult parasitoids). Exposure to host, plant, or host and plant was initiated and maintained as described for the 0- to 4-h treatment group in the first experiment. We assayed searching responses of 85 individual females, as described above.

This experiment was designed as a two-way ANOVA using SAS GLM (SAS Institute, 1985) to test for main and interactive effects of the type of postemergence exposure provided (wild cherry and host, wild cherry only, host only, or no plant or host exposure) and plant species (wild cherry or cabbage) on searching time. To correct for normality of residuals, data were transformed by SQRT (searching time + 0.5) prior to analysis. Treatment means were compared as described for the first experiment.

Experiment 3: Constancy and Longevity of Searching Responses Induced Through Postemergence Exposure to Plant and Host

This experiment was designed to determine the constancy and the longevity of the searching responses induced in *C. congregata* through postemergence experience with a host-associated plant, as identified in the first experiment. Newly emerged *C. congregata* were exposed either to wild cherry and their caterpillar hosts or to their caterpillar hosts only, as described for the second experiment. We then assayed the searching responses of individual females drawn from each of the treatment groups (two to four cohorts each) to either cabbage or wild cherry over several days. Individual females ($N = 120$) were used only once during the course of the experiment, as described above.

For analysis of this experiment, we chose an analysis of variance approach, rather than a linear regression, i.e., "decay," approach for two reasons: (1) we wished to examine further the inhibitory effects of postemergence exposure to wild cherry on searching responses to cabbage found in the first experiment, and (2) our related studies suggested that induced searching responses would decay abruptly (Kester, unpublished). We judged that both of these effects would be obscured by the "decay" approach because searching responses were assayed on only three dates. The experiment was designed as a three-way ANOVA to test the main and interactive effects of the type of exposure provided (wild cherry and host or host only), the number of days elapsed from adult emergence to assay of searching responses (2–3, 4–5, or 6–7), and plant species (wild cherry or cabbage) on searching time. Results from two separate experiments were grouped for analysis. Means comparisons were performed as described above.

RESULTS

Effect of Time Period of Postemergence Exposure to Plants on Induction of Searching Responses. Results of the first experiment support our hypothesis that induction of searching responses to plants during the preovipositional period of *C. congregata* requires exposure to both plants and hosts during the time period immediately following adult emergence. Results of the analysis of variance performed are shown in Table I. Mean searching responses of females in each of the three treatment groups on wild cherry or cabbage are presented in Fig. 1. As demonstrated by the insignificant three-way interaction of experimental replication, treatment group (exposure period), and plant assayed, these responses were remarkably consistent (Table I).

Females exposed to both wild cherry and their caterpillar hosts for the 4-h period immediately following adult emergence ("0- to 4-h treatment group") searched longer on wild cherry than those exposed only to their caterpillar hosts

Table I. Results of Analysis of Variance Performed to Test the Effects of Postemergence Exposure Period on the Searching Response of *Cotesia congregata* (Say) to Wild Cherry or Cabbage[a]

Source of variation	df	*F* value	*P*
Experimental Replication	3	1.41	0.2440
Exposure Period	2	0.21	0.2100
Plant Assayed	1	153.15	0.0001
Experimental Replication × Exposure Period	6	1.62	0.1502
Experimental Replication × Plant Assayed	3	0.35	0.7881
Exposure Period × Plant Assayed	2	28.57	0.0001
Experimental Replication × Exposure Period × Plant Assayed	6	0.48	0.8252
Error	102		

[a]Analysis was performed using SAS GLM (SAS Institute, 1985); all assumptions for ANOVA were met.
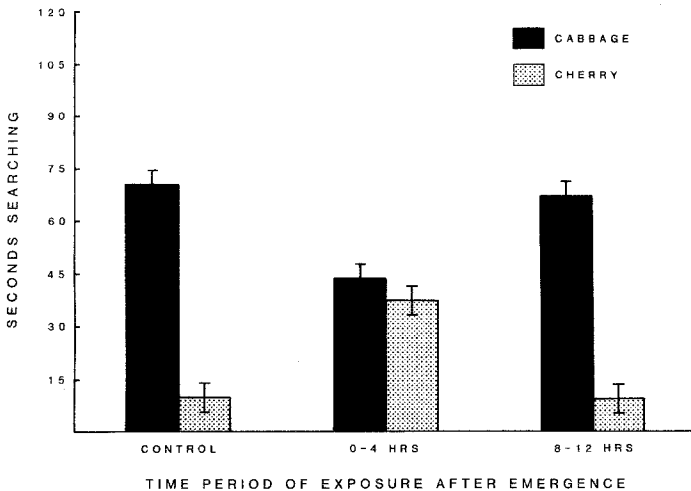

Fig. 1. Critical period for induction of searching responses to an inherently unattractive (wild cherry) or attractive (cabbage) plant in preovipositional *Cotesia congregata* (Say). Females in the control group were exposed only to their caterpillar hosts 0–4 h after adult emergence; 0- to 4-h females were exposed to both hosts and wild cherry for 0–4 h after adult emergence. The 8- to 12-h females were exposed to their caterpillar hosts for 0–12 h and to wild cherry 8–12 h after adult emergence. Each bar represents the mean (±SE) response for 21 individuals assayed 48 h after emergence. See text for further explanation.

("control treatment group") during this 0- to 4-h period ($P = 0.0001$). Also, females in the 0- to 4-h treatment group searched as long on wild cherry as they did on cabbage ($P = 0.4248$), whereas females exposed to their hosts only searched longer on cabbage than on wild cherry ($P = 0.0001$). These results demonstrate that exposure to wild cherry and hosts induced an increased searching response to wild cherry. However, similarity of the searching responses of the 0- to 4-h females to the two plants was due, in part, to a reduction in searching time on cabbage in that control females searched longer on cabbage than females in the 0- to 4-h treatment group ($P = 0.0001$). This finding suggests that exposure to wild cherry induced an inhibited searching response to cabbage.

Overall, searching responses of females exposed to their caterpillar hosts for the first 12 h but not exposed to wild cherry until the 8- to 12-h period after adult emergence ("8- to 12-h treatment group") resembled those of females exposed only to their hosts, as clearly seen in Fig. 1. Females in the 8- to 12-h group searched longer on cabbage than on wild cherry ($P = 0.0001$), and these searching responses were the same as those of the control females to cabbage ($P = 0.4835$) and to wild cherry ($P = 0.8529$). These results indicate that induction of increased searching responses to wild cherry during the preovipositional period of *C. congregata* required exposure to wild cherry and the caterpillar host within a narrow window of time following adult emergence. Given our observations of newly emerged adults and the design of this experiment, this critical period may be as short as 30 min.

In the absence of plant cues, parasitoids exposed to their caterpillar hosts at emergence but not offered wild cherry until 8 h later may have learned to recognize other chemotactile cues, e.g., the plastic cup or other host-related cues, prior to their exposure to wild cherry (Wardle and Borden, 1986). If so, our results would demonstrate that postemergence learning is not reversible through similar experience within the preovipositional period and, thus, would offer further support of our initial hypothesis.

Effect of Type of Postemergence Exposure on Induction of Searching Responses. Overall, exposure to either caterpillar hosts, wild cherry, or a combination of these, during the 0–4 h following adult emergence affected later searching responses of *C. congregate* to wild cherry and to cabbage, as indicated by the results of the second experiment. Results of the analysis of variance performed to test for differential effects of postemergence experience are shown in Table II. Mean searching responses to the two plants assayed for the four treatment groups are presented in Fig. 2.

Females exposed only to their caterpillar hosts ("host-only treatment group") searched longer on cabbage than on wild cherry ($P = 0.0001$), as did the females in the control group, which received no host or plant exposure ($P = 0.0001$). Also, females in the host-only group searched as long on wild cherry

Table II. Results of Analysis of Variance Performed to Test for Differential Effects of Postemergence Exposure to Host, Plant, or Host and Plant on the Searching Response of *Cotesia congregata* (Say) to Wild Cherry or Cabbage[a]

Source of variation	df	F value	P
Type of Exposure	3	15.82	0.0001
Plant Assayed	1	113.95	0.0001
Type of Exposure			
× Plant Assayed	3	14.22	0.0001
Error	76		

[a] ANOVA was performed using SAS GLM (SAS Institute, 1985); data were transformed by SQRT (searching time + 0.5) to correct for normality of residuals.
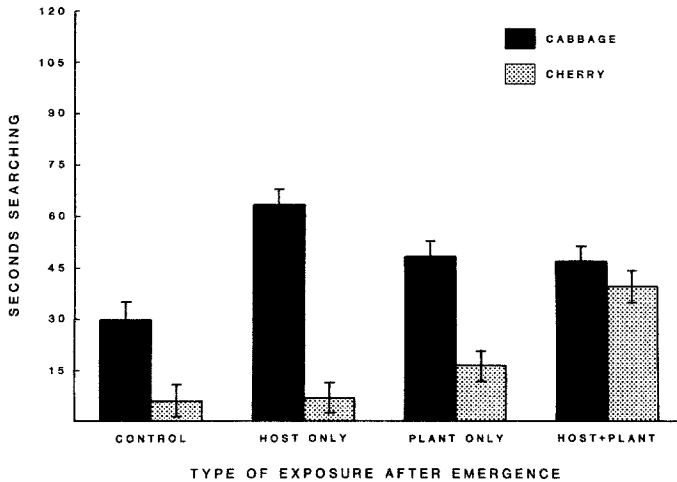

Fig. 2. Differential induction of searching responses to an inherently unattractive (wild cherry) and attractive (cabbage) plant due to postemergence exposure to caterpillar hosts, to wild cherry, or to wild cherry and hosts in *Cotesia congregata* (Say). Control females received no exposure to hosts or wild cherry. Each bar represents the back-transformed mean (±SE) response of 12 individuals assayed 48 h after emergence. See text for further explanation.

as females in the control group ($P = 0.8587$), indicating that exposure to caterpillar hosts only did not affect searching response to wild cherry. However, females exposed to caterpillar hosts after emergence searched longer on cabbage than those in the control group ($P = 0.0001$), suggesting that exposure to caterpillar hosts may augment inherent searching responses.

Females exposed only to wild cherry ("plant-only treatment group") searched longer on wild cherry than females receiving no host or plant exposure

(P = 0.0023) or than females exposed only to their caterpillar hosts (P = 0.0032). Also, females exposed only to wild cherry searched longer on cabbage than those with no exposure to either hosts or wild cherry (P = 0.0034) but for a similar amount of time as females exposed only to their caterpillar hosts (P = 0.0946). Unfortunately, clear interpretation of the effect of postemergence exposure to plants in the absence of the host cannot be made, due to the strong possibility that host cues were available in the cocoons of the newly emerged parasitoids.

The weaker but similar searching responses of females exposed to wild cherry and parasitoid cocoons ("plant-only treatment group") compared to those of females exposed to wild cherry, caterpillar hosts, and cocoons ("plant and host treatment group") may reflect the effects of postemergence exposure to plants with respect to limited or unlimited contact with host cues. For example, females exposed only to wild cherry searched longer on wild cherry than females in either of the no-plant treatments, as noted above, but females exposed to wild cherry and caterpillar hosts searched longer on wild cherry than those exposed only to wild cherry (P = 0.0003). These results suggest that increased contact with the host reinforced the searching response induced by postemergence exposure to wild cherry and more limited contact with host cues provided by parasitoid cocoons. Similarly, females exposed to both wild cherry and their caterpillar hosts searched less time on cabbage than those exposed only to wild cherry (P = 0.0034), suggesting that inhibition of the searching response to cabbage was reinforced through increased contact with the host.

Constancy and Longevity of Searching Responses Induced Through Post-emergence Exposure. Overall, the searching responses induced through postemergence exposure to wild cherry in the presence of the caterpillar host was surprisingly long-lived and differed from those found for females exposed only to their caterpillar hosts. Results of the analysis of variance performed are shown in Table III. Searching responses of the two exposure groups on wild cherry or cabbage are presented in Figs. 3A and B.

When exposed to both wild cherry and their caterpillar hosts for the 0- to 4-h period following adult emergence, females searched as long on wild cherry at 4–5 days as they did at 2–3 days after emergence (P = 0.2769). However, the mean searching time on wild cherry of females in this same treatment group showed an abrupt decline at 6–7 days, when compared with those measured at 2–3 (P = 0.0001) or at 4–5 days (P = 0.0001). In contrast, the searching response of females exposed only to their caterpillar hosts remained constant on wild cherry over the three dates they were assayed (P > 0.05 for all possible comparisons). Decay of the induced response to wild cherry was so complete that at 6–7 days, there was no difference in the mean searching time of females exposed to wild cherry and their hosts and of females exposed only to their hosts (P = 0.1395).

Table III. Results of Analysis of Variance Performed to Test the Effects of Postemergence Exposure to Hosts or to Hosts and Wild Cherry on the Constancy and Longevity of Searching Responses to Wild Cherry or Cabbage in *Cotesia congregata* (Say)[a]

Source of variation	df	F value	P
Type of Exposure	1	10.07	0.0020
Plant Assayed	1	356.30	0.0001
Day Assayed[b]	2	15.98	0.0001
Type of Exposure × Plant Assayed	1	38.33	0.0001
Type of Exposure × Day Assayed	2	8.39	0.0004
Plant × Day Assayed	2	19.86	0.0001
Type of Exposure × Plant × Day Assayed	2	13.43	0.0001
Error	108		

[a] ANOVA was performed using SAS GLM (SAS Institute, 1985); data were transformed by SQRT (searching time + 0.5) to correct for normality of residuals.
[b] Refers to the age of the insect (2–3, 4–5, or 6–7 days after adult emergence).

Interestingly, searching responses to cabbage over the three dates assayed were similar for the two treatment groups, but were not constant. When exposed to wild cherry and their caterpillar hosts after emergence, females searched longer on cabbage at 4–5 days than they did at 2–3 days after emergence ($P = 0.0010$) and for a similar amount of time at 4–5 days as they did at 6–7 days ($P = 0.1614$). Females exposed only to their hosts searched longer on cabbage at 4–5 days than they did at 2–3 days ($P = 0.0317$) but searched for a similar amount of time at 4–5 days as they did at 6–7 days ($P = 0.0816$). As reported for the two earlier experiments, females exposed to wild cherry and their hosts searched on cabbage for less time at 2–3 days than females exposed only to their hosts. However, searching responses on cabbage were similar for the two treatment groups at 4–5 days ($P = 0.3425$) and at 6–7 days ($P = 0.5519$). Overall, these results suggest a release of the inhibitory effects of postemergence exposure to wild cherry (or to unknown cues provided to females exposed only to their hosts) at 4–5 days.

DISCUSSION

Exposure to an relatively unattractive plant (wild cherry) in the presence of the caterpillar host within the first 4 h after adult emergence induced an increased searching response to this plant and an inhibited searching response to an attractive plant (cabbage) in females of *C. congregata* (Fig. 1). Exposure to wild cherry and parasitoid cocoons immediately following emergence induced similar but weaker searching responses to wild cherry and cabbage (Fig. 2).
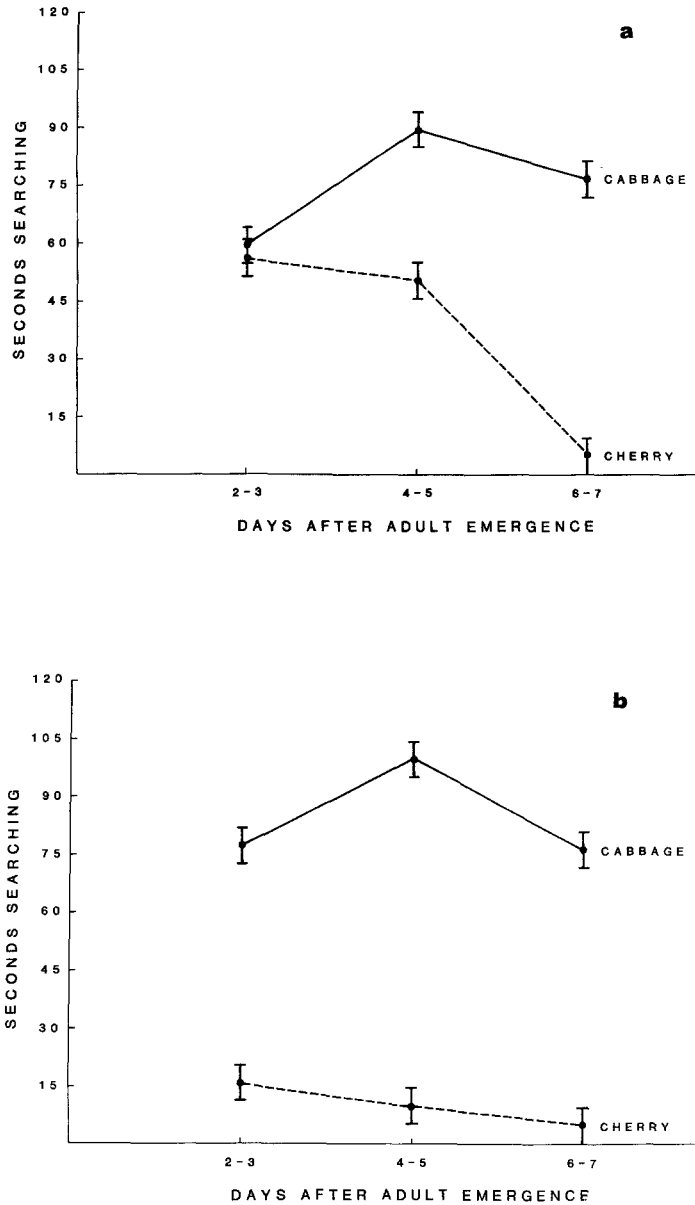
Fig. 3. Searching responses of *Cotesia congregata* (Say) to an inherently attractive (cabbage) or unattractive (wild cherry) plant. (A) Females exposed to wild cherry and their caterpillar hosts for 0–4 h after adult emergence. (B) Females exposed only to their caterpillar hosts 0–4 h after adult emergence. Each point represents the back-transformed mean (±SE) searching response of 10 individuals. See text for further explanation.

However, because host cues were probably available in parasitoid cocoons, these weaker induced responses were probably not due to postemergence contact with wild cherry alone but, instead, reflected the intensity of exposure to host cues. This is further suggested by the augmented searching response to cabbage of parasitoids exposed to both parasitoid cocoons and caterpillar hosts compared to those exposed only to parasitoid cocoons (Fig. 2). If contact with any source of host cues is required for induction of searching responses in *C. congregata*, then postemergence learning without oviposition could be classified as a type of associative learning (Papaj and Prokopy, 1989).

The types of exposure provided in our second experiment may appear to be highly artificial. However, our field observations of *C. congregata* on tobacco and tomato suggest that each of these types of exposure may occur under natural conditions. For example, parasitoid cocoons can remain attached to the caterpillar host or they can become dislodged and fall onto the plant or ground below. Under these conditions, females will have different postemergence experiences. Our results suggest that without exposure to novel plant cues after emergence, positive searching responses to inherently attractive plants remain intact, whether or not females have contact with their caterpillar hosts, in the absence of ovipositional experience (Figs. 2 and 3B).

Searching responses induced by postemergence exposure to wild cherry in the presence of the caterpillar host were relatively long-lived, considering that adult females of *C. congregata*, more long-lived than males, typically live for only 2 weeks (Kester, personal observation). The induced response to wild cherry was consistently high until its disappearance at 6–7 days, although inhibition of the searching response to cabbage appeared to be released earlier, at 4–5 days after emergence (Fig. 3A). These features suggest that postemergence learning in *C. congregata* may involve several mechanisms including changes at the sensory level.

Although associative learning of plants or plant habitats has been demonstrated among several insect orders and is generally assumed to involve complex changes in the brain, little is known about the actual mechanisms involved. However, at least some cases of associative learning in insects may involve changes in sensitivity of the olfactory receptor neurones (Vet *et al.*, 1990). For example, females of *Leptopilina heterotoma*, a parasitoid of larval drosophilids, show inhibited electroantennogram (EAG) responses to beet odors when they are permitted a 1-h ovipositional experience with hosts in a yeast habitat (Vet *et al.*, 1990). The inhibited EAG response to beet odor in yeast-trained *L. heterotoma* parallels the inhibited searching response to cabbage in *C. congregata* exposed to wild cherry. In future investigations, we hope to compare the behavioral responses induced by postemergence experience to EAG responses of *C. congregata*.

Since we did not consider the effects of postemergence exposure on flight

responses to plants, we do not know if, or how, postemergence experience will affect host-habitat orientation. Overall, studies investigating the effects of early adult experience on habitat orientation have yielded mixed results (Jaenike, 1982, 1983; Hoffman, 1988; Sheehan and Shelton, 1989; Kaas *et al.*, 1990). However, females of *C. congregata* show complete ovipositional responses to appropriately aged host larvae at 1–2 days after adult emergence (Kester, personal observation) and the effects of postemergence experience with cherry lasted for at least 2–3 days beyond. Therefore, postemergence experience with plants could affect the foraging behavior of reproductively mature females. Due to the complexity of host-habitat location, postemergence experience may influence only a part of the full sequence of behaviors comprising this process, such as the amount of time an insect will remain in the habitat it encounters (Sheehan and Shelton, 1989; Kester and Barbosa, in preparation). In addition to its role in foraging behavior, postemergence induction of plant searching responses in *C. congregata*, and other related species, may serve other functions as well.

We suggest that the primary function of early adult experience in *C. congregata*, and other related species which must locate hosts on many different plants, is to retain newly emerged adults within the original host-habitat for mating. This hypothesis is supported by our findings that (1) postemergence learning required plant experience within a narrow period of time following adult emergence, (2) postemergence experience with wild cherry (an inherently unattractive plant) induced a positive searching response to this plant but also inhibited the searching response to cabbage (an inherently attractive plant); and (3) these responses lasted throughout the preovipositional period of 24–48 h and for several days beyond. Retention of newly emerged adults for mating may be particularly important for short-lived gregarious species which can utilize several host species occurring on many plants.

As previously hypothesized for phytophagous insects (Bush, 1969; Smith, 1987; Papaj and Prokopy, 1989), retention of newly emerged adults on suitable plants during the preovipositional period of insect parasitoids would increase the likelihood of assortative mating, would enhance linkage of inherent plant preferences and progeny survival, and could lead to local specialization for specific plants. For example, *C. congregata* is specialized for the Sphingidae but can be viewed as a host habitat or plant generalist in that, cumulatively, its potential hosts may occur on over 40 plant families in Maryland alone (Kester and Barbosa, 1991). However, we have found that populations of *C. congregata* which differ in their historical exposure to tobacco also differ in their searching responses to tobacco and to nicotine, as well as their survivorship on hosts fed artificial diets containing nicotine (Kester and Barbosa, 1991). Such interpopulation differences may reflect local adaptations to abundant plants and may be facilitated through postemergence learning.

Our hypothesis that postemergence experience functions to retain newly

emerged adults within the host habitat in *C. congregata* is not exclusive of its possible role in foraging. Responses induced through postemergence experience may be subsequently reinforced through ovipositional experiences with hosts in the original habitat. In the absence of such reinforcement, induced responses to the novel plant would disappear, inherent responses would be reinstated, and parasitoids would most likely disperse from the original habitat. Although this proposed scenario is speculative, it is based on the experimental work reported herein and contains several hypotheses that can be directly tested. Hopefully, our continued work with *C. congregata* will provide greater insight into both the mechanisms and the functions of postemergence learning.

ACKNOWLEDGMENTS

REFERENCES

Barbosa, P., Gross, P., and Kemper, J. (1991). Influence of plant allelochemicals on the performance of the tobacco hornworm and its parasitoid, *Cotesia congregata. Ecology* (in press).

Bush, G. L. (1969). Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**: 237–251.

Corbet, S. A. (1985). Insect chemosensory responses: A chemical legacy hypothesis. *Ecol. Entomol.* **10**: 143–153.

Hérard, F., Keller, M. A., Lewis, W. J., and Tumlinson, J. H. (1988). Beneficial arthropod behavior mediated by airborne semiochemicals. IV. Influence of host diet on host-oriented flight chamber responses of *Microplitis demolitor* Wilkinson. *J. Chem. Ecol.* **14**: 1597–1606.

Hoffman, A. A. (1988). Early adult experience in *Drosophila melanogaster. Insect Physiol.* **34**: 197–204.

Jaenike, J. (1982). Environmental modification of oviposition behaviour in *Drosophila. Am. Nat.* **119**: 784–802.

Jaenike, J. (1983). Induction of host preference in *Drosophila melanogaster. Oecologia* **58**: 320–325.

Jaenike, J. (1988). Effects of early adult experience on host selection in insects: Some experimental and theoretical results. *J. Insect Behav.* **1**: 3–15.

Kaas, P. J., Elzen, G. W., and Ramaswamy, S. B. (1990). Learning in *Microplitis croceipes* Cresson (Hym., Braconidae). *J. Appl. Entomol.* **109**: 268–273.

Kester, K. M., and Barbosa. P. (1991). Behavioral and ecological constraints imposed by plants on insect parasitoids: Implications for biological control. *Biol. Control.* (in press).

Papaj, D. R., and Prokopy, R. J. (1988). The effect of prior adult experience on components of habitat preference in the apple maggot fly (*Rhagoletis pomonella*). *Oecologia* **76**: 538–543.

Papaj, D. R., and Prokopy, R. J. (1989). Ecological and evolutionary aspects of learning in phytophagous insects. *Annu. Rev. Entomol.* **34**: 315–350.

Prokopy, R. J., Averill, A. L., Cooley, S. S., and Roitberg, C. A. (1982). Associative learning in egglaying site selection by apple maggot flies. *Science* **218:** 76–77.

SAS Institute (1985). *Statistical Analysis Systems, Version 5,* SAS Institute, Cary, NC.

Sheehan, W., and Shelton, A. M. (1989). The role of experience in plant foraging by the aphid parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae). *J. Insect Behav.* **2:** 743–759.

Smith, M. J. (1987). When learning guides evolution. *Nature* **329:** 761–762.

Smith, M. A., and Cornell, H. V. (1979). Hopkins host-selection in *Nasonia vitripennis* and its implications for sympatric speciation. *Anim. Behav.* **27:** 365–370.

Vet, L. E. M. (1983). Host-habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym.: Eucoilidae), a parasitoid of fungivorous *Drosophila*: The influence of conditioning. *Neth. J. Zool.* **33:** 225–248.

Vet, L. E. M., de Jong, R., van Giessen, W. A., and Visser, J. H. (1990). A learning-related variation in electroantennogram responses of a parasitic wasp. *Physiol. Entomol.* **15:** 243–247.

Wardle, A. R., and Borden, J. H. (1985). Age-dependent associative learning by *Exeristes roborator* (F.) (Hymenoptera: Ichneumonidae). *Can. Entomol.* **117:** 605–616.

Wardle, A. R., and Borden, J. H. (1986). Detrimental effect of prior conditioning on host habitat location by *Exeristes roborator. Naturwissenenschaften* **73:** 559–560.