Postemergence Experience Affects Sex Ratio Allocation in a Gregarious Insect Parasitoid

Amanda J. Lentz · Karen M. Kester

Abstract We tested the hypotheses that postemergence experience with plants ("early adult learning") modifies sex ratio and clutch size allocations of *Cotesia congregata* (Say) (Hymenoptera: Braconidae), a gregarious larval endoparasitoid of *Manduca sexta* L. (Lepidoptera: Sphingidae). Emerging wasps were exposed for 2–3 h to (a) one of two host plants (tomato or tobacco) or no plant, and (b) one of two novel plants (arugula or parsley) or no plant. Each female was permitted a single oviposition in a host offered with one of the two plant species 24 h later. Hosts were reared on laboratory diet before and after parasitization. Wasps exposed to either host plant allocated proportionately more females to hosts offered with the plant species experienced at emergence than wasps with the alternate species, but clutch sizes did not differ. Irrespective of plant species, wasps exposed to novel plants allocated proportionately more females to hosts than wasps without plant experience, and larger clutches to hosts offered with parsley than with arugula. Differential responses to host and novel plants suggest inherent recognition of host foodplants by *C. congregata*. Results demonstrate a direct effect of learning on reproductive potential.

Keywords Learning · sex ratio theory · ovipositional decision-making · tritrophic interactions · Hymenoptera · Braconidae · *Cotesia congregata* (Say)

Introduction

Successful reproduction in parasitic wasps begins with the location of suitable hosts for future offspring. Parasitic wasps locate potential hosts using a complex array of stimuli emanating from the host and host habitat (Vinson 1976). These stimuli include both constitutive and induced odors from host plants that can be learned by

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parasitoids before adult emergence (Cortesero and Monge 1994; Gandolfi et al. 2003), immediately following emergence (Kester and Barbosa 1991a), or during oviposition (Vet 1983; Turlings et al. 1993). By enhancing female responsiveness to host-linked stimuli and refining foraging skills, learning increases the likelihood of host encounter and thus the opportunity for reproduction, and in so doing affects fitness indirectly (Vet and Dicke 1992). We hypothesized that learning operates beyond the host location stage by modifying ovipositional decisions based on plant cues, thereby impacting fitness more directly. This hypothesis is based on evidence that parasitoid survival varies with respect to the host foodplant or diet (Barbosa et al. 1986, 1991; Benrey and Denno 1997) and evidence that many parasitoids are egg or sperm limited (Rosenheim and Rosen 1991; Ode and Rosenheim 1998).

Oviapositional decision-making in insect parasitoids has been well-studied (Waage 1986; Godfray 1994). Clutch size allocation varies with respect to parasitoid attributes such as age and egg supply, intrinsic host factors including host quality, size and sex, as well as ecological factors such as host density and intraspecific and interspecific competition. Similarly, sex ratio allocation is affected by parental and host characteristics, environmental conditions, and local mate competition (Charnov 1982; King 1987; Godfray 1994). Modifications of clutch size and sex ratio allocations as a result of experience have been implied by many studies, but the role of learning on oviapositional decision-making has been studied rarely (Dukas and Duan 2000; Morris and Fellowes 2002). Further, a single study has investigated the direct effect of plant species on sex allocation in two solitary ichneumonids (Fox et al. 1996), but to our knowledge, the role of learned plant cues in oviapositional decision-making in parasitic wasps has not been studied.

Cotesia congregata (Say) (Hymenoptera: Braconidae) is a gregarious endoparasitoid of the tobacco hornworm, *Manduca sexta* (L.) (Lepidoptera: Sphingidae) and other larval sphingids, most of which are specialized for one to a few plant families (Kester and Barbosa 1991b). Generally, females of *C. congregata* mate with siblings on the natal host foodplant immediately following emergence (Kester and Barbosa 1991a). This species is typical of arrhenotokous hymenopterans in that males develop from unfertilized eggs and females from zygotes, and ovipositing females adjust clutch size and sex ratio allocations in response to environmental cues (Godfray 1994). Clutch size ranges from 10–200 individuals, and sperm received in a single mating is depleted after *ca*. 10 oviapositions over 5 days (unpublished data). Sex ratio allocations in the wild ranges from 23–99% females, depending on the host plant complex; for example, $x\pm SD=48\pm23\%$, *M. sexta* on tobacco, and $72\pm17\%$, *Ceratomia catalpae* on catalpa. Related studies have demonstrated that behavioral responses of newly-emerged females of *C. congregata* are modified through a single 2–3 h exposure to plant material in the presence of the host ("postemergence learning"), and changes remain intact for 4 days without further reinforcement (Kester and Barbosa 1991a). Postemergence learning (sometimes referred to as "early adult learning") can also modify parasitoid responses to other plant species not experienced ("cross induction"), and further, searching and flight responses may be affected differentially (Kester and Barbosa 1992).

We hypothesized that postemergence experience with plant material in the presence of the host would influence the oviapositional decisions of *C. congregata* to

favor greater reproductive investment of females in hosts encountered on the natal plant species. This hypothesis is based on the biology of *C. congregata* and work with related species. Females of *C. congregata* are sperm and egg limited (Kester, unpublished), and larger than males, therefore, more females should be allocated to high quality hosts, and males to low quality hosts because they are most likely to disperse. For example, Tagawa and Kitano (1981) reported that males of a closely related gregarious species, *C. glomeratus*, often disperse immediately after emergence, and immigrant males accounted for 40% of observed mating under field conditions. We also hypothesized that inherent recognition of host plants would result in differential effects of postemergence experience to host and novel plant species. To test these hypotheses, we compared the effects of postemergence experience with one of two host plant species and one of two novel plant species on clutch size and sex ratio allocations. Since behavioral responses to plants can differ among parasitoid populations (Kester and Barbosa 1994), we also assayed searching responses to both host and novel plant species. Host plants, tomato (Solanaceae: *Lycopersicon esculentum* Miller 'Westover') and tobacco (Solanacaeae: *Nicotiana tabacum* L. 'NC95'), both elicit strong searching responses in tobacco-derived strains of *C. congregata* (Kester and Barbosa 1994). Compared to tomato, the novel plant arugula (Brassicaceae: *Eruca sativa* Miller) elicits a moderate searching response, and parsley (Apiaceae: *Petroselinium crispum* L.) elicits a weak searching response. Novel plant species are from two families not in the host range of any *Manduca* species in North America (Hodges 1971), and were selected on the basis of a previous study (Kester and Barbosa 1992). As we report herein, both innate and learned responses to plant cues affect ovipositional decision-making in *C. congregata*.

Materials and Methods

Insects and Plants Parasitoids and hornworms were obtained from colonies that originated from tobacco (D. Dahlman, University of Kentucky). Hornworms were reared exclusively on a semi-synthetic casein diet. Parasitoids had no experience with plants other than experimental exposure, as described in Kester and Barbosa (1991a). Plants were grown in 3.8 L pots in a glasshouse without pesticides, and fertilized weekly with Miracle Grow®. All plants used in this study were pre-reproductive and free of apparent disease or infestation. Tobacco (rosette stage) and tomato plants were *ca*. 3 months old, arugula plants, were no more than 2 months old, and parsley plants were *ca*. 6 months old. Plants were planted in ascension, so that each plant species could be assayed at a uniform age.

Experimental Design and Analyses Experimental design and procedures were based on those developed previously (Kester and Barbosa 1991a). Briefly, each parasitoid clutch, still attached to the natal host, was held in an individual clear plastic cup, and randomly assigned to a treatment group (one of the two plant species or no plant). Leaf material was added to each cup when the first adult emerged. Plants from which leaf material was taken were herbivore-free, and natal hosts generally are lethargic and do not feed following parasitoid egression. Therefore, plant cues, both contact and volatile, were constitutive or induced by mechanical damage only. Parasitoid

clutches, still attached to natal hosts, were exposed to plants and hosts, or hosts only for the first 2–3 h following emergence. Then, plants and hosts were removed and parasitoid clutches were held in separate containers with honey and water. Parasitoids were left undisturbed for the 24-h preovipositional period. This allowed sufficient time for mating and a refractory period to control for possible short-term effects due to sensitization (Smith 1993). To ensure mating success and control for possible effects due to local mate competition, parasitoid clutches used in all experiments had *ca*. equal numbers of males and females. Host and novel plants were tested in separate experiments due to time constraints, and experiments were replicated two and three times respectively ($n=$ 12–20 replicates per treatment in each experimental replication).

At the time of testing, individual females were selected randomly from each treatment group and transferred to glass vials. Searching responses were measured as time spent in active antennal palpation on the surface of a 0.8-cm leaf disc during a 2-min trial. Each female was tested once; those searching <2.0 s were considered unresponsive and excluded from all analyses. Each responsive female was then offered a 3rd-instar hornworm (0.05–0.12 g) in proximity to the leaf disc and permitted a single uninterrupted oviposition. As determined in preliminary studies, clutch size and sex ratio allocations were not affected by variation in weight of 3rd-instar larvae (ANCOVA, $n=30$; $P>0.05$). Parasitized hornworms were reared individually on laboratory diet until egression of parasitoid larvae was observed. The number of cocoons per clutch was counted, and all resulting adults were sexed. Sex ratios were calculated as the proportion of females per clutch. Because mating status of ovipositing females was not confirmed and the mean production of all male clutches did not vary among treatment groups (host plants: 17.5±8.8%, $n=248$; novel plants: 25.0±1.9%, $n=226$; $P>0.05$), all-male clutches were excluded from all analyses.

Data were analyzed using SAS, Proc GLM (SAS Institute 1990). The block effect (experimental replication) was not significant ($P>0.05$) in both host and novel plant experiments, and therefore was eliminated in final analyses. Separate two-way analyses of variance were performed to test the main and interactive effects of: (1) the type of postemergence experience (one of two plants or no plant), and (2) the plant offered for searching and oviposition. Data were transformed to correct for normality of residuals: host plant searching times by square root $(x)+0.5$, novel plant searching times by ln (x), and the proportion of females per clutch by arcsin (square root $(x)+1$). Assumption for normality failed in one case, but sample size was adequate ($n>30$) and data were symmetrical, so parametric analyses were performed (Ott 1993); otherwise, assumptions for parametric analysis were met. A Boneferroni's correction was used to adjust α values for all *post hoc* comparisons ($P=0.05$ (# of independent comparisons-1)/ # of all comparisons). For all comparisons, significance was determined at $P\leq0.03$.

Results

Host Plants

Searching Responses Searching time on host plants varied with respect to the interaction of postemergence experience and the plant species assayed ($P=0.002$;

Table 1A, Fig. 1a). Inherent searching responses to tobacco and tomato did not differ ($P=0.15$). Postemergence experience with tomato did not increase searching time on tomato (tomato-experienced wasps vs. control wasps, $P=0.49$), but inhibited searching responses to tobacco ($P=0.0007$). Females with postemergence experience with tobacco did not differ in searching responses to either tobacco or tomato ($P=0.15$; Fig. 1a).

Clutch Size Allocations Postemergence experience had no effect on clutch size allocations ($P>0.05$; Table 1B, Fig. 1b). The mean number of cocoons produced per clutch across all treatment groups was 131 ± 7 ($n=242$).

Sex Ratio Allocations The proportion of females produced per clutch varied with respect to the interaction of postemergence experience and the plant assayed ($P=0.001$; Table 1C, Fig. 1c). Proportionately more females were allocated to hosts offered with the plant species experienced at emergence than on the alternative host plant species. For example, wasps that emerged on tobacco produced more ($P=0.0001$) females per clutch in hosts offered with tobacco than tomato, and wasps that emerged on tomato produced more ($P=0.0001$) females in hosts offered with tomato (Fig. 1c). The proportion of females produced per clutch was similar ($P=0.13$) for wasps with tomato experience at emergence and oviposition, and wasps with tobacco experience at emergence and oviposition (Fig. 1c). Innate responses to host plants differed; females without plant experience produced proportionately more ($P=0.03$) females on tomato than on tobacco (Fig. 1c).

Table 1 Host Plants: Main and Interactive Effects of Postemergence Experience (Tobacco, Tomato, or No Plant) and Plant Species Offered (Tobacco or Tomato) on Searching Responses and Ovipositional Decisions of *Cotesia congregata* (Say)

| Source of variation	Df	F	P
A. Searching responses (active antennal palpation in a 2-min trial)			
Postemergence experience	2	1.69	0.19
Plant Species	1	1.60	0.21
Postemergence experience * Plant species	2	6.94	0.002
Error	110		
B. Clutch size allocations (number of cocoons produced per clutch)			
Postemergence experience	2	0.88	0.41
Plant species	1	0.27	0.60
Postemergence experience * Plant species	2	0.66	0.51
Error	241		
C. Sex ratio allocations (proportion of females produced per clutch)			
Postemergence experience	2	4.73	0.01
Plant species	1	0.83	0.36
Postemergence experience * Plant species	2	24.28	0.001
Error	197		

Results shown are from separate 2-way ANOVAs.
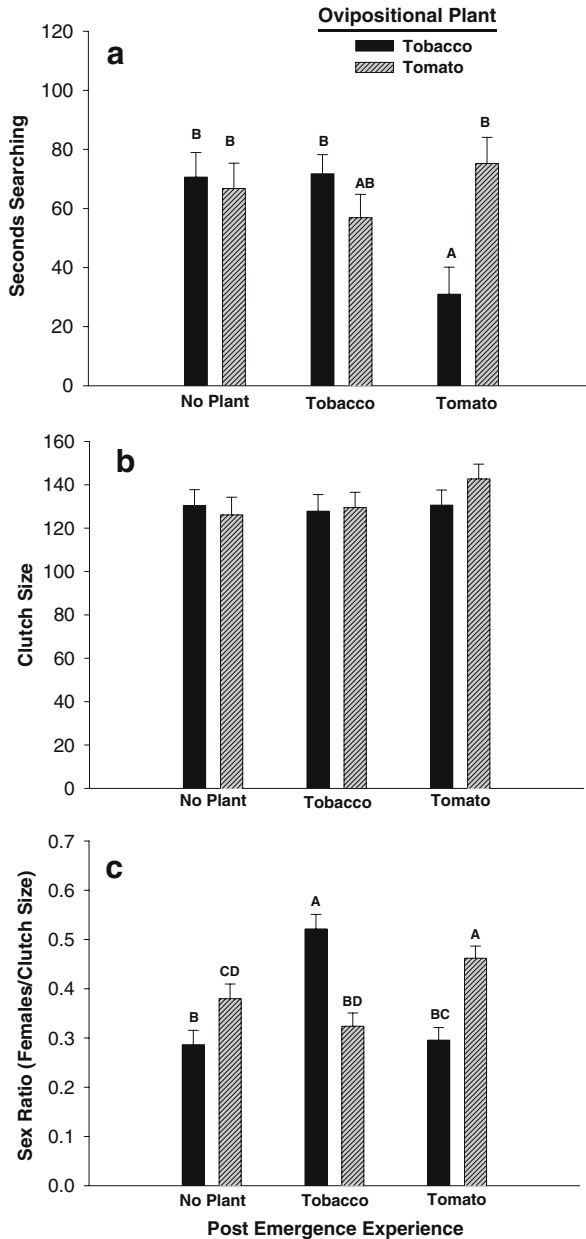
Fig. 1 Effects of postemergence experience on searching responses, clutch size and sex ratio allocations of *Cotesia congregata* (Say) to two host foodplants of *Manduca sexta* L. (tobacco or tomato). *Each bar* represents the untransformed lsmean±SE for each treatment group; means with *different letters* differ significantly ($P \leq 0.03$). **a** Searching responses. Searching time was affected ($P=0.002$) by the interaction of postemergence experience and the plant species assayed. **b** Clutch size allocations. The number of cocoons produced per host was affected by the main or interactive effects of postemergence experience ($P > 0.41$). **c** Sex ratio allocations. The proportion of females produced per clutch was affected ($P=0.001$) by the interaction of postemergence experience and the plant species offered at oviposition.

Novel Plants

Searching Responses Searching time on novel plant species varied with respect to the main effects of postemergence experience and species of plant assayed (Table 2A, Fig. 2a). Females with postemergence experience searched longer ($P=0.003$) than those without plant experience; however, searching responses did not differ between arugula-experienced wasps and parsley-experienced wasps ($P=0.11$). Overall, arugula elicited a stronger inherent response than parsley, and regardless of postemergence experience, females searched longer ($P=0.003$) on arugula than on parsley ($x=28.0\pm3.0$ s, $x=9.0\pm2.0$ s, respectively).

Clutch Size Allocations Clutch size differed with respect to the plant offered at oviposition ($P=0.03$; Table 2B, Fig. 2a). Wasps tended to oviposit larger ($P=0.07$) clutches in hosts offered with parsley ($x=111\pm6$ cocoons, $n=66$) than with arugula ($x=91\pm6$ cocoons; $n=81$).

Sex Ratio Allocations The proportion of females produced per clutch differed with the type of postemergence experience (Table 2C, Fig. 2c). Irrespective of the plant species offered, wasps with plant experience at emergence produced proportionately more ($P=0.001$) females than wasps without plant experience. The proportion of females produced per clutch did not differ between wasps that emerged on arugula or parsley ($P=0.29$).

Table 2 Novel Plants: Main and Interactive Effects of Postemergence Experience (Arugula, Parsley, or No Plant) and Plant Species Offered (Arugula or Parsley) on Searching Responses and Ovipositional Decisions of *Cotesia congregata* (Say)

Source of variation	Df	F	P
A. Searching responses (active antennal palpation in a 2-min trial)			
Postemergence experience	2	4.57	0.01
Plant species	1	25.97	0.0001
Postemergence experience * Plant species	2	0.26	0.77
Error	140		
B. Clutch size allocations (number of cocoons produced per clutch)			
Postemergence experience	2	1.69	0.19
Plant species	1	4.58	0.03
Postemergence experience * Plant species	2	0.12	0.89
Error	141		
C. Sex ratio allocations (proportion of females produced per clutch)			
Postemergence experience	2	7.51	0.0009
Plant species	1	0.69	0.41
Postemergence experience * Plant species	2	0.38	0.69
Error	103		

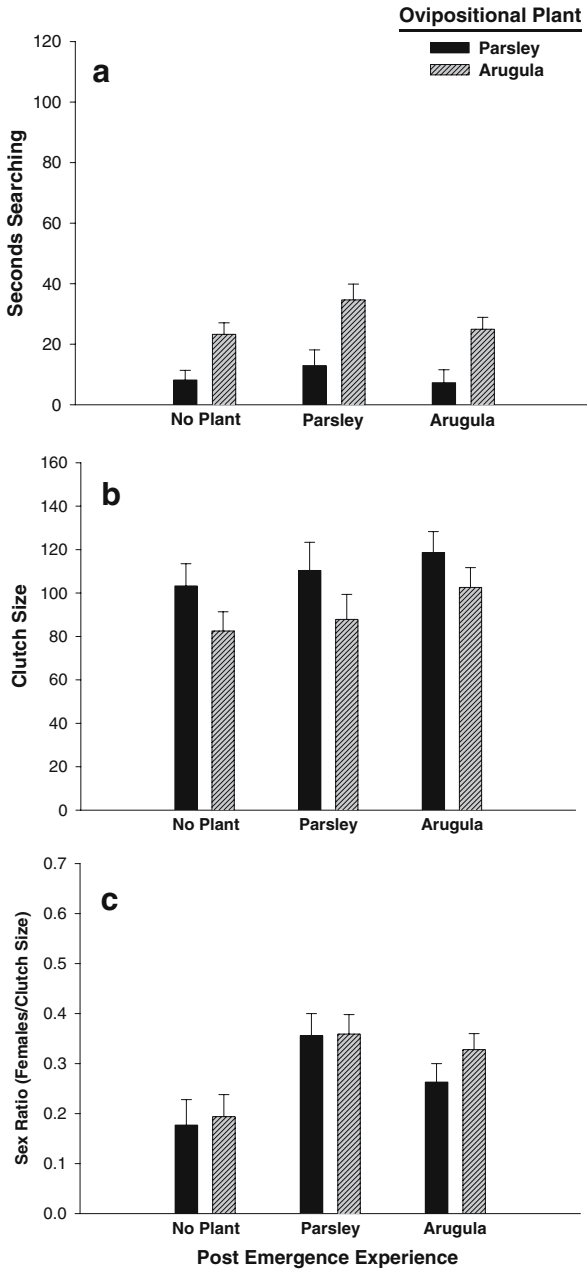Results shown are from separate 2-way ANOVAs.

Fig. 2 Effects of postemergence experience on searching responses, clutch size and sex ratio allocations of *Cotesia congregata* (Say) to two novel plants (arugula or parsley). The interaction between postemergence experience and the plant species offered had no effect ($P=0.69$) on response variables. *Each bar* represents the untransformed lsmean±SE for each treatment group. **a** Searching responses. Searching time was affected ($P\leq0.01$) by both main effects. **b** Clutch size allocations. Clutch size differed ($P=0.03$) only with respect to the plant species offered with the host. **c** Sex ratio allocations. The proportion of females produced per clutch was affected ($P=0.0009$) by postemergence experience (plant vs. no plant) only.

Discussion

Learning of host-finding cues in parasitic wasps is generally regarded as adaptive because it increases the probability of host encounter and, in turn, the opportunity for reproduction (Vet et al. 1990). Indirect effects of learning on parasitoid fitness are well documented (e.g., Wäckers and Lewis 1994; Turlings et al. 1995) but only a few studies have considered the direct effects of learning on fitness (Dukas and Duan 2000; Morris and Fellowes 2002). Results of the present study support our initial hypothesis that postemergence learning increases the allocation of female progeny to hosts encountered on the natal host plant species, and thereby increases parasitoid reproductive potential and fitness directly. Results also support our second hypothesis that effects of postemergence experience with host or novel plants differ, and suggest inherent recognition of host plant species by *C. congregata*.

Females of *C. congregata* that received a postemergence experience with one of two host plant species (tobacco or tomato) allocated proportionately more females to hosts offered with the plant species experienced at emergence (Table 1C, Fig. 1c). In contrast, the effect of postemergence experience with one of two novel plant species (arugula or parsley) was not plant specific, i.e., more generalized. Wasps experienced with either plant species allocated proportionately more females to hosts than control wasps, irrespective of the plant species offered at oviposition (Table 2B, Fig. 2b; Table 2C, Fig. 2c). Host and novel plant experiments should be compared cautiously because they were not conducted concurrently. However, evidence suggests that irrespective of plant experience at emergence, wasps allocated more females to hosts offered with a host plant than to hosts offered with a novel plant. In combination, results indicate that *C. congregata* nherently recognizes tomato and tobacco as host foodplants and that postemergence experience amplifies sex ratio allocation responses. Further, plant-specific effects were limited to host plants, suggesting that the effects of postemergence experience on sex ratio allocations is constrained by inherent host plant recognition.

Postemergence learning had no effect on clutch size allocation. Most likely, clutch size decisions in *C. congregata* are based on factors other than plant cues such as host developmental stage or weight (e.g., King 1987). Clutch size was not affected by the type of host plant offered at oviposition, but wasps oviposited larger clutches to hosts offered with parsley than to hosts offered with the more attractive arugula (Table 1B, Fig. 1b, Table 2B, Fig. 2b). Allocation of larger clutches to hosts feeding on suboptimal foodplants may offset increased larval mortality. For example, nicotine has a detrimental effect on the survival of larval *C. congregata* (Barbosa et al. 1991), and both parasitoid load and offspring mortality are greater when hosts feed on a high rather than a low nicotine variety of tobacco (Thorpe and Barbosa 1986).

Our study tested the direct effect of learned host plant cues associated with the natal host foodplant, i.e., postemergence experience or early adult learning, on clutch size and sex ratio allocation decisions made by a gregarious larval parasitoid at first oviposition. Only two other studies have tested the effects of learning on ovipositional decision-making in parasitic wasps, and neither addressed the role of learned plant cues on sex ratio allocation. Dukas and Duan (2000) tested the effect of learning on parasitism rates in host patches of the solitary egg-pupal parasitoid of

tephritid flies, *Biosteres (= Fopius) arisanus* (Hymenoptera: Braconidae) and found that wasps offered host-infested guava, lemon or kumquat parasitized more eggs in the fruit species they experienced at prior oviposition. Similarly, Morris and Fellowes (2002) tested the effects of natal host species on parasitism rates in host patches and sex ratio allocations in the solitary idiobiont, *Pachycrepoideus vindemiae* Rondani (Hymenoptera: Pteromalidae). In this study, individual wasps were offered patches of twenty pupae of *Musca domestica* L. or *Drosophila melanogaster* L. Results of these studies and of the present one, demonstrate that learning influences ovipositional decision-making.

Induction of host–habitat preferences through early adult experience has been hypothesized to enhance potential linkage of host or host–plant preferences and progeny survival (Papaj and Prokopy 1989). By augmenting inherent searching and sex allocation responses to host foodplants, postemergence experience would increase the efficiency of host location and exploitation of available host populations, thus optimizing fitness of *C. congregata*. In our study, postemergence learning resulted in allocation of proportionately more females to hosts with the host foodplant experienced at emergence. However, naïve wasps searched as long on tobacco as they did on tomato yet allocated more females to hosts offered with tomato. In contrast, naïve wasps searched longer on arugula than on parsley yet allocated the same proportion of females to hosts on both plant species (compare Fig. 1a and c, and Fig. 2a and c). Most likely, responses of naïve wasps reflect past selective pressures. For example, Kester (1991) reported that wasps originating from a tobacco population had a higher tolerance to dietary nicotine than wasps originating from tomato, but larval performance in the field was higher on tomato than tobacco plants for both populations. This finding could explain why naïve wasps in the present study, originating from *M. sexta* on tobacco, allocated proportionately more females in hosts offered with tomato than tobacco. Likewise, *C. congregata* has one host (*Hyles lineata* (F.)) reported to feed on *Brassica rapae*) and no recorded hosts utilizing plants in the Apiaceae (Tietz 1972), which may account for the incongruent searching and sex allocation responses to arugula, as well as the weak searching and male-biased sex allocation responses to parsley. Certainly, the linkage between behavioral, ovipositional and developmental responses deserves further investigation.

Our work demonstrates that postemergence learning provides a mechanism for tracking and optimizing reproductive investment to hosts that will predictably support successful development, i.e., hosts encountered on the same plant species on which the foraging wasp underwent development. By enhancing responsiveness and focusing reproductive investment to hosts on locally abundant host foodplants, postemergence learning could facilitate local adaptation and ultimately, genetic differentiation of populations (Jensen et al. 2002). We hypothesize that learned natal plant cues play an important role in the ovipositional decision-making of many larval parasitoid species.

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