Entomologia Experimentalis et Applicata **98:** 123–132, 2001.

Early oviposition experience affects patch residence time in a foraging parasitoid

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Accepted: June 8, 2000

Key words: biological control, dynamic state model, habitat selection, learning, parasitoid, *Trichogramma thalense*

Abstract

Parasitoids learn olfactory and visual cues that are associated with their hosts, and use these cues to forage more efficiently. Classical conditioning theory predicts that encounters with high-quality hosts will lead to better learning of host-associated cues than encounters with low-quality hosts. We tested this prediction in a two-phase laboratory experiment with the parasitoid *Trichogramma thalense* Pinto & Oatman (Hymenoptera: Trichogrammatidae) and the host *Anagasta kuehniella* Zeller (Lepidoptera: Pyralidae).

Host quality during the first exposure to hosts affected later foraging behavior for some experimental treatments, as predicted. We used a learning model, followed by patch-time optimization, to interpret our findings. We first simulated the parasitoids' host encounters during the experiment, and predicted their estimate of patch quality after each encounter. We then used dynamic optimization to predict the parasitoids' optimal patch residence times. The model reproduces the trends of the experimental results.

Introduction

Various biological control programs for agricultural pests are based on mass rearing and release of local natural enemies to supplement field populations (augmentative biological control, van Emden & Peakall, 1996). The population densities of these natural enemies are presumably regulated by their own set of coevolved predators and parasites. Multiple releases are therefore needed to ensure that large enough populations of biocontrol agents are maintained in the field. The natural enemies are reared in insectaries and released on a regular basis. This raises the possibility for behavioral manipulation of the biocontrol agents during the rearing stage. Ideally, one would like to direct the post-release behavior of biocontrol agents through pre-release manipulation (Lewis & Martin, 1990; Papaj & Vet, 1990). At the very least, one would like to avoid a wrong pre-release experience that might decrease the post-release performance of natural enemies (Wardle & Borden, 1986; Vet & Groenewold, 1990).

Behavioral studies show that both recent and past foraging experience can affect habitat choice or host choice in insect parasitoids, which are common biocontrol agents (reviewed by Turlings et al., 1993). Simulation studies suggest that such learning can eventually shape the spatial distribution of the population (Bernstein et al., 1988, 1991). Response to very recent experience includes adjustment of residence time in host patches in response to oviposition (e.g., Waage, 1979; Roitberg & Prokopy, 1984; Hemerik et al., 1993; Driessen et al., 1995) or to host-associated cues (e.g., Ayal, 1987; Driessen et al., 1995; Henneman, 1998). The suggested proximate mechanisms associated with these responses include sensitization and habituation to host kairomones and to ovipositions in hosts (Waage, 1979; Driessen et al., 1995). Evidence for the effects of more distant experience on foraging behavior is based on two-phase stud-

ies where phase-I foraging conditions were shown to affect phase-II decisions. For example, *Leptopilina* wasps preferred, in a choice test, substrates on which they had previously oviposited (Vet, 1988; Vet & Schoonman, 1988; Papaj & Vet, 1990; Poolman Simons et al., 1992). *Trichogramma pretiosum* remained longer in host patches after a single pre-release oviposition than without previous experience (Gross et al., 1981). *Trichogramma maidis* increased its affinity to a given host species after oviposition on the same host (Kaiser et al., 1989). Past conditions of photoperiod, barometric pressure and host availability affected the tendency of *Leptopilina* to accept hosts that were already parasitized (Roitberg et al., 1992, 1993). Past exposure of *Trichogramma principium* to young hosts decreased the likelihood of later host rejection (Reznik et al., 1997). These findings suggest learning mechanisms that differ from those involved in short-term responses. Vet & Groenewold (1990) suggest that past foraging experience modifies habitat selection in parasitoids through associative learning of host-related cues. Roitberg et al. (1992) and Reznik et al. (1997) on the other hand, suggest that past experience affects host selection through modification of host acceptance thresholds.

In the present study, we test the hypothesis that oviposition experience on high-quality hosts would result in higher subsequent parasitism rates than similar experience on low-quality hosts. This hypothesis is based on classical conditioning theory, which predicts greater reinforcement of the response to host-related cues when hosts are of high quality than when their quality is low (Atkinson et al., 1990). We test this hypothesis through a two-phase laboratory experiment. We then use a dynamic state variable model (Mangel & Clark, 1988; Mangel & Ludwig, 1992; Clark & Mangel, 1999) to suggest how learning may modify the parasitoids' habitat choice behavior.

Materials and methods

Parasitoids and hosts

Trichogramma thalense parasitoids were collected in Santa Cruz county, CA in 1997, and were reared in the insectary of the UC Santa Cruz Center for Agroecology and Sustainable Food Systems (UCSC-CASFS). These are pro-ovigenic, gregarious parasitoids that oviposit and feed on a wide range of moth eggs. Generation time of *T. thalense* is 10.1 ± 0.13 days, and mean lifetime fecundity is 36.9 ± 1.9 at 25 °C (Abbinanti, 1994). We used mated females that were 24–48 h old for experiments. Preliminary experiments showed that female of this age group parasitize more readily than younger and older wasps. *Anagasta kuehniella* moths were obtained from Beneficial Insects Inc., Canada, and were supplemented by collections from Santa Cruz county. They were reared, mated, and allowed to oviposit in the insectary of the UCSC-CASFS. Their eggs were collected daily and were used as hosts for the experiments. In a few cases of host shortage we also used the commercially obtained eggs as hosts. *Trichogramma thalense* parasitize fresh *Anagasta* eggs more readily than eggs that are a few days old (Figure 1). These findings are consistent with reports on other *Trichogramma* species (Pak, 1986; Hintz & Andow, 1990; Calvin et al., 1997). We therefore considered fresh hosts to be 'good' (in the sense that they are favored by *Trichogramma*) and older hosts to be 'bad'. 'Good' hosts were used immediately after collection. 'Bad' hosts were incubated for 72 h at 25 °C before use.

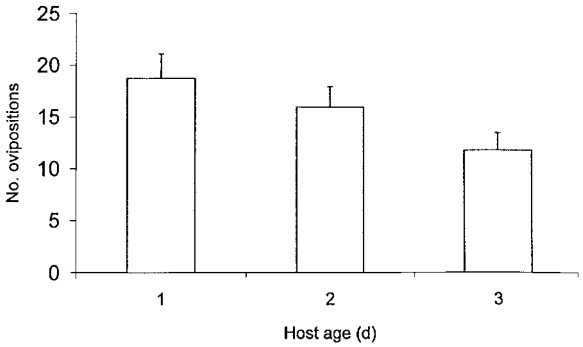

Figure 1. The mean number of hosts parasitized by *T. thalense* during 24 h. d-1 hosts (n=47) were 0–24 h old, d-2 hosts (n=46) were 24–48 h old, d-3 hosts (n=48) were 48–72 h old. d-2 and d-3 hosts were incubated at 25 °C before use. Error bars are 1 SEM.

Experimental procedure

Experiments were conducted at 25 °C in a laboratory under constant illumination. Hosts were prepared on 2 × 1 cm egg-cards in petri dishes. Parasitoids were chilled briefly (<10 min at 5 °C) prior to manipulation, and were then placed on the hosts. Parasitoids that did not start inspecting the hosts immediately were replaced. The experiments consisted of two phases. In the first phase, we placed a single parasitoid on an egg card with either good or bad hosts. The number of hosts, and the duration of exposure, varied between experiments (see below for details). In

Table 1. Design of experiment 1

Treatment	*n*	Phase-I hosts	Phase-II hosts
GG	32	10 good	>50 good
BG	34	10 bad	>50 good
GM	36	10 good	>25 good+>25 bad
BM	37	10 bad	>25 good+>25 bad
GB	35	10 good	>50 bad
BB	36	10 bad	>50 bad

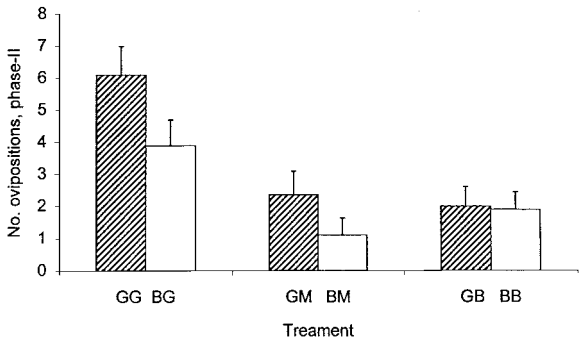

Figure 2. Mean number of ovipositions in the second phase of experiment 1. Error bars are 1 SEM. Hatched bars are treatments with good phase-I hosts, white bar are treatments with bad phase-I hosts. Host type in phase-I and in phase-II had a significant effect on the number of phase-II ovipositions (2-way ANOVA, df=5, F=4.37, P<0.05 for phase-I hosts, F=13.49 P<0.001 for phase-II hosts). Good hosts in phase-II differ significantly in their effect from medium hosts (mean difference -3.10 ± 0.70, P<0.001) and from bad hosts (mean difference 3.33 ± 0.69, P<0.001). The effects of medium and bad hosts in phase-II are not significantly different (mean difference 0.23 ± 0.66, *post-hoc* Bonferroni tests).

the second phase, which followed the first phase immediately, we moved the parasitoid to a new dish that contained >50 hosts. The second-phase hosts were either good, bad, or both good and bad, depending on experiment. We removed the parasitoid 7 h later, and incubated the phase-I and phase-II hosts at 25 °C. Preliminary observations showed that *T. thalense* can oviposit their whole egg complement (20–30 eggs) within 4 h. Therefore, parasitoids were not host- or time-limited (but probably egg-limited) in the second phase. We identified parasitized hosts by their black color six days after exposure to the parasitoid. We tested whether the number of parasitized hosts in phase-II is affected by the quality of hosts in the first phase, by the number of ovipositions in the first phase, or by the duration of the first phase.

Experiment 1: Does host quality in phase-I affect foraging behavior in phase-II?

In the first phase of the experiment we exposed a single parasitoid to either ten good hosts or ten bad hosts, glued to a black egg card, for 4 h. In the second phase we moved each parasitoid to another black egg card with >50 hosts that were either good, bad, or approximately half good and half bad (medium patch). We created the medium patch by gluing the good hosts to one half of the egg card, bad hosts to the other half. Thus we used six experimental treatments (Table 1).

Experiment 2: Does the number of ovipositions in phase-I affect foraging behavior in phase-II? The first phase consisted of exposing a single parasitoid to either >50 good hosts (n=174) or >50 bad hosts (n=342) for 15–100 min, depending on treatment. In the second phase, we allowed the wasps to oviposit on >50 good hosts for 7 h. *Trichogramma thalense* requires, on average, 45 min to parasitize ten hosts (preliminary observations). By using some phase-I durations that were shorter and others that were longer we obtained a large variability in the number of phase-I ovipositions. We then regrouped the data according to the number of hosts parasitized in phase-I, regardless of its duration. We tested for correlations between the numbers of phase-I and phase-II ovipositions.

Experiment 3: Does the duration of phase-I affect foraging behavior in phase-II? We exposed a single parasitoid to either ten good or ten bad hosts in phase-I, and to >50 good hosts in phase-II. The duration of phase-I in this experiment varied from 45 min to 24 h. When phase-I lasted longer than 45 min, the wasps spent part of it in the presence of hosts, but without ovipositing, since most of the hosts had already been parasitized. That could be a time of possible habituation, or forgetting. If wasps need to oviposit continually in order to retain a learned association, then the effect of phase-I host quality on phase-II behavior is expected to diminish as the length of phase-I increases.

Direct observations: does host quality and fresh host depletion affect the movements of the wasps? We conducted direct observations in order to test (a) whether the wasps reject bad hosts more frequently than good hosts, (b) whether they leave patches of bad hosts sooner than patches of good hosts, (c) whether they travel larger distances within patches of bad hosts than within patches of good hosts, and (d) whether

they treat unparasitized hosts differently from hosts that had already been parasitized. We placed 25 hosts in a 5×5 array on a 2×1 cm black egg card, and allowed a single parasitoid with no previous experience to forage on them. We observed the parasitoid's activities through a dissecting microscope and recorded them directly onto computer. We recorded the sequence of hosts touched by the parasitoid, and the time spent on host inspection, rejection, oviposition and host-feeding. We stopped the observation after the parasitoid left the patch and stayed away from it for more than ten min. Then we removed the parasitoid, and repeated the observation with another inexperienced wasp on the same patch. Most of the hosts in this patch had been already parasitized by the first parasitoid. Thus, the second observation allowed us to record movement patterns and time budgets on parasitized hosts. We defined the distance between two hosts as the minimal number of movements between neighbors on the grid required for traveling between them. Thus the smallest distance on a 5×5 grid is 1, and the largest distance is 4. A parasitoid that selects its hosts randomly is expected to travel an average distance of 2.33 between consecutive hosts. We calculated average movement distances for each observed individual. We observed 11 pairs of parasitoids in arrays of good unparasitized hosts, and on good parasitized hosts. We observed eight parasitoids on bad unparasitized hosts and seven parasitoids on bad parasitized hosts in a similar manner.

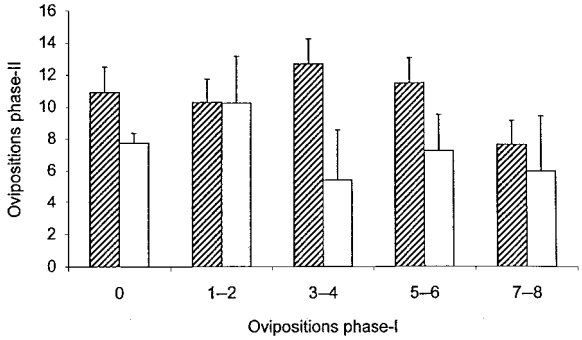

Figure 3. The mean number of ovipositions in phase-II of experiment 2 as a function of the number of ovipositions in phase-I for treatments GG (hatched bars) and BG (white bars). The Error bars are 1 SEM.

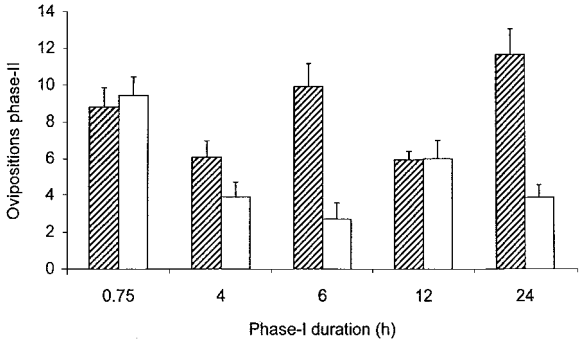

Figure 4. The mean number of ovipositions in phase-II of experiment 3 as a function of the duration of phase-I for treatments GG (hatched bars) and BG (white bars). Error bars are 1 SEM. Host type in phase-I, but not the duration of phase-I, had a significant effect on the number of ovipositions in phase-II (two-way ANOVA, df=7, F=18.13, P<0.001 for phase-I host type, F=1.494, P>0.05 for phase-I duration).

Results

Experiment 1. Parasitoids that foraged in a good patch during phase-II oviposited more than parasitoids that foraged in a medium or bad patch (Figure 2). Parasitoids that were exposed to good hosts in phase-I oviposited more in phase-II than parasitoids that experienced bad hosts in phase-I. However, this effect was statistically significant only for the GG and BG treatments (for abbreviations see Table 1). In the GM and BM treatments, the parasitoids were given the opportunity to choose between good and bad hosts in phase-II. We found no statistically significant preference for the good hosts in this mixed-patch situation: 1.47 ± 0.69 good hosts and 0.75 ± 0.50 bad hosts were parasitized in treatment GM (power = 0.80, Zar 1996, p. 136), 0.89 ± 0.36 good hosts and 0.35 ± 0.17 bad hosts were parasitized in treatment BM (power = 0.91). The mean number of ovipositions in phase-I was similar across treatments and did not show a clear trend.

Experiment 2. Parasitoids that were exposed to good hosts in phase-I oviposited more during phase-II than parasitoids with a similar number of ovipositions on bad hosts in phase-I. This trend was statistically significant only for cases with 0 ovipositions in phase-I (df=37, $t=-1.84$, P<0.05). The number of hosts parasitized in phase-II peaked after 3–4 ovipositions on good hosts, and after 1–2 ovipositions on bad hosts in phase-I (Figure 3).

Experiment 3. The duration of phase-I did not have a significant effect on the number of phase-II ovipositions. The number of phase-II ovipositions was significantly higher in treatment GG than in treatment BG (Figure 4, see legend for statistics).

Direct observations. The *Trichogramma* individuals spent more time, and parasitized more, in patches with good hosts than in patches with bad hosts. They also rejected hosts more frequently, and oviposited twice in the same host more frequently, in good patches than in bad patches. All wasps moved between directly neighboring hosts more than expected from a randomly moving individual. This area-restricted movement pattern was less pronounced in patches of parasitized hosts than in patches of mainly unparasitized hosts (Table 2). These data suggest that differing rejection rates of good and bad hosts cannot explain the results of experiment 1, but that differing residence durations in good and bad patches may be important. We tested this idea through a model, which tries to reproduce the results of experiment 1 by using patch residence duration as the only behavioral decision.

Modeling. We used a model that simulated learning, and a dynamic state variable optimization model in order to reproduce the results of experiment 1. Direct observations showed that the parasitoids stayed for a longer time, and oviposited more, on patches with good hosts than on patches with bad hosts (Table 2). Therefore, the behavior that we modeled was the residence time in the phase-II patch.

The learning model simulates the host encounters of a parasitoid in a second-phase patch in the six experimental treatments of experiment 1. Each modeled parasitoid had already encountered ten good hosts or ten bad hosts in phase-I. The model makes the following assumptions:

(a) Parasitoids that experienced good hosts in phase-I have a high initial estimate for the quality of the phase-II patch. Parasitoids that experienced bad hosts in phase-I have a lower initial estimate for the phase-II patch.

(b) During each time-step the parasitoid encounters a host that is either good, bad, good and parasitized, or bad and parasitized. Each host type contributes differently to the parasitoid's fitness. We estimated these contributions by looking at the average patch time on each type of hosts in the direct observations (Table 2). We transformed these values by defining the time in a patch of good hosts as 1, and calculated patch time for other host types accordingly (0.7 for good and parasitized, 0.39 for bad, 0.29 for bad and parasitized). We transformed the values for total number of parasitized hosts (Table 2) in the same manner. This resulted in the following values: 1 for good hosts, 1 for good and parasitized hosts, 0.84 for bad hosts, 0.44 for bad and parasitized hosts. We then averaged the transformed parameters for patch time and number of parasitized hosts for each host type. This estimate assumes that the wasps' foraging preferences reflect the relative contributions of the various host types to their fitness.

(c) The parasitoid always oviposits in the encountered host. This assumption reflects our observations that host rejection is not more frequent in bad hosts than in good hosts (Table 2), suggesting that differential host rejection cannot account for the results of experiment 1. Differential rejection was therefore not included in our model.

(d) Following each encounter the parasitoid updates its estimate of patch quality. This estimate is based on the number of good, bad, and parasitized hosts so far encountered (in phase-I or -II), weighed by how recent the encounters were. In the model, we estimated the frequency of each host type h {h = good, bad, good and parasitized, bad and parasitized} during t encounters as follows. The weight w_i of encounter i was $(i/t)^{\delta}$ if host of type h was encountered, 0 otherwise; here δ is a memory parameter that gives more weight to recent experience when large, and more influence to past encounters when small. The total estimated frequency of hosts of type h is the sum of weights

$$\text{Sum of weights} = \frac{\sum_{i=1}^{t} w_i}{\sum_{i=1}^{t} (i/t)^{\delta}} \qquad (1)$$

The frequency of all host types sums up to 1, since the parasitoid encounters a host during each time-step.

(e) The longer a parasitoid remains in the patch, the higher its probability of encountering a parasitized host. *Trichogramma* move mainly between neighboring hosts (that is, a parasitoid typically encounters some of the hosts more than once, and others not at all). We let g(t), b(t), gp(t), bp(t) denote, respectively, the numbers of good, bad, good-parasitized, and bad-parasitized hosts at the start of time period t. The probability $E_p(t)$ of encountering a parasitized host is then

$$Ep(t) = \left(\frac{gp(t) + bp(t)}{g(t) + b(t) + gp(t) + bp(t)} \right)^{\gamma}, \qquad (2)$$

where γ is a search parameter that ranges $0 < \gamma \leq 1$. Small values of γ describe parasitoids that search a small part of the patch; $\gamma = 1$ specifies random search. The encounter probabilities with good and bad hosts are

Table 2. Behavioral parameters from direct observations. The effect of host type (good vs. bad, and parasitized vs unparasitizied) was tested through two-way ANOVAs. Proportions were arcsine-transformed prior to analysis. *- P<0.05, ** - P<0.01, *** - P<0.001, NS – non-significant

Parameter	Host type				Statistical significance	
	Good	Good + parasitized	Bad	Bad + parasitized	Good/bad host	Parasitized unparasitized host
n	11	11	8	7		
Time in patch (min)	98.18 ± 8.30	69.54 ± 9.24	38.13 ± 2.55	28.43 ± 3.68	F=41.93 ***	F=6.020 *
# of hosts parasitized	18.09 ± 1.23	18.18 ± 1.92	15.13 ± 2.41	8.00 ± 2.31	F=11.29 **	F=3.23 NS
Freq. of host rejection	0.67 ± 0.12	1.41 ± 0.25	0.13 ± 0.06	0.11 ± 0.06	F=28.03 ***	F=4.36 *
Freq. of 2 ovipositions in same host	0.18 ± 0.03	0.27 ± 0.04	0.09 ± 0.02	0.10 ± 0.07	F = 8.663 **	F=1.39 NS
Movement distance	1.21 ± 0.03	1.43 ± 0.06	1.44 ± 0.08	1.79 ± 0.20	F=13.15 **	F=12.30 **

$$E_g(t) = \frac{g(t)}{g(t)+b(t)}(1-E_p(t))$$
$$E_b(t) = \frac{b(t)}{g(t)+b(t)}(1-E_p(t)) \quad (3)$$

Using data from direct observations (Table 2), we set a higher value for γ following an encounter with a parasitized host than after oviposition in a fresh host. Using these assumptions, we simulated a series of host encounters in each run of the model, and updated the parasitoids' estimate of the quality of the patch following each encounter.

We used a dynamic state variable model to determine the optimal patch residence time. The modeled decision was whether to stay in the patch for an additional time-step or to leave the patch and search for better hosts. We assumed that the parasitoids evaluate patch leaving as better than foraging in a patch of parasitized hosts, but as less profitable than foraging in a patch of unparasitized hosts. We set

$$F(t) = \text{maximum expected reproductive success between } t \text{ and } T, \quad (4)$$

where the maximum is taken over remaining in the current patch or leaving and seeking another patch. We assume that oviposition in good, bad and parasitized hosts increments lifetime fitness by amounts β_g, β_b, β_p, respectively, and that leaving increments lifetime fitness by an amount β_l. The fitness value of leaving the patch at the start of period t is $V_l(t) = \beta_l + F(t+1)$ and the fitness value of remaining in the patch is

$$V_r(t) = E_g(t)[\beta_g + F(t+1)] + E_b(t)[\beta_b + F(t+1)] + E_p(t)[\beta_p + F(t+1)] \quad (5)$$

combining these, we have

$$F(t) = \max\{V_l(t), V_r(t)\} \quad (6)$$

We assume that β_l is genetically determined, rather than learned. Mortality during our experiments was lower than 5% and preliminary observations indicated no survival costs associated with ovipositions, in agreement with Bai & Smith (1993). For these reasons we did not include a mortality term in Equation (5). We performed 1000 runs of each set of simulations, resulting in 1000 predicted patch residence times for each simulated experimental treatment. We report on their means and standard deviations.

The predicted numbers of ovipositions in phase-II for the six treatments of experiment 1 reproduce the two main trends observed in the experiment (Figure 5): (1) more ovipositions are predicted when the phase-II patch is good than when it is medium or bad. (2) more ovipositions are predicted when the phase-I hosts are good than when they are bad, but this trend is more significant when the phase-II hosts are good as well. We also calculated the predicted phase-II patch times for different values of the search parameter and the memory parameter, while keeping other parameter values constant (Figures 6 and 7). These analyses show that the qualitative predictions of the model are more sensitive to the value of the memory parameter than to the search parameter. For example, the model predicts

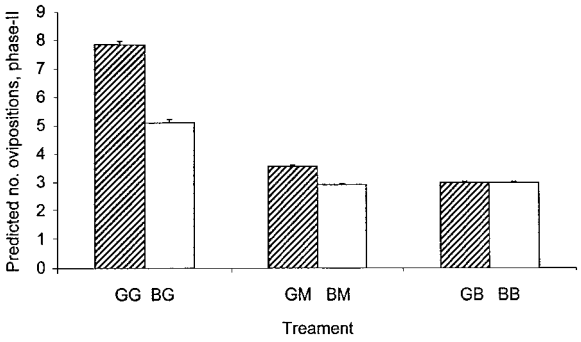

Figure 5. The mean number of ovipositions in phase-II of experiment 1, as predicted by the dynamic state variable model. The prediction for each treatment is an average over 1000 simulations of host encounters. Error bars are 1 SD. Model parameters were: γ=0.2 for unparasitized hosts, γ=0.4 for parasitized hosts, δ=7. The fitness values of ovipositing in good, good and parasitized, bad, and bad and parasitized hosts were 1, 0.84, 0.62 and 0.37, respectively. The fitness value of leaving the patch was 0.8. The model was run for 30 time steps.

more phase-II ovipositions in treatment GB than in treatment BB for low values of the memory parameter, but similar numbers of ovipositions for high values (Figure 6). The prediction for the two treatments is similar, on the other hand, for all values of the search parameter (Figure 7).

Discussion

The present study agrees with previous demonstrations of associative learning that later affects habitat selection in parasitoid wasps. Our working hypothesis was that host-related cues are learned more effectively when paired with good hosts than when paired with bad ones. This hypothesis was only partly supported by our experiment, namely only when the parasitoids were exposed to high-quality hosts in phase-II. This suggests that the working hypothesis was too simple to predict the wasps' behavior even in our artificial controlled environment. The model, which included learning and forgetting by the parasitoid, as well as non-random host encounters, reproduced the parasitoids' patch choice decisions. We think that the model is important in pointing to these factors as candidates for empirical investigation.

An alternative interpretation of our results is that the wasps' host exposure in phase-I affected their rates of egg maturation (e.g., wasps that experienced bad hosts slowed down their egg development, or wasps that experienced good hosts accelerated egg development). Such a response, which does not involve

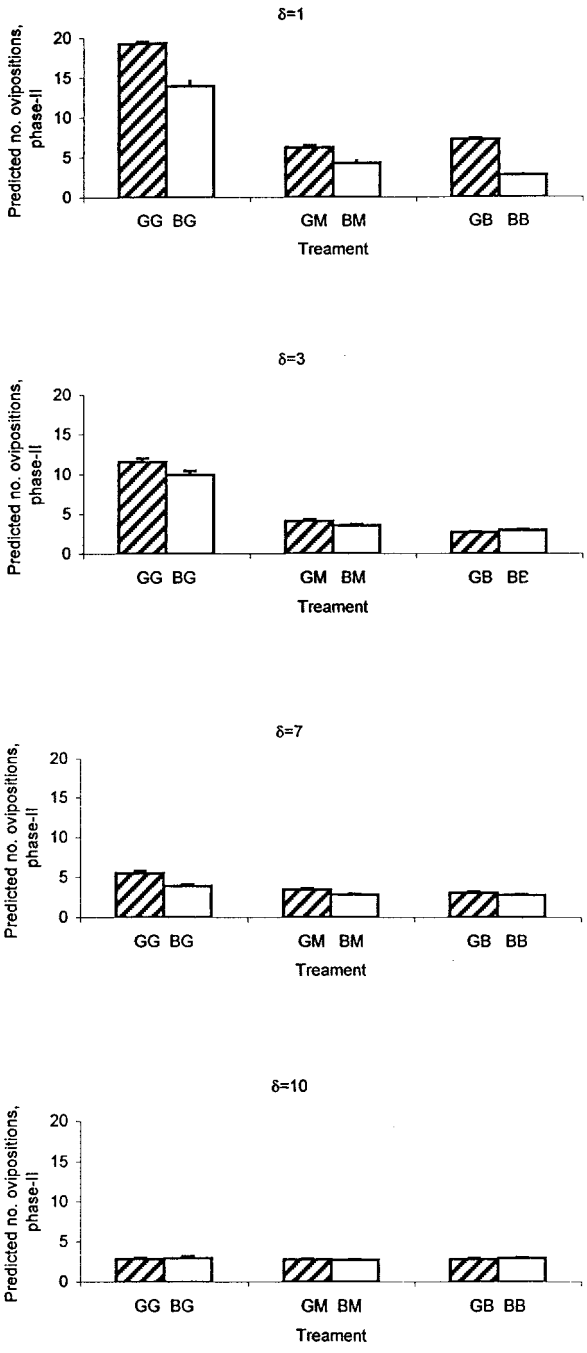

Figure 6. The mean number of ovipositions in phase-II of experiment 1, as predicted by the dynamic state variable model. The value of the memory parameter δ was varied between 1 (large weight to old experience) and 10 (large weight to recent experience in the evaluation of patch quality). The values of the remaining parameters were the same as in Figure 5.

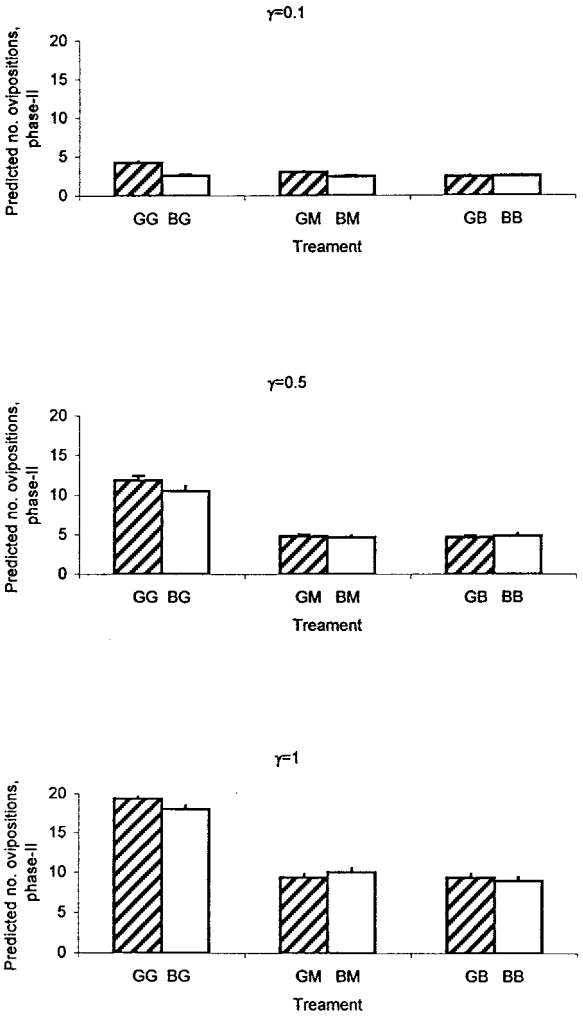

Figure 7. The mean number of ovipositions in phase-I of experiment 1, as predicted by the dynamic state variable model. The value of the search parameter γ was varied between 0.1 (movement mainly between adjacent hosts) and 1 (random host selection), and was identical for parasitized and unparasitized hosts. The values of the remaining parameters were the same as in Figure 5.

learning, could also produce differences between treatments in the number of phase-II ovipositions. This interpretation seems less likely for the following reasons: (1) Phase-II followed immediately after the end of phase-I in our experiments, leaving the wasps little time for adjustment of ovarian development, (2) *Trichogramma thalense* is largely pro-ovigenic, and (3) The number of ovipositions in phase-I was similar for good and bad hosts.

Our results indicate that phase-I exposure to hosts affected the wasps' later affinity to host patches, i.e., habitat choice. We have no strong evidence for effects of the phase-I exposure on later host-choice behavior. For example, individuals in the GM and BM treatments (experiment 1) chose similar proportions of good and bad hosts in the second phase of the experiment, regardless of their phase-I exposure. It seems that a first exposure to hosts or host-related cues affects habitat selection in some of the systems studied (Gross et al., 1981; Vet & Schoonman, 1988; Vet, 1988; Papaj & Vet, 1990; Poolman Simons et al., 1992), and host selections in others (Kaiser et al., 1989; Roitberg et al., 1992, 1993). At this stage, we cannot predict whether learning would influence host choice or habitat choice for a given parasitoid species. One possible relevant factor for making such a prediction may be the gregariousness of the parasitoid (i.e., whether more than one parasitoid can successfully develop within one host). The cost of ovipositing in an already-parasitized host is much higher for solitary than for gregarious parasitoids. We therefore speculate that host selection may be easily affected by previous experience in solitary parasitoids (as in Reznik et al., 1997). Habitat selection may be more influenced by learning in gregarious species, such as *T. thalense* in the present study. This speculation can be tested in a comparative experimental study.

Our experiments show that a 'good' host exposure makes parasitoids more likely to oviposit later than a 'bad' exposure. A possible proximate interpretation is that the phase-I 'good' exposure increased the wasps' responsiveness to patch cues, and caused them to search the second-phase patch harder than the phase-I 'bad' exposure. A similar mechanism was suggested by Waage (1979) to explain patch-time decisions in *Nemeritis*. Other experiments and models (Roitberg et al., 1992, 1993), on the other hand, suggest that selectivity increases after an initial exposure to 'good' conditions, because individuals now have knowledge about the state of the environment. The arguments in the latter cases are based on ultimate trade-offs concerning mortality of the ovipositing individual and fitness from oviposition in different kinds of patches. What remains to be done is linking proximate and ultimate approaches.

Experiments 2 and 3 were designed to find the number of phase-I ovipositions and the duration of phase-I that would maximize the wasps' performance in phase-II. Experiment 2 showed that maximal parasitization is phase-II is achieved after one to four ovipositions in phase-I. This finding possibly reflects a balance between two tendencies: learning may increase, but the parasitoid's egg load probably de-

creases with increased exposure to hosts in phase-I. 1-4 ovipositions in phase-I are possibly long enough to affect the wasps' habitat selection, but short enough to avoid egg limitation in phase-II. Host quality in phase-I of experiment 3 influenced the number of phase-II ovipositions, but the duration of phase-I did not have a clear effect. We suspect that interference with the wasps' circadian rhythm in these experiments, and possibly egg resorption (Bai & Smith, 1993; Fleury & Boulétreau, 1993), may underlie some of these erratic results. *Trichogramma* requires 45 min on average for ten ovipositions (preliminary observations). Thus, the phase-I patch of experiment 3 was possibly less depleted when phase-I lasted 45 min than when phase-I was longer. It is therefore possible that the wasps experienced varying patch quality via differential depletion in experiment 3. This depletion effect may also have masked possible effects of phase-I duration.

The parasitoids in our experiments were held without hosts for 24–48 h, a long time compared to the situation in nature. Although our preliminary observations show that the wasps' tendency to oviposit is maximal at this age, we cannot rule out the possibility that egg development was arrested, or that eggs were resorbed in the experiments until hosts were provided. This possibility can be checked by repeating the experiments with younger animals.

Our results suggest that pre-release exposure of parasitoids to high-quality target hosts may affect their performance in biological control programs. *Trichogramma* are generally released as pupae within hosts, ca. 24 h before the expected emergence of adults. They are usually housed in containers that allow adults to fly out, but prevent potential predators from getting in. Pre-release hosts may be provided within the same container together with habitat-specific cues, so that parasitoids can encounter them shortly after emergence. Such exposure may increase the parasitoids' initial affinity to their target habitat, although this effect will likely decay rapidly as the parasitoids acquire further experience in the field.

Acknowledgements

We thank Cathy Carlson, Maggie Barton and Sarah Barnett for technical assistance. This work was partially supported by a USDA grant to Marc Mangel.

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