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Influence of Experience on the Sequential and Temporal Organization of Host-Acceptance Behavior in *Brachymeria intermedia* (Chalcididae), an Endoparasitoid of Gypsy Moth

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Experienced Brachymeria intermedia *females are almost twice as likely to accept a* Lymantria dispar *pupa as inexperienced parasitoids. The sequence of parasitoid behaviors that leads to host acceptance is highly canalized. Experienced parasitoids, however, have a higher probability of initiating host investigation and making a transition from drumming to grasping, which in turn almost invariably leads to ovipositor insertion. Experienced females found the host more quickly than inexperienced females. Host-handling time did not change with experience but was longer in females that accepted rather than rejected the host. Females exposed to gypsy moth odor but not contacting pupae behaved similarly to females that never experienced host-related stimuli.*

KEY WORDS: *Brachymeria intermedia*; *Lymantria dispar*; parasitoid; experience; foraging; learning.

INTRODUCTION

The influence of adult experience on the foraging behavior of parasitoids has been shown in many recent papers (Vet, 1983; Vet and van Opzeeland, 1984; Wardle and Borden, 1985; Drost *et al.*, 1986, 1988; Hérard *et al.*, 1989; Lewis and Tumlinson, 1988; Zanen et al., 1989; Kaiser *et al.*, 1989; Cardé and Lee, 1989; Turlings *et al.*, 1990). However, as noted by Vet and Schoonman (1988), most of the data available deal with host finding and host-habitat finding by

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means of olfactory cues. Less is known about the influence of experience on foraging decisions made by parasitoids once the host has been found, i.e., close-range host finding and host-acceptance behavior. Although parasitoids of moving hosts (larvae) generally have a very short host-acceptance phase, parasitoids of sessile hosts (eggs, pupae) often go through an elaborate examination of the host before oviposition (Vinson, 1984). Behavioral plasticity at this level of the foraging process may therefore be more likely in parasitoids of sessile hosts.

The endoparasitic chalcidid *Brachymeria intermedia* was introduced into the United States at the beginning of this century as a biological control agent for gypsy moth, *Lymantria dispar* (Burgess and Crossman, 1929; Leonard, 1966). *B. intermedia* has been recovered from many species of Lepidoptera in Europe (Dowden, 1935) and has been reared from lepidopterous and dipterous pupae in the laboratory (Dowden, 1935; Minot and Leonard, 1976), but its natural polyphagy in the United States is largely unknown.

The host-finding behavior of *B. intermedia* is guided partly by volatile kairomones (Cardé and Lee, 1989) and partly by contact kairomones (Leonard *et al.*, 1975; Minot and Leonard, 1976). Adult experience in *B. intermedia* affects the time needed to find the kairomone odor source in an olfactometer as well as the propensity to accept a host (Cardé and Lee, 1989). In the present paper we investigate the behavioral sequence leading to host acceptance, the behavioral changes that occur as a result of prior oviposition experience, and whether exposure of the wasps to odor of gypsy moth pupae affects host acceptance.

MATERIALS AND METHODS

Insects

Gypsy moth egg masses were supplied by the USDA Methods Development Laboratory at the Otis ANG Base, Mass. The larvae were reared on a wheat germ diet at 28 ± 1°C in LD 16:8 h and at 1400 lux (Bell *et al.*, 1981). Pupae were collected from this laboratory colony or obtained directly from the USDA.

B. intermedia was reared on female gypsy moth pupae according to the method of Minot and Leonard (1976) and maintained at 28 ± 1°C and 60 ± 15% RH. Parasitoids were collected randomly on the day of emergence, distributed equally over two experimental groups that were held separately in cages (20 × 20 × 20 cm) with water and honey. The female/male ratio was 2:1 in all cages. Females generally mate once within 2 days after emergence (Dowden, 1935) but males continue to court mated females (Leonard and Ringo, 1978). To avoid possible influences of courting males on the "physiological state" of the female, males were removed at the third day after emergence. One experimental group was withheld from hosts until the test (the inexperienced group). The other experimental group was provided with fresh gypsy moth pupae daily at a one pupa-per-female ratio, starting 3 days after emergence, until the day before the test (the experienced group). In a separate experiment, females were kept in separate growth chambers, one with pupal odor (a petri dish with 10 live pupae, covered with wire gauze, so that the parasitoids could not contact the pupae) and one without pupal odor, again starting three days after emergence until the day before the test.

Data Collection and Behavioral Repertoire

Tests were conducted between the eighth and the twelfth hours of the photophase (Minot and Leonard, 1976) when females were 5–12 days old (Barbosa *et al.*, 1986), at 28°C and 11,000 lux. Behavioral assays were carried out in 10-cm-diameter plastic petri dishes with a Whatman No. 1 filter paper on the bottom. One female *L. dispar* pupa, 3–5 days old, was placed on the center of the filter paper. The pupa could move freely; however, it generally did not move until the wasp inserted her ovipositor and this occasionally resulted in the parasitoid being thrown off the host. One female parasitoid was transferred to the lip inside of the dish cover and the dish was closed. The observation time was 10 min, unless a female left the pupa after drumming or was thrown off earlier. The occurrence and duration of the following behaviors of *B. intermedia* were recorded continuously with a TRS-80 Model 100 computer.

Not on host: walking or standing still while the parasitoid is not in contact with the host.

Preening not on host: all preening activities, while not in contact with the host.

Preening: all preening activities, while standing on the host.

Antennal encounter: standing beside the pupa while drumming it with the tips of the antennae.

Walking: walking on the pupa, while the antennae are mostly parallel to the host surface and the tips of the antennae are touching the host surface intermittently.

Drumming: walking or standing still on the pupa, while the flagella are perpendicular to the host surface and the tips of the antennae drum the host surface intermittently.

Standing still: standing still on the pupa while none of the other described behaviors occur.

Grasping: grasping of the pupa by spreading the hind legs.

Inserting ovipositor: insertion of the ovipositor into the host.

Throwoff: loss of contact with the host as a result of the host's defensive behaviors [spinning and arching as described by Rotheray and Barbosa (1984)].

Some of the above behaviors have been described previously for *B. intermedia* ovipositing in *Galleria mellonella*, the wax moth (Tucker and Leonard, 1977). Lashcomb *et al.* (1983) reported that feeding on host fluids commonly occurs in the laboratory; however, we and Tucker and Leonard (1977) rarely observed it and in the present experiments it was never seen.

Sequence Analysis

To determine significant sequences of behavior and the influence of experience, a 10 × 10 × 2 contingency table was constructed, where variable A was the preceding behavior (10 possible behaviors), variable B the following behavior (10 possible behaviors), and variable C the history of the parasitoid (two possible values: inexperienced and experienced), and analyzed by log-linear models (Bishop *et al.*, 1975; Fienberg, 1980). Because there were so-called structural zeros in the table (impossible transitions as a result of the observer's definitions), the expected frequencies could not be calculated directly from the marginal totals, requiring iterative procedures (Bishop *et al.*, 1975). We used the iterative proportional fitting (IPF) function of PROC IML of SAS (SAS Institute Inc., 1988).

The expected frequency f_{exp} of one cell of the table can be expressed as

$$\log (f_{\mathrm{exp}}) = \mu + I_{\mathrm{A}} + I_{\mathrm{B}} + I_{\mathrm{C}} + I_{\mathrm{AB}} + I_{\mathrm{AC}} + I_{\mathrm{BC}} + I_{\mathrm{ABC}}$$

μ is the geometric mean of the cell probability; I_{A}, I_{B}, and I_{C} are the effects of variables A, B, and C; I_{AB}, I_{AC}, and I_{BC} are the effects of assocation between pairs of variables; and I_{ABC} is the parameter representing association between all variables. The log-linear models used in the analysis all contained the parameters μ, I_{A}, I_{B}, I_{C}, and I_{AC}. μ sets the overall effect, and I_{A}, I_{B}, and I_{C} adjust for internal variation, because the margins were not fixed for any variable. I_{AC} needed to be included because the frequency of the preceding behavior (variable A) was not equal for inexperienced and experienced (variable C) females. Including the parameter I_{AC} ensured that the transition probabilities sum to 1.00 over each row.

The log-linear model assuming behavioral independence excludes parameter I_{ABC} and I_{AB}, i.e., $I_{\mathrm{ABC}} = I_{\mathrm{AB}} = 0$. Rejection of this model rejects the hypothesis of random association between acts or a zeroth-order Markov chain (Colgan, 1978) in favor of a first order Markov chain. The model assuming a first-order Markov chain, but no influence of the history of the parasitoid on the transition probabilities, includes I_{AB} and sets $I_{\mathrm{ABC}} = I_{\mathrm{BC}} = 0$. The model assuming influence of parasitoid history in addition to a first-order Markov chain sets only $I_{\mathrm{ABC}} = 0$.

The fit of the log-linear models to the observed data was determined with the G test. The degrees of freedom for the G test were adjusted to the number of structural zeros and the number of estimated parameters according to Bishop *et al.* (1975):

$$\mathrm{df} = (T_{\mathrm{e}} - z_{\mathrm{e}}) - (T_{\mathrm{p}} - z_{\mathrm{p}})$$

where T_e is the number of cells in the table (200), z_e is the number of structural zeros (60), T_p is the number of parameters fitted by the model, and z_p is the number of cells obtaining $f_{exp} = 0$ under the fitted model.

Freeman–Tukey deviates (Sokal and Rohlf, 1981)

$$\sqrt{f_{obs}} + \sqrt{(f_{obs} + 1)} - \sqrt{(4f_{exp} + 1)}$$

where f_{obs} is the observed cell frequency and f_{exp} the expected cell frequency, show which transitions account for the poor fit of the fitted log-linear model, i.e., which transitions are affected by the excluded parameter(s). As a criterion for the deviates being large, the deviates were compared with

$$\sqrt{(\text{df} * 3.841)/\text{Number of estimated cells}}$$

(Sokal and Rohlf, 1981), where 3.841 is the chi-square value for $\alpha = 0.05$, df $= 1$.

Result Categories

At the end of each observation we categorized the outcome of the behavioral sequence as follows:

ACCEPT—ovipositor insertion;
REJECT—drumming the pupa but never ovipositor insertion;
NODRUM—mounting the pupa but never drumming;
NOMOUNT—no mounting;
THROWOFF—observation stopped because the parasitoid was thrown off by the pupa.

Time Analysis

For each female the cumulative time engaging in a behavior was calculated. The nonparametric Wilcoxon two-sample test (Sokal and Rohlf, 1981) was used to compare durations between groups.

RESULTS

Sequence Analysis

A kinematic graph of all behavioral transitions occurring is given in Fig. 1. To determine which of these behavioral transitions were significant and whether experience influenced the behavior, log-linear models were fitted to the data with *G* tests.

The first model assumed random association between acts and no influence of experience. When this model was fitted to the data, the *G* test gave a $P < 0.0001$ (Fig. 2A), which means that this model is not satisfactory to explain

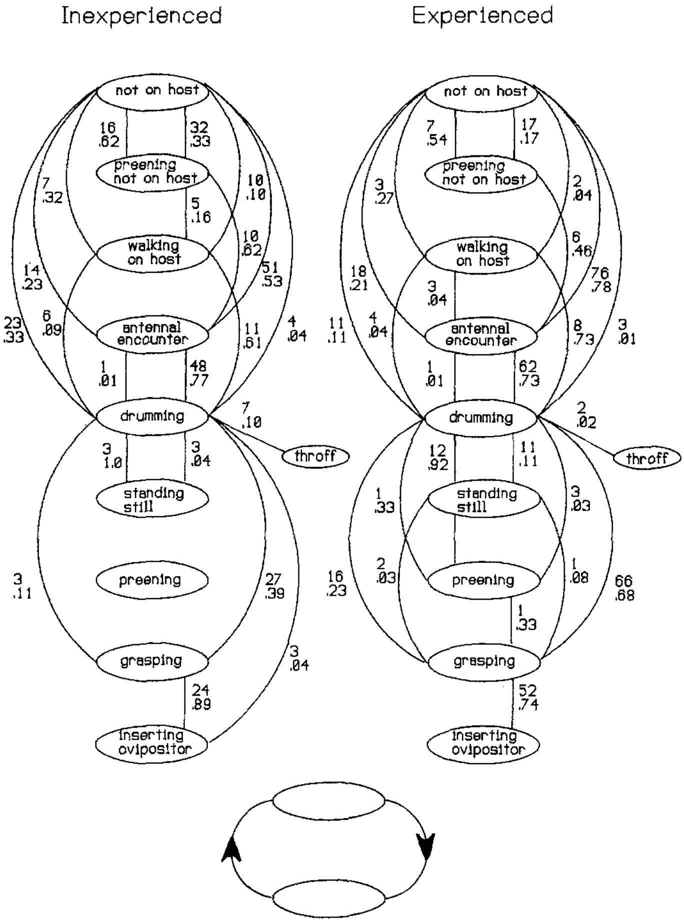

Fig. 1. Numbers of occurrence (first entry) and transition probabilities (second entry) of host acceptance behavior in *B. intermedia.*

all the variability in the data. The significant Freeman–Tukey deviates indicate nonrandom transitions and are graphically represented in Fig. 3. For this model we did not consider negative deviates, because we were not interested in behavioral transitions that do not or rarely occur. As is clear from Fig. 3, the sequential relationship between behaviors is remarkably similar in inexperienced and experienced females. For many transitions, however, the Freeman–Tukey deviates were greater in experienced females, meaning that they were more likely to occur in experienced females (Fig. 2A).

The second model assumed a first-order Markov chain and no influence of experience. Fitting this model to the data with the G test gave a $P = 0.0412$ (Fig. 2B), which means that some of the variation in our data is explained by behavioral interactions. The unexplained variation must have been due to the history of the female, i.e., experience. Figure 4 shows how inexperienced and experienced females differ in their behavior: the transitions influenced by female history are drumming to grasping and drumming to not on host. The transition probability of drumming to grasping increases after experience, while drumming to not on host decreases. Thus, after experience the association between drumming and grasping becomes stronger, because females do not leave the host and instead go over to grasping.

The third model assumes that, in addition to behavioral interaction, there are changes in transition probabilities after experience. Fitting this model to the data with the G test gave a $P = 0.99$, which means that this model is satisfactory because it explains nearly all the variability in the data.

Thus, the main change in behavior with experience is that the transition probability from drumming to grasping, which precedes ovipositor insertion, increases.

Result Categories

The number of females accepting the host was almost twice as high in experienced females as in inexperienced females (69.3%, $n = 75$; 36.0%, $n = 75$; $P = 0.05$, G test). For all other result categories there was no significant difference between inexperienced and experienced females. Some inexperienced females walked over the pupa without drumming it (NODRUM). This never happened with experienced females.

Time Analysis

Time spent not on host is significantly shorter in experienced females than in inexperienced females (Table I). Time expenditures for all other behaviors were highly variable and are not significantly different between the experimental groups.

To determine whether experienced females were faster in finding and handling the host and whether there were differences in host-finding and host-handling times between accepting and rejecting females, we analyzed behavioral durations separately for accepting and rejecting females within each experimental group. Because observations ended when a parasitoid that drummed the host departed the host, host-finding time can be calculated as the sum of all behaviors off the host (not on host + preening not on host). The host-handling time is the sum of durations of all behaviors on the host. Host-finding time appears to decrease with experience, and females that eventually reject the host tend to have a longer host-finding time (Table II). Host-handing time did not

(A)

INEXPERIENCED

	n	p	W	E	D	T	S	P	G	I
n	-	12.01 4.40	7.53 0.90	26.52 4.01	30.73 -6.90	-	1.03 0.15	0	9.98 -3.98	9.21 -3.74
p	6.30 2.28	-	2.01 1.68	7.08 1.06	8.21 -3.40	-	0.28 0.96	0	2.66 -1.00	2.46 -0.88
W	4.46 1.13	1.73 -0.40	-	3.81 -1.61	4.41 2.46	0.69 0.47	0.15 1.16	0	1.43 -0.18	1.32 -0.09
E	18.40 -1.02	7.12 -3.01	4.46 -1.93	-	18.20 5.34	2.85 -1.11	0.61 0.56	0	5.90 -2.55	5.46 -2.36
D	21.29 0.41	8.23 -3.41	5.16 0.44	18.17 -8.17	-	3.29 1.71	0.71 1.78	0	6.83 5.17	6.31 -1.39
S	0.71 0.46	0.27 0.97	0.17 1.12	0.60 0.57	0.70 1.78	0.11 1.22	-	0	0.23 1.03	0.21 1.06
P	0	0	0	0	0	0	0	-	0	0
G	6.82 -2.91	2.64 -0.99	1.66 -0.35	5.82 -2.52	6.75 -1.56	1.08 0.13	0.23 1.03	0	-	2.02 6.88

EXPERIENCED

	n	p	W	E	D	T	S	P	G	I
n	-	3.98 4.25	2.57 0.88	24.43 7.56	31.87 -8.92	-	3.28 -1.34	0.69 0.48	19.34 -8.92	11.85 -4.54
p	1.42 2.89	-	0.32 0.91	3.01 1.48	3.93 -1.67	-	0.40 0.80	0.08 1.26	2.38 -0.83	1.46 -0.20
W	1.18 1.34	0.41 0.79	-	2.50 -0.90	3.26 2.08	0.06 1.30	0.34 0.88	0.07 1.28	1.98 -0.57	1.21 0.00
E	11.41 1.77	3.95 -1.69	2.54 0.39	-	31.61 4.52	0.61 0.56	3.25 -1.33	0.68 0.48	19.19 -5.67	11.75 -4.51
D	14.41 -0.88	4.99 -2.16	3.21 0.51	30.59 -8.89	-	0.77 1.13	4.11 2.61	0.86 1.62	24.23 6.41	14.83 -5.35
S	1.40 -0.15	0.48 0.70	0.31 0.91	2.97 -1.18	3.88 3.01	0.07 1.27	-	0.08 1.26	2.35 -0.81	1.44 -0.19
P	0.32 0.91	0.11 1.22	0.07 1.28	0.67 0.50	0.87 0.29	0.02 1.38	0.09 1.25	-	0.53 0.65	0.32 0.90
G	8.87 -3.63	3.07 -1.23	1.98 -0.57	18.84 -6.32	24.57 -1.84	0.47 0.71	2.53 -0.19	0.53 0.65	-	9.13 8.36

(B)

	n	p	W	E	D	T	S	P	G	I
n	-	24.37 1.48	6.96 1.11	63.17 -1.58	2.49 0.93	-	0	0	0	0
p	16.20 0.01	-	3.52 0.80	11.27 -0.31	0	-	0	0	0	0
W	6.21 1.13	0	-	0	11.79 -0.16	0	0	0	0	0
E	13.62 0.17	0	1.28 -0.06	-	46.82 0.21	0.43 0.77	0	0	0.85 0.32	0
D	14.17 2.10	0	4.17 0.89	0.83 0.33	-	3.75 1.47	5.83 -1.20	1.25 0.33	38.75 -2.00	1.25 1.28
S	0	0	0	0	2.81 0.23	0	-	0	0.19 1.09	0
P	0	0	0	0	0	0	0	-	0	0
G	0	0	0	0	5.29 -0.97	0	0.56 0.62	0	-	21.15 0.65

	n	p	W	E	D	T	S	P	G	I
n	-	24.63 -1.61	7.04 -1.16	63.83 1.48	2.51 -0.91	-	0	0	0	0
p	6.80 0.17	-	1.48 -0.21	4.73 0.63	0	-	0	0	0	0
W	3.79 -0.29	0	-	0	7.21 0.37	0	0	0	0	0
E	18.38 -0.03	0	1.72 0.92	-	63.18 -0.12	0.57 0.60	0	0	1.15 0.78	0
D	19.83 -2.18	0	5.83 -0.70	1.17 0.03	-	5.25 -1.54	8.17 0.98	1.75 0.90	54.25 1.54	1.75 -0.41
S	0	0	0	0	12.19 0.02	0	-	0	0.81 0.35	0
P	0	0	0	0	1.00 0.18	0	1.00 0.18	-	1.00 0.18	0
G	0	0	0	0	13.71 0.65	0	1.44 0.54	0	-	54.85 -0.35

(C)

	n	p	W	E	D	T	S	P	G	I
n	-	17.00 0.06	4.87 -0.29	74.98 0.15	1.67 -0.35	-	0	0	0	0
p	5.07 0.86	-	1.09 0.10	6.86 -0.25	0	-	0	0	0	0
W	3.91 -0.36	0	-	0	7.07 0.42	0	0	0	0	0
E	18.72 -0.11	0	1.75 0.91	-	62.22 0.00	0.38 0.82	0	0	1.76 0.31	0
D	11.30 -0.02	0	3.30 0.47	1.14 0.05	-	1.62 0.41	11.03 0.06	3.00 0.13	66.28 0.00	0.47 0.72
S	0	0	0	0	12.01 0.07	0	-	0	0.96 0.22	0
P	0	0	0	0	0	0	0	-	0	0
G	0	0	0	0	16.04 0.05	0	1.97 0.17	0	-	51.53 0.10

	n	p	W	E	D	T	S	P	G	I
n	-	32.00 0.04	9.14 0.35	52.04 -0.11	3.35 0.44	-	0	0	0	0
p	17.93 -0.40	-	3.90 0.61	9.10 0.36	0	-	0	0	0	0
W	6.09 0.44	0	-	0	11.94 -0.20	0	0	0	0	0
E	13.27 0.26	0	1.25 -0.04	-	47.75 0.07	0.62 0.55	0	0	0.25 1.00	0
D	22.72. 0.11	0	6.70. -0.18	0.86. 0.31	-	7.38. -0.05	2.95 0.15	0	26.71. 0.10	2.58 0.37
S	0	0	0	0	2.97 0.15	0	-	0	0.04 1.33	0
P	0	0	0	0	0.41 0.79	0	0.18 1.11	-	0.72 0.44	0
G	0	0	0	0	2.99 0.13	0	0.05 1.33	0	-	24.42 -0.03

Fig. 2. Expected frequencies (first entry) and Freeman–Tukey deviates (second entry) when different log-linear models are fitted to the transition frequencies. (n) Not on host; (p) preening not on host; (W) walking; (E) antennal encounter; (D) drumming; (T) throwoff; (S) standing still; (P) preening on host; (G) grasping; (I) inserting ovipostior. T and I do not occur in rows because they are not followed by any behavior according to the definition. (A) Model I, assuming random association between acts: $G = 1189.87$, df = 108, $P = 0.0000$, $T_p = 38$, $z_p = 6$, number of estimated cells = 124, critical value for the Freeman–Tukey deviates (cv) = 1.83. (B) Model II, assuming interaction between behaviors but no influence of experience: $G = 62.74$, df = 45, $P = 0.0412$, $T_p = 110$, $z_p = 15$, number of estimated cells = 56, cv = 1.76. (C) Model III, assuming behavioral interactions as well as influence of experience: $G = 11.18$, df = 37, $P = 0.9999$, $T_p = 119$, $z_p = 16$, number of estimated cells = 56, cv = 1.59.

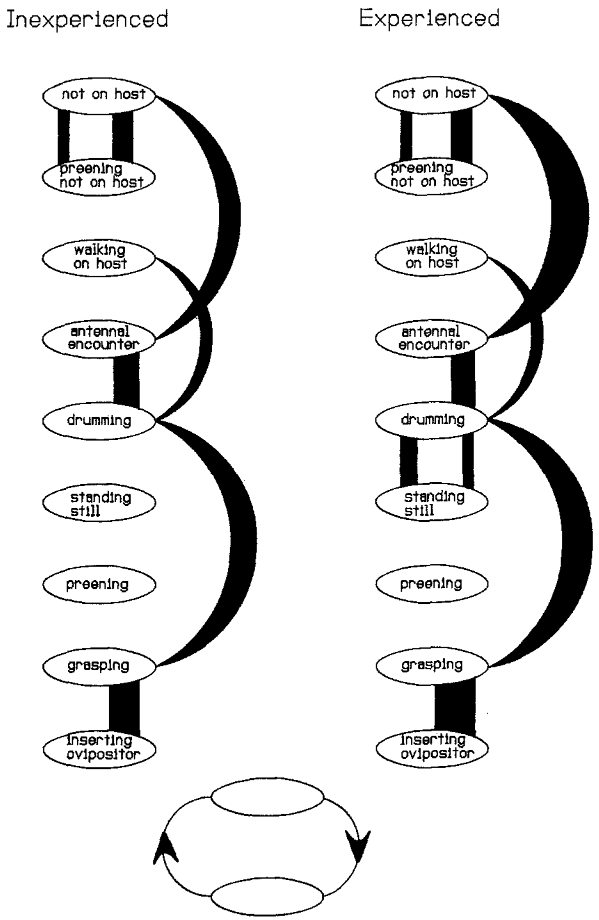

Fig. 3. Sequential organization of host acceptance behavior in inexperienced and experienced *B. intermedia.* The arrows indicate transitions where the occurrence of the succeeding behavior depends significantly on the occurrence of the immediately preceding behavior (first-order Markov chain). The width of the arrows corresponds to the magnitude of the Freeman–Tukey deviates, fitting the log-linear model and assuming independence of behavioral acts (Model I).

change with experience and was longer in accepting females irrespective of experience.

Exposure to Odor

When referring to experienced females, we have to consider whether it was the cues encountered, the performance of behaviors, or both that were vital to

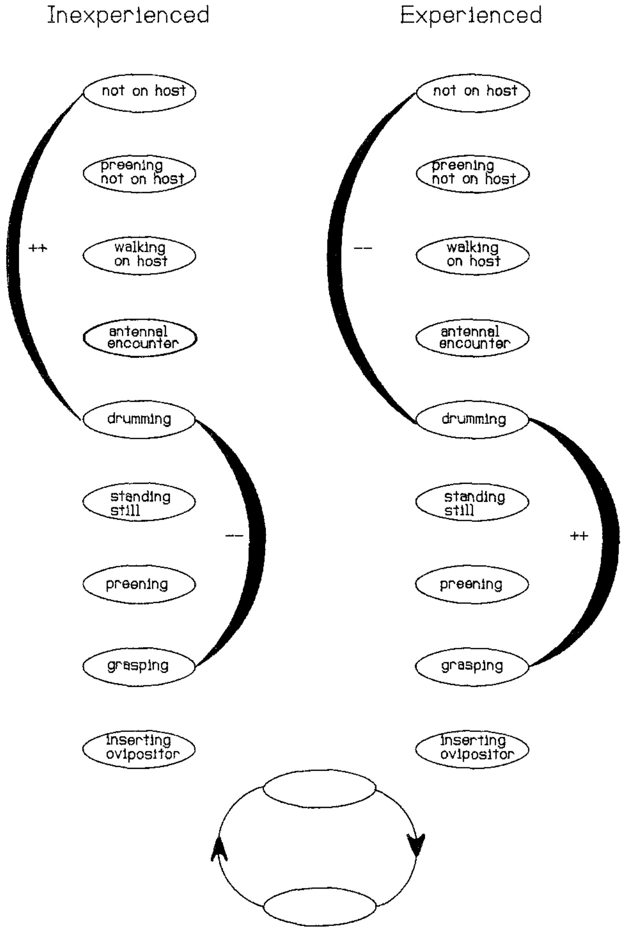

Fig. 4. Behavioral transitions that are significantly different between inexperienced and experienced females. The width of the arrows corresponds to the magnitude of the Freeman–Tukey deviates, fitting the log-linear model and assuming no influence of experience on the interaction between behavioral acts (Model II). "++" indicates stimulation, while "--" indicates inhibition.

the change from being inexperienced, i.e., Does a female have to find a pupa, contact the kairomone, and perhaps oviposit, or is exposure to the odor of the pupae sufficient to improve host acceptance behavior? To determine whether exposure to odor alone is sufficient, we tested females that were exposed to odor of gypsy moth pupae and females that were witheld from odor (by keeping them in another environmental chamber) in the same way as we did for the other experiments. Females had no oviposition experience when tested. We

Table I. Time Spent (in Seconds) per Behavioral Component Performed by Inexperienced and Experienced *B. intermedia*

Behavioral component	Female history								
	Inexperienced				Experienced				
	n	Mean	Min	Max	n	Mean	Min	Max	P^a
n, not on host	73	76	2	181	73	47	2	180	<0.001
p, preening	26	50	9	137	15	48	9	92	NS
W, walking	13	7	0	24	9	3	1	10	NS
E, antennal encounter	49	12	1	62	67	11	0	72	NS
D, drumming	54	57	2	269	62	71	3	235	NS
S, standing still	13	10	8	12	10	52	2	272	NS
P, preening on host	—	—	—	—	2	14	11	17	NA
G, grasping	25	4	0	14	53	9	0	77	NS
I, inserting ovipositor	27	82	2	229	52	76	6	390	NS

[a] Wilcoxon two-sample test, $\alpha = 0.05$.

Table II. Comparison of Time Spent Host Finding and Host Handling by Inexperienced and Experienced Female *B. intermedia*, Based on Whether They Accepted or Rejected the Host

Result category	Female history	N	Time (mean ± SE)[a]	
			Host finding	Host handling
Accept	Inexperienced	27	53.9 ± 9.7 ab	153.9 ± 13.1 ba
	Experienced	52	33.7 ± 4.8 a a	165.1 ± 14.7 a b
Reject	Inexperienced	19	78.5 ± 11.6 a a	57.5 ± 10.3 a a
	Experienced	8	58.3 ± 14.4 ab	91.6 ± 17.0 aa

[a] Values followed by the same letters connected by vertical lines are not significantly different (Wilcoxon two-sample test, $\alpha < 0.05$).

found that the percentage of tested females accepting the host was not different between these groups (inexperienced, 33.3%, $n = 24$; odor exposed, 37.5%, $n = 24$; $P = 0.549$, G test) and was similar to that of inexperienced females in the first experiment (36%).

DISCUSSION

There are two points in the oviposition behavioral sequence of *B. intermedia* females affected by oviposition experience. First, females with foraging experience approached the host significantly faster and were more apt to investigate it with their antennae than inexperienced females. Second, the transition from drumming to grasping was more likely to occur in experienced females, which resulted in a higher frequency of host acceptance, whereas the transition from drumming to not on the host, leading to host rejection, was inhibited in experienced females.

Interestingly, only experienced females that accepted the host were faster in host finding, whereas the individuals that rejected the host were not significantly different from inexperienced females with regard to host-finding time. It is surprising that a considerable number of females in both experimental groups rejected the host, while the host quality was kept as uniform as possible throughout the experiment. Perhaps the parasitoids detect subtle differences in pupae that appear of equal quality to our standards. Alternatively, there may be individual variation in the parasitoids for the ability to determine host quality. Both inexperienced and rejecting females had long host-finding times. Perhaps this should be interpreted as low searching activity. The fact that they mounted and investigated the pupa thus would be an artifact of the small test arena. Most of the females that eventually made an antennal encounter with the host investigated it, and this did not change with experience, i.e., the transition antennal encounter to drumming did not change with experience, nor did the time spent drumming.

Papaj and Prokopy (1989) reviewed definitions of learning and proposed to use several criteria to determine whether a change in behavior is due to learning. Aside from (1) repeatability of the behavioral change, the criteria are that (2) the behavior changes gradually with experience and (3) the change in behavior wanes when continued experience of the same type is absent. Using criteria 2 and 3 we cannot yet verify if the change in behavior with experience in *B. intermedia* is due to learning. It is possible that physiological differences between inexperienced females and experienced females are responsible for the changes in behavior. The physiological state of the parasitoids was influenced by whether they were given pupae, but individual variation in physiological state, perhaps due to the number of eggs produced, may also be a factor influencing the behavioral response. For example, in *Venturia canescens* there is a positive correlation between the number of eggs in the oviducts and the time spent foraging (Trudeau and Gordon, 1989).

Thus, we have shown that in *B. intermedia* the foraging behavior for a gypsy moth pupae changes with experience at two points in the behavioral sequence. Further research is needed to reveal whether this is due to learning or a change in the physiological state of the female (apart from learning) and how plastic the foraging behavior is when different host species are encountered.

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