

Learning of Host Microhabitat Form by *Exeristes roborator* (F.) (Hymenoptera: Ichneumonidae)

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Females of the polyphagous, ichneumonid ectoparasitoid, Exeristes roborator (F.), learned the form of artificial host microhabitats in the laboratory. Females given hosts only in a microhabitat of one form subsequently concentrated their responses on this microhabitat when given a choice between it and a microhabitat of another form, neither of which contained hosts. Control females did not display similar preferences. The parasitoid did not appear to distinguish the form of a microhabitat until after it contacted it. When hosts were present in test microhabitats, learning of form was apparently overridden, possibly because the parasitoids detected the presence of hosts before they assessed form or because their responses were shaped by learning of host-related factors. Together with learning of other microhabitat characteristics, learning of form may contribute to recognition of plant structures that are likely to contain suitable hosts by E. roborator.

KEY WORDS: *Exeristes roborator*; learning; host microhabitat form; host-finding; parasitoid.

INTRODUCTION

For some insects, cues involved in responses to food sources or oviposition sites can be provided by the form of these resources. Responses to aspects of host form such as size, shape, orientation, and pattern of arrangement of component parts occur in pollinators (Faegri and van der Pilj, 1979), phytophagous insects (Prokopy and Owens, 1983), and biting flies (Allan *et al.*, 1987) and may also occur in predatory insects (Hagen *et al.*, 1976). Such cues appear to be involved in the responses of a considerable number of parasitoids to their

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hosts, through either visual or tactile perception (Vinson, 1976, 1985; Arthur, 1981).

In a few cases, insects' responses to the form of feeding or oviposition sites are known to be influenced by learning. After contact with host plants, or host-plant extracts applied to nonhost plants, the pipevine swallowtail butterfly, *Battus philenor* L., selectively searches for plants with similar leaf shape or leaf buds on which to oviposit (Papaj, 1986a-d). Worker honey bees, *Apis mellifera* L., can learn the size, shape, pattern, and orientation of elements of food source markers (von Frisch, 1971; Wehner, 1981; Gould, 1984, 1985; Gould and Marler, 1987). Ovipositional experience with a specific host fruit can affect the propensity of female apple maggot flies, *Rhagoletis pomonella* (Walsh), and Mediterranean fruit flies, *Ceratitidis capitata* (Wiedemann), to respond with ovipositional behavior to fruits and artificial fruit models of different sizes. Experienced flies may reject fruits and models not resembling the familiar host fruit in size (Papaj and Prokopy, 1986; Papaj *et al.*, unpublished, reported by Prokopy and Fletcher, 1987). Arthur (1967) showed that the ichneumonid parasitoid, *Itopectis conquisitor* (Say), could learn to discriminate between different host shelters on the basis of size and overall configuration, but not on the basis of orientation.

The polyphagous, ichneumonid ectoparasitoid, *Exeristes roborator* (F.), learns to respond to artificial host microhabitats in the laboratory, from exposure to hosts in them (Wardle and Borden, 1985). The parasitoid can learn the color and odor of these objects (Wardle, 1988). In nature, females attack hosts concealed in a variety of plant structures (Thompson, 1957). Our objective was to determine whether or not *E. roborator* could learn host microhabitat form and, if so, to determine whether or not the parasitoid could be influenced by this learning when given the opportunity to attack hosts in microhabitats of different forms.

MATERIALS AND METHODS

Insect Rearing and Maintenance

Female *E. roborator* came from a stock colony kept in the insectary at Simon Fraser University. Immature stages were reared on coddled larvae of a factitious host, the greater wax moth, *Galleria mellonella* (L.), according to Syed's (1985) method.

All experiments were conducted in a small room illuminated with cool white fluorescent lights on an 8-h L:16-h D cycle. The temperature normally ranged between 22 and 26°C. Experimental females were held for pretest treatment in 30 × 30 × 45-cm cages with water, honey-coated sugar cubes, and males. Test cages were identical to pretest treatment cages, except that males were not present.

Experiments 1 and 2

Pretest Treatments. Female *E. roborator* eclosing over a 2-day period were assigned to four groups of 10–12 insects each and placed in pretest treatment cages. Each of the four groups was subjected to a different treatment for 1 week (Table I, Experiments 1 and 2). Parasitoids in all groups were exposed to two artificial microhabitats that differed in their form. Insects in group I were given hosts in one of the microhabitats only, to determine if they could learn the form of this object. Similarly, parasitoids in group II were given hosts in the other microhabitat only, to determine if the second form could also be learned. As

Table I. Pretest Treatments and Testing Regimes for *E. roborator* in Experiments 1–3

Experiment	Group	<i>N</i>	Pretest treatment ^{a, b}	Testing regime ^b
1	I	24	Given 1 cylinder containing hosts and 1 sphere not containing hosts (hosts in cylinder)	Given 1 cylinder and 1 sphere, neither containing hosts, simultaneously for 1 h
	II	26	Given 1 cylinder not containing hosts and 1 sphere containing hosts (hosts in sphere)	Given 1 cylinder and 1 sphere, neither containing hosts, simultaneously for 1 h
	III	23	Given 1 cylinder and 1 sphere, both containing hosts (hosts in both microhabitats)	Given 1 cylinder and 1 sphere, neither containing hosts, simultaneously for 1 h
	IV	24	Given 1 cylinder and 1 sphere, neither containing hosts (hosts in neither microhabitat)	Given 1 cylinder and 1 sphere, neither containing hosts, simultaneously for 1 h
2	I	24	As for group I, Experiment 1	Given 1 cylinder and 1 sphere, both containing hosts, simultaneously for 1 h
	II	25	As for group II, Experiment 1	Given 1 cylinder and 1 sphere, both containing hosts, simultaneously for 1 h
	III	24	As for group III, Experiment 1	Given 1 cylinder and 1 sphere, both containing hosts, simultaneously for 1 h
	IV	23	As for group IV, Experiment 1	Given 1 cylinder and 1 sphere, both containing hosts, simultaneously for 1 h
3	IV'	10	As for group IV, Experiment 1	As for Experiment 1
	V	10	Held without exposure to microhabitats or hosts	As for Experiment 1

^aClean microhabitats and fresh hosts were placed in cages each day for 7 days.^bHosts were five coddled larvae of *G. mellonella*.

controls, females in groups III and IV were offered hosts in both microhabitats and hosts in neither microhabitat, respectively, to determine if general access to hosts in the microhabitats or exposure to the microhabitats themselves could produce behavior resembling learning of either form in *E. roborator*.

The microhabitats (Fig. 1) were created using two Styrofoam objects with approximately equal surface areas, a sphere 6.35 cm in diameter (surface area = 126.68 cm²) and a cylinder 2.54 cm in diameter and 14.6 cm in height (surface area = 126.64 cm²). These forms were chosen because they resembled plant structures (fruits, shoots, stalks) in which some of the hosts of *E. roborator* are found. Each microhabitat was mounted on the tip of a disposable Pasteur pipette (Fisher Scientific, Toronto, Ontario), shortened to a length of 13 cm for spheres and 9 cm for cylinders. The blunt end of the pipette was attached to the centre of the overturned bottom half of a 60 × 15-mm disposable petri dish (Labtek, Miles Laboratories Inc., Naperville, Ill.). With this mount, the microhabitats could be placed in cages with their centers at the same height, approximately 15 cm off the cage floor. Compartments in which hosts could be concealed were created in the surface of each microhabitat. A heated cork borer was used to melt five circular pits, 1.3 cm in diameter and 0.5 cm in depth. These depressions were arranged 1 cm apart in a straight line along the long axis of the cylinder, with the highest and lowest depressions 2 cm from the top and bottom of the cylinder, respectively. On the sphere, the depressions followed the surface curve around one side in a straight, vertical, line from a point 1 cm above the insertion of the Pasteur pipette to the top of the sphere. Each pit was covered by a taut, 1.5 × 1.5-cm piece of Kimwipe (Kimberly-Clark Ltd., Toronto, Ontario) held in place with a 1.3-cm (outer diameter) white plastic ring (Tailorform, Symark Sales Co. Inc., Montreal, Quebec) pushed a few millimeters into the mouth of the pit. When hosts were required in the microhabitat, a single coddled larva of *G. mellonella* was concealed in each depression beneath the Kimwipe "membrane." Female *E. roborator* freely probed, fed, and oviposited on hosts in both the cylinder and the sphere (Fig. 1).

Each day clean microhabitats and fresh host larvae were placed in the cages. The positions of the cylinder and sphere were reversed to prevent possible learning of host microhabitat position. All microhabitats were cleaned between uses with 95% ethanol, and those used to present host larvae to females were never subsequently used without hosts.

At the end of their seventh day of pretest treatment, parasitoids from each group were distributed, as evenly as possible, between four test cages. Due to mortality during pretest treatment, each cage held 8–10 females. For individual and group identification, each female in a test cage was marked on the thorax with a dot of paint (Testor Corp., Weston, Ontario) of a different color.

Testing Regimes. On the following day, testing was carried out on all test

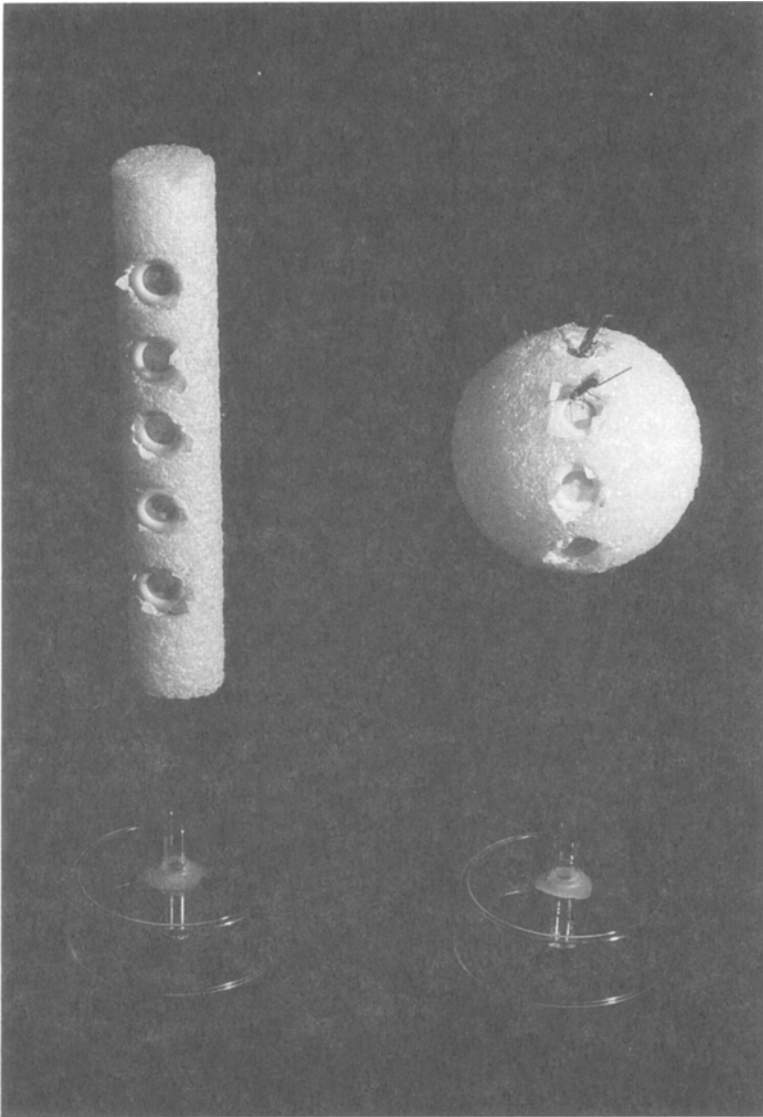


Fig. 1. Styrofoam microhabitats, with *E. roborator* probing host larvae in the sphere.

cages in random order. In Experiment 1, females in two randomly chosen cages were monitored for evidence that they had learned host microhabitat form. They were simultaneously given one spherical and one cylindrical microhabitat, neither containing hosts (Table I, Experiment 1), and their responses to these

microhabitats were observed for 1 h. A record was kept of whether or not each female contacted each microhabitat and, if she did, of how long she was in contact and how many times she probed with her ovipositor. This behavior indicated that she was searching for hosts in the microhabitat. A probe was counted if a female inserted her unsheathed ovipositor into any part of the microhabitat. The positions of the cylinder and the sphere were reversed in the two test cages.

Concentration of response by females in groups I and II on the cylinder and the sphere, respectively, when similar concentration by control groups III and IV females did not occur, would indicate that the parasitoid had learned host microhabitat form.

In Experiment 2, females in the remaining two test cages were treated in an identical manner, except that the two Styrofoam microhabitats simultaneously placed in their cages each contained five fresh coddled larvae of *G. mellonella* (Table I, Experiment 2). These insects were monitored to determine whether or not any learning of microhabitat form revealed in Experiment 1 influenced females' choice of microhabitats in which to attack hosts.

Procedures were repeated until >20 females from each group were tested in each experiment.

Experiment 3

Pretest Treatments. Exposure of control females in group IV (Experiments 1 and 2) to the cylinder and the sphere repeatedly without reward might have decreased their responsiveness and prevented detection of an innate attraction to one form or the other. To test this possibility, females eclosing over a 3-day period were divided into two groups (Table I, Experiment 3). Group IV' females were exposed to the same pretest treatment as group IV females in Experiment 1. Group V females were not given hosts or microhabitats, so that the responses of insects with no exposure to the experimental system could be measured. After 7 days of treatment 10 females from each group were marked on the thorax with a dot of paint for identification and divided equally between two test cages.

Testing Regime. On the following day, testing was carried out in random order on the two cages as in Experiment 1 (Table I, Experiment 3). A reduction in responsiveness to a form due to exposure to the microhabitats alone would be suggested by significantly greater and more concentrated responses to either the cylinder or the sphere by group V females than by group IV' females.

Statistical Analysis

Experiments 1 and 2. Females were classified according to whether or not they contacted and probed the microhabitat of either form alone, both microhabitats, or neither microhabitat. For each experiment the numbers of females

in these response categories were compared with a $4 \times 4 \chi^2$ test. When χ^2 values were significant ($\alpha = 0.05$), simultaneous 95% confidence intervals were calculated for the differences between group I and groups II–IV in the proportion of females responding only to the cylinder and between group II and groups I, III, and IV in the proportion of females responding only to the sphere (Miller, 1981). When intervals did not contain 0, the proportions being compared were significantly different. In addition, females in each group in Experiment 1 were classified according to whether or not they contacted the cylinder or the sphere first, or did not contact either microhabitat, and $4 \times 3 \chi^2$ analysis ($\alpha = 0.05$) was used to detect differences between groups in the numbers of females in these first choice categories.

The mean proportions of total responses that were directed to the cylinder were calculated for the responding females in each group. These means, and also mean total responses to microhabitats by all females in each group, were compared ($\alpha = 0.05$) using the Kruskal–Wallis test and multiple-comparisons procedure of Conover (1980).

The percentages of all females in each group responding in total to microhabitats were compared ($\alpha = 0.05$) using a test for comparing >2 proportions and a modified Newman–Keuls multiple-comparisons procedure (Zar, 1984).

Experiment 3. Females were divided into four response categories as in Experiments 1 and 2, and $2 \times 4 \chi^2$ analysis ($\alpha = 0.05$) was used to test for differences between the groups in the numbers of females in these categories. The mean proportions of total responses devoted to the cylinder by responding females were determined as in Experiments 1 and 2, and these means, along with mean total responses to microhabitats, were compared with the Mann–Whitney test (Conover, 1980) ($\alpha = 0.05$). The proportions of all females in each group responding in total to the microhabitats were compared with the Fisher exact test (Zar, 1984) ($\alpha = 0.05$).

RESULTS

Exeristes roborator learned host microhabitat form, although detection of form appeared to occur after contact with the microhabitats (Fig. 2, Table II). In Experiment 1, females exposed to hosts only in the cylinder (group I) or the sphere (group II) during pretest treatment subsequently concentrated much of their host-seeking activities on these forms when they did not contain hosts (Fig. 2, Table II). There were no significant differences between groups in the first contact choices of females (χ^2 test, $P > 0.05$), in the numbers of females contacting either microhabitat alone, both microhabitats, or neither microhabitat over the course of the test hour (χ^2 test, $P > 0.05$), or in the total numbers of females contacting microhabitats (Table III, Experiment 1), suggesting that orientation to these microhabitats was not affected by prior experience with hosts in them. Highly significant differences did occur in the numbers of females

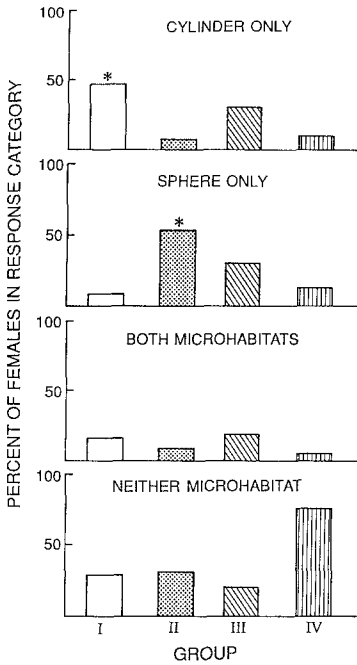


Fig. 2. Percentage of *E. roborator* in groups I-IV in Experiment I probing the cylinder or sphere alone, both microhabitats, or neither microhabitat when hosts were not present in the microhabitats. Bars marked with an asterisk are not significantly different from the next lowest bar but are significantly different from the two lowest bars in the same subgraph [simultaneous 95% confidence intervals for differences between proportions (Miller, 1981)]. Pretest treatment for group I (open bars) = hosts in cylinder, for group II (stippled bars) = hosts in sphere, for group III (diagonally hatched bars) = hosts in both microhabitats, and for group IV (vertically hatched bars) = hosts in neither microhabitat.

Table II. Mean Percentage of Total Contacting and Probing Responses to Microhabitats Directed at the Cylinder by Responding *E. roborator* in Groups I-IV During Testing in Experiment I

Group (pretest treatment)	No. females contacting microhabitats	Mean % (\pm SE) of total contact time spent on cylinder ^a	No. females probing microhabitats	Mean % (\pm SE) of total probes executed on cylinder ^a
I (hosts in cylinder)	18	72.4 \pm 8.8 a	17	81.1 \pm 8.2 a
II (hosts in sphere)	20	24.4 \pm 8.9 b	18	13.9 \pm 7.7 c
III (hosts in both microhabitats)	18	54.3 \pm 10.7 ab	18	52.0 \pm 10.9 b
IV (hosts in neither microhabitat)	16	53.0 \pm 11.5 ab	6	41.2 \pm 20.0 bc

^aMeans in a column followed by the same letter are not significantly different, Kruskal-Wallis test and multiple-comparisons procedure (Conover, 1980), $\alpha = 0.05$. Mean percentage of total response on sphere = 100 - mean % of total response on cylinder.

in the four probing response categories ($\chi^2 = 36.6$, $df = 9$, $P < 0.001$), with both group I and group II differing from one another and from control group IV in the proportions of females responding exclusively to the cylinder and the sphere, respectively (Fig. 2). However, groups I and II females did not differ from control females in group III in this respect (Fig. 2). There were also significant differences between group I and group II in the distribution of responses by females between the cylinder and the sphere, with responding females in each group spending more than 70% of contact time and executing more than 80% of their ovipositor probes on the only microhabitat in which they previously had experience attacking hosts (Table II). Neither group I nor group II differed from groups III and IV in distribution of contact time between forms, but responding females in group I favored the cylinder with their probing responses more than responding females in both control groups (Table II). Responding females in group II differed significantly from those in group III in probe distribution, but the very large difference in distribution of probes between group II and group IV lacked significance statistically, probably due to the small number of probing females in group IV and the large variation in their distribution of probes between the cylinder and the sphere (Table II). However, the significant difference between the two groups in propensity to probe only the sphere (Fig. 2) indicates that responding females in group II, like those in group I, showed a greater preference for the only microhabitat form in which they had previously attacked hosts.

In Experiment 1 females in groups I–III differed from group IV females in total numbers probing microhabitats, and in the strength of their total responses to microhabitats, but did not differ from one another in these responses (Table III, Experiment 1). Thus exposure to hosts in microhabitats of different forms appeared to cause females in all three groups to learn equally to respond to these microhabitats. This general ability to learn to respond allowed disclosure of the differences caused by learning of specific microhabitat forms by females in groups I and II (Fig. 2, Table II).

In Experiment 2, no influence of form learning could be detected in the responses of females in groups I and II to a cylinder and a sphere containing host larvae. There were no significant differences between groups in the numbers of females contacting or probing (χ^2 test, $P > 0.05$) either microhabitat alone, both microhabitats, or neither microhabitat or in the distribution of contact time and ovipositor probes between the cylinder and the sphere by responding females (Kruskal–Wallis test, $P > 0.05$). Females with prior experience attacking hosts in Styrofoam microhabitats (groups I–III) were superior to group IV females only in their total probing responses (Table III, Experiment 2), indicating that the role of learning in response to forms was much reduced when the forms contained hosts.

Table III. Total Contacting and Probing Responses to Microhabitats by *E. roborator* in Groups I-IV During Testing in Experiments 1 and 2

Experiment	Group (pretest treatment)	Percentage of females ^a		Mean total (\pm SE) ^b	
		Contacting microhabitats	Probing microhabitats	Minutes in contact with microhabitats	Probes executed on microhabitats
1	I (hosts in cylinder)	75.0 a	70.8 a	15.0 \pm 2.9 a	9.3 \pm 2.1 a
	II (hosts in sphere)	76.9 a	69.2 a	14.7 \pm 3.4 a	8.5 \pm 1.7 a
	III (hosts in both microhabitats)	78.3 a	78.3 a	18.7 \pm 2.9 a	11.2 \pm 1.8 a
	IV (hosts in neither microhabitat)	66.7 a	25.0 b	6.0 \pm 1.7 b	1.7 \pm 0.8 b
2	I (hosts in cylinder)	83.3 a	83.3 a	27.3 \pm 3.6 a	9.8 \pm 1.7 a
	II (hosts in sphere)	76.0 a	76.0 a	25.2 \pm 3.7 a	8.2 \pm 1.5 a
	III (hosts in both microhabitats)	79.1 a	79.1 a	24.7 \pm 3.4 a	10.3 \pm 1.9 a
	IV (hosts in neither microhabitat)	69.6 a	69.6 a	18.7 \pm 4.1 a	5.3 \pm 2.1 b

^aWithin each experiment percentages in a column followed by the same letter are not significantly different, test for comparing >2 proportions and modified Newman-Keuls multiple-comparisons procedure (Zar, 1984), $\alpha = 0.05$.

^bWithin each experiment means in a column followed by the same letter are not significantly different, Kruskal-Wallis test and multiple-comparisons procedure (Conover, 1980), $\alpha = 0.05$.

Exposure to the Styrofoam cylinder and sphere without hosts for 7 days did not reduce the responses of *E. roborator* to microhabitats of either form. In Experiment 3, group IV' and V females did not differ in numbers contacting or probing (χ^2 test, $P > 0.05$) either microhabitat alone, both microhabitats, or neither microhabitat, in the proportions of total contact time and ovipositor probes they directed to the cylinder, or in the strength of their total responses to microhabitats (Mann-Whitney test, $P > 0.05$). Similar total numbers of females also contacted and probed microhabitats in both groups (Fisher exact test, $P > 0.05$).

DISCUSSION

The respective concentration of ovipositor probes by female *E. roborator* in both group I and group II in Experiment 1 on cylindrical and spherical microhabitats without hosts must have been caused by learning of microhabitat form. Females in groups III and IV, that together were exposed to the same stimuli as females in groups I and II, but without specific pairing of hosts with one form, did not concentrate their probing activities on either microhabitat. The lack of a strong response to either the cylinder or the sphere by group IV females was not the result of prolonged exposure to the microhabitats without reward, because females given this experience did not differ in their responses from females never exposed to the microhabitats (Experiment 3).

Considerable examination of the microhabitats during initial contact, and possibly initial probing, probably was necessary for clear discrimination between them by group I and II females, since insects in these two groups differed from those in both control groups only in their probing responses to the cylinder and the sphere. Thus, females probably devoted most of their probing activity to a microhabitat after distinguishing its form.

After contact, females could not have learned to use some distinguishing feature other than form, as the cylinder and sphere did not differ in their surface texture or appearance, consistency, or chemical composition.

There are approximately 30 reported natural hosts for *E. roborator* (Thompson, 1957). Their microhabitats can differ considerably in form from both surrounding vegetation and each other. Examples include apples [the codling moth, *Cydia pomonella* (L.)], cotton bolls [the pink bollworm, *Pectinophora gossypiella* (Saunders)], corn stalks (the European corn borer, *Ostrinia nubilalis* Hübner), and "shepherd's crook" pine shoots [the European pine shoot moth, *Rhyacionia buoliana* (Denis and Schiffermüller)]. If such differences in form are perceptible to *E. roborator*, they could be used by the parasitoid in the identification of host microhabitats. While these natural host microhabitats are not unique examples of plant architecture, learning of their form, when combined with learning of other distinctive features, could contribute to recognition by the parasitoid of plant structures that are likely to contain suitable hosts.

Since learning of form did not affect females' responses to a host microhabitat until after contact in Experiment 1, it may not have influenced females in Experiment 2 because they detected the presence of larvae of *G. mellonella* on or before contact and probed for them without assessing the form of the objects that housed them. If so, learning of form would probably only influence responses to plant structures in natural situations in which hosts are not imme-

diately detected. A female might search for a longer time on a structure of familiar form, even if she did not initially detect a host in that microhabitat. However, an alternative explanation for the similarity of response by females in groups I–III in Experiment 2 could be that learning of host-related factors, such as odor, shaped their responses, overriding any influence of learning of form.

The apple maggot, *Rhagoletis pomonella*, can learn to discriminate after contact between fruit models of different sizes (Papaj and Prokopy, 1986). Städler (1977) has suggested that proprioceptors in the leg joints and mechanoreceptors on the ovipositor of this and other insects could be involved in the perception of the size and surface curvature of objects. Similar mechanisms may have allowed female *E. roborator* to determine the form of the cylinder and sphere when in contact with them. Alternatively, the parasitoid could also have been using features that it detected visually during contact. Visual or tactile assessment of the form of an object after contact with it could have several advantages. The insect would not need a clear line of sight from a distance to the object, or need to have it contrast in some way with its background. The form perceived by the insect would not depend on its angle of view, and tactile senses might allow detection of details too subtle to be distinguished visually.

In some cases, learning of form by insects affects their response to an object before contact. For example, the shapes and sizes of flowers provide distinctive visual cues that worker honey bees learn to use in conjunction with other flower features to identify profitable resources from a distance (von Frisch, 1971; Gould, 1984; Gould and Marler, 1987). The lack of effect of form learning on orientation to host microhabitats from a distance by *E. roborator* could reflect either the experimental conditions or the fact that the parasitoid does not learn to use form in this way.

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