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Some Aspects of Host Selection by *Perilitus coccinellae*^{1,2}

J. V. RICHERSON³ AND C. J. DELOACH⁴

ABSTRACT

Host selection by *Perilitus coccinellae* (Schrank), a parasite of adult Coccinellidae, was studied in a cage where beetles and models revolved at a constant rate. The parasite successfully parasitized all 7 species of coccinellids presented, *Coccinella novemnotata* Herbst, *Hippodamia convergens* Guérin-Ménéville, *Colomegilla maculata* (De Geer), *H. parenthesis* (Say), *Adalia bipunctata* (L.), *Cycloneda munda* (Say), and *Brachyacantha ursina* (F.). It also attacked models made of

colored paper, metal, and wood. The parasite was initially attracted by movement of any of the beetles or models. It attacked the larger species more often than the smaller species, and survival of the parasite from egg to adult was much greater in the larger species. However, factors other than the size which are associated with the larger species may determine host selection. Odor, and to a lesser extent color, influenced host selection, but shape or texture were of little importance.

The general biology of *Perilitus coccinellae* (Schrank), the major parasite of adult entomophagous coccinellids (Richerson 1970), was studied by Balduf (1926) and Cushman (1913). Balduf (1926), Bryden and Bishop (1945), and Walker (1961) reported that *P. coccinellae* attacked only moving hosts. Walker (1961) concluded that visual stimuli were the most important factors in host selection, and the parasite would attack if the host was moving and was red or black. Shape and odor did not seem to be important. The present study was conducted at the Biological Control of Insects Research Laboratory at Columbia, Mo., to determine more exactly how host movement, odor, size, and color influenced host selection by the parasite.

MATERIALS AND METHODS

The beetle hosts and parasites originated from material collected in Boone County, Mo., during June 1968. The coccinellids (Fig. 1) were swept from clover and alfalfa, held in a 1.8×0.9×0.9-m cage, and fed cabbage aphids, *Brevicoryne brassicae* (L.); turnip aphids, *Hyadaphis pseudobrassicae* (Davis); and green peach aphids, *Myzus persicae*

(Sulzer), on turnip and cabbage plants. The sizes listed in Fig. 1 are the average from 50 insects of each species which were reared in a laboratory culture. For the tests, beetles of about the same average size were selected from field collections but were not measured. The parasites were reared from hosts randomly selected from a colony of about 35 beetles.

All studies of host selection were made in a circular-motion cage 15 cm high and 30 cm diam that had clear plastic around the perimeter and a plywood top and bottom (Fig. 2). The shaft of the sweep-second hand of an electric clock which was attached beneath the cage extended through the center of the cage to a point 10 cm above the floor, and 4 rods 7.5 cm long were attached at right angles to the shaft. Using rubber cement, both models and living beetles were suspended from each rod by wires, so that they rotated just above the cage floor. The parasites were introduced through a door at the top of the cage. When the clock was started, the models revolved in a circle (15-cm diam) at 1 rpm.

In the series of tests, the response of the parasite to nonhosts was compared by using paper models of different colors and metal and wooden models; also, nonhost beetles were used, all with and without coxal secretion. The paper models were made from black, red, and yellow construction paper in 4 shapes: a 7-mm circle, a 5×7-mm rectangle, a 7-mm square, and

¹ Hymenoptera: Braconidae.

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³ Present address: Department of Biological Science, Pestology Centre, Simon Fraser University, Burnaby 2, B. C., Canada.

⁴ Now Research Entomologist, Biological Control of Weeds Investigations, Buenos Aires, Argentina, FAS, Department of State, Washington, D. C. 20521.

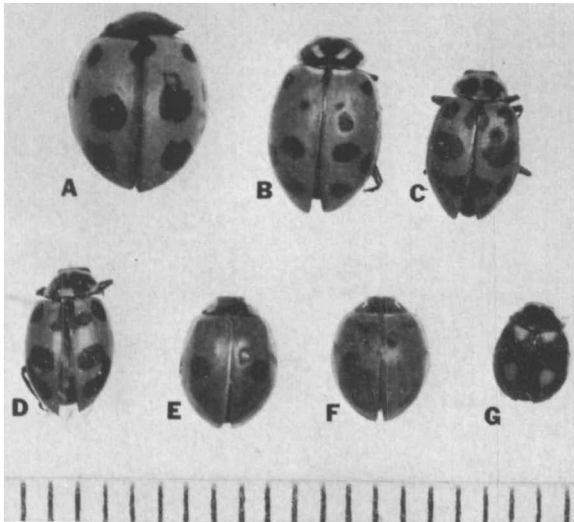


FIG. 1.—Coccinellids presented to *P. coccinellae* and average size of each species (in millimeters): A, *C. novemnotata* (6.5×4.6); B, *H. convergens* (6.0×4.0); C, *C. maculata* (6.0×4.0); D, *H. parenthesis* (5.0×3.5); E, *A. bipunctata* (4.5×3.5); F, *C. munda* (4.5×3.5); G, *B. ursina* (3.8×2.5). Scale in millimeters.

a 5×7-mm oval, all folded and glued so they were 2 mm high (Fig. 3). A brass pin which resembled a red coccinellid with black spots (19×9.5 mm) and a wooden model of the same color (11×9.5 mm) also were used (Fig. 3). The 2 nonhost beetles were *Epilachna varivestis* Mulsant, a coccinellid that has not been recorded as a host, and *Diabrotica undecim-*



FIG. 2.—Motion cage used for analysis of host selection behavior.

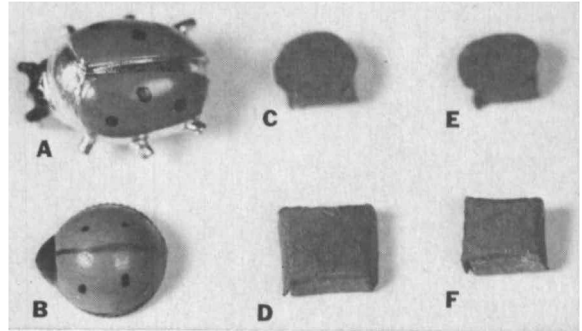


FIG. 3.—Models presented to *P. coccinellae* in the motion cage: A, metal pin; B, wooden model; C-F, paper models.

punctata howardi Barber, a chrysomelid which resembles coccinellids in size and shape.

The coxal secretion applied to the models was obtained by impaling 1 *H. convergens* on a pin and transferring all its coxal secretion to the dorsal surface of the model or nonhost beetle with a camel's hair brush.

The ovipositional responses of the parasite to the stimuli were defined as follows: (1) *pursuit*—the act of following the host without making prior contact and without taking the ovipositional stance; it was considered the 1st level of response; (2) *ovipositional stance*—the position in which the abdomen and the ovipositor are extended ventrally and cephalad between the legs and held against the thorax so the end of the ovipositor is in front of the head of the parasite. Included in this response are jabs with the ovipositor at a host which had previously been moving but had stopped. These jabs were not considered ovipositional, because no eggs were found when these beetles were dissected. They were probably attempts to stimulate movement of the host, which would expose the abdominal membranes and facilitate an ovipositional attack; (3) *ovipositional attack*—the actual insertion of the ovipositor into the host.

RESULTS

P. coccinellae attacked and successfully parasitized all 7 species of coccinellids in preliminary tests in ½-pint cartons, but the number of attacks varied with each species. The ovipositor was inserted through the membrane between the last 2 abdominal segments, either dorsally or ventrally; however, this area was vulnerable only when the beetle was moving, so the behavior of *H. convergens* in the field appeared to make it more vulnerable to parasitism than other species. For example, *Cycloneda munda* (Say), *Adelia bipunctata* (L.), and *Coccinella novemnotata* Herbst became immobile when attacked, and *Colcomegilla maculata* (De Geer) was too active and often escaped. Also, in the field the elytra of the beetles offered good protection because attacked beetles that became immobile drew in their legs and tightened the elytra over the abdomen, thus prevent-

Table 1.—Ovipositional attacks by *P. coccinellae* on 6 species of beetles with and without elytra in the motion cage.

| Species | Avg size of beetle (mm) | Number of attacks to beetles ^a | |
|-----------------------------------|-------------------------|---|----------------|
| | | With elytra | Without elytra |
| <i>C. novemnotata</i> | 6.5×4.6 | 13.75 a | 13.50 a |
| <i>H. convergens</i> | 6.0×4.0 | 12.25 b | 12.00 b |
| <i>C. maculata</i> | 6.0×4.0 | 12.00 b | 11.75 b |
| <i>A. bipunctata</i> | 4.5×3.5 | 9.00 c | 8.75 c |
| <i>C. munda</i> | 4.5×3.5 | 6.75 d | 6.50 d |
| <i>D. undecimpunctata howardi</i> | | 0.00 e | 0.00 e |

^a Means with the same letter within or between columns are not significantly different at the 5% level by Duncan's multiple range test. Mean of 10 replications; parasites exposed 15 min each.

ing oviposition by the parasite. In the motion cage, the elytra offered little protection, because the attachment to the wires prevented this defense.

One series of test (5 replications) was made in the motion cage to determine whether *P. coccinellae* could recognize a host with the elytra removed. Thus, 2 beetles of each species with elytra were presented along with 2 like beetles with the elytra removed.

The response to the same species of beetle with or without elytra did not differ significantly, but the larger of the 2 species was attacked significantly more often than the smaller species; the nonhost beetle was not attacked at all (Table 1).

The effect of exchanging elytra between species was also compared in the motion cage. Again, living beetles of 6 species (all hosts) were used, and the elytra were removed and glued on with rubber cement. In each of the tests 2 reciprocal pairs (2 each of 2 species) were compared by placing them together in the motion cage with 1 parasite for 15 min. A different parasite was used with each of the 30 combinations of beetles, and 5 replications were made. The total number of attacks varied directly with the size of the body of the beetle, but there was no apparent relationship between the total number of attacks and the size of the elytra (Table 2).

The effects of fastening 2 species together by tying them side by side about 4 mm apart (using thread and rubber cement) was compared in the motion cage for all combinations of 6 species. The beetles used had been dead 1 month so the effects of odor were assumed to have been minimized. Four identical pairs were placed together in the motion cage with 1 parasite for 15 min, a different parasite was used for each of the 15 combinations tested, and

Table 2.—Ovipositional response of *P. coccinellae* to coccinellid species (reciprocal exchanges of the elytra).^a

| Elytra | Total no. of ovipositional attacks and stances to beetles with indicated body sizes (mm) | | | | | | Total |
|-----------------------|--|-----------------------------------|---------------------------------|------------------------------------|-----------------------------------|------------------------------|-------|
| | <i>C. novemnotata</i> (6.5×4.6) | <i>H. convergens</i> (6.0×4.0) | <i>C. maculata</i> (6.0×4.0) | <i>H. parenthesis</i> (5.0×3.5) | <i>A. bipunctata</i> (4.5×3.5) | <i>C. munda</i> (4.5×3.5) | |
| <i>C. novemnotata</i> | | 46 | 43 | 44 | 65 | 44 | 242 |
| <i>H. convergens</i> | 54 | | 50 | 45 | 36 | 35 | 220 |
| <i>C. maculata</i> | 40 | 49 | | 45 | 20 | 28 | 182 |
| <i>H. parenthesis</i> | 61 | 51 | 48 | | 41 | 21 | 222 |
| <i>A. bipunctata</i> | 61 | 48 | 49 | 37 | | 45 | 240 |
| <i>C. munda</i> | 59 | 46 | 43 | 40 | 47 | | 235 |
| Totals | 275 | 240 | 233 | 211 | 209 | 173 | 1341 |

^a 5 replications each of 4 pairs (2 of each species) of beetles in the motion cage for 15 min.

Table 3.—Ovipositional response of *P. coccinellae* to each of 6 species of coccinellids when paired with the other 5 species.^a

| Partner species | Total no. ovipositional attacks and stances on target species of indicated size (mm) | | | | | |
|-----------------------|--|-----------------------------------|---------------------------------|------------------------------------|-----------------------------------|------------------------------|
| | <i>C. novemnotata</i> (6.5×4.6) | <i>H. convergens</i> (6.0×4.0) | <i>C. maculata</i> (6.0×4.0) | <i>H. parenthesis</i> (5.0×3.5) | <i>A. bipunctata</i> (4.5×3.5) | <i>C. munda</i> (4.5×3.5) |
| <i>C. novemnotata</i> | | 53 | 51 | 44 | 47 | 35 |
| <i>H. convergens</i> | 58 | | 50 | 47 | 43 | 43 |
| <i>C. maculata</i> | 55 | 53 | | 44 | 45 | 39 |
| <i>H. parenthesis</i> | 61 | 53 | 52 | | 47 | 39 |
| <i>A. bipunctata</i> | 55 | 49 | 52 | 47 | | 46 |
| <i>C. munda</i> | 58 | 45 | 47 | 49 | 48 | |
| Totals | 287 | 253 | 252 | 231 | 230 | 202 |

^a 4 replications, each with 4 identical pairs of beetles in the motion cage for 15 min.

Table 4.—Effect of host species on mortality of *P. coccinellae*.^a

| Host species | Avg size of beetle (mm) | No. parasites dying in indicated stage | | | | | No. parasites reaching adult stage |
|-----------------------|-------------------------|--|----|----|-------|-----------------|------------------------------------|
| | | Stadium | | | Pupae | Adult in cocoon | |
| | | 1 | 2 | 3 | | | |
| <i>C. novemnotata</i> | 6.5×4.6 | 0 | 0 | 0 | 0 | 1 | 24 |
| <i>H. convergens</i> | 6.0×4.0 | 0 | 0 | 0 | 1 | 1 | 23 |
| <i>C. maculata</i> | 6.0×4.0 | 0 | 0 | 0 | 0 | 1 | 24 |
| <i>H. parenthesis</i> | 5.0×3.5 | 0 | 0 | 1 | 4 | 2 | 18 |
| <i>C. munda</i> | 4.5×3.5 | 0 | 0 | 4 | 16 | 2 | 3 |
| <i>A. bipunctata</i> | 4.5×3.5 | 0 | 1 | 15 | 6 | 0 | 3 |
| <i>B. ursina</i> | 3.8×2.5 | 1 | 14 | 6 | 3 | 0 | 1 |

^a Total of 5 replications for each species; 5 coccinellid adults in each replication.

4 replications were made. Again, the larger species were attacked more often (Table 3).

The relationship between host size and survival of parasites was determined by placing each of the 7 host species in ½-pint cartons and exposing them to parasites until 25 were parasitized. Thereafter, the beetles were fed aphids and water until the parasite larvae emerged and spun cocoons. All living beetles from which a parasite larva did not emerge were dissected after 35 days, the time required for complete development of the parasite, and dead beetles were dissected immediately. Parasite cocoons were dis-

sected after 9 days if no adult emerged. The stage of development of the parasite at death was noted, using the stadial description established by Balduf (1926). The size of the host and parasite mortality were related: a greater portion of the parasite larvae and pupae died in the 3 smaller host species, *Cycloneda munda*, *A. bipunctata*, and *Brachyacantha ursina* (F.) than in the 4 larger species. Most of the parasites completed their development in the larger host species (Table 4). There was no evidence of encapsulation of the parasite egg in any host.

In a series of tests made to determine the response

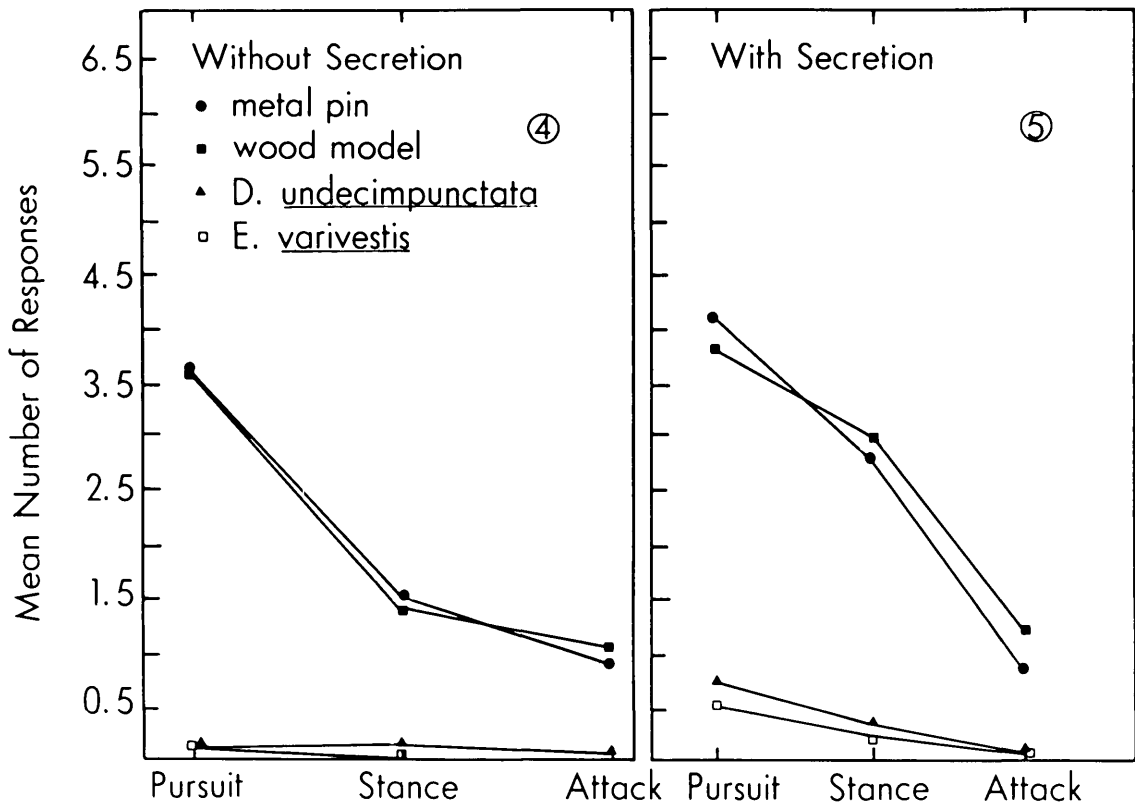


FIG. 4-5.—Mean number of responses of *P. coccinellae* to nonhost beetles, a metal pin, and wooden model without coxal secretion of *H. convergens* (Fig. 4) and with the secretion (Fig. 5).

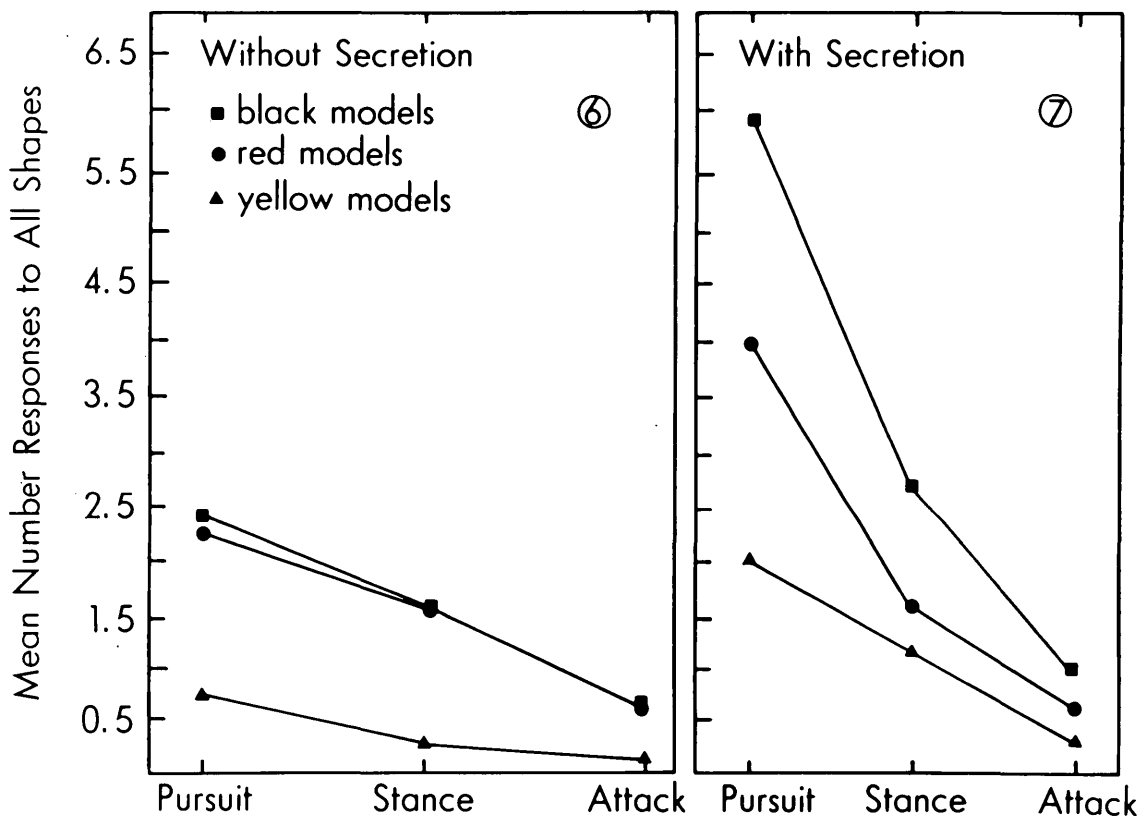


FIG. 6-7.—Mean number of responses of *P. coccinellae* to colored-paper models without coxal secretion of *H. convergens* (Fig. 6) and with the secretion (Fig. 7). Each point is the mean of all 4 shapes of models presented.

of the parasite to nonhosts, *P. coccinellae* was presented in the motion cage with each of the following combinations in the order listed for 15 min. A different parasite was used in each of the 10 replications.

1. *E. varivestis*, *D. undecimpunctata howardi*, metal pin, and wooden model.
2. Black-paper models in circular, rectangular, oval, and square shapes.
3. Red-paper models in the same 4 shapes.
4. Yellow-paper models in the same 4 shapes.

The parasite responded to the nonhost beetles, *E. varivestis* and *D. undecimpunctata howardi*, significantly less than to the metal pin and wooden model (Fig. 4); however, the addition of coxal secretion to these beetles significantly increased the number of pursuits although the response still was less than to the metal pin and wooden model. The responses to the metal pin and wooden model were not significantly increased by addition of the coxal secretion, except that the number of stances increased (Fig. 5).

Black and red models induced a significantly greater number of pursuits and stances than the yellow models, but the difference in number of attacks was not significant (Fig. 6). When coxal secretion was applied to the models, the number of pursuits and stances increased, but the number of attacks did not (Fig. 7). No significant difference was apparent in the response to the 4 shapes (Table 5).

DISCUSSION AND CONCLUSIONS

Some inferences can be made about the way the behavior of *P. coccinellae* fits into the general phases of host selection as defined by Salt (1935) and Doutt (1964). The 1st phase, ecological selection or host-habitat finding, was not investigated. However, the sampling in Boone County, Mo., revealed that *P. coccinellae* was found in all habitats where its hosts were found, and similar findings were reported in Illinois (Balduf 1926). Doutt's 2nd phase, host finding, is demonstrated in *P. coccinellae* by pursuit, and his 3rd phase, host acceptance, is demonstrated as ovipositional stance and attack. Thus, the occurrence of pursuit only or of pursuit and stance with-

Table 5.—Response of *P. coccinellae* to 4 shapes of paper models in the motion cage.

| Shape | No. responses ^a | | |
|-----------|----------------------------|--------|--------|
| | Pursuit | Stance | Attack |
| Rectangle | 46 a | 28 b | 9 c |
| Oval | 45 a | 20 b | 11 c |
| Square | 45 a | 28 b | 10 c |
| Circle | 41 a | 25 b | 9 c |

^a Total of 10 replications of 15 min each. Numbers followed by the same letter either between or within columns are not significantly different at the 5% level by Duncan's multiple range test.

out attack suggests that each phase of host selection requires a discreet, or at least an additional, stimulus.

The studies of host selection showed that the initial attraction was a moving object, whether dead or living hosts, paper models, metal or wooden models, or nonhost beetles. Thus the findings of Bryden and Bishop (1945) and Walker (1961) are confirmed. However, when the parasite is attracted by movement, the odor, size, and color of the moving object are further stimuli to host recognition.

The response of the parasite increased when coxal secretion from *H. convergens* was smeared on the models and nonhost beetles, but only the number of pursuits and stances increased for *E. varivestis*, *D. undecimpunctata howardi*, and the paper models, and only the number of stances for metal and wooden models. The number of attacks did not, which fact suggests that odor is an important stimulus for host recognition but not for oviposition. Also, odor proved important in the preference for coccinellids of about the same size. Walker (1961) made his tests with paper models smeared with whole crushed coccinellids and concluded that odor had no effect on recognition. However, his crude mixture included coxal secretion and possibly other competitive or masking odors. Rudinsky (1968) reported that extracts obtained from the gut of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, masked the sex pheromone of females ready to mate, and Jacobson (1965) cited other cases of masking of insect odors.

P. coccinellae seemed to prefer the larger species of coccinellids; preference (Tables 1-4) generally diminished in accordance with size (see Fig. 1). However, the mechanism of selection was not clear. Oviposition in the large species was advantageous, because survival of the immature stages of the parasite was much higher in them, but the parasite may use the odor of the particular species as a criterion in making the size distinction. When the elytra were exchanged between species, the parasite preferred the body of the larger species and showed little regard as to which elytra were attached, though the overall appearance of size was more related to the elytra than to the body of the beetle. (Odor probably is more associated with the body than with the elytra, since the site of coxal secretion is on the body.) Also, the species preference was unchanged when the elytra were removed (Table 1). Odor apparently influenced host selection, because pursuits and stances increased when paper models and nonhost beetles were smeared with coxal secretion. However, there was no clear demonstration that size alone was important, because size was always confounded with species in the comparisons, and different sizes of the same species were not compared.

Host color is probably a minor factor in host recognition and preference, but red- and black-paper models and the metal and wooden models (red with black spots) were attacked more often than the yellow-paper models. Walker (1961) also reported that *P. coccinellae* preferred red and black. Since the paper models were uniformly pigmented and the elytral pattern varied between coccinellid species, color but not pattern was concluded to be a factor in host recognition. The parasite maintained the same order of host-species preference based on size, even when the elytra were removed, so color and pattern are relatively minor factors in host recognition; again, odor was probably the principal factor.

P. coccinellae showed no preference for the 4 shapes of paper models presented, so we conclude that shape is not important in host selection. Paper, metal, and wooden models were all pursued, examined, and attacked by the parasite; therefore, texture of the host also seems to be of little importance.

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