Host-Acceptance Behavior of *Dinocampus coccinellae* (Hymenoptera: Braconidae)

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ABSTRACT *Dinocampus coccinellae* (Schrank) spent >80% of a 300-s observation period in host-handling activities (orienting toward, pursuing, and attacking hosts) when exposed to individual adult *Coleomegilla maculata* (DeGeer) or *Coccinella septempunctata* (L.). When *D. coccinellae* was exposed to two populations of *Hippodamia variegata* (Goeze) from Canada or France and *Propylea quatuordecimpunctata* (L.) from Canada or Turkey, host-handling activities decreased to <70% of 300 s. *D. coccinellae* oriented toward and attacked *C. maculata* and *C. septempunctata* in 10–12 s, compared with 18–38 s for *H. variegata* and *P. quatuordecimpunctata*. Additionally, *C. maculata* and *C. septempunctata* were attacked more frequently (mean = 3.3 and 2.6 in 300 s, respectively) than *H. variegata* or *P. quatuordecimpunctata* (mean = 2 and 1.5 in 300 s, respectively). No differences in *D. coccinellae* behavior were observed in response to the two *H. variegata* and two *P. quatuordecimpunctata* populations. *D. coccinellae* successfully emerged from 58% of *C. maculata*, 47% of *C. septempunctata*, 7–15% of *H. variegata*, and 1% of *P. quatuordecimpunctata*. Total mortality of adults exposed to *D. coccinellae* was 80% for *C. maculata*, 76% for *C. septempunctata*, 50% for *H. variegata* (France), 38% for *H. variegata* (Canada), and 11% for both *P. quatuordecimpunctata* populations. Based upon our observations, we expanded the description of *D. coccinellae* selection behavior to include orientation, which precedes forward motion toward a host.

KEY WORDS parasitoid, biological control, Coccinellidae

Dinocampus (=*Perilitus*) *coccinellae* (Schrank) is a solitary, thelytokous, koinobiont parasitoid that attacks aphidophagous coccinellid species throughout the world (Richerson 1970, Hodek 1973, Richerson & DeLoach 1973, Marsh et al. 1987). This parasitoid typically attacks adults; however, it also parasitizes immature stages of coccinellids (Obrycki et al. 1985, Shaw 1988). During the past three decades, several Palearctic hosts of *D. coccinellae* have fortuitously established in North America (e.g., *Coccinella septempunctata* [L.], *Hippodamia variegata* [Goeze], and *Propylea quatuordecimpunctata* [L.]) (Gordon 1985, 1987; Schaefer & Dysart 1988; Wheeler 1990). The current biological control program for the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) is continuing to introduce Palearctic populations of these species into the United States (Flanders et al. 1991). How the establishment of Palearctic hosts will affect relationships between *D. coccinellae* and native coccinellid hosts is unknown.

In previous laboratory studies, differences in host suitability were observed among these Palearctic species and selected Nearctic species (Obrycki 1988, 1989). However, no quantitative comparative behavioral studies of *D. coccinellae* in response to Nearctic and Palearctic coccinellid species have been conducted. Host-selection behavior was described initially by Doutt (1959) as habitat location, host location, host acceptance, and host suitability. More recently, host-acceptance behavior was divided into host examination, ovipositor probing, drilling, and oviposition (Vinson 1985). Close-range host location by *D. coccinellae* occurs within a few centimeters of the host, and, during host examination, odor and movement appear to stimulate oviposition (Balduf 1926, Walker 1961, Richerson & DeLoach 1972, Semyanov 1975). Previously, oviposition was assumed to occur only when the host was moving. Attacks on immobile coccinellid hosts were thought to stimulate host movement, which then resulted in an attack (Balduf 1926, Richerson & DeLoach 1972).

In this study, we quantify and compare the host-acceptance behavior of *D. coccinellae* in response to mobile and immobile adults of selected Nearctic and Palearctic coccinellid species and determine if *D. coccinellae* discriminates between geographic populations of *H. variegata* and *P. quatuordecimpunctata*.

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Materials and Methods

Host Species. Adult *C. maculata* were collected from aggregation sites in Story County, IA, during 1988 and 1989. *P. quatuordecimpunctata* (F_4–F_5) from Turkey and Canada, *H. variegata* (F_4–F_5) from France and Canada, and field-collected *C. septempunctata* from Peach County, GA, were provided by the USDA–APHIS Biological Control Laboratory in Niles, MI. Field-collected *C. septempunctata* and *C. maculata* adults were held for 6 wk at 22 ± 1°C and a photoperiod of 16:8 (L:D) h, until *D. coccinellae* had emerged. Individuals of *C. septempunctata* and *C. maculata* from which no parasitoids emerged were used as hosts in the experiments. A random sample of 50 of the *C. maculata* was dissected, and no evidence of parasitism (eggs, head capsules, or immatures) by *D. coccinellae* was observed. From 18 to 30 unexposed adults from each species (control) were held for 28–35 d under similar conditions as the exposed coccinellids, then frozen and dissected for the presence of *D. coccinellae*. No *D. coccinellae* were recovered from any of the control individuals.

Preceding exposure to *D. coccinellae*, between 5 and 6 adults of the same species were held in 0.24-liter paper cartons (Fonda, Union, NJ) at 26 ± 1°C and a photoperiod of 16:8 (L:D) h, with water, a 1:1 mixture of honey and Wheast (Qualcepts, Minneapolis, MN), and pea aphids (*Acyrthosiphon pisum* Harris).

Parasitoid Females. All *D. coccinellae* were reared from adult *C. septempunctata* collected in GA during 1988 and held at 22 ± 1°C and a photoperiod of 16:8 (L:D) h. On the day of eclosion, *D. coccinellae* were placed individually into 0.24-liter paper cartons and provided with water, a mixture of honey and Wheast, and honey. All experiments were initiated with 1-d-old *D. coccinellae* females.

Experimental Design. Eighteen *D. coccinellae*, six in each of three replicates, were exposed to 24–36 individual coccinellids over 5–6 d. An individual *D. coccinellae* was removed from its carton and gently shaken into a 0.24-liter paper carton (the arena) with a 1-cm-grid paper liner and a plastic petri dish lid (100 mm by 9 mm, Fisher Scientific). An adult coccinellid was added, and observations began when both insects were in the arena. Three parasitoid behaviors recorded during a 300-s exposure period were: (1) orientation: *D. coccinellae* facing host, antennae waving or motionless, no forward motion; (2) pursuit: included movement toward host, ovipositor distad or ventrad and cephalad; encircling a stationary host, ovipositor distad or ventrad and cephalad; or a combination of these; and (3) attack: insertion of the ovipositor into the host. Terminology describing *D. coccinellae* behavior generally follows that of Richerson &

DeLoach (1972); however, we modified the definitions of their terminology slightly (see *Discussion*).

To determine if attacks into the membranous areas of the head and membranous region between the prothorax and the mesothorax (the anterior region), legs (from the coxa to the distal end of the femur), and abdomen resulted in oviposition, we recorded parasitism (presence of immature *D. coccinellae* in dissected host or successful eclosion) that occurred when a host had been attacked in only one region (anterior region, legs, or abdomen) of its body. We also recorded parasitism resulting from attacks made into immobile and mobile hosts. Hosts that were moving during an attack were defined as *mobile*. Hosts that had been moving but then stopped and were attacked, and hosts that did not move during the observation period were defined as *immobile*.

The six host populations were designated as: (1) *H. variegata* (Canada), (2) *P. quatuordecimpunctata* (Turkey), (3) *P. quatuordecimpunctata* (Canada), (4) *C. septempunctata*, (5) *H. variegata* (France), and (6) *C. maculata*. Daily, the first of six hosts exposed to each of six female parasitoids came from a different source population. Hosts were rotated on each of the 6 consecutive d until individuals from each coccinellid population had been offered first to each female parasitoid. For example, on day 1 of the experiment, the first host offered to parasitoid 1 was *H. variegata* (Canada). Host 2, the second host offered on day 1, was the first host offered on day 2, and so on through day 6 of the experiment. Female parasitoids 2–6 were offered hosts 2–6, as their first host on day 1, respectively, and their first host for each day rotated in the same order as for parasitoid 1. The sequence of hosts and the initiation within the sequence was the same for replicates 2 (parasitoids 7–12) and 3 (parasitoids 13–18). Observations were made between 0745 and 1600 hours at 22 ± 3°C under natural and fluorescent room lighting.

Following exposure to *D. coccinellae*, adult coccinellids were removed from the arena and placed individually into paper cartons provisioned with water, and a mixture of honey and Wheast. Pea aphids were provided on alternate days. Hosts were maintained at 26 ± 1°C and a photoperiod of 16:8 (L:D) h until *D. coccinellae* emergence, or for 28–35 d. From 18 to 30 adults of each population were maintained at 26 ± 1°C and a photoperiod of 16:8 (L:D) h to determine the survival of nonexposed individuals. All coccinellids from which a *D. coccinellae* did not exit were dissected for the presence of immature *D. coccinellae*. Voucher specimens are deposited in the Iowa State University Insect Collection, Ames.

Host mortality and parasitism by *D. coccinellae* were classified as: A, host dead, successfully

Table 1. Behavioral responses ±SEM of *D. coccinellae* to, and percentage successful parasitism of, selected Nearctic and Palearctic coccinellid hosts

	C. mac	C7	Hv Ca	Hv Fr	P14 Ca	P14 Tu	ANOVA[a] df	ANOVA[a] P	LSD
Parasitoid behavior									
Total handling time(s)[b,c]	247 ± 16.6	253 ± 10.7	206 ± 26.5	214 ± 25.5	195 ± 30.2	194 ± 21.6	5, 10	0.002	28.45
Time to first orientation(s)[c]	10 ± 3.3	12 ± 3.4	18 ± 1.1	24 ± 8.6	38 ± 6.6	33 ± 6.1	5, 10	0.014	16.16
Time to initial attack(s)[c]	59 ± 9.9	72 ± 2.2	77 ± 9.2	87 ± 4.0	118 ± 6.9	125 ± 17.7	5, 10	0.004	32.71
Mean no. attacks per host[c,d]	3.3 ± 0.04	2.6 ± 0.1	2.0 ± 0.34	2.1 ± 0.1	1.7 ± 0.1	1.5 ± 0.1	5, 10	0.0001	0.500
% Hosts attacked[e]	95 ± 0.03	95 ± 0.02	92 ± 0.02	93 ± 0.02	85 ± 0.03	78 ± 0.06	5, 10	0.014	9.94
No. exposed each rep	36, 30, 34	36, 28, 35	36, 29, 35	36, 34, 34	36, 28, 35	36, 29, 35			
% Successful parasitism[f]	60 ± 0.08	48.5 ± 0.06	17.4 ± 0.1	8.7 ± 0.04	1.2 ± 0.01	0 ± 0	5, 10	0.0002	20.12
No. eclosed adults	45	57	15	7	1	0			
No. eclosed per rep	13, 17, 15	19, 12, 26	6, 9, 0	4, 3, 0	0, 0, 1	0, 0, 0			

C. mac, *C. maculata;* C7, *C. septempunctata;* Hv Ca, *H. variegata* (Canada); Hv Fr, *H. variegata* (France); P14 Ca, *P. quatuordecimpunctata* (Canada); P14 Tu, *P. quatuordecimpunctata* (Turkey).

Standard errors based on the means of three replicate means.

[a] Error term is rep*species.

[b] Time spent orienting, charging, encircling, and attacking a host in a 300-s observation period.

[c] Female nested within rep as a factor in the ANOVA.

[d] Total number of attacks/number of hosts attacked.

[e] (Number of hosts attacked/number of hosts exposed) × 100.

[f] (Number of hosts from which *D. coccinellae* eclosed/total number attacked) × 100.

parasitized (i.e., successful *D. coccinellae* eclosion); B, host alive at the end of 28–35 d, evidence of either unsuccessful parasitism or delayed development of *D. coccinellae* (i.e., egg, first instar head capsule(s), or later immature stages found during dissection); C, host dead, evidence of unsuccessful parasitism or delayed development; D, host attacked but alive at the end of 28–35 d, no evidence of parasitism found during dissection; E, host dead, no evidence of parasitism found during dissection; and F, host not attacked.

Statistical Analysis. We examined *D. coccinellae*'s behavior toward the various coccinellid species with analysis of variance (ANOVA) (SAS Institute 1985) and least significant difference (LSD; not adjusted for multiple comparisons) (Snedecor & Cochran 1967). Responses included the number of seconds used to handle a host (sum of seconds orienting toward, charging, encircling, and attacking a host), and the number of seconds required for first orientation and first attack of a host. The percentage in each host mortality-parasitism category was calculated as the number of individuals in each category divided by the total number of exposed individuals of each host population (minus those lost during the 28–35-d holding period) × 100.

Results

Intraspecific Host Comparisons. *D. coccinellae* responded statistically similarly to the two populations of *H. variegata* and to the two populations of *P. quatuordecimpunctata* (Table 1; Fig. 1). Therefore, results are combined for the

two populations of *H. variegata* and *P. quatuordecimpunctata,* unless otherwise noted.

Host Acceptance. *D. coccinellae* spent more time handling *C. maculata* and *C. septempunctata* (mean, 246 and 253 s, respectively) than either *H. variegata* or *P. quatuordecimpunctata* (mean ranges from 194 to 214 s) (ANOVA; df = 5, 10; P = 0.002) (Table 1). *D. coccinellae* first oriented toward *C. maculata* and *C. septempunctata* in <12 s, toward *H. variegata* in 19–26 s, and toward *P. quatuordecimpunctata* in 34–38 s (ANOVA; df = 5, 10; P = 0.014) (Table 1). *D. coccinellae* first attacked *C. maculata* and *C. septempunctata* in less time (59 and 73 s, respectively) than *H. variegata* (≈80 s) and *P. quatuordecimpunctata* (>110 s) (ANOVA; df = 5,10; P = 0.004) (Table 1). *C. maculata* and *C. septempunctata* were attacked more frequently (mean, 3.3 and 2.6 times) than *H. variegata* (mean, 2.0 times) and *P. quatuordecimpunctata* (mean, 1.5 and 1.7 times) (ANOVA; df = 5, 10; P = 0.0001) (Table 1; Fig. 2). Less than 10% of the *C. maculata, C. septempunctata,* and *H. variegata* were not attacked, whereas 15–20% of the *P. quatuordecimpunctata* were not attacked by *D. coccinellae* (ANOVA; df = 5, 10; P = 0.014) (Table 1, Fig. 2).

D. coccinellae successfully parasitized relatively few immobile hosts: four *C. septempunctata* and three *H. variegata.* Additionally, three immobile *C. septempunctata* and six immobile *H. variegata* were parasitized unsuccessfully (contained immature *D. coccinellae*) (Table 2). Mobile *C. septempunctata* attacked in more than one body region were successfully parasitized more frequently than when attacked in only the abdomen or anterior region (Table 2). Thirty-one
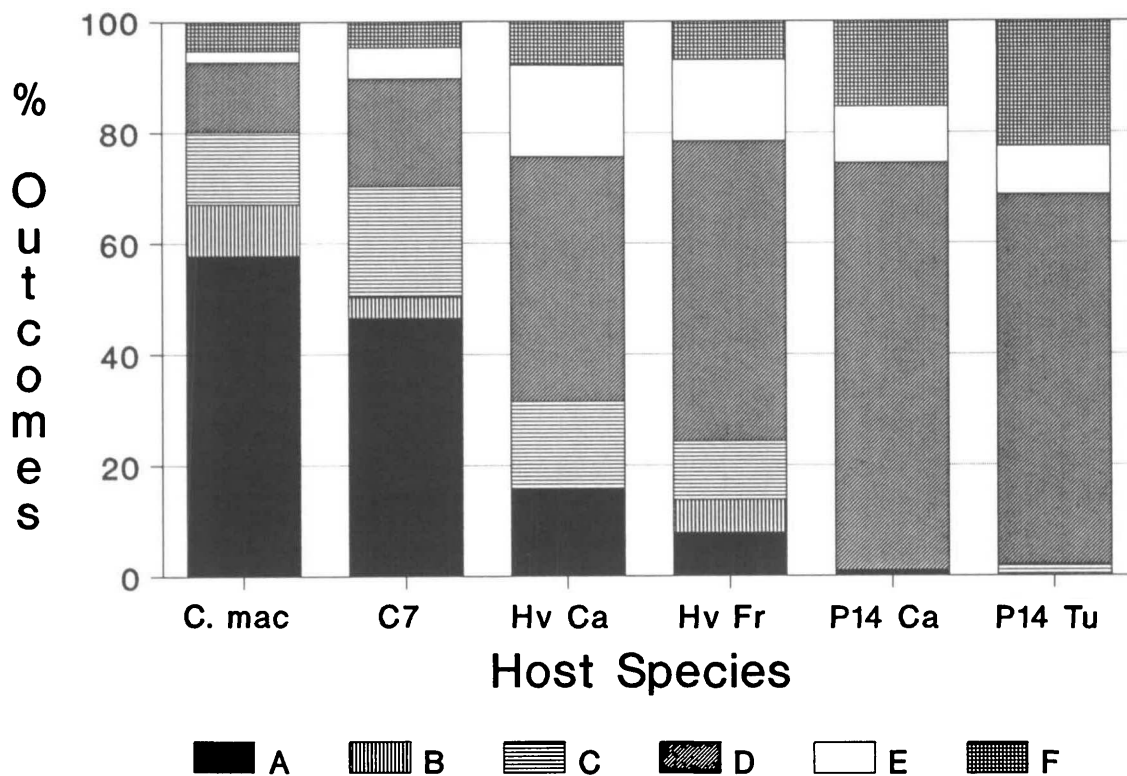
Fig. 1. Percentages of hosts which, following a 300-s exposure to *D. coccinellae* and a 28–35-d holding period, were: A, dead and successfully parasitized; B, alive and unsuccessfully parasitized (*D. coccinellae* eggs, head capsules, or later immature stages found when dissected); C, dead and unsuccessfully parasitized; D, alive and attacked but not parasitized; as determined by dissection; E, dead and attacked but not parasitized; or F, not attacked. C. mac, *Coleomegilla maculata;* C7, *Coccinella septempunctata;* Hv Ca, *H. variegata* (Canada); Hv Fr, *H. variegata* (France); P14 Ca, *P. quatuordecimpunctata* (Canada); P14 Tu, *P. quatuordecimpunctata* (Turkey).

mobile *C. maculata* attacked in two body regions and 26 attacked only in the abdomen were parasitized successfully. However, no moving *C. maculata* attacked only in the anterior region were parasitized successfully (Table 2). Moving *H. variegata* hosts were parasitized successfully in approximately equal numbers when attacked in only the abdomen or anterior region or when attacked in both regions.

Host Suitability. *D. coccinellae* successfully eclosed from 58% of the *C. maculata,* 47% of *C. septempunctata,* 16% of *H. variegata* (Canada), 8% of *H. variegata* (France), and 1% of *P. quatuordecimpunctata* (Canada) (Fig. 1, category A). Relatively few *C. maculata, C. septempunctata* and *H. variegata* (France) (9, 4, and 6%, respectively), were alive and contained *D. coccinellae* eggs or larvae after 28–35 d (Fig. 1, category B). The percentage of hosts that died before 28–35 d, and contained life stages of *D. coccinellae* ranged from <2% for the *P. quatuordecimpunctata* to 20% for *C. septempunctata,* (Fig. 1, category C).

The percentage of hosts attacked but not parasitized and alive at the end of 28–35 d varied from 13% for *C. maculata* and 19% for *C. sep-*

tempunctata to between 40 and 50% for *H. variegata,* to ≈70% for *P. quatuordecimpunctata* (Fig. 1, category D). Less than 15% of all hosts were attacked and not parasitized and died in <35 days (Fig. 1, category E). Approximately 20% of the *P. quatuordecimpunctata* were not attacked (Fig. 1, category F).

Percentage mortality was four times higher in *C. maculata* and *C. septempunctata* populations exposed to *D. coccinellae* than in control populations. Percentage mortality of the exposed *H. variegata* (Canada) population was three times higher than the control population, whereas mortality in the exposed population of *H. variegata* (France) was 1.5 times higher than the control population. There was only a negligible difference in percentage mortality of exposed versus control *P. quatuordecimpunctata* (7 versus 11%) (Fig. 3).

Discussion

Intraspecific Host Comparisons. Based on our measures of *D. coccinellae* acceptance behavior and host suitability, *H. variegata* from Canada
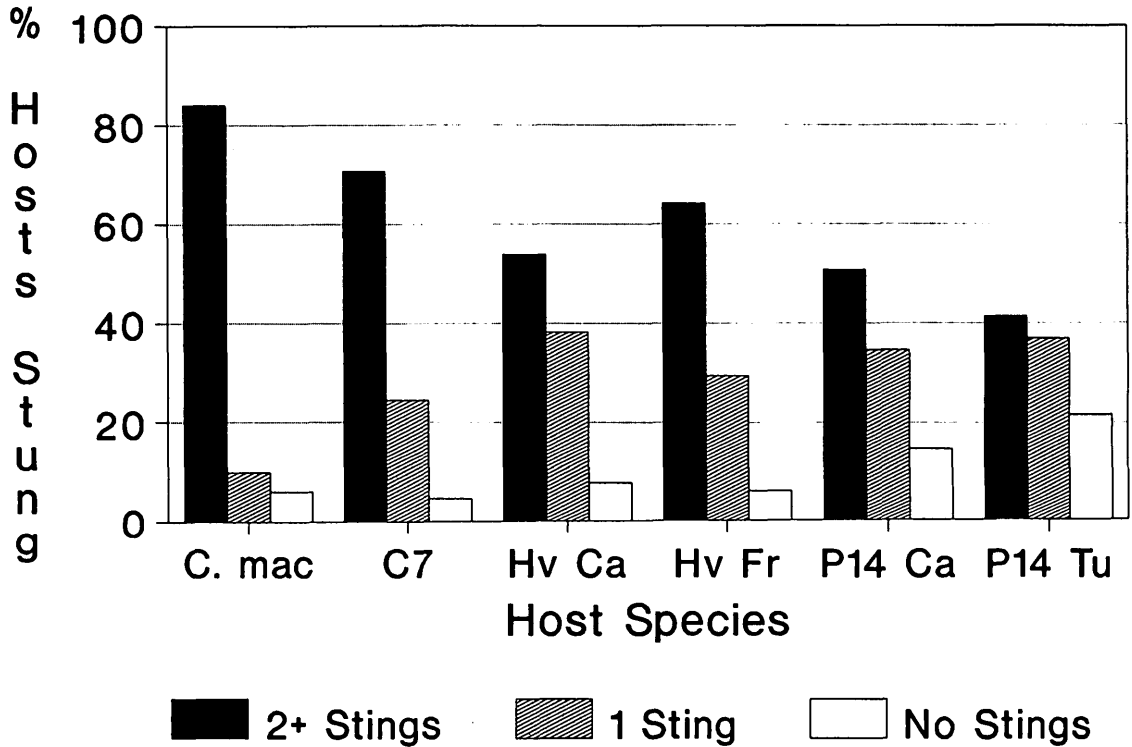
% 100
H
o 80
s
t 60
s
40
S
t 20
u
n 0
g

C. mac   C7   Hv Ca   Hv Fr   P14 Ca   P14 Tu

Host Species

■ 2+ Stings   ▨ 1 Sting   ☐ No Stings

Fig. 2. Percentage of six populations of coccinellid hosts attacked more than once, once, or not attacked by *D. coccinellae* in 300 s (species abbreviations as in Fig. 1).

and France are equivalent hosts (Table 1). Previously, in France, 12–25% of field-collected *H. variegata* adults dissected were parasitized by *D. coccinellae* (Iperti 1964). In our study, *D. coc-* *cinellae* eclosed from 8% of *H. variegata* (France); however, percentage parasitism increases to 24% if unsuccessful and delayed parasitism are included. Similarly, 15% of the *H.*

Table 2. Number of mobile and immobile coccinellids that were attacked in various body regions by *D. coccinellae* during a 300-s observation period

Outcome	More than one body region[a]			Anterior only			Abdomen only		
	A	B	C	A	B	C	A	B	C
	Location of attacks in mobile coccinellid hosts								
Host Species									
C. mac	6	13	31	3	0	0	5	8	26
C7	10	16	24	8	6	6	6	3	0
Hv Ca[b]	21	5	6	10	2	3	30	7	6
Hv Fr[b]	27	9	1	11	3	2	23	4	4
P14 Tu	18	0	0	8	1	0	46	1	0
P14 Ca	10	1	0	16	0	0	42	0	1
	Location of attacks in immobile coccinellid hosts								
Host Species									
C. mac	0	0	0	0	0	0	1	0	0
C7	0	2	1	3	1	1	0	0	2
Hv Ca	0	0	0	6	0	1	4	1	0
Hv Fr	1	2	0	3	1	2	2	2	0
P14 Tu	1	0	0	3	0	0	6	0	0
P14 Ca	2	0	0	3	0	0	5	0	0

A, attacked but not parasitized; B, attacked and parasitized but *D. coccinellae* eclosion did not occur; C, successful *D. coccinellae* eclosion.

C. mac, *C. maculata;* C7, *C. septempunctata;* Hv Ca, *H. variegata* (Canada); Hv Fr, *H. variegata* (France); P14 Ca, *P. quatuordecimpunctata* (Canada); P14 Tu, *P. quatuordecimpunctata* (Turkey).

[a] Host attacked in two or more of the following: anterior region (head and thorax), coxa, abdomen.

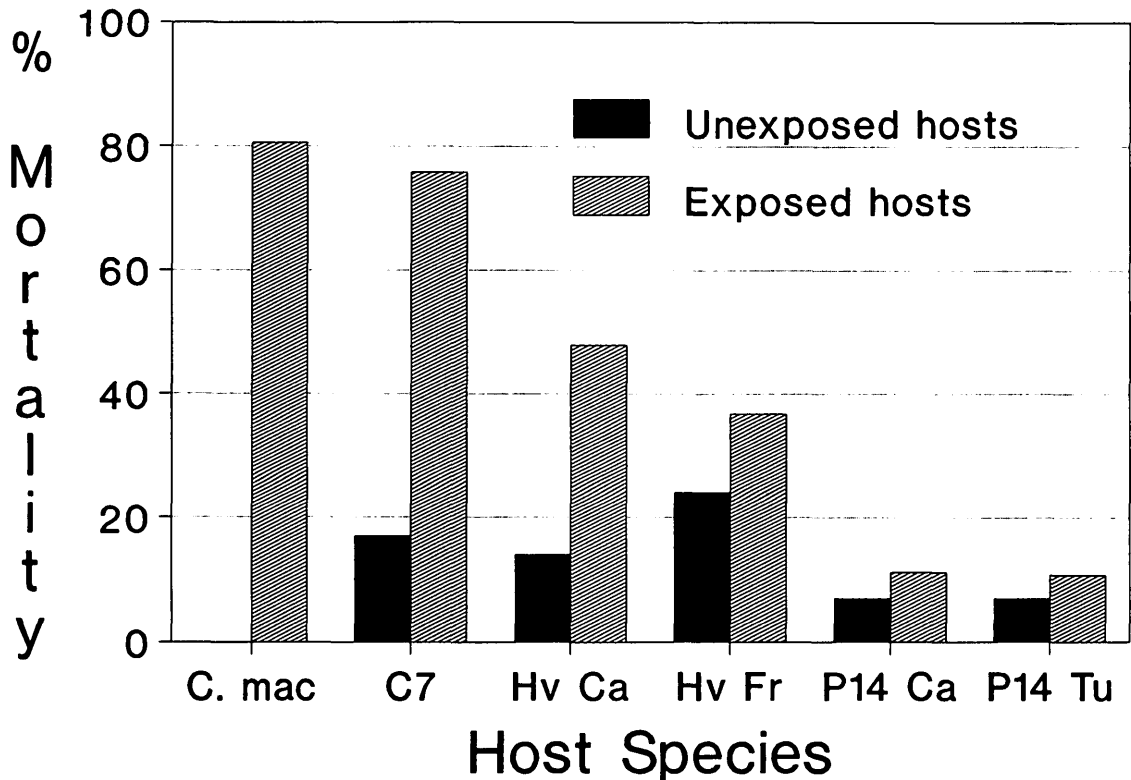[b] Single host was attacked in the coxa only, but parasitism did not occur.

Fig. 3.   Percentage mortality in unexposed, control populations (*n* = 18–30 adults for each of the six host populations) compared with individuals exposed to *D. coccinellae* for 300 s. C. mac, 0% versus 80%; C7, 17 versus 70%; Hv Ca, 14 versus 47%; Hv Fr, 24% versus 38%; P 14 (either Canada or Turkey) 7 versus 11%. All individuals were maintained for 28–35 d at 26 ± 1°C and a photoperiod 16:8 (L:D) h (species abbreviations as in Fig. 1).

variegata (Canada) were parasitized successfully, and an additional 15% were parasitized unsuccessfully. These results differ considerably and inexplicably from a previous laboratory study in which no *H. variegata* (Canada) were parasitized successfully by *D. coccinellae* (Obrycki 1989).

Iperti (1964) reported that, based on dissections, <8% of the *P. quatuordecimpunctata* collected over several months were parasitized by *D. coccinellae*. This is much higher than our data and that of Obrycki (1989), in which percentage parasitism of *P. quatuordecimpunctata* (Canada) was 2%. Our study demonstrates that the low percentage of successful parasitism of *P. quatuordecimpunctata* results from both fewer attacks per host and the low number of attacked hosts that were accepted for parasitism (determined by dissection) (Table 1; Fig. 1). More than 70% of exposed *P. quatuordecimpunctata* were attacked but not parasitized, indicating that this species is marginally acceptable for *D. coccinellae* (Fig. 1).

Host Acceptance. Although *D. coccinellae* will attack coccinellid adults in any membranous part of the body, there are inconsistancies in the literature on the location of oviposition. For example, Sluss (1968) observed that ≈50% of the attacks by *D. coccinellae* resulted in egg deposition in *Hippodamia convergens;* attacks in the abdomen were twice as common as in the coxa. Similarly, Richerson & DeLoach (1972) reported that oviposition into several coccinellid species was only between the last two abdominal segments. Conversely, Iperti (1964) and Semyanov (1975) reported that ovipositional attacks occurred in the membranous regions of the head, and between the prothorax and the mesothorax, as well as between the abdominal tergites. We also observed considerable interspecific host variation in the location of *D. coccinellae* oviposition sites (Table 2). These observations are consistent with previous studies in which parasitization of *C. maculata* was reported from abdominal attacks (Balduf 1926, Richerson & DeLoach 1972), whereas *C. septempunctata* was parasitized from attacks in the anterior region (head and thorax) (Iperti 1964, Semyanov 1975).

D. coccinellae also has been reported to oviposit only in mobile hosts (Balduf 1926, Bryden

& Bishop 1945, Richerson & DeLoach 1972). However, we found that motionless hosts were parasitized (Table 2). Considerable variation existed in the ability of *D. coccinellae* females to attack immobile hosts successfully. Of 18 parasitoids observed (24–36 observations per female), two did not attack immobile hosts and 10 attacked but did not parasitize immobile hosts. Six *D. coccinellae* attacked an average of five (range from three to six) immobile hosts; of these, ≈54% were parasitized (range, 33–67%). A single *D. coccinellae* parasitized all the immobile hosts that it attacked ($n = 3$). The responses observed are presumed to be the result of intraspecific variation in response to hosts, a common characteristic of many parasitoid species (Lewis et al. 1990). It is also possible that some of the parasitoid females may have been infected with a microsporidian, which may affect host-acceptance behavior (Sluss 1968).

Previously, Richerson & DeLoach (1972) described the close range sequence of host-selection behavior of *D. coccinellae* as pursuit, following a host without contacting it or assuming the ovipositional stance; ovipositional stance, bringing the ovipositor cephalad and ventral to the body of *D. coccinellae* (included in this behavior are attacks into motionless hosts); and oviposition attack, inserting the ovipositor into mobile hosts. They considered pursuit to be host location (Doutt 1959) and ovipositional stance and attack to be host-acceptance behavior (Doutt 1959). We found that these three activities did not always occur in a well-defined sequence. When following a host, *D. coccinellae* females frequently alternated the ovipositor from a distal position to a cephalad position, the ovipositional stance of Richerson & DeLoach. Therefore, pursuit and oviposition stance often occur simultaneously as part of host-examination behavior (Vinson 1985). Host examination by *D. coccinellae* often occurs rapidly, and in most cases the examination, ovipositor drilling, probing, and oviposition are completed in <2 s.

We observed host-location behavior when *D. coccinellae* oriented, or turned toward a host. Similar observations of turning toward a host before forward movement were made by Sluss (1968). This behavior may be a response to chemicals emanating from coccinellid hosts or host movement during the introduction of the host to the parasitoid arena. It is possible Richerson & DeLoach (1972) did not quantify this behavior because they used a circular-motion cage device in which hosts were attached to an arm and rotated at a constant speed, whereas our observations were based upon the natural movements of hosts and *D. coccinellae*.

On the basis of our observations, we conclude that the terminology used by Richerson & DeLoach (1972) does not fully describe the variation in *D. coccinellae* close-range host selection behavior. We propose the following changes to describe *D. coccinellae* selection behavior: orientation, turning toward host; pursuit, following or encircling a host, a behavior which may occur concurrently with ovipositional stance, body position with the abdomen cephalad and ventrad; and attack, attacks of either mobile or immobile hosts.

The concepts of parasitoid host acceptance generally are based on behavior of parasitoids of sessile hosts. The behavior of parasitoids attacking mobile hosts was recognized by Doutt (1959), and recently Vinson (1985) concluded that parasitoids attacking active hosts have a relatively short host-handling time. However, following host examination, parasitoids of active hosts may overcome or stimulate movement of an active host. Yeargan & Braman (1989b) concluded that the concepts of host acceptance need to include parasitoid behavior that alters the behavior of mobile hosts to increase the chances of successful parasitism. For example, *D. coccinellae* encircles and probes nonmoving hosts to initiate movement, which may be necessary for some *D. coccinellae* females to complete oviposition (Balduf 1926, Bryden & Bishop 1945, Walker 1961). Similarly, *Microtonous vittatae* Muesebeck uses its antennae to induce movement in its host *Phyllotreta* spp. before oviposition (Smith 1952). *Mesochorus discitergus* Say, a hyperparasite of three primary parasitoids of the green cloverworm, *Plathypena scabra* (F.), uses its legs to reel up second instars which had spun a silk thread off the edge of a leaf (Yeargan & Braman 1989a). In these examples, oviposition would either be more difficult or impossible without manipulation of the active host.

Host Suitability. The two species most often successfully parasitized, *C. maculata* and *C. septempunctata*, were attacked repeatedly and were more likely to be either unsuccessfully parasitized or to contain *D. coccinellae* larvae showing delayed development. These two coccinellid species also suffered the greatest overall mortality compared with mortality of nonexposed individuals (Fig. 3). The high mortality of two otherwise acceptable and suitable hosts may be the result of having been attacked repeatedly. Superparasitism did not play a major role in this mortality—only two *C. maculata* and one *C. septempunctata* contained two *D. coccinellae* head capsules.

Implications for Aphid Biological Control Programs. *D. coccinellae* parasitized and nonparasitized *H. convergens* consumed a similar number of aphids until the time of parasitoid larval emergence (Sluss 1968). *D. coccinellae* is multivoltine, and several generations attack larval, pupal, and adult coccinellids (Obrycki & Tauber 1978). *D. coccinellae* could limit the level of predation, and therefore the degree of aphid suppression, expected from a coccinellid species. Parasitoid

activities of *D. coccinellae* may be similar to biotic interference by native predators and parasitoids of exotic phytophagous insects introduced for weed control (Goeden & Louda 1976). For example, we hypothesize that because *D. coccinellae* seldom parasitizes *P. quatuordecimpunctata,* this coccinellid species may be relatively more effective in suppressing Russian wheat aphid populations.

Acknowledgments

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