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Author(s): William Sheehan and A. M. Shelton

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## PARASITOID RESPONSE TO CONCENTRATION OF HERBIVORE FOOD PLANTS: FINDING AND LEAVING PLANTS<sup>1</sup>

WILLIAM SHEEHAN<sup>2</sup> AND A. M. SHELTON

Department of Entomology, New York State Agricultural Experiment Station,  
Cornell University, Geneva, New York 14456 USA

**Abstract.** We hypothesized that a parasitoid of an herbivore would be attracted to large rather than small patches of plants that provide food for the herbivore. We conducted experiments to determine whether such parasitoids would be more likely to find and/or less likely to leave large patches of their victims' host plants. We also examined whether prey density (independent of patch size) affects plant finding or leaving. These aspects of plant foraging behavior were examined for *Diaeretiella rapae* (Hymenoptera: Aphidiidae), a parasitoid wasp that attacks aphids primarily on cruciferous plants.

Arrival rates of naturally occurring *D. rapae* in artificial patches of 5, 10, 20, and 40 potted collard plants were measured in a field experiment. There was no patch-size effect (plants in larger patches were not more likely to be found), and plants with aphids were not more likely to be found than aphid-free plants. Furthermore, there was no dosage response to water bowl traps baited with chemical plant attractant placed in the same field. Leaving rates were measured in a greenhouse experiment using dispersal cages containing 1, 4, or 16 plants and 0, 10, or 100 aphids. Leaving rate decreased in larger patches independently of aphid density, which also affected leaving rate.

We conclude that plant leaving may be equally or more important than plant finding in determining abundance of *D. rapae* in patches of crucifers. The significance of this result is discussed.

**Key words:** *Brevicoryne brassicae*; cabbage aphid; crucifers; *Diaeretiella rapae*; parasitoid; patch size; plant finding; plant foraging; plant leaving; plant-specialist; resource concentration.

### INTRODUCTION

The "resource concentration hypothesis" suggests that specialist insect herbivores should be more abundant where their food plants are concentrated because those insects are more likely to find, and less likely to leave, concentrated patches of host plants (Root 1973). Many insect parasitoids must also locate certain plants to find suitable hosts (Vinson 1981, van Alphen and Vet 1986). By analogy with the resource concentration hypothesis for herbivores, such plant-specialist parasitoids may be more likely to find, or less likely to leave, concentrated patches of their prey's food plants.

Concentration of host-plant resources involves at least five interdependent variables: patch size, or number of plants in a patch; plant density, or spacing, of plants within a patch; distance between patches; plant diversity, or presence of associated non-host plants; and plant quality (Kareiva 1983). We tested the effect of one of these variables, patch size, on the foraging behavior of *Diaeretiella rapae* M'Intosh (Hymenoptera: Aphidiidae), a parasitoid that usually attacks aphids on cruciferous plants (Mackauer and Stary 1967,

Nemeç and Stary 1984). To the extent that plants or habitat have been considered at all in work on parasitoid foraging, usually habitat or plant location has been emphasized (see reviews by Vinson 1976, 1981, van Alphen and Vet 1986), and properties of plant populations, such as patch size, have received almost no attention (Price et al. 1980). We investigated the effect of increasing patch size on the rates at which wasps found and left collard plants. Furthermore, since theoretical work on parasitoid foraging has focused almost exclusively on interactions between parasitoids and hosts (e.g., Hassell 1978, Murdoch et al. 1985), we also investigated how presence of aphids affects plant finding and how patch size compares with aphid density in affecting plant leaving rates. Finally, we performed experiments on one potential mechanism, response to the characteristic crucifer volatile, allylthiocyanate, that could lead to a positive patch-size effect on plant-finding rates.

### METHODS

In all experiments we used laboratory-reared cabbage aphids (*Brevicoryne brassicae*) and collards (*Brassica oleracea* cv Vates). We used cabbage aphids because they are the preferred hosts of *D. rapae* (Hafez 1961) and collards because the 2 mm long wasps are easy to see on the large flat leaves. Field experiments

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<sup>2</sup> Present address: Division of Biological Control, University of California at Berkeley, 1050 San Pablo Avenue, Albany, California 94706 USA.

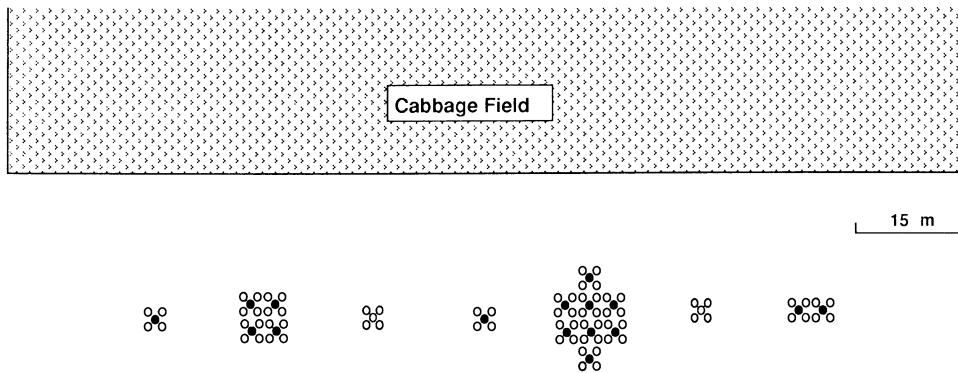


FIG. 1. Diagram of artificial patch layout used in "Plant Finding" and "Attraction to Plants vs. Aphids" experiments. Circles represent potted collard plants: ●, with aphids (trap plants); ○, without aphids (nontrap plants).

were conducted at the Vegetable Research Farm of the New York State Agricultural Experiment Station in Geneva, New York, USA. Insect specimens described in this study have been deposited in the Cornell University Insect Collection under lot number 1162.

#### *Plant finding*

To investigate the effect of patch size on parasitoid plant-finding we created artificial patches of 5, 10, 20, and 40 potted collards in a mowed grass field adjacent to a 1.2 ha unsprayed cabbage field. We placed the patches 15 m apart and 20 m from one edge of the cabbage field to intercept naturally occurring, dispersing wasps (Fig. 1). Confounding differences in plant diversity between patches were minimized by the homogeneity and short stature of the mowed grass background (cf. Bach 1986). To census patches quickly for wasps we used a mixture of trap (aphid-infested) and nontrap (uninfested) potted plants, and censused only trap plants. In preliminary observations on both trap and nontrap plants we established that arriving wasps tend to find infested plants quickly and then to stay on those plants for at least 2 h at low (<6 wasps/plant) densities. To equalize the probability of capture between patches, we used a ratio of one infested plant to four uninfested plants in all but two patches (discussed below). All plants were grown outdoors in 2-L (soil volume) pots and each had  $\approx 2000\text{-cm}^2$  leaf surface area (including both surfaces). Trap plants were then infested in greenhouse cages and thinned to  $\approx 1000$  apterous aphids each before use in experiments.

Wasps become remarkably quiescent on plants following oviposition, and with practice it was possible to capture virtually all wasps on aphid-infested plants. We aspirated all wasps from trap plants at 90-min intervals during daylight hours on 9, 22, 23, and 28 August 1985. Between aspiration days, we redistributed pots between patches and randomly reassigned patch locations. Wasp species and sex were verified in the laboratory. Mean number of wasps arriving per

day, both per plant and per patch, was modeled using least squares regression.

We included in the above experimental layout 5-pot patches without trap plants to compare attraction of wasps to patches with and without aphids (Fig. 1). All plants in 5-pot patches with and without aphids (2 of each) were examined during regular censuses.

#### *Plant leaving*

To test the effect of both patch size and aphid density on wasp leaving-rate from patches, we released wasps onto potted collard plants placed in organdy-covered dispersal cages in a greenhouse. Cages were  $1 \times 1$  m with 0.5 m high sides fitted with pyramid-shaped tops (Fig. 2). Dispersing wasps tended to fly upwards and get trapped in vials attached to inverted funnels. Akinlosotu (1973) used small cages of similar design to show that *D. rapae* dispersal from single plants depends on the density of searching conspecifics. We tested three patch sizes (1, 4, and 16 collards), and three aphid densities (0, 10, and 100), giving nine treatment combinations, with six to nine replicates of each. At first three, and later six, cages were used simultaneously, with treatments randomly and pots haphazardly assigned to cages. Similar-sized plants (range: 1170–2000  $\text{cm}^2$  leaf surface area) that had never had aphids were used on each day. Aphids were placed on a central plant, reflecting the clumped distributions commonly found at low population densities in nature (Trumble 1982). We then released eight <3-day-old female wasps onto the central plant in each cage between 0900 and 1100 on 14 mostly sunny days during June and July 1986 and we counted wasps collected in the vials after 3 and 6 h. Wasps were taken from a laboratory population started in May 1986 and infused twice with field-collected specimens. Stock cultures were maintained in  $1\text{-m}^3$  cages in a greenhouse.

During the experiments temperature (measured in a 4-plant cage) ranged from 20° to 34°C; relative humidity ranged from 45 to 85%; and maximum light ranged

from 85 to 170 lx. We measured temperature and humidity simultaneously in 1-, 4-, and 16-plant cages on 26 July, a warm, sunny day, using thermistor temperature probes and metallic, capacitive, relative humidity probes connected to a weather datalogger. Temperature varied little between cages (mean of three readings was 29.3°, 28.5°, and 28.1° in 1-, 4-, and 16-plant cages, respectively); relative humidity was higher in 16-plant cages (mean of three readings was 73.3, 72.7, and 82.7%, respectively).

Patch size (number of plants) and aphid density were modeled using ANOVA in the SAS statistical package. Results of a regression model substituting leaf area for number of plants yielded similar results, except where noted.

#### Attraction to mustard oil

*Diaeretiella rapae* is attracted to the synthetic mustard oil allylisothiocyanate, both in Y-tube olfactometers (Read et al. 1970, Chua 1975, Akinlosotu 1977) and in a wind tunnel (W. Sheehan, *personal observation*). A dosage-dependent response to mustard oil could result in the concentrating of wasps in large patches of crucifers. To test the null hypothesis that no such concentrating effect occurs, we used 24 water bowl traps to provide three different release rates of allylisothiocyanate (Aldrich Chemical Company) plus a control. We placed the bowls in a randomized block design within a 1-ha cabbage plot (three replicates), and also 5 m outside the plot, along its perimeter (three replicates). The insides of the 20 cm diameter bowls were painted dark green (Krylon "Hunter Green"; Borden Incorporated), the color most attractive to *D. rapae* (Vater 1971). Bowls were placed on wooden platforms 20 cm above soil level, filled with water plus a small amount of detergent, and left for 3 d. A 15 mL glass vial filled with 6 mL allylisothiocyanate (or yellow-colored water for the controls) was fixed in the center



FIG. 2. Dispersal cages used to measure plant-leaving rate. Cages contained 1, 4, or 16 plants and 0, 10, or 100 aphids; eight wasps were released in each cage. Wasps that left patches flew upward and were trapped in vials.

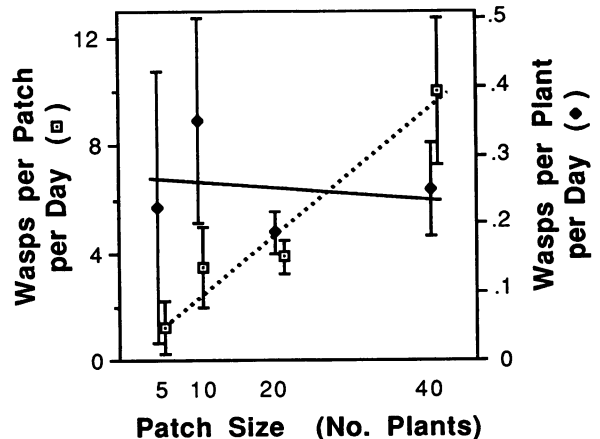


FIG. 3. Mean number of *D. rapae* females captured per patch per day (◆) and per plant per day (◻) plotted against patch size. Least squares regressions: for wasps per patch per day,  $Y = (0.237 \pm 0.056)\text{patch size} - 0.043$ ;  $r^2 = 0.50$ ;  $P < .0005$ ; for wasps per plant per day,  $Y = (-0.0003 \pm 0.006)\text{patch size} + 0.753$ ;  $r^2 = .0002$ ;  $P > .95$ . Each vertical line through a point represents  $\pm 1$  SE of the variation between plants within patches.

of each bowl. Release rate was varied by increasing the size of a hole drilled in the caps and by placing a cotton dental wick in the highest release treatment. Actual release rates were determined by weighing vials before and after the experiment. Mean rates ( $\pm$ SE) for the three treatments were  $61.9 \pm 6.6$ ,  $217 \pm 6.2$ , and  $2063 \pm 86.7$  mg/d. Least squares regression was used to analyze capture rate as function of allylisothiocyanate release rate.

## RESULTS

### Plant finding

Analysis of variance showed both experimental day and patch size to be significant, but no significant interaction between experimental day and patch size ( $F = 0.55$ ;  $df = 3, 19$ ;  $P > .65$ ). Consequently "day" was dropped as a factor in the subsequent regression analysis. More naturally occurring *D. rapae* did enter large rather than small patches ( $P < .0005$ ), but individual plants in large patches were not more likely to be found than were plants in small patches ( $P > .95$ ; Fig. 3). For example, 8.8 times as many wasps were captured per patch per day in the 40-pot patches (10.0) as in the 5-pot patches (1.13), but there were also 8 times as many plants in the 40-pot patches. Consequently, on a per-plant basis there was no patch-size effect.

An identical number of wasps (nine) was captured in patches with and without aphids (means = 1.125 wasps per patch per day; SE = 2.8 and 0.99, respectively).

### Plant leaving

Not surprisingly, wasps stayed longer in patches with more aphids ( $P = .0001$ , Table 1). This is represented

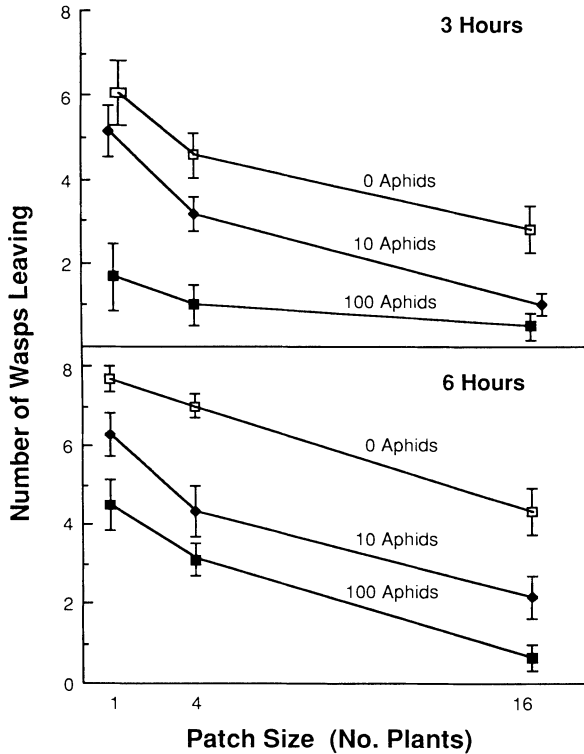


FIG. 4. Number of *D. rapae* collected in vials atop dispersal cages containing different numbers of plants (i.e., different patch sizes) and different densities of aphids. Top: number of wasps collected after 3 h. Bottom: cumulative number of wasps collected after 6 h. Each cage started with eight female wasps. There were 6–9 replicates for each treatment combination. Each vertical line through a point represents  $\pm 1$  SE.

graphically by the descending intercepts in Fig. 4. More interesting to the present study, wasps stayed significantly longer in larger patches at both 3 and 6 h (given by the patch-size terms in Table 1), and this effect was independent of aphid density at 6 h (given by the interaction term in Table 1). Wasps stayed longer in larger aphid-free patches after both 3 and 6 h (Fig. 4). At 3 h the effect of aphids on retaining wasps within patches may have depended on patch size, as shown by the low interaction probability between patch size and aphids ( $P = .1376$ , Table 1). When leaf area was modeled, rather than number of plants per patch, the interaction term was highly significant ( $F = 4.74$ ;  $df = 2,50$ ;  $P < .013$ ).

*Attraction to mustard oil*

Within the cabbage plot female wasps were not captured in water bowl traps in greater numbers at higher release rates (Fig. 5), except that the highest release rate (2 g/d) resulted in more captures than the mean of the others ( $P < .05$ ). Regressing the number of wasps captured per bowl per day against the logarithm of the release rate of allylisothiocyanate gives a slope that is not significantly different from zero. Outside the cab-

TABLE 1. ANOVA results for the influence of aphid density and patch size on *D. rapae* emigration rates in dispersal cages, after 3 and 6 h.

Source of variation		MS	df	F	P
3 h	Aphids	119.37	2	29.87	.0001
	Patch size	76.52	2	19.15	.0001
	Aphids $\times$ patch size	14.63	4	1.83	.1376
	Error	99.90	50		
6 h	Aphids	125.51	2	37.36	.0001
	Patch size	133.85	2	39.84	.0001
	Aphids $\times$ patch size	2.73	4	0.41	.8033
	Error	83.98	50		

bage plot, in similar locations where we had caught wasps at trap plants, we caught only one female wasp in a control bowl. (We caught twice as many males as females [211 vs. 105] within the cabbage plot; outside the plot we trapped only three males in bowls.)

DISCUSSION

Random patch encounter could result in a positive correlation between the absolute number of colonists per patch and patch size (Strong 1979). However, a correlation between colonist density per unit plant and patch size suggests a response to patch size per se ("patch size effect" of Bach 1986). Although sample sizes are small, our data suggest that increasing patch size did not increase finding rates per plant by *D. rapae* (Fig. 3). However, the decrease in leaving rates per plant with increasing patch size (Fig. 4) indicates that leaving rates (or tenure times) may be equally or more important than finding rates in determining the abundance of *D. rapae* in patches of crucifers. Mechanisms

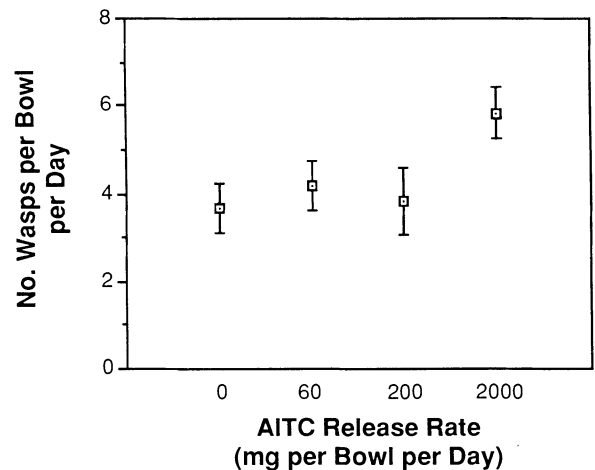


FIG. 5. Number of *D. rapae* females captured per bowl per day within a cabbage field as a function of allylisothiocyanate (AITC) release rate. There were six replicate bowls per release rate.  $Y = 3.34 + 0.242 \ln(\text{release rate})$ ,  $SE = 0.263$ ,  $r^2 = 0.04$ ,  $P < .37$ . Each vertical line through a point represents  $\pm 1$  SE of the variation within treatments.

underlying the retention effect of increasing patch size are unknown, but may involve more favorable microclimate or wasp-movement behavior (cf. Bach 1988).

The result is surprising, considering the emphasis that has been placed on plant and habitat location by parasitoid workers (e.g., Vinson 1981, van Alphen and Vet 1986). Analogous findings, however, have been reported by recent workers studying herbivore response to plant density and diversity (Bach 1980, Risch 1981, Stanton 1983) as well as to patch size (Kareiva 1985). Furthermore, the effect of patch size, independent of aphid density, on reducing wasp leaving-rate would not have been predicted from most existing parasitoid foraging models, in which patch time is solely a function of host and parasitoid parameters (e.g., Hassell 1978; but see Huffaker 1958, Kaiser 1983, Kareiva 1987). Our results with *D. rapae* suggest that more attention could profitably be paid to interactions between parasitoids and dispersion of the food plants of their hosts.

Ayal (1987) has elegantly shown that when a searching *D. rapae* encounters aphid honeydew she changes her behavior in ways that retain her in the patch and often lead her to the host source. However, plant finding apparently occurs prior to aphid finding since, in our study, wasps were not preferentially attracted to patches with aphids. This conclusion is consistent with other evidence. Wasp response to honeydew is due primarily, if not exclusively, to contact chemicals (Ayal 1987, W. Sheehan, *personal observation*), and wasps searching on leaves often walk within millimeters of an aphid without arresting (W. Sheehan, *personal observation*). Furthermore, Akinosotu (1977) presented *D. rapae* in an olfactometer with a choice between brussels sprout leaves and cabbage aphids that had been exposed to an air current for 45 min and found a significant preference for leaf odor. Read et al. (1970) found that *D. rapae* was attracted in an olfactometer to aphids removed from collard leaves for 15 min but not to aphids that had been removed 24 h earlier, suggesting that it is plant rather than aphid odor that is attractive.

Little is known about the ability of other parasitoid species to distinguish host-infested from uninfested plants or microhabitats. There is limited evidence for some species of attraction directly to hosts or to plant cues altered by host feeding (reviewed by Vinson 1981, see also Drost et al. 1986). However other parasitoid species locate particular plants or microhabitats independently of the presence of hosts. Vinson (1981) cited several anecdotal field examples. In the laboratory Vet (1983, 1985) used olfactometers to show that only three of eight parasitoid species attacking *Drosophila* could distinguish between odors of host-infested and uninfested substrates; those that did use host cues only acquired the ability through conditioning during oviposition. Selection must be strong, especially on specialist parasitoids, for the ability to distinguish

at a distance host-infested plants or microhabitats. Absence of this ability in parasitoids may reflect an evolutionary physiological constraint.

The absence of a dosage-dependent response to mustard oil in the field (Fig. 5) is consistent with the absence of evidence of synergism in attractancy by plants in large patches (Fig. 3). These findings are seemingly inconsistent with data showing a dosage-dependent response by *D. rapae* to mustard oils in Y-tube olfactometers (Read et al. 1970, Akinosotu 1977). A possible resolution of this discrepancy is that *D. rapae* may only respond to crucifers at very close range; that is, they may have chemoreceptors for mustard oils that are specific but not highly sensitive. This condition is predicted by Chapman (1982: 315), who notes that small insects tend to have relatively few antennal sensilla. A high level of sensitivity in small, feebly flying insects, he suggests, might actually be disadvantageous if it causes insects to attempt to fly to distant hosts which they are physically incapable of reaching. Specific receptors in small insects, then, may instead function in close-range detection and acceptance of important resources, and possibly in retention following acceptance. Electroantennogram recordings from *D. rapae* in response to a range of plants are consistent with this hypothesis (P. White and W. Sheehan, *personal observation*).

The higher number of captures in bowls with the highest release rate (Fig. 5) may not be relevant to normal foraging behavior since this rate is orders of magnitude greater than the rate of volatilization from plants (Finch 1978). On the other hand, our lowest release-rate treatments (within or exceeding the range of actual plant release rates) yielded no more captures than controls. This suggests that mustard oils released from plants are unlikely, by themselves, to provide attractive stimuli in the field. Probably other chemicals, and other sensory modalities besides olfaction, are involved in short-range orientation to crucifers by *D. rapae*, as appears to be the case with some crucifer herbivores (Renwick 1983).

A hypothesis analogous to the resource concentration hypothesis for herbivores is partially supported for a plant-specialist parasitoid: concentration of plant "resources" reduces plant-leaving rates by *D. rapae*. However, this finding gives rise to a paradox. In systems where plant-specialist natural enemies are effective mortality agents, we might expect specialist herbivores to be less, not more, abundant in areas where their host plant resources are concentrated. This hypothesis remains to be tested.

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