Foraging Behavior of Field Populations of *Diadegma* Spp. (Hymenoptera: Ichneumonidae):Testing for Density-Dependence at Two Spatial Scales[1]

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Abstract The foraging behavior of populations of *Diadegma* spp. (Hymenoptera: Ichneumonidae) attacking the diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), was studied in the field. The effect of host density on percentage parasitism was investigated at two spatial scales: that of the individual plant, as well as a "cluster of plants" at low, medium and high densities. Using binoculars, parasitoid searching was observed on host plants at different host densities over an 8-h period. Behavior was compared to that predicted under the Patch Selection Theory. Percentage parasitism was independent of host density at both spatial scales. However, the behavioral studies showed parasitoid aggregation behavior at higher host densities. The population displayed an imperfect preference for higher host densities in the first 4 h of foraging. In the second 4-h period, no preference was observed.

Key Words density dependence, spatial scale, Patch Selection, optimal foraging, *Diadegma, Plutella xylostella*

Patch selection theory is a variation of Optimal Foraging Theory that describes the behavior of a forager whose prey is concentrated in small areas with a significant travel time between them. In nature, prey items are typically distributed nonrandomly, such that food distribution occurs in aggregations or "patches" of varying food quality. The optimal forager seeks the most profitable patches first, and then includes less profitable ones when rich patches become scarce. Optimal predators should stay in patches until the rate of food intake drops to a level equal to the average of the habitat as a whole. The predator should leave a patch when it can consume more prey per unit of time by traveling to another one. Thus, the "marginal" capture rate should be equalized across all patches in the environment, i.e., Charnov's (1976) "marginal value theorem." When applied to insect parasitoids, the individual female is expected

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to maximize the number of eggs laid instead of energy obtained by feeding (Cook and Hubbard 1977, Hubbard and Cook 1978). A general prediction of the marginal value theorem is that patch residence time should increase with increased travel time between patches–a prediction supported by experimental evidence in *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae) foraging for the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Wang and Keller 2003).

Optimal Patch Selection predicts that parasitoids will spend more searching time in patches of high host density. In spite of overwhelming evidence of such aggregation behavior in both the laboratory and field (Hassell 1978), parasitism is not always density-dependent (Lessells 1985, Force and Moriarty 1988, Hassell 2000). Stiling (1987) provided 171 case studies of which 43 (25.2%) were density-dependent, 39 (22.8%) were inversely density-dependent and 89 (52%) were density-independent. In a field study of *Diadegma* spp. foraging for the diamondback moth, Waage (1983) found clear aggregation at high host densities, but parasitism was density-independent. Furthermore, *Diadegma* did not appear to visit the most profitable patches first, as predicted in optimal foraging models.

When studying Patch Selection Theory, the experimenter must address the spatial scale at which to define a patch. Because the physical definition of a patch is largely arbitrary, some researchers have attempted to investigate density-dependent patch effects at more than one spatial scale. At the level of individual trees, *Mastrus ridibundus* (Gravenhorst) (Hymenoptera: Ichneumonidae), produced no consistent pattern of percentage parasitism against the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) (Bezemer and Mills 2001). When data were pooled across orchards, percentage parasitism was inversely density-dependent. Density-dependent parasitism by the specialist parasitoid *Psyllaephagus pachypsyllae* Howard (Hymenoptera: Encyrtidae) on nipplegall makers, *Pachypsylla celtidismamma* (Fletcher) (Homoptera: Psyllidae), was studied using three spatially nested scales: leaves, branches, and trees of hackberry, *Celtis occidentalis* L. (Lill 1998). At the level of the individual leaf, parasitoids appeared to be attracted to higher host densities, but did not produce density-dependent parasitism. At the branch level, parasitism was density-independent, indicating that parasitoids also did not respond to host density at that spatial scale. However, at the tree level, a significant positive relationship was found between parasitism and host density. In field pine, parasitism of *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae) eggs by *Trichogramma* spp. was density independent at the level of the whole tree, but was strongly inversely density dependent in the top whorl in the spring-generation (McCravy and Berisford 1998). Density dependent parasitism of the bagworm, *Thyridopteryx ephemeraeformis* Haworth (Lepidoptera: Psychidae) by *Itoplectis conquisitor* (Say) was studied at two spatial scales: individual trees and small patches of trees (Cronin 1989). At the individual tree level, percentage parasitism was inversely density-dependent. In large area (12-90 ha) habitats of red clover (*Trifolium pretense* L.), parasitism of stem-boring weevils (Coleoptera: Curculionidae) (*Catapion seniculus* Kirby and *Ischnopterapion virens* [Herbst]) averaged 80%, declining to about 40% on small habitats (0.03-0.2 ha) (Tscharntke and Kruess 1999). Thus, different patterns of parasitism can emerge from the same host–parasitoid system at different spatial scales.

In this paper, we test if field populations of *Diadegma* spp. exhibit foraging behavior consistent with predictions of patch selection theory, and if these behaviors result in density-dependent percentage parasitism at either of two spatial scales: individual host plants or clusters of plants placed within a field crop.

Materials and Methods

Patch effects at different spatial scales. The experiments were conducted in the Brussels sprouts crop (*Brassica oleracea* L. var. "Winter Harvest") planted in the study field at the Imperial College at Silwood Park, Ascot, Berkshire, England (1981 and 1982 field seasons). Potted Brussels sprouts plants (≈30-40 cm height) were infested with second- or third-instar *P. xylostella* larvae in numbers ranging varying from 4, 8, or 16 per plant. Larvae were allowed 24-h feeding prior to field exposure so that they could secure themselves to the test plants. Patch effects on percentage parasitism were tested at two spatial scales: (1) individual plant; (2) "cluster" of plants (within ≈3 x 3 m area). Plants with 4, 8, or 16 larvae per plant were designated "low", "medium" and "high" patch densities at the plant level. Corresponding densities at the "cluster" level were obtained by increasing the numbers of plants at each cluster: (1) "low": 3 plants (1 each of 4, 8 and 16 larvae per plant); (2) "medium": 6 plants (2 each of 4, 8 and 16 larvae per plant); (3) "high": 9 plants (3 each of 4, 8 and 16 larvae per plant). Individual plants were placed about 1.0 m apart; plant clusters about 30 m apart. Holes were dug within the host crop to accommodate the potted plants, so that the soil level within the pot was flush with the level of the soil in the field. Cylindrical cardboard catches with plastic borders were placed around each plant to minimize larval loss.

To assess parasitism rates at different periods of exposure to the parasitoid population the experiment was repeated 6 times: (1) 3-h exposure period (performed on 22 July 1982); (2) 5-h (25 July 1982); (3) 5-h (5 August 1982); (4) 8-h (28 August 1981); (5) 8-h (28 June 1982); and (6) 72-h (21-23 August 1981). After exposure to the endemic *Diadegma* population, larvae were collected in plastic containers and returned to the laboratory. Parasitoid eggs were given 2 days to develop prior to dissection.

Observations on foraging behavior in the field. Direct observations on foraging behavior in field populations of *Diadegma* may be made using binoculars to observe wasps foraging on plants with known densities of host larvae (Waage 1983). Potted Brussels sprouts plants were infested with second- and third-instar larvae of *P. xylostella* using the methods described above at densities of 0, 4, 8, 12 or 16 larvae per plant (4 replicates each). The plants were placed in a bare field, inside holes with larval catches in a 5 x 4 grid at interplant distances of 2 m. Host densities were marked on the pots that were placed in the field randomly in an unspecified order to minimize experimental bias.

At 15-min intervals from 1000-1800h, plants were observed using binoculars (Zeiss 10 x 50w). Parasitoid sightings on the plants were recorded at each period: a sighting was defined as either the observation of a parasitoid searching on the host plant or hovering in its immediate vicinity. Three trials were performed on 21 June 1983, 6 July 1983, and 19 July 1983.

Statistical analysis. In the study on patch effects at different spatial scales, percentage parasitism was analyzed by pairwise *t*-tests for low, medium and high density patches at both spatial levels. The *t*-statistic was computed using a modified *t*-test based on the binomial distribution for proportions:

$$t = \frac{|p_1 - p_2|}{\sqrt{\frac{p_1 q_1}{n_1} + \frac{p_2 q_2}{n_2}}}$$

where p_1 and p_2 are proportions parasitized for samples 1 and 2; q_1 and q_2 are ($1 - p_1$ and $1 - p_2$, respectively); and n_1 and n_2 are sample sizes of samples 1 and 2, respectively. The statistic was compared against tabulated t-values with $n_1 + n_2 - 2$ degrees of freedom (Gravetter and Wallnau 2003).

In observations on foraging behavior in the field, percentage parasitism during each trial was analyzed for effects of host density by one-way ANOVA (arc sine transformation). Numbers of observations as affected by host plant density were analyzed by Chi-square. Effects of host density on numbers of observations blocked by 2-h time period were analyzed by linear regression.

Results and Discussion

Patch effects at different spatial scales. The *Plutella–Diadegma* system was chosen because it enabled us to manipulate host densities in the field easily. The experimental site hosted populations of *Diadegma* species comprised almost entirely of *D. eucerophaga* (Waage 1983), but the numbers of *P. xylostella* were low (Legaspi 1984, 1986). Furthermore, the use of binoculars permitted observations from a distance, without disturbing parasitoid behavior (Waage 1983). Independent sampling revealed that the sex ratio of *D. eucerophaga* in the field was approximately 1:1 (177♂♂: 194 ♀♀) (Legaspi 1984). We found no clear and consistent patch effects to be evident at the level of either the individual plant or cluster of plants (Fig. 1). We suggest that percentage parasitism is independent of host density at either spatial scale. Furthermore, when overall percentage parasitism in each trial is plotted by exposure time, percentage parasitism increases to an asymptote of ≈70% suggesting that a proportion of hosts will always escape parasitism. Percentage loss also increases to ≈60% after 72 h (Fig. 2). Percentage of superparasitism also increases with increased field exposure time, rising to an asymptote of about 15% after 72 h. However, no consistent density-dependent trends in percentage superparasitism were found at either spatial scale (Table 1). Shown are proportions of hosts superparasitized for Trials D to F. Superparasitism in Trials A to C were too low to analyze (overall percentage superparasitism levels were 1.33, 2.63 and 0.42%, respectively).

Observations on foraging behavior in the field. Effects of host plant density on percentage parasitism and numbers of wasp observations are summarized in Fig. 3. As in the analysis at different spatial scales, percentage parasitism was independent of host density (Figs. 3A, 3C, and 3E). Despite density-independent parasitism, behavioral observations indicated higher numbers of wasp sightings at higher host densities, consistent with the findings of Waage (1983). To determine whether searching behavior of the *Diadegma* population changed as a result of parasitism, the observations were pooled across all three trials and analyzed by time period (Fig. 4). Therefore, time period 1 represents the first 2 h of exposure to the *Diadegma* population, through to time period 4 which is the last 2 h. During the first 4 h of the trials, parasitoid sightings were higher at the higher host densities, indicating aggregation behavior (Regression statistics for Time period 1: $F = 45.13$; df = 1, 4; $P < 0.01$; Time period 2: $F = 169.9$; df = 1, 4; $P < 0.01$). In the later time periods, the effects of host density on parasitoid sightings were not significant (Time period 3: $F = 4.36$; df = 1, 4; $P = 0.128$; Time period 3: $F = 2.49$; df = 1, 4; $P < 0.212$). These observations are consistent with broad predictions of optimal foraging that high quality patches are exploited first. However, the effect is not perfect in that not all parasitoids search the currently most profitable patches. When patch quality equalizes throughout the en-

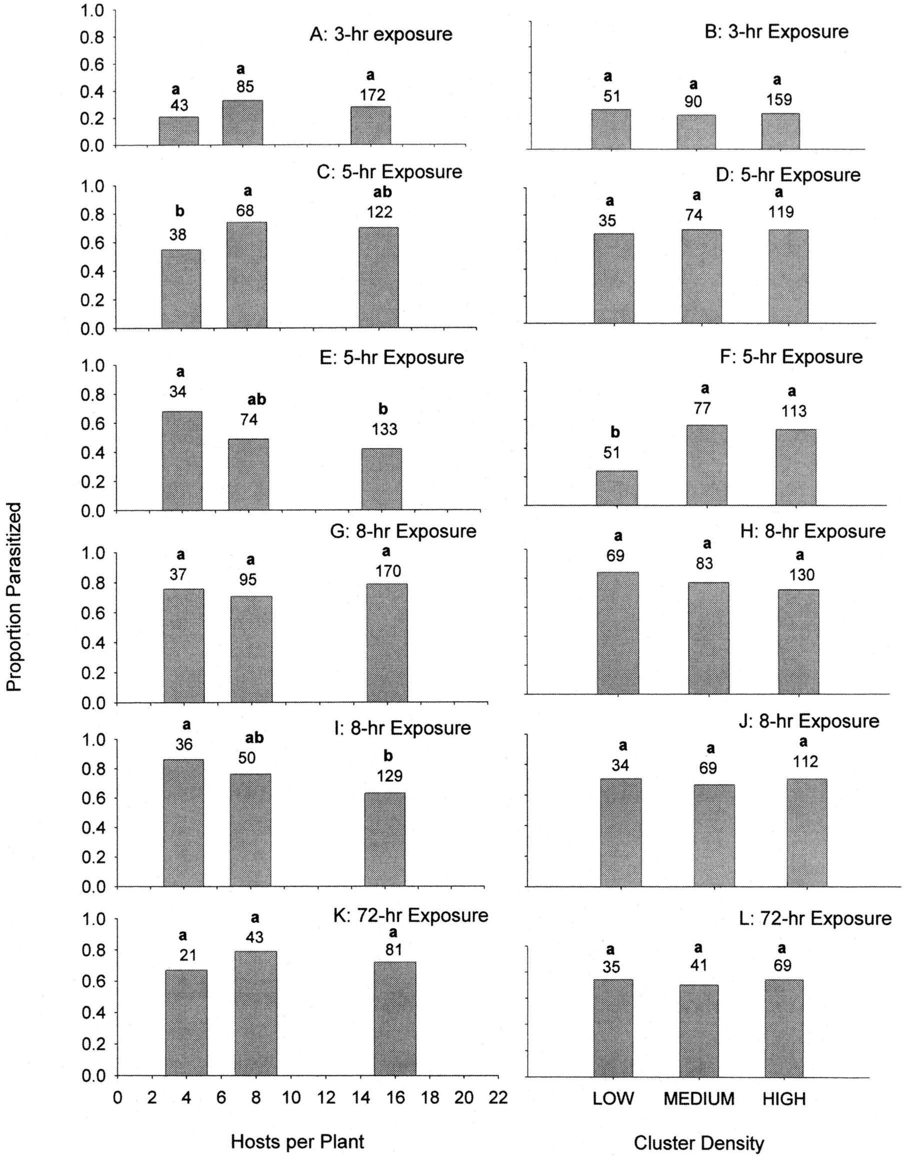

Fig. 1. Proportions of *Plutella xylostella* larvae parasitized by field populations of *Diadegma* spp. The left column indicates testing at the level of the host plant; column on the right indicates the cluster level. Numbers above the bars indicate number of host insects examined. Identical letters above the bars indicate means are not significantly different ($P = 0.05$) using the modified *t*-test described in the text.

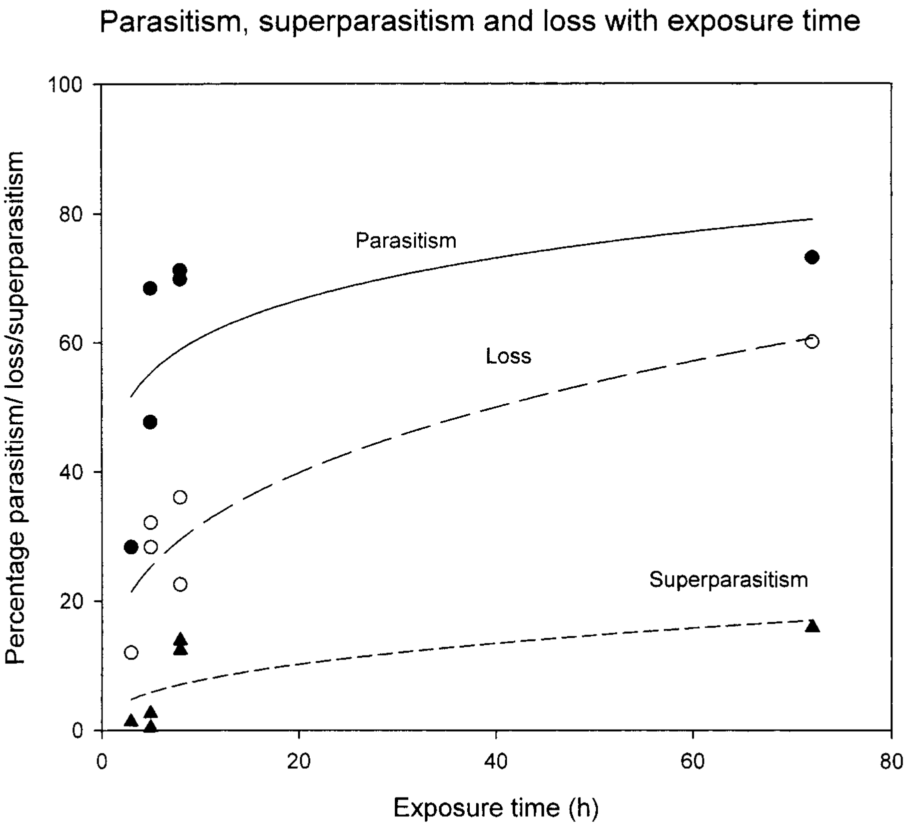

Fig. 2. Percentages of parasitism, superparasitism and larval loss with exposure time to field populations of *Diadegma* spp.

vironment as a consequence of patch exploitation, parasitoids spend equal amounts of time in all patches

In choosing a spatial scale to test for patch effects, a natural choice is that of the individual plant or tree, which was used in the present study and in others (e.g., Bezemer and Mills 2001, Lill 1998, McCravy and Berisford 1998, Cronin 1989). Larger or smaller scales will be determined by such biological factors as parasitoid mobility (Corbett and Plant 1993) and host distribution, as well as practical concerns such as the availability of resources, manpower and equipment to perform the experiments. Determining spatial scales and attempting to define the hierarchy of patchiness in physical terms is largely arbitrary, and any patch effects are influenced by the experimental design.

We found inconsistent density effects on percentage parasitism at both spatial scales, despite apparent aggregation behavior at higher host densities. Waage (1983) suggested two possible explanations: (1) increased superparasitism at high host densities; and (2) an increased proportion of time spent in nonsearching activi-

Table 1. Superparasitism in field populations of *Diadegma* spp. attacking *Plutella xylostella* at two spatial scales

Trial	Patch	Density	Superparasitism*
Trial D (8 h)	Plant	4	5/37 = 0.135 a
		8	12/75 = 0.16 a
		16	18/170 = 0.106 a
	Cluster	Low	12/69 = 0.174 a
		Medium	8/83 = 0.096 a
		High	15/130 = 0.115 a
Trial E (8 h)	Plant	4	5/36 = 0.139 ab
		8	3/50 = 0.06 b
		16	22/129 = 0.17 a
	Cluster	Low	6/34 = 0.176 a
		Medium	11/69 = 0.159 a
		High	13/112 = 0.116 a
Trial F (72 h)	Plant	4	5/21 = 0.238 a
		8	7/43 = 0.163 a
		16	11/81 = 0.136 a
	Cluster	Low	3/35 = 0.086 a
		Medium	5/41 = 0.122 ab
		High	15/69 = 0.217 b

* Within each trial and spatial scale, proportions designated by identical letters are not significant at $P = 0.05$ using modified t-test described in text

ties. Field populations of *Diadegma* have shown avoidance of superparasitism (Legaspi 1986). However, we found no evidence of density-dependent percentage superparasitism at either spatial scale studied. Although superparasitism may not be a direct cause of density-independent parasitism, time spent examining and rejecting previously-parasitized hosts may have been one of the nonsearching activities Waage (1983) postulated. Another such activity may have been the handling time spent in waiting for hosts hanging on silken threads to avoid parasitism (Wang and Keller 2002). A limit on percentage parasitism may be attributed to the inability of *Diadegma* to find a significant proportion of the hosts. Even after 72-h exposure, about 30% of the hosts were unparasitized (Fig. 2). Finally, experimental error may be introduced by larval loss in the field. A combination of these factors may have resulted in the inconsistent parasitism patterns and generally density-independent parasitism. The result is not surprising in light of the findings of Hassell (1982) that aggregation behavior can actually result in inverse density-dependent parasitism as observed in *Trichogramma pretiosum* Riley parasitizing the stored product moth, *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae)

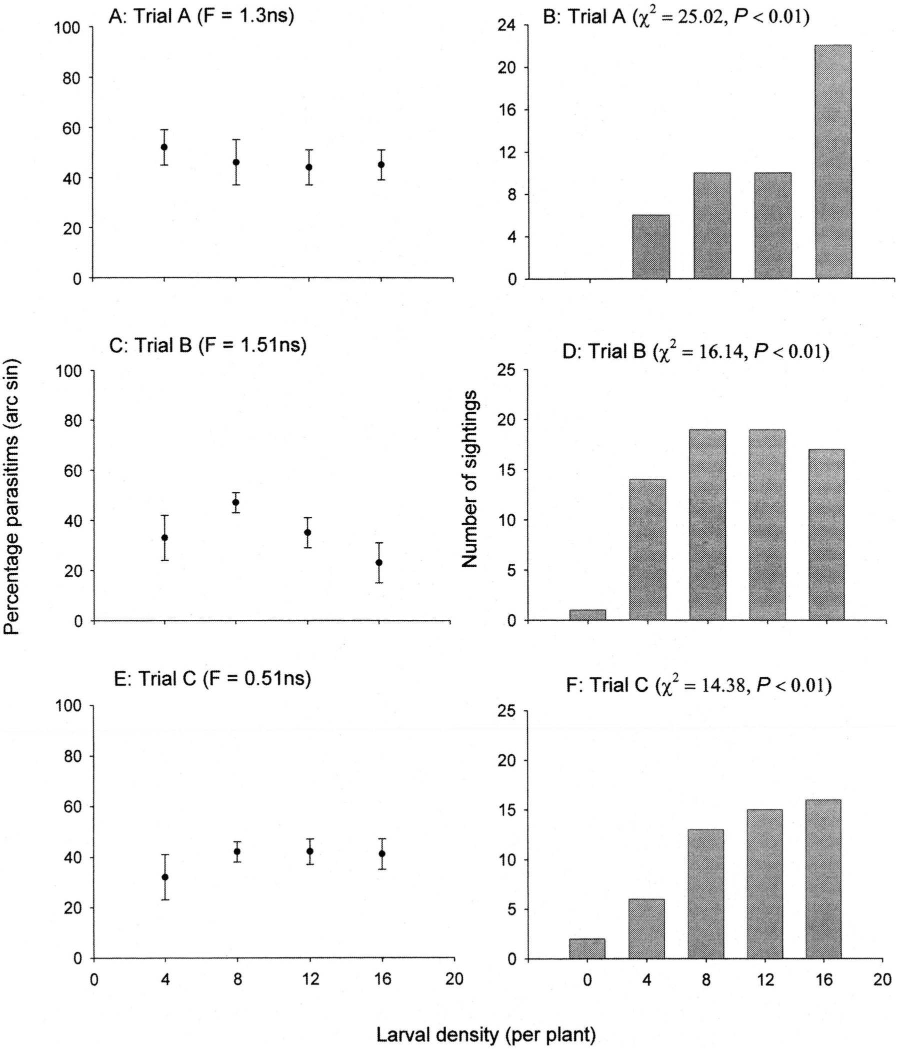

Fig. 3. Effects of *Plutella xylostella* host density per plant on percentage parasitism and number of parasitoid sightings.

Experimental evidence supports predictions of optimal foraging and patch selection in insect parasitoids. Using *Nemeritis canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae), Waage (1979) proposed a mechanistic model wherein a parasitoid entering a patch was motivated by previous experience and kairomones. Failure to locate hosts results in a decline in motivation and subsequent departure from the patch. However, each oviposition event results in an increase in motivation to search. The initial motivation, followed by rates of subsequent ovipositions determines residence time in the patch. This model was modified to include detrimental effects of encounters with parasitized hosts (van Alphen and Jervis 1996).

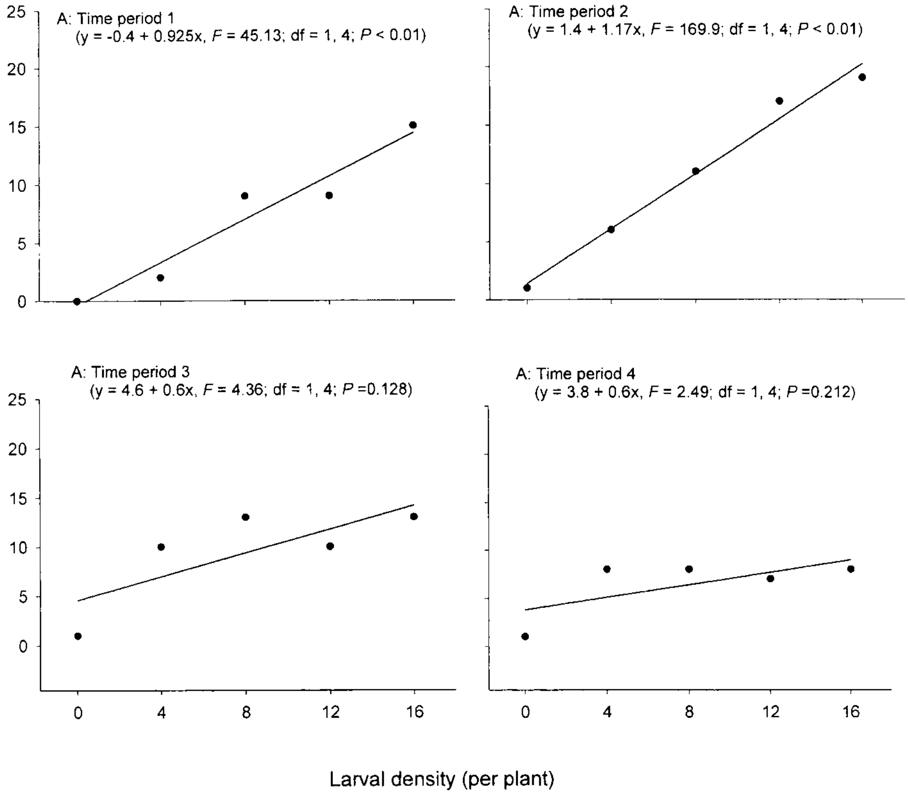

Fig. 4. Regressions of parasitoid sightings as a function of host density per plant by time period. Each figure (A to D) represents a 2-h block of time from the start of the experiment at 1000h to 1600h.

Unlike the case of a truly omniscient forager, biological mechanisms can be proposed to account for *Diadegma* spp. behavior observed in this study. The adult female parasitoid initially seeks host patches with high levels of profitability. Host location is undoubtedly mediated by the host plant kairomones. Oilseed rape (*Brassica napus* L.) plants that were damaged mechanically or through feeding by *P. xylostella* larvae attracted the parasitoid *Cotesia plutellae* (Kurdjumov) (Hymenoptera: Braconidae) (Potting et al. 1999). Intact cabbage leaves or host larvae alone elicited no response in *Cotesia rubecula* (Marshall) (Hymenoptera: Braconidae) seeking *Pieris rapae* L. (Lepidoptera: Pieridae) (Agelopoulos and Keller 1994a). Numerous studies have shown that parasitoids can differentiate among different kairomones. *Cotesia rubecula* was most attracted to cabbage leaves damaged by insect feeding over those damaged by snails or mechanical means (Agelopoulos and Keller 1994b). Geervliet et al. (1998) found that naïve females of *Cotesia glomerata* L. and *C. rubecula* could distinguish between odors of plants with high versus low host densities. In only 3 of 168 (1.8%) parasitoid observations occurred on plants that had no host insects, suggesting that the *Diadegma* population selected host plants based on cues indicating presence of the host. this study, only 3 parasitoid observations were made in undamaged host plants, suggesting the role of kairomones in host plant selection. Higher numbers of observations at the higher host densities may have been a response to higher kairomone levels.

Patch residence time is probably determined by encounter rates with parasitized and unparasitized hosts (Wajnberg et al. 2000), kairomone levels (Shaltiel and Ayal 1998), “expectation levels” due to conditioning (Keasar et al. 2001), and handling time spent waiting for hosts that are suspended from silken threads. As higher quality patches are exploited, patch profitability throughout the environment tends to equalize and parasitoids tend to spend equal amounts of time searching the relatively homogenous environment.

The possibility that different density relationships may exist at different spatial scales complicates the process of evaluating the efficacy of biological control agents. Researchers may need to measure predation or parasitism rates at several spatial scales as in the case of estimating natural control. For example, *Chilocorus kuwanae* (Silvestri) (Coleoptera: Coccinellidae) was evaluated at three spatial levels as a biological control agent against the scale *Unaspis euonymi* (Comstock) (Homoptera: Diaspididae) in New England from 1991-1995 (van Driesche et al. 1998). At the field site level, *C. kuwanae* suppressed the scale in 9 of 14 release sites. In a 32-ha apartment site, *C. kuwanae* spread to 64% of host plants within 4 months. At the statewide level, no significant spread of the predator was found in Massachusetts by 1994. The experimental design of methods to measure pest suppression at several levels is often strongly influenced by natural enemy mobility. Corbett and Plant (1993) caution that this influence complicates the interpretation of small-scale experiments and extrapolation to larger scales. After all, natural enemies and their targets do not operate in isolation from the larger environment. The degree of success of a biological control agent may be affected by complex relationships between size of crop area, and proximity to other crop and noncrop habitats (Tscharntke and Brandl 2004). In the case of the *Diadegma–Plutella–Brassica* system, parasitoids may not need to be released in close proximity to the host insects because *Diadegma* spp. are able to locate hosts within a cropping area, and density-dependent effects may not be evident even at large spatial scales than those we examined. However, the fact that maximal parasitism levels did not exceed ≈70% suggests the *Diadegma* spp. alone may be an ineffective control agent against *P. xylostella*.

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