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Response by coccinellids to spatial variation in cereal aphid density

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Abstract The objectives of this study were to determine if coccinellids adjusted their distribution within spring wheat fields in response to spatial variation cereal aphid density in the fields and to describe the patterns of cereal aphid population growth that resulted. Field experiments were completed in which the physical dimensions of patches infested with cereal aphids, cereal aphid density, and access to patches by coccinellids were varied. Aphid infestations consisted of naturally occurring densities (natural patches) and much greater densities created by supplementing patches with aphids (supplemented patches). Coccinellids were denied access to some supplemented patches (exclusion patches) but allowed unlimited access to others. Densities of adult *Hippodamia convergens* and *Coccinella septempunctata* were correlated with aphid density in patches whereas density of *Coleomegilla maculata* was not. Aggregation by coccinellids was independent of patch area. The realized aphid population growth rate (r) was lower in supplemented than natural patches in all four trials but was significantly lower in only one trial. The lower r in supplemented patches was not exclusively caused by coccinellid predation, and emigration of aphids from patches probably also contributed. r was significantly greater in exclusion patches than supplemented and natural patches, indicating that coccinellids markedly reduced aphid numbers in patches even when aphid density was extremely high.

Key words Aphididae · Biological control · Coccinellidae · Predation · Density dependence · Functional response

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Introduction

Natural enemies that aggregate in local patches with high prey density and increase their attack rate on prey in such patches can suppress prey populations more than enemies that do not (Murdoch and Briggs 1996). The increased population suppression achieved by such spatially density-dependent predation does not stabilize prey or predator populations if predators frequently adjust their spatial distribution to optimize their attack rate (Murdoch and Stewart-Oaten 1989; Rohani et al. 1994). However, the important characteristic for managing pests in ephemeral agroecosystems is not population stability but the ability of natural enemies to suppress the pest population before it reaches economically damaging levels. This effect is more likely to occur if natural enemies concentrate their attacks in patches with high prey density than if they do not (Murdoch and Briggs 1996).

Aphidophagous Coccinellidae are important predators of aphids in agricultural crops (Hodek and Honek 1996). Aggregation by coccinellids in patches of aphids in fields has frequently been observed (e.g., Wright and Laing 1980; Frazer et al. 1981; Turchin and Kareiva 1989; Ives et al. 1993), and can reduce aphid population growth in patches with high aphid density compared to patches with low aphid density. For example, Frazer et al. (1981) found that coccinellids aggregated in patches in alfalfa fields with high aphid density, and when aphid density in the field as a whole was relatively low, the coccinellids were capable of reducing aphid density in patches in a positive density-dependent manner. However, others have observed aggregation by coccinellids but no evidence of positive spatially density-dependent predation (Cappuccino 1988; Turchin and Kareiva 1989). There can be differences among coccinellid species in their tendency to aggregate, which could explain discrepancies among studies. Furthermore, habitat features such as relative humidity, plant density, and abundance of alternate foods and other resources can influence the spatial distribution of coccinellids, and may sometimes be more influential than the presence of aphids (Ewert and Chiang

1966; Honek 1982, 1983, 1985a; Coderre et al. 1987; Cottrel and Yeargan 1998a,b).

Cereal aphids are pests of spring wheat in eastern South Dakota, United States, and typically exhibit a patchy distribution in fields (Elliott and Kieckhefer 1987). Coccinellids are often numerically dominant aphid predators in spring wheat fields (Elliott and Kieckhefer 1990). Little is known of the nature of the predator–prey interaction between coccinellids and aphids in spring wheat in South Dakota, and this study was undertaken to address three questions concerning that interaction. First, do coccinellids alter their spatial distribution in response to spatial variation in cereal aphid density, and if so, do all species respond similarly? Second, does aggregation by coccinellids depend on the physical size of aphid-infested patches? In other words, are coccinellids capable of finding and aggregating in aphid patches regardless of their physical dimensions, or do patches below a particular size escape detection by coccinellids? Finally, how do cereal aphid numbers change over time in relation to spatial variation in numbers of coccinellids and aphids?

Materials and methods

Study sites

Experiments were accomplished during 1988 and 1989 in 1.5-ha spring wheat fields (cv. "Guard") near Brookings, South Dakota. Two trials of the experiment were undertaken each year, the first in June, in a field planted in early April, and the second in July, in a field planted in mid-May.

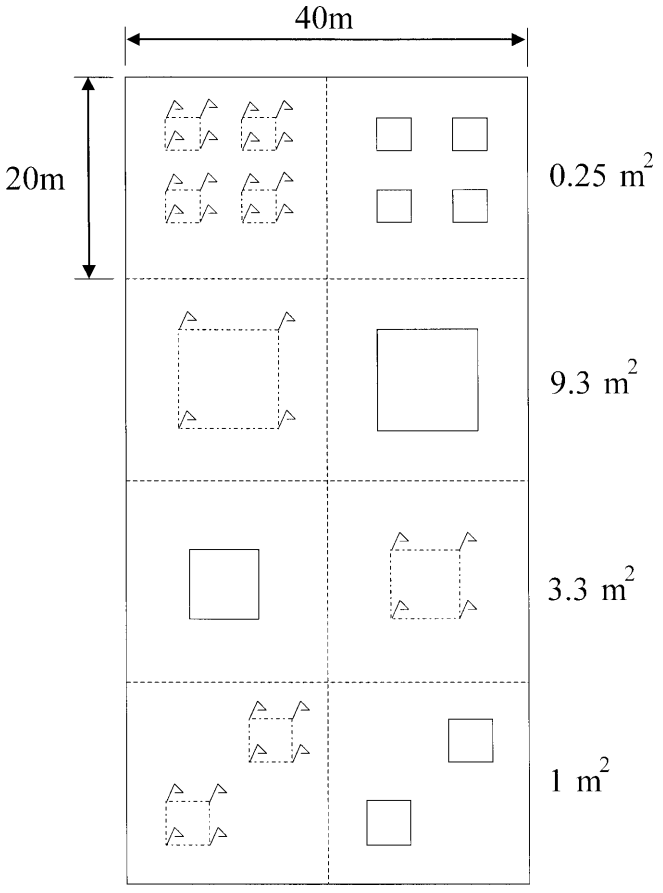

Fig. 1. Hypothetical replicate of the split-plot design used in 1988 trials. *Squares with solid lines*, locations of supplemented patches; *squares with dashed lines*, natural patches (not drawn to scale)

1988 field experiments

A split-plot experimental design was used in 1988 for each trial of the experiment. A replicate consisted of four levels of the physical area of aphid infested patches and two cereal aphid infestation levels. Therefore, one replicate required eight experimental units (Fig. 1). The entire experiment was replicated four times. To establish the experiment, four rows of eight plots, each 20 × 40 m, were established in the field. Distance between rows of plots was about 5 m. Each of four patch sizes (0.25, 1, 3.3, and 9.3 m^2) was assigned randomly to a 20 × 40 m plot in each row. Each 20 × 40 m plot was divided into two 20 × 20 m subplots, each of which was randomly assigned one of two aphid infestation levels. Aphid infestation levels consisted of naturally occurring densities (natural patches) and elevated densities created by infesting field cages with laboratory-reared cereal aphids (supplemented patches). Field cages were square with wooden (0.25- and 1-m^2 cages) or aluminum (3.3- and 9.3-m^2 cages) frames covered by screen material (~6 strands/cm mesh size). The 0.25- and 1-m^2 cages were 0.75 m in height and the 3.3- and 9.3-m^2 cages were 1.8 m in height.

In each of the four subplots assigned 0.25-m^2 patches, four 0.5 × 0.5 m cages were placed approximately equidistant from one another and from the edge of the subplot. Two 1 × 1 m cages were placed in a similar manner in each subplot assigned 1-m^2 patches. A single 1.8 × 1.8 m or 3.05 × 3.05 m cage was placed in the center of each subplot assigned 3.3- or 9.3-m^2 patches. In subplots assigned natural aphid infestation levels, the same number of square areas of the appropriate size were established in an identical arrangement by placing marking flags at each of the four corners of a square (Fig. 1).

Cages were maintained in the field for about 3 weeks, during which time they were infested with a mixture of four cereal aphid species: *Rhopalosiphum padi* (L.), *R. maidis* (Fitch), *Schizaphis graminum* (Rondani), and *Sitobion avenae* (F.). The aphids were reared in a greenhouse on spring wheat growing in standard greenhouse flats. Primarily *R. padi* and *S. graminum* were used to infest cages, but small numbers of *S. avenae* and *R. maidis* were also used. Aphids were added to a cage by cutting the wheat in the greenhouse flats and distributing it between the rows of wheat in the cage. The aphid-infested wheat was divided so that each cage received an amount proportional to its area. However, no attempt was made to estimate the absolute number of aphids added to each cage. Aphids were added to cages every 5–7 days, whenever enough became available in the laboratory colonies to infest the cages.

Field cages were maintained essentially free of coccinellids by covering their edges with soil and conducting periodic searches in which all coccinellids found were removed. After about 3 weeks, cages were removed, the four corners where the cage had been were marked with flags, and the experiment was begun. In trial 1, the density of coccinellids was measured in all plots (caged and uncaged) at 0, 24, and 48 h after cage removal, and at the end of the trial, 3 days later. In trial 2, coccinellid density was measured at 0, 4, 24, and 48 h after cage removal, and every 1–3 days until the end of the trial. Coccinellid density was measured by counting the number of each species in 0.5 × 0.5 m quadrats. In 9.3- and 3.3-m^2 patches, the quadrat was placed at four arbitrarily selected nonoverlapping locations within the square circumscribed by the flags. In 1-m^2 patches, the quadrat was placed at two nonoverlapping locations. The quadrat was centered over each 0.25-m^2 patch for counting coccinellids. Using this approach, the same area (1 m^2) was sampled for coccinellids in each size patch.

Cereal aphid density was measured in each trial at less frequent intervals than coccinellid density. Cereal aphids were sampled by counting the number of aphids on 80 arbitrarily selected tillers taken from within each 9.3- and 3.3-m^2 patch, 40 tillers in each 1-m^2 patch, and on 20 tillers in each 0.25-m^2 patch. This sampling approach provided uniform sampling intensity across treatments. The number of tillers per 0.3 m of crop row was estimated for each patch at the end of the experiment by counting 4, 8, 16, and 16 0.3-m lengths of row in 0.25-, 1-, 3.3-, and 9.3-m^2 patches, respectively. Aphid density (number/m^2) at a particular time was estimated as the product of the mean number of aphids per tiller, the mean number of tillers per meter of row, and the number of meters of row/m^2. Wheat plant growth stage was recorded periodically during each trial using a widely accepted method (Zadoks et al. 1974).

Cereal aphid species composition during the study was typical of that in spring cereals in eastern South Dakota, with *Rhopalosiphum padi* and *Schizaphis graminum* predominating, and *Sitobion avenae* and *R. maidis* present in low numbers. These aphids respond to abiotic and biotic factors in a qualitatively similar manner (Elliott et al. 1988; Walgenbach et al. 1988; Elliott and Kieckhefer 1989; Kieckhefer et al. 1989). Thus, comparing densities of combined species was considered appropriate for estimating the influence of coccinellids on the growth rate of cereal aphid infestations, and this was the method used. In the first trial, cereal aphid density was measured immediately after cages were removed and at the end of the experiment 5 days later. In the second trial, cereal aphid density was measured on the day of cage removal, again 3 days later, and a third time at the end of the 7-day experiment.

1989 field experiments

Procedures in 1989 were modified somewhat from those in 1988. We found that aggregation by coccinellids was unrelated to patch size in 1988, so patch size was not included as an independent variable in the experimental design in 1989; rather, a single patch size (1 m^2) was used. Furthermore, we decided that it would be informative to monitor cereal aphid population growth in the absence of coccinellids, so we added a third treatment. The three treatments were arranged in a completely randomized experimental design with seven replicates of each treatment. To establish a trial, three rows of seven plots (~20 × 20 m) each were established in a spring wheat field. Each plot was randomly assigned one of three treatments: (1) naturally infested patches to which coccinellids had free access (natural patches); (2) patches supplemented with greenhouse-reared cereal aphids to which coccinellids had free access (supplemented patches); and (3) patches supplemented with greenhouse-reared cereal aphids to which coccinellids had no access (exclusion patches). Field cages were infested with laboratory-reared cereal aphids as in 1988. In the third treatment, cages were left in place for the duration of the experiment, and were maintained essentially free of coccinellids by periodically opening them and removing with an aspirator all coccinellids seen in a visual search of the foliage and ground in the cage. Coccinellids removed from cages were released outside the experimental field.

Coccinellid density was measured in all patches at 0, 4, 24, 48, 72, and 96 h after cage removal, and periodically for the duration of each trial. Coccinellid density in each patch was determined by complete enumeration of coccinellids in the entire 1-m^2 area of the patch rather than by sampling using 0.5 × 0.5 m quadrats as in 1988. Aphid density was measured periodically by counting aphids on 25 tillers in each 1-m^2 patch. The number of tillers per 0.3 m of crop row was estimated for each patch at the end of the experiment by counting six 0.3-m lengths of row in each patch. Wheat plant growth stage was determined periodically as in 1988.

During 1989, samples of 100 cereal aphid nymphs taken from arbitrary locations in natural and supplemented patches were inspected on one occasion during trial 1 (the last day of the trial) and two occasions during trial 2 (the first and last days of the trial). This sampling was done to determine if the proportion of winged aphids produced, that could disperse from patches and thereby cause a difference in the aphid population growth rate in different patch types, differed among supplemented and natural patches.

Statistical analysis

A heterogeneity of slopes regression model (Littell et al. 1991) was used to test for differences in coccinellid aggregation in different size aphid patches. This step involved calculating linear regression equations for coccinellid density versus aphid density for each size patch and testing whether unique regression parameters were needed for some or all patch sizes, or whether a single regression line adequately fit all data. Adequate fit by a single line would indicate that patch size was unimportant in determining the extent to which coccinellids aggregate in aphid patches of different size.

Pearson correlation coefficients were calculated to determine if the density of adult and larval coccinellids of each

species and coccinellid egg masses was related to cereal aphid density in patches. Correlation coefficients for each trial were calculated using aphid and coccinellid density averaged over all dates for each experimental unit. Estimates of coccinellid density made before cages had been off patches for at least 24 h were excluded from calculations. Because coccinellid and aphid densities varied over the course of a trial, this approach was probably less sensitive than if correlation coefficients had been calculated from observations of coccinellid and aphid density made at precisely the same time. However, the latter approach was not possible because aphids and coccinellids were not usually sampled on the same day. Data for all size patches in 1988 were used in calculating correlation coefficients because the heterogeneity of slopes analyses as described yielded no evidence for an affect of patch size on aggregation by coccinellids.

The realized rate of cereal aphid population growth for supplemented and naturally infested plots in each trial was estimated using the equation:

$$r = \{\ln(n_{t+\Delta t}) - \ln(n_t)\}/\Delta t$$

where n_t is aphid density on day t and $n_{t+\Delta t}$ is aphid density Δt days later. r summarizes the change in aphid density per day that results from all causes. r was calculated for each pair of adjacent estimates of aphid density made during a particular trial. Analysis of variance for a split-plot (trial 1, 1988) or split-split-plot design (trial 2, 1988) was used to determine if r differed among dates or treatments. Patch area was the main plot factor and patch type (natural or supplemented) was the subplot factor for trial 1, 1988; date was the main plot factor, patch area was the subplot factor, and patch type was the subsubplot factor for trial 2, 1988; and date was the main plot factor and patch type (natural, supplemented, or exclusion) was the subplot factor in both 1989 trials (Littell et al. 1991). Estimates of r for time intervals before or on the date of cage removal for a trial were deleted from the data before analysis of variance. The least significant difference test was used to test for differences in r among patch types and time intervals and for testing for differences in r among date × patch type means in cases where this interaction was significant.

All statistical analyses were accomplished using appropriate procedures from the Statistical Analysis System (SAS Institute 1988). Statistical hypotheses were tested with an $\alpha = 0.05$ probability of rejecting the null hypothesis.

Results

General patterns

Wheat plant growth stage varied over the course of each trial and among trials. Wheat was in boot stage at the beginning of trial 1, 1988, and was heading by the end of that trial, whereas plants progressed from the stem elongation stage to the boot stage during trial 2, 1988. In 1989 trials, wheat plants ranged from stem elongation to milky ripe stage, and from boot to soft dough stage in trials 1 and 2, respectively.

Mean cereal aphid density in supplemented patches varied from 1233 m^{-2} in trial 2, 1988 to 42 613 m^{-2} in trial 1, 1988 (Table 1). Aphid density was approximately 3 times greater in supplemented than natural patches in trial 1, 1988, but about 30 times greater in other trials.

Hippodamia convergens and *Coccinella septempunctata* (L.) were the most abundant coccinellids in wheat fields during the study, with *Coleomegilla maculata lengi* Timberlake, *H. tredecimpunctata tibialis* (Say), and *H. parenthesis* (Say) consistently present at lower densities (Table 1). Two other species, *Coccinella transversoguttata richardsoni* Brown and *Cycloneda munda* (Say), were present but were so infrequently encountered that their densities are not presented individually.

Adult coccinellid density varied among patch types in trials, from 5.8 m^{-2} in supplemented and 4.5 m^{-2} in natural patches in trial 1, 1988, to 12.2 m^{-2} in supplemented and 2.0 m^{-2} in natural patches in trial 2, 1989 (Table 1). Coccinellid larvae were present in three trials. Larvae were not identified to species in 1988, but were identified in 1989.

Table 1. Number of coccinellids and cereal aphids per square meter (±SE) averaged across sampling dates in naturally infested and supplemented patches in each of two trials in 1988 and 1989

Life stage/species	Trial 1, 1988		Trial 2, 1988		Trial 1, 1989		Trial 2, 1989	
	Natural	Supplemented	Natural	Supplemented	Natural	Supplemented	Natural	Supplemented
Coccinellid adults	4.5 (0.57)	5.8 (0.65)	2.9 (0.63)	7.9 (1.7)	1.5 (0.25)	11.4 (0.97)	2.0 (0.67)	12.2 (3.1)
Hippodamia convergens	2.1 (0.29)	3.2 (0.38)	1.7 (1.6)	4.8 (1.4)	1.0 (0.22)	7.3 (0.63)	1.5 (0.21)	7.5 (1.9)
Hippodamia tredecimpunctata	2.0 (0.38)	1.9 (0.35)	0.50 (0.17)	0.41 (0.11)	0.05 (0.03)	0.15 (0.08)	0.04 (0.03)	0.14 (0.11)
Coccinella septempunctata	0.05 (0.03)	0.19 (0.07)	0.16 (0.05)	0.88 (0.28)	0.15 (0.08)	3.5 (0.54)	0.43 (0.12)	4.2 (1.1)
Coleomegilla maculata	0.20 (0.05)	0.03 (0.13)	0.38 (0.10)	0.33 (0.08)	0.25 (0.06)	0.43 (0.15)	0.04 (0.04)	0.14 (0.07)
Hippodamia parenthesis	0.10 (0.04)	0.15 (0.06)	0.21 (0.03)	0.40 (0.09)	0.03 (0.03)	0.05 (0.03)	0.0	0.0
Coccinellid larvae	22.4 (6.2)	32.6 (7.6)	0.0	0.0	1.3 (0.29)	7.2 (1.6)	0.54 (0.17)	5.3 (1.2)
H. convergens	–	–	–	–	1.2 (0.27)	7.0 (1.6)	0.28 (0.09)	2.6 (0.42)
H. tredecimpunctata	–	–	–	–	0.0	0.07 (0.03)	0.06 (0.03)	0.30 (0.13)
C. septempunctata	–	–	–	–	0.0	0.01 (0.01)	0.10 (0.04)	2.3 (0.70)
C. maculata	–	–	–	–	0.12 (0.05)	0.10 (0.05)	0.10 (0.03)	0.15 (0.04)
Coccinellid egg masses	–	–	–	–	0.02 (0.01)	0.14 (0.04)	0.03 (0.02)	0.05 (0.03)
Cereal aphids	12 262 (1927)	42 613 (5253)	35.9 (6.7)	1233 (220)	791 (121)	22 798 (3364)	493 (73)	15 407 (4938)

The ranking of larval abundance in 1989 was similar to that of adults, with *H. convergens* larvae being most abundant followed by *C. septempunctata*, and other species being less abundant.

Aggregation by adult coccinellids

Aggregation by adult coccinellids in supplemented patches was evident within 4 h of cage removal and was complete within 24 h of cage removal (Fig. 2). Species differed markedly in the extent to which they aggregated in supplemented patches (Table 2). For data pooled across treatments, density of *H. convergens* was strongly correlated with aphid density in each trial, whereas density of *Coccinella septempunctata* was correlated with aphid density in three of four trials. Density of *Coleomegilla maculata* was never correlated with aphid density (Table 2). The lower density of *C. maculata* may have partially accounted for the lack of correlation with aphid density. However, we do not think this was the primary factor because high correlations were found for species with similarly low densities, such as *C. septempunctata* and *H. tredecimpunctata* in trial 2, 1988 (see Table 1). Density of all adult coccinellids was correlated with aphid density in three of four trials (Table 2); this was a reflection of the dominance in the fauna of species that strongly aggregated in patches with high aphid density.

There was no evidence that aggregation by adult coccinellids in patches was related to the physical area of a patch. Heterogeneity of slope regression models with

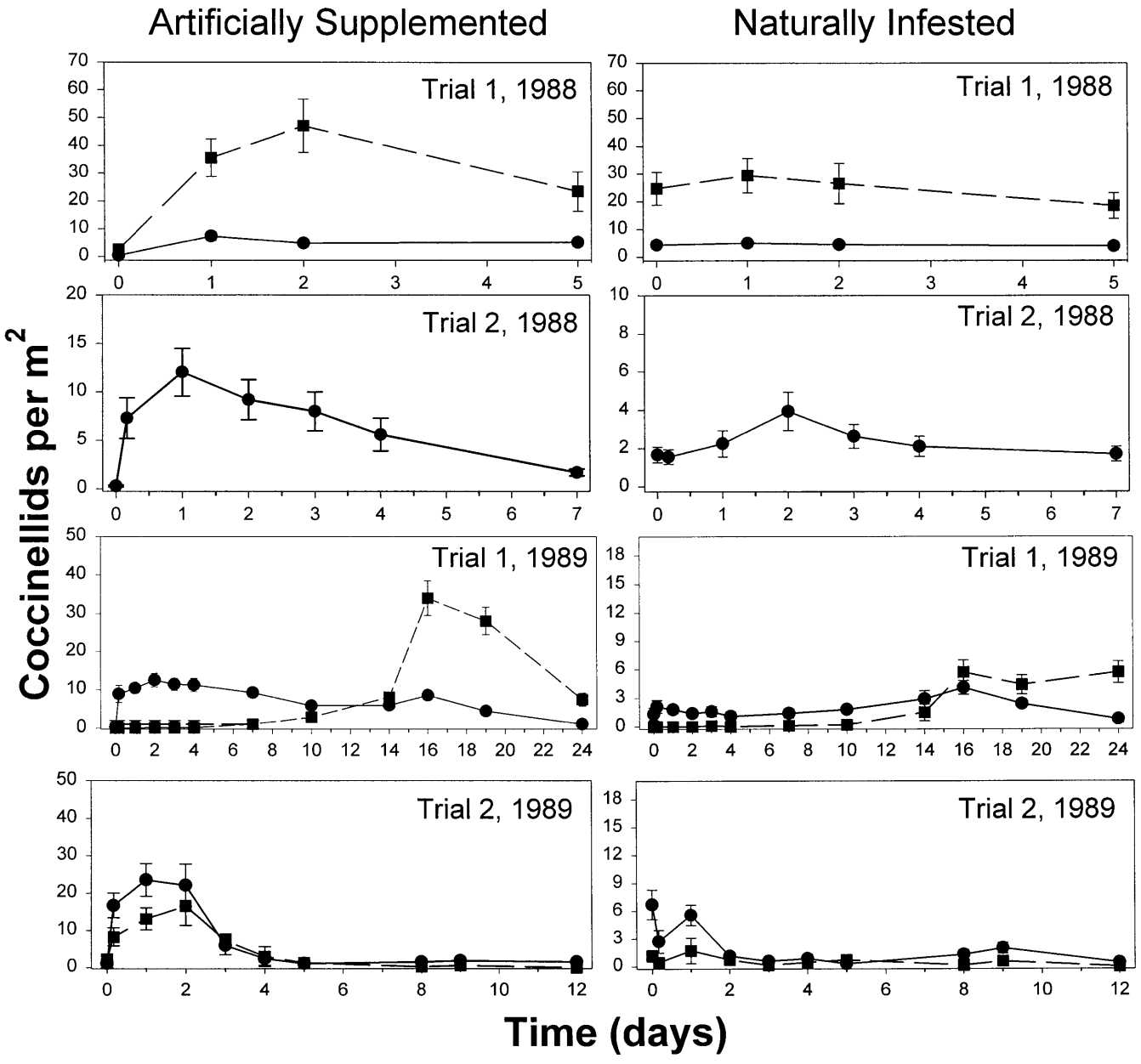

Fig. 2. Adult (●) and larval (■) coccinellid density in naturally infested and supplemented patches (*bar* width is 1 SE)

Table 2. Pearson correlation coefficients between coccinellid and cereal aphid density in spring wheat patches infested with cereal aphids

Life stage/species	Trail 1, 1988[a]	Trail 2, 1988[a]	Trail 1, 1989	Trail 2, 1989
Sample size	32	32	14	14
Adult coccinellids	0.20	0.64*	0.83*	0.67*
H. convergens	0.40*	0.61*	0.88*	0.65*
C. septempunctata	0.07	0.76*	0.68*	0.61*
C. maculata	0.04	0.06	0.08	–
H. tredecimpunctata	−0.05	0.70*	–	–
Coccinellid larvae	0.34*	–	0.78*	0.85*
H. convergens	–	–	0.79*	0.81*
C. septempunctata	–	–	–	0.89*
C. maculata	–	–	−0.17	0.40
H. tredecimpunctata	–	–	–	0.48*
Coccinellid egg masses	0.13	–	0.40*	−0.18

Correlation coefficients were not calculated when coccinellid density averaged <0.10 individuals/m^2

[a] Coccinellid larvae were not identified to species in 1988

*, differs significantly from zero

unique slope and intercept parameters for each size patch did not fit adult coccinellid density versus aphid density relationships significantly better for any species than a simple linear regression model (results not shown). Thus, over the range of patch sizes examined, aggregation by coccinellids in aphid patches was unrelated to patch area.

Aggregation by immature coccinellids

For data pooled across treatments, the density of coccinellid larvae was correlated with aphid density in each trial in which larvae were present (see Table 2). The timing of peak larval density was inconsistent among trials (see Fig. 2). Larval density peaked about 15 days after cage removal in trial 1, 1989, but about 2 days after cage removal in trial 1, 1988 and trial 2, 1989. The density of coccinellid egg masses was relatively high and was correlated with aphid density in trial 1, 1989 (Tables 1 and 2). Thus, the greater numbers of larvae in supplemented patches in trial 1, 1989, was partially the result of in situ recruitment of larvae in patches.

In trial 2, 1989, large numbers of larvae were present in the field when cages were removed (Fig. 2), but coccinellid egg masses were uncommon and about equally dense in natural and supplemented patches (Table 1). In this trial, density of coccinellid larvae peaked in supplemented patches within 48 h of cage removal. Aggregation by larvae in supplemented patches must have been primarily due to the foraging activity of larvae rather than larvae that hatched from eggs laid in supplemented patches. A similar pattern was observed in trial 1, 1988, when larvae were abundant in the field when cages were removed. Aggregation by larvae occurred more slowly than aggregation by adults, with larvae requiring about twice as long as adults to reach peak density (48 compared to 24 h).

Coccinellid species differed in the extent to which their larvae aggregated in aphid-infested patches. Densities of *Hippodamia convergens and Coccinella septempunctata* larvae were correlated with aphid density, while *Coleomegilla maculata* larval density was not correlated with aphid density. The lack of correlation for *C. maculata* larvae may have been related to their very low density in both 1989 trials, which could have made it difficult to detect such a relationship unless it was very strong. A heterogeneity of slopes regression model with slope and intercept parameters for each size patch did not fit data for larval coccinellid (combined species) versus aphid density in trial 1, 1988, significantly better than a simple linear regression model. Thus, aggregation by larvae apparently did not depend on patch size.

Aphid population growth

Aphid populations decreased from initial densities by the end of each trial. In general, aphid numbers declined most in supplemented patches, by intermediate amounts in natural patches, and least in exclusion patches.

In 1988, the realized rate of aphid population growth, r, was negative for the duration of each trial, indicating that aphid populations decreased in both natural and supplemented patches (Fig. 3). Estimates of r for trial 1, 1988 are not shown in Fig. 3 because only one estimate could be made from the two aphid density measurements taken; these were $r = -0.30$ (SE = 0.020) and $r = -0.32$ (SE = 0.019) for natural and supplemented patches, respectively.

r was greater than zero during the early part of trial 1, 1989, in natural and supplemented patches, but became negative in both patch types during the latter part of the trial. r was positive in exclusion patches during the entire trial. In trial 2, 1989, r was negative in all patch types for estimates made after cages were removed, but was lower in natural and supplemented patches than in exclusion patches.

Wheat is known to become less suitable for cereal aphid survival and reproduction after the boot stage of growth (Burton et al. 1985; Dixon 1987). Wheat plants progressed beyond boot stage during trials 1 and 2, 1989. Thus, decreases in aphid density in 1989 trials probably resulted partly from the effect of advanced wheat plant age on aphid

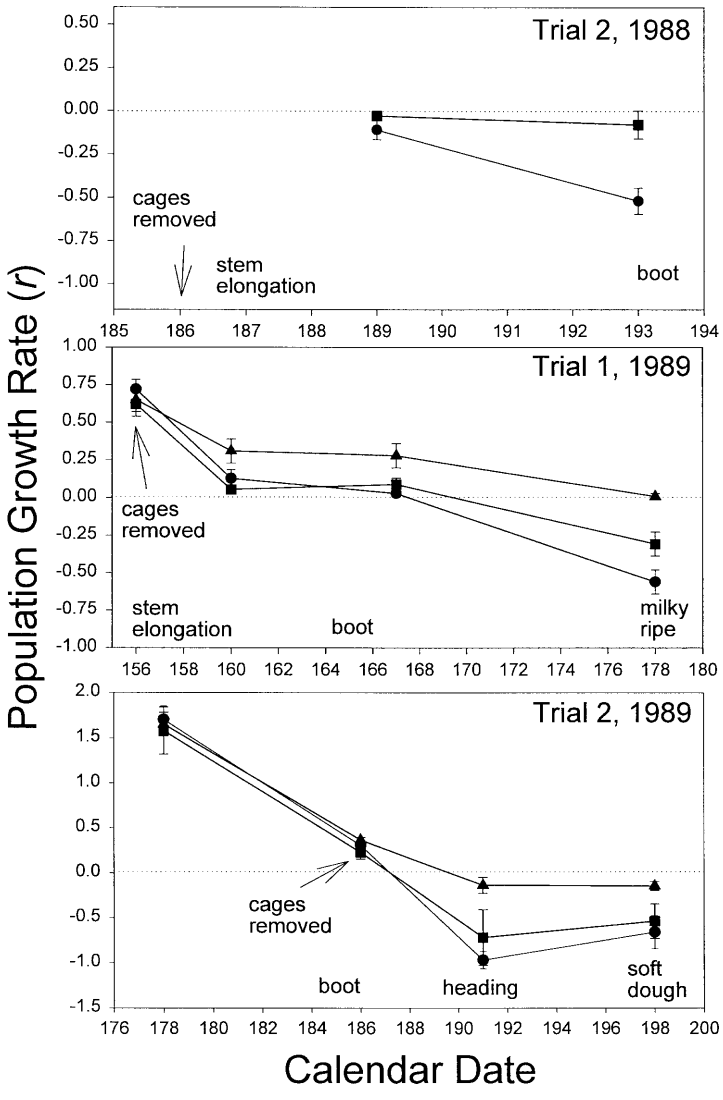

Fig. 3. Rate of cereal aphid population growth in supplemented (●) and naturally infested (■) coccinellid inclusion patches and supplemented coccinellid exclusion patches (▲). Also illustrated is wheat plant growth stage at various times during each trial (*bar* width is 1 SE)

survival and reproduction, and partly from emigration of aphids from patches. Reduced host plant quality may also have been a factor in the decline in aphid density during trial 1, 1988, in which plants were heading when the last measurement of aphid density was taken. However, the effect of plant quality could not be distinguished from that of coccinellids in trial 1, 1988 because we did not include a coccinellid exclusion treatment.

r did not differ among treatments in trial 1, 1988, but was lower in supplemented than natural patches in trial 2, 1988 ($F = 67.5$; df = 1, 30; $P < 0.01$), and there was a date × patch type interaction ($F = 54.1$; df = 1, 30; $P < 0.01$). r did not differ among patch types during the first 3 days of the trial, but was lower in supplemented than natural patches during the subsequent 4 days ($t = -12.5$; df = 54; $P < 0.01$).

r differed among patch types in both 1989 trials ($F = 25.7$; df = 2,18; $P < 0.01$ for trial 1 and $F = 5.43$; df = 2,18; $P < 0.05$ for trial 2). The date × patch type interaction was not significant for either trial. r was greater in supplemented exclusion patches than in natural patches and supplemented patches in both trials ($t = -5.6$; df = 18; $P < 0.01$ and $t = -3.1$; df = 18; $P < 0.01$ for comparisons with natural patches in trials 1 and 2; and $t = -6.2$; df = 18; $P < 0.01$ and $t = -4.4$; df = 18; $P < 0.01$ for comparisons with supplemented patches in trials 1 and 2). r was usually lower in supplemented patches than natural patches, especially for measurements taken toward the end of each trial (see Fig. 3). However, the two treatments did not differ significantly in either trial, nor was there a date × patch type interaction.

The ratio of aphids to coccinellids differed among patch types within a trial and among trials (Table 3). For example, there were 7347 aphids per adult coccinellid in supplemented patches and 1991 aphids per coccinellid when larvae and adults were combined in trial 1, 1988. In the same trial, there were 2725 aphids per adult coccinellid in natural patches and 951 aphids per coccinellid when larvae were included. In trial 2, 1988, there were 179 aphids per adult coccinellid in supplemented and 12.4 aphids per adult coccinellid in natural patches; larvae were absent during the trial.

There were 2.7 times more aphids per adult coccinellid in supplemented than natural patches in trial 1, 1988, but 14.4

Table 3. Average ratio of cereal aphids to coccinellids in natural and supplemented aphid patches in each of two trials in 1988 and 1989

	Aphids/coccinellids		
	Supplemented	Natural	Supplemented/ natural
Trial 1, 1988			
Adults	7347	2725	2.7
Adults plus larvae	1991	951	2.1
Trial 2, 1988			
Adults	179	12.4	14.4
Adults plus larvae	179	12.4	14.4
Trial 1, 1989			
Adults coccinellids	1999	527	3.8
Adults plus larvae	1226	283	4.3
Trial 2, 1989			
Adults	1263	247	5.1
Adults plus larvae	880	194	4.5

The ratio is listed for adult coccinellids and adults plus larvae
Also listed is the ratio of aphids to coccinellids in supplemented compared to natural patches

more aphids per adult coccinellid in supplemented than natural patches in trial 2, 1988 (Table 3). This ratio was greatest when aphid abundance in the field was low, irrespective of the degree of difference in aphid density in natural versus supplemented patches, and lowest when aphid abundance was high (Tables 1 and 3).

Chi-square tests indicated that the proportion of alatoid nymphs did not differ significantly among natural and supplemented patches in either 1989 trial. Thus, greater emigration of aphids by flight from supplemented patches than natural patches was unlikely to have caused the lower *r* values in supplemented compared to natural patches. We do not have similar data for 1988 trials. However, alate production is primarily a response to host plant decline caused by overcrowding and plant senescence and to short day length (Watt and Dixon 1981; Summy and Gilstrap 1983; Debarro 1992). Overcrowding by aphids was the main factor differing among patch types that would be expected to cause alate production. Aphid densities were high in both supplemented and natural patch types in trial 1, 1988, and relatively low in both patch types in trial 2, 1988. In light of the 1989 trials, which showed high aphid densities and large differences in aphid density among natural and supplemented patches, it is reasonable to assume that alate production was similar in supplemented and natural patches in 1988.

Discussion

Aggregation by coccinellids

Zhang and Sanderson (1993) observed strong aggregation by a specialist predatory mite with respect to spatial variation in the density of its prey, an herbivorous mite, *Tetranychus urticae*, whereas a polyphagous predatory mite exhibited a weak aggregative response. Variation in aggregation among coccinellids may also be related to differences to prey specificity. *Coleomegilla maculata* eats a variety of plant and animal foods in addition to aphids, whereas *Hippodamia convergens* and *Coccinella septempunctata* are primarily aphidophagous (Hodek 1973; Hodek and Honek 1996). The lack of strong aggregation by *C. maculata* may be related to lower searching efficiency of this highly polyphagous species. However, other studies have documented aggregation by *C. maculata* in patches with high aphid density (Wright and Laing 1980; Coderre et al. 1987; Cottrell and Yeargan 1998a,b), suggesting that aggregation by this species may depend more on the quantity and distribution of acceptable food or other resources than on inferior aphid searching ability. Regardless of the reason, the species composition of a coccinellid assemblage may influence the spatial pattern of predation on aphids in spring wheat fields and possibly the effectiveness of cereal aphid biological control.

Coccinellid species that aggregated responded similarly to variation in aphid density in patches differing more than 40 fold in area. Ives et al. (1993) demonstrated that *H. convergens* and *C. septempunctata* responded to spatial variation in aphid density at a very fine scale, the scale of individual fireweed plants. It is not surprising that we did not observe differences in aggregation in relation to patch area because the scale at which beetles respond to spatial variation in aphid density is apparently finer than the smallest patches included in our study.

Aphid population growth

In spite of aggregation by coccinellids in supplemented patches there were always 2.1 to 14.4 more aphids per coccinellid in supplemented than in natural patches (see Table 3). Without increasing their feeding rate or otherwise contributing to greater aphid mortality, coccinellids would be incapable of killing as great a proportion of aphids in supplemented patches as in natural patches. Honek (1985b) observed an approximately tenfold increase in predation rate on aphids in densely populated alfalfa fields compared to sparsely populated fields, whereas Turchin and Kareiva (1989) observed an approximately threefold increase in feeding rate by coccinellids in fireweed patches with aphid dense populations compared to those with sparse populations. Laboratory functional response studies show two- to fivefold increases in predation rate by adult coccinellids for high compared to low aphid densities (Hodek and Honek 1996, page 208). If coccinellids in spring wheat fields exhibit a similar range of variation in feeding rate, spatially density-dependent predation by coccinellids would not be a consistent phenomenon; this may partially explain why we observed spatially density-dependent predation in only one of four trials. Wheat decreases in quality as a host for some cereal aphids after plants progress beyond the boot stage of development (Burton et al. 1985; Dixon 1987). Because wheat plants had progressed beyond boot stage in three of four trials, coccinellids, probably in combination with host plant quality and other factors, reduced aphid populations in a spatially density-independent manner.

Foraging by coccinellids disturbs aphids, causing them to fall from plants (Roitberg and Myers 1978) and increasing the chance they will emigrate from a patch or succumb to some other mortality agent. Englund (1997) demonstrated that prey densities should decrease faster in small than large prey patches when predators are present because a proportionately greater number of prey emigrate from small patches. We did a retrospective analysis of our data to see if *r* decreased faster in small than large patches. Regression of *r* versus patch area for trial 1 was not significant, but regressions for the two time intervals for which *r* was estimated in trial 2 were significant ($F = 5.9$; df = 1, 15; $P = 0.03$ and $F = 7.8$; df = 1, 15; $P = 0.01$, respectively). Slope parameters were greater than zero for both regressions, indicating a greater population growth rate in large than small patches; this would be expected if coccinellids were causing large numbers of aphids to disperse from plants, and suggests that there was greater net emigration of aphids from small than large patches. Emigration may have been particularly high in trial 2, 1988, because adult coccinellid density was high and beetles were probably hungry and actively searching for cereal aphids (Honek 1985b) that were present at very low densities in the field except in supplemented patches. Previous studies have observed increased mortality of cereal aphids on the ground (Winder 1990; Growling and van Emden 1994), indicating that cereal aphids that dispersed from plants may have suffered disproportionately high mortality.

Including larval coccinellids did not change the disparity in the aphid to coccinellid ratio between supplemented and natural patches in a consistent way. Larvae were nearly as efficient as adults at accumulating in supplemented patches, either by in situ recruitment into such patches or by immigration from surrounding areas. Data summarized by Hodek and Honek (1996, page 208) indicate that larval coccinellids increase their feeding rate more in response to an increase in aphid density than adults. Thus, combined predation by adults and larvae would be more likely to cause spatially density-dependent mortality than predation by adults alone.

Adult coccinellids are capable of dramatically reducing aphid numbers in high aphid density patches in spring wheat fields when density in the field as a whole is low. This situation occurs most frequently early in the growing season, and the greatest contribution by coccinellids to cereal aphid biological control may be made by adults preying on aphids during this time. Greater knowledge of temporal and spatial aspects of predation by adult coccinellids during the early phases of cereal aphid population development in spring wheat would help elucidate their value in cereal aphid biological control.

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