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Response of coccinellids to their aphid prey at different spatial scales

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Abstract Predators that have an increasing numerical response for aggregation, attack and oviposition to increasing prey density are thought to be ideal for biological control. However density-dependent processes are infrequently detected and explanations include differences in the scales at which observations are made, behavioral differences among species, and habitat features. We examined the aggregation of four species of colonizing adult coccinellids to varying prey densities at two spatial scales in a maize system. Three of the species, *Adalia bipunctata*, *Hippodamia tredecimpunctata*, and *Hippodamia convergens*, responded to aphid abundance at the plant scale, and one species, *Coleomegilla maculata*, responded to the average aphid density at the plot (10×10 m) scale. In addition, *H. convergens* responded to individual plants with high aphid abundance in those plots with many plants of high aphid abundance. These results suggests that *C. maculata* (and possibly *H. convergens*) may be better able to colonize fields before aphid populations reach high levels, whereas *A. bipunctata* and *H. tredecimpunctata* may only be able to respond to high aphid abundance at the plant scale. This study suggests that spatial scale can affect predator–prey dynamics in a species-specific manner. However, the differences among coccinellid species in the community appear to be complementary, potentially contributing to greater aphid suppression.

Keywords Coccinellids · Aphids · Spatial scale · Species-specific behavior · Aggregation

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Introduction

How predators respond to variation in prey density has been a central theme in ecology theory (Hassell and May 1974; Kareiva and Odell 1987) and biological control (Beddington et al. 1978; Murdoch et al. 1985). A predator that responds numerically by aggregating attacks and oviposition to locations with higher prey density is thought to be ideal for suppressing pest populations before they reach damaging levels (Murdoch et al. 1985; Waage and Greathead 1988; Murdoch and Briggs 1996). However, there are numerous inconsistencies among published reports on the detection of density-dependent processes. Possible explanations for these discrepancies include differences in the spatial scales at which observations are made (Stiling and Strong 1982; Heads and Lawton 1983; Ives et al. 1993; Ray and Hastings 1996), the treatment of interacting populations (e.g. predator and prey) as spatially homogenous (Kareiva 1990, 1994; Noda 2004), behavioral differences among species, habitat features such as plant density, and availability of alternative prey (Elliot and Kieckhefer 2000).

In particular, numerous studies have examined the response of predators to variation in prey density using ladybird beetle (Coccinellidae)-aphid systems. Some studies have shown positive numerical responses for oviposition (Dixon 1959; Wratten 1973; Wright and Laing 1980; Mills 1982), aggregation (Neuschwander et al. 1975; Sakuratani et al. 1983; Karieva 1990; Evans and Youssef 1992; Elliot and Kieckhefer 2000), and dispersal (Ives et al. 1993) by some species of adult coccinellids in response to varying prey density, while other studies on the same and different species have not found this (Foote 1973; Frazer and Raworth 1985; Coderre et al. 1987; Karieva 1990; Schellhorn and Andow 1999a; Elliot and Kieckhefer 2000). Of these studies, only two have compared multiple species responses to prey density at more than one spatial scale (Ives et al. 1993; Elliot and Kieckhefer 2000). The work by Ives et al. (1993) found that the strength of adult aggregation and tenure was related to the spatial scale, whereas work by Elliot and Kieckhefer (2000) found that aggregation by coccinellids was unrelated to spatial scale, and that one species did not exhibit an aggregative response to prey density. These differences may be due to behavioral differences among species and the spatial scales examined.

In maize systems several species of coccinellids contribute to pest suppression (Forbes 1883; Ewert and Chiang 1966) and exhibit specific oviposition, larval foraging and dispersal behavior (Schellhorn 1999a, b). We were interested in the coccinellid community response to variations in aphid density. In this study we compared the aggregation response of the four most abundant species of adult coccinellids to variations in aphid density at two spatial scales—aphid abundance on a plant and the average aphid density on a group of plants. We show that coccinellid species aggregate to their aphid prey, but at different spatial scales, and that these differences among species in the community appear to be complementary, possibly contributing to greater aphid suppression.

Natural history

The study was conducted in maize fields in southeastern Minnesota, USA. Four species of coccinellids, *Coleomegilla maculata* (DeGeer), *Hippodamia tredecimpunctata* (Say), *Hippodamia convergens* (Guerin) and *Adalia bipunctata* (L.) (Coccinellidae: Coleoptera) were consistently prevalent, and all of them used aphids as a main food source. The corn leaf aphid, *Rhopalosiphum maidis* (Fitch) (Aphididae: Hemiptera) was the dominant aphid in maize, and formed large aggregations in the whorl. *Rhopalosiphum padi* (L.), and *Sitobion avenae* (F.) were also present and formed small aggregations scattered onthe leaves and stalk of the plant. In Minnesota, *C. maculata, H. tredecimpunctata* and *H. convergens* are found in wetlands, meadows, and small-grain and alfalfa fields in early spring and in maize fields from late spring until fall. They feed on aphids, lepidopteran eggs and larvae (Conrad 1959; Andow 1990), maize pollen (Forbes 1883), extrafloral nectaries (Schuster et al. 1976) and maize rust spores (personal observation, NAS). *A. bipunctata* is found on shrubs, trees, and weeds from early spring until mid-summer, and maize from mid-summer to early fall. It is primarily aphidophagous (Hodek and Honěk 1996), but also feeds on pollen (Hemptinne and Desprets 1986).

Materials and methods

To determine if four different species of colonizing adult coccinellids aggregate to aphids at two spatial scales (Noda 2004), a plant or a group of plants, we conducted a series of experiments during the summers of 1994 and 1996 on the St. Paul Campus of the University of Minnesota, Ramsey County, MN, USA. To create conditions of varying aphid densities, we used a variety of maize that is susceptible to aphids (cv. Green Giant, “Code 40”) and a variety of maize that is resistant to aphids (cv. Green Giant, “Code 39”). Morphologically the varieties appear similar in every way and share parent material. With these varieties we established high aphid-density plots and low aphid-density plots, and by mixing the varieties and planting dates, we established plots of spatially varying aphid densities. The three aphid-density treatments were planted in 10×10 m plots at a density of 49,400 seeds/ha (or 494 plants per plot), and replicated four times in a randomized complete block design both years. The seeds were planted into a plowed, harrowed and herbicide-treated (Lasso) field in late May.

For this study, we considered only those plots with variable aphid densities among plants (see categories below) for three sampling events during a 2-week period when both aphids and coccinellids were present. Aphid populations peak and crash within a 3- to 4-week period (Schellhorn and Andow 1999b), and the seasonal phenology of aphid density is such that for a 2-week period aphid density is variable, otherwise the majority of the plants have either high (>300) or low (0–50) aphid densities. We chose the plots by establishing categories of aphid densities and plotting a frequency distribution of plants in each plot with 0, 1–50, 51–300, >300 aphids per plant. Plots were chosen if three of the four aphid categories were represented and no single category comprised more than 66% of the plants; 39 plots met these conditions. At weekly intervals on three occasions (13, 20, and 28 July 1994, and 24 and 31 July and 7 August 1996) we counted aphids and colonizing coccinellid adults by species on 64–80 randomly selected plants per chosen plot (16–20 plants per replicate). We minimized disturbance to the insects by using hand mirrors to check the undersides of leaves. The coccinellids were colonizing immigrants because the first coccinellid pupa observed in maize plots was after the third sampling period. In 1996, *H. tredecimpunctata* was absent.

Statistical analysis

A homogeneity-of-slopes model was used to test the aggregation of coccinellids to aphid abundance on a plant and the average aphid density of a group of plants, i.e., within a plot. The homogeneity-of-slopes model included a regressor effect (aphid abundance on a plant), a main effect (plot), and an interaction term. The analysis was conducted with the general linear model (GLM) procedure that uses the method of least squares to fit GLMs with normal errors (SAS 1999). The analysis of coccinellid aggregation to aphids on a plant addressed the fine scale plant-to-plant variability. The analysis of coccinellid aggregation to the average aphid density of a plot addressed the variability in aphid densities among large groups of plants. The plot variable included groups of plants from both years sampled on three occasions. A significant interaction ($P < 0.05$) between aphid abundance on a plant and plot indicated that coccinellid colonization response to aphid density varied with year and date and for characteristics of large plot size (e.g., a group of plants). If the interaction term was not significant, it was removed from the model, and an analysis was run with the regressor and main effect. If the interaction term was significant, the full model was presented and the relationship discussed. If the plot variable was significant, coccinellid density was evaluated for each component of the plot variable (year, date and characteristics of large plot size) using ANOVA. The predictor, aphid density, was $\ln(X+1)$ transformed to standardize error variance for all analyses. Statistical analysis was conducted using SAS version 7.1 (SAS 1999).

Results

Hippodamia convergens, H. tredecimpunctata and *A. bipunctata* were only found on plants with aphids (Fig. 1), whereas seven *C. maculata* were recorded on plants without aphids. Furthermore, 23% of *C. maculata*, 3% of *H. tredecimpunctata*, 5% of *H. convergens* and no *A. bipunctata* were recorded on plants with less than 50 (=3.9 in natural logarithm) aphids (Fig. 1).

However, 35% of *C. maculata*, 65% of *H. tredecimpunctata*, 73% of *H. convergens* and 71% of *A. bipunctata* were recorded on plants with more than 300 (=5.7 in natural logarithm) aphids (Fig. 1). The average number (±SD) of aphids per plant for each species was 3,833±5,924 for *H. convergens*, 2,782±862 for *H. tredecimpunctata*, 2,809±1,133 for *A. bipunctata*, and 1,009±220 for *C. maculata*. Of the 39 plots used in the analysis, *C. maculata* was present in 37, *H. tredecimpunctata* and *H. convergens* were present in 15, and *A. bipunctata* was present in 12 (Fig. 2).

Coccinellid species aggregated differently to varying aphid densities at each spatial scale. *A. bipunctata* and *H. tredecimpunctata* responded to the fine-scale, plant-to-plant variation in aphid abundance, indicated by the significant term for plant (Table 1). The interaction term was nonsignificant (*A. bipunctata*: $F=0.95$, df=38, $P=0.5534$; *H. tredecimpunctata*: $F=1.06$, df=24, $P=0.3881$), hence it was removed and the models were run with the regressor, plant, and main effect, plot (Table 1). *H. convergens* also responded to aphid abundance at the plant scale (Table 2). However, the combination of a significant response to the fine-scale aphid abundance and significant interaction term suggested that they responded to individual plants with high aphid abundance in those plots with many plants with high aphid abundance.

Coleomegilla maculata was different and responded to the average aphid density of the large spatial scale, the plot, indicated by the significant plot term (Table 2). However, other components contributing to plot variability were not significant (year: $F=0.62$, df=1, $P=0.4319$; date: $F=0.01$, df=1, $P=0.918$). For *C. maculata*, the combination of the significant response to the average aphid density at the plot scale and significant interaction term suggested that they responded to the average aphid density of a plot, but once there they moved to plants with aphids. Not surprisingly, all coccinellid species combined responded to both the aphid abundance at the plant scale and to the average aphid density of the plot (plant: $F=23.14$, df=1, $P<0.0001$; plot: $F=1.80$, df=1, $P=0.0026$). For the initial model the interaction term was nonsignificant (plant*plot: $F=1.30$, df=38, $P=0.1138$), hence removed and the model was run with plant and plot.

Discussion

For all four colonizing coccinellid species, we found statistically significant aggregation to their prey, but at

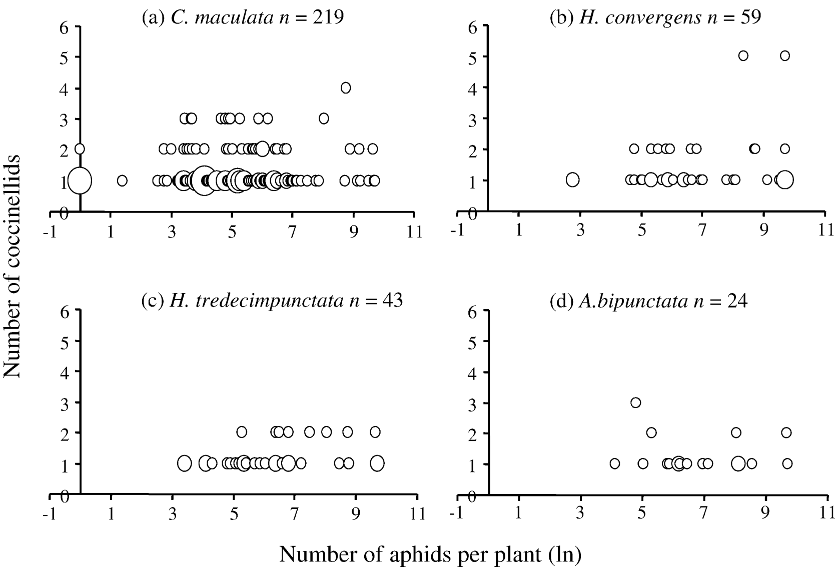

Fig. 1a–d The relationship between the number of aphids per plant (ln) and the number of adult coccinellids for **a** *C. maculata*, **b** *H. convergens*, **c** *H. tredecimpunctata*, and **d** *A. bipunctata*. The size of the *circle* represents the frequency of events (e.g. the smallest circle equals one and the largest circle equals five)

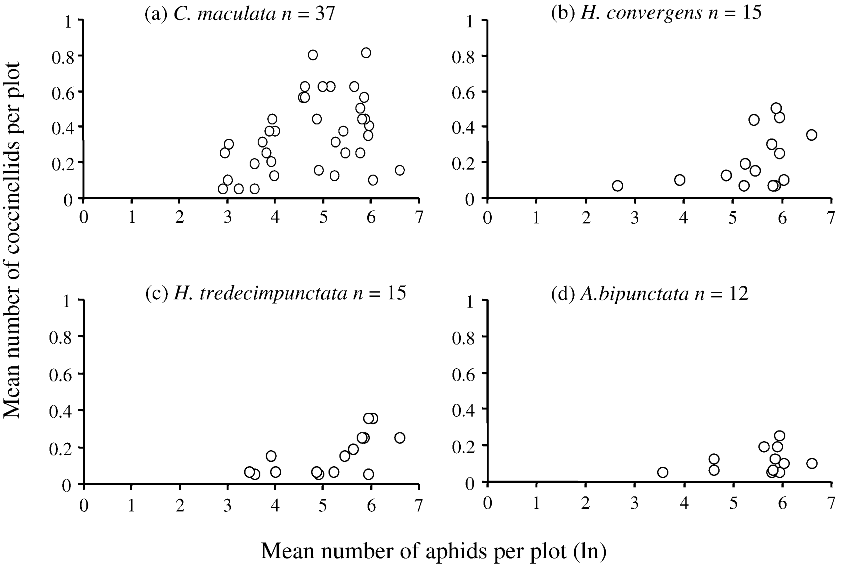

Fig. 2a–d The relationship between the mean number of aphids per plot (ln) and the mean number of adult coccinellids per plot for **a** *C. maculata*, **b** *H. convergens*, **c** *H. tredecimpunctata*, and **d** *A. bipunctata*

Table 1 Homogeneity-of-slopes model excluding the nonsignificant interaction term, for the effect of aphids at the plant and plot scale on *A. bipunctata* and *H. tredecimpunctata* adult density

Source	df	MS	*F*	*P*
A. bipunctata				
Plot	38	0.0574	1.13	0.2697
Plant	1	0.2504	4.95	0.0265
Error	636	32.1995		
H. tredecimpunctata				
Plot	24	0.1684	1.49	0.0642
Plant	1	0.9508	8.43	0.0039
Error	426	48.0366		

Aphid density was log-transformed

Table 2 Homogeneity-of-slopes model for the effect of aphids at the plant and plot scale on *C. maculata* and *H. convergens* adult density

Source	df	MS	*F*	*P*
C. maculata				
Plot	38	0.5599	1.46	0.0002
Plant	1	0.6565	1.71	0.1919
Grid plot*plant	38	0.5878	1.53	0.0241
Rid error	597	0.3845		
H. convergens				
Plot	38	0.1199	0.81	0.7832
Plant	1	1.5524	10.51	0.0013
Plot*plant	38	0.2430	1.65	0.0098
Error	598	0.1477		

Aphid density was log-transformed

different spatial scales. In a patchy aphid environment where aphid abundance among plants was variable, *A. bipunctata* and *H. tredecimpunctata* aggregated to aphids at the scale of the individual plant. Both species colonized plants with aphids independently of the average aphid density across the maize plot. *H. convergens* responded similarly to local aphid variation except that they aggregated only in plots with numerous plants with high aphid abundance. *C. maculata* was different from the other three species and aggregated only to the average aphid density at a larger spatial scale, the plot. The reason why *C. maculata* responds to the large spatial scale while other species respond more locally may have to do with their habitat preference and greater utilization of pollen as food. *C. maculata* is more likely to be found in crops that span large areas (e.g., forage, cereals and grain), and they can complete their development on pollen, whereas *A. bipunctata* is more likely to be found in trees, shrubs and isolated patches of weeds (Hodek and Honěk 1996). Hodek and Honěk (1996) also reported a minimum of 50 aphids needed to attract *A. bipunctata*. The two *Hippodamia spp.* are likely to be found in a range of habitats including those where *C. maculata* and *A. bipunctata* are found (Hodek and Honěk 1996), thus they may be able to respond to aphids at multiple spatial scales. Of course, all four species of coccinellids may response to aphids at scales other than the two that we examined, finer (e.g., within plant) and coarser (e.g., entire fields). If species are responding at multiple spatial scales then they may be able to track the scale-dependent spatial pattern of aphids. For example, *R. maidis* formed large aggregations in the maize whorl, while the other two species of aphids, *R. padi* and *S. avenae*, formed small aggregations on the leaves and stalks throughout the plant.

Earlier we provided possible explanations as to why density-dependent processes are infrequently detected. We found that coccinellid predators aggregate in species-specific ways that appear to depend on the scale at which they detect/respond to their prey. These results may explain some of the inconsistencies in the coccinellid literature. For example, some authors have found that *C. maculata* adults aggregate to aphids (Wright and Laing 1980; Coderre et al. 1987), while others have not

(Elliot and Kieckhefer 2000). Each paper was conducted at a single spatial scale. Although Elliot and Kieckhefer (2000) considered different spatial scales, after finding that aggregation by all species of coccinellids was unrelated to patch size, they proceeded with experiments at a single spatial scale. It is unclear whether they considered each coccinellid species separately. *H. tredecimpunctata* (Wright and Laing 1980) and *H. convergens* (Elliot and Kieckhefer 2000) aggregated to aphids, but this was shown at a single spatial scale. Our results and those of Ives et al. (1993) have highlighted the species-specific behavioral response of coccinellids to varying densities of prey when data are collected from more than a single spatial scale.

Interestingly, differences in adult aggregative response may influence oviposition, foraging and interspecific interactions in our system. The species of coccinellids discussed here have distinct oviposition strategies (Schellhorn and Andow 1999a). *C. maculata* has no oviposition preference for plants with aphids, but does prefer to oviposit at the bottom of the plant (Schellhorn and Andow 1999a). Since *C. maculata* responded to the average aphid density of a plot, they may not oviposit near aphids (Schellhorn and Andow 1999a) because they do not respond to aphids at such a fine scale. Other authors have explained that *C. maculata* oviposits away from aphids because it is a weak host searcher (Corderre et al. 1987) or is negatively phototactic (Ewert and Chiang 1966). *H. tredecimpunctata* did not have an oviposition preference for low or high densities of aphids or location on the plant (Schellhorn 1998). However they did aggregate to aphids at the scale of the individual plant. This suggests that *H. tredecimpunctata* may aggregate at a spatial scale that is different from the scale at which they oviposit, for example, clusters of adjacent plants. *A. bipunctata* has an oviposition preference for high densities of aphids at the top of the plant (Schellhorn and Andow 1999a). This suggests that *A. bipunctata* aggregates and oviposits at the same spatial scale.

Furthermore, the differences among these four coccinellid species in their response to varying aphid densities at different spatial scales may reduce the strength of the interaction among them. Previous studies have shown that *C. maculata* and *A. bipunctata* do not search in the same part of the plants (Ewert and Chiang 1966; Foott 1973; Schellhorn and Andow 1999a), and that intraspecific interference was greater than interspecies interference (Schellhorn and Andow 1999a). In the field, larvae of *A. bipunctata* prefer to forage near the top of the maize plant near clusters of aphids, while larvae of *C. maculata* prefer to forage near the bottom of the maize plant (Schellhorn and Andow 1999a). These foraging differences may reduce interference between *A. bipunctata* and *C. maculata* by reducing encounters and interspecific predation of coccinellid eggs, molting larvae, and pupae (Schellhorn and Andow 1999a). The interaction between *C. maculata*, the most abundant species, and all three of the less abundant species may be reduced because they do not aggregate to aphids at the same scale. The three less abundant species will tend to be found on plants with high aphid densities, while *C. maculata* will be found more uniformly on nearby plants, thereby reducing interaction strength. Sunahara and Mogi (2004) also suggest that two insect predators coexist because they aggregate to spatial scales differently.

Ultimately what is important is how coccinellid communities suppress aphid populations. Based on our findings, *C. maculata* is more likely to be found in groups of plants with high mean aphid density, but will not aggregate to individual plants with high aphid abundance. Thus they will encounter lower densities of aphids on some plants, and may prevent further aphid increase on these plants—the ultimate goal of biological control (Murdoch et al. 1985). Although their prey suppression ability was not tested in this study, they were the most abundant species at all aphid densities (Schellhorn 1998), and are known to suppress aphid populations in maize (Sparks et al. 1966; Corderre and Torneur 1986; Campbell and Cone 1994). The three other coccinellid species complement *C. maculata*. In patchy aphid environments, *A. bipunctata*, *H. tredecimpunctata* and *H. convergens* should be aggregated on plants with moderate-to-high aphid densities regardless of the average aphid density in the surrounding neighbourhood. Moreover, *A. bipunctat*a and *H. tredecimpunctata* may be able to find and colonize these plants even when the surrounding aphid density is extremely low. Therefore these species may be able to reduce aphid populations on the plants that will be overlooked by *C. maculata*. Several examples exist of predator combinations that produce either enhanced or reduced biological control (see Rosenheim 1998). Our results suggest that a community of coccinellids may provide better biological control than a single species alone.

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