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Coleomegilla maculata (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions

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Abstract The impact of a predator on its prey may depend on the presence of other species in the community. In particular, if predators are attracted to areas containing one prey species, another prey species may suffer greater predation if it occurs in the same areas. If the predator is omnivorous, this may occur even if one prey species is an animal and the other is a plant. We investigated the role of local dandelion densities on the impact of the predator *Coleomegilla maculata* on pea aphids in alfalfa fields. At small spatial scales, increased dandelion densities were associated with high *C. maculata* densities, presumably because these omnivorous ladybird beetles aggregated to pollen resources. In turn, the high *C. maculata* densities were associated with low aphid densities, presumably because of increased predation. We used laboratory cages to simulate *C. maculata* foraging in two adjacent patches of alfalfa, one with dandelions and one without. As in the field, the laboratory experiment showed that *C. maculata* aggregated to alfalfa interspersed with dandelions, which resulted in increased predation on aphids on alfalfa. This study demonstrates that a pollen-producing plant can indirectly decrease nearby herbivore densities by attracting an omnivorous predator.

Keywords Predation · Generalist predator · Indirect interactions · Apparent predation · Biological control

Introduction

Although predator-prey systems are generally discussed as two strongly interacting species, many predator-prey systems are influenced indirectly by other species in the community. Indirect effects occur when the impact of one species on a second depends on the presence of a third species (Holt 1977; Abrams 1987a,1987b; Strauss 1991). Indirect interactions arise through chains of direct interactions with the additional organism or through the third organism changing direct interactions between the other species (Wootton 1994). A variety of indirect effects are possible depending on the third species involved and how that species affects the others. Indirect interactions resulting from the addition of predators can facilitate predation in some cases (Soluk 1993; Kotler et al. 1993; Losey and Denno 1998), while in other cases, additional predators that prey on other predators or cannibalize their own species can act to decrease predation (Rosenheim et al. 1993; Letourneau and Dyer 1998; Schellhorn and Andow 1999). The addition of a prey species can affect a predator's functional or numerical response, resulting in increased or decreased predation on the focal prey species (Murdoch 1969; Murdoch and Oaten 1975; Holt 1977; Holt and Lawton 1994). In fact, predator-mediated indirect effects between non-competing prey species can in principle result in any combination of positive, negative, or neutral interactions (Abrams 1987a; Holt and Kotler 1987). Understanding how additional organisms influence the behavior of predators or prey may be a useful approach for predicting the consequences of indirect interactions on predator-prey population dynamics (Holt and Kotler 1987; Huang and Sih 1990; Losey and Denno 1998; Sih et al. 1998; Schellhorn and Andow 1999).

In this paper, we present evidence for an indirect interaction between the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), and the common dandelion *Taraxacum officinale* (Weber) in alfalfa fields. Pea aphids do not feed on dandelions, so there is no direct interaction between them. Nonetheless, there are at

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least two possible ways dandelions could have a negative effect on aphid populations: indirectly through a negative effect on the aphids' host plant, alfalfa, or indirectly through a positive effect on the generalist ladybird beetle *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae). Here, we test whether dandelions have a negative indirect impact on pea aphids by attracting *C. maculata* into areas of high dandelion density. This type of indirect interaction has previously been described as “apparent predation” (Holt 1977) or “indirect antagonism” (Huang and Sih 1990).

Materials and methods

Study organisms

C. maculata is a native coccinellid beetle that is widely distributed east of the Rocky Mountains in North America (Gordon 1985). It is a polyphagous species known to feed on a broad range of aphid species, pollen, nectar, lepidopteran eggs, and a variety of other homopterans and immature insects (Smith 1960; Putnam 1964; Hodek 1973; Mareida et al. 1992; Hodek and Honek 1996).

The pea aphid, *A. pisum*, is a Palearctic aphid species that was first introduced into North America in the mid-19th century (Clausen 1978). In Wisconsin, it is commonly found in alfalfa, peas, and other agricultural legumes. In some areas it reaches levels high enough to cause significant economic damage (Clausen 1978; Losey et al. 1997). Pea aphids are not known to feed on dandelion plants or flowers.

The common dandelion is an apomictic, perennial weed that blooms abundantly, producing large amounts of nectar and pollen (Solbrig and Simpson 1974; Sheaffer and Wyse 1982). It commonly invades many agricultural fields, including fields of alfalfa. Dandelions can compete with alfalfa for light, water, potassium, and phosphorus (Sheaffer and Wyse 1982; Mueller and Fick 1987). Weed competition may hinder growth, development, and quality, especially in alfalfa seedlings. However, dandelion control has not been shown to consistently increase total alfalfa yield or quality (Sheaffer and Wyse 1982; Mueller and Fick 1987).

Alfalfa, as a perennial legume, provides a more stable environment for roots and belowground organisms; however, in Wisconsin alfalfa is cut and harvested two to three times per growing season causing an almost complete removal of aboveground vegetation. This management scheme presents an excellent environment for plants and insects that can withstand aboveground disturbances such as cutting, or can quickly reinvade from nearby habitats after cutting. All fields in this study were surveyed before the first cutting of the growing season.

The known direct interactions among the four study organisms are reflected in a community diagram (Fig. 1). Drawing the direct interactions among species in the system allows us to predict the possible indirect interactions between species.

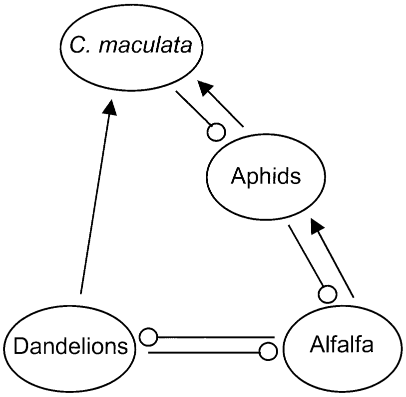

Fig. 1 Community diagram of the study organisms. Positive effects of one organism on another are denoted by *lines with arrows*; negative effects by *lines with circles* (Levins 1973)

Field observations

To determine associations between population densities of *C. maculata*, pea aphids, and dandelions, 12 alfalfa fields with varying dandelion densities were sampled at the University of Wisconsin Arlington Research Station, Arlington, Wisconsin, United States. Three parallel transects were created in each field. The transects were 10 m apart, and each contained seven 2 m×2 m quadrats spaced every 10 m. The transects were placed to sample a gradient of naturally occurring dandelion densities within fields. Transects were at least 10 m from the edge of the field to minimize any possible edge effects. In each quadrat the number of dandelion flowers was counted visually, the number of *C. maculata* was assessed by a visual search followed by sweep-netting the entire quadrat (with 33-cm-diameter sweep nets), and the number of pea aphids was quantified by sweep-netting.

We analyzed the data to determine whether the local density of dandelions (within quadrats) affected the abundances of *C. maculata* and pea aphids. Because many quadrats contained low numbers of *C. maculata* and pea aphids (including zero), we used Poisson regression (SAS Institute 1990, pp. 1168–1175). Unlike ordinary least-squares regression, which assumes that errors are normally distributed, Poisson regression assumes that the errors are Poisson distributed, thereby explicitly accounting for the variability associated with small numbers. Among the 12 fields, the ranges in mean dandelion, *C. maculata*, and pea aphid numbers per quadrat were 0.33–39.5, 0.048–1.10, and 0.29–6.33, respectively. Because we were interested in the effect of local dandelion density on *C. maculata*, and pea aphid numbers, rather than differences among fields, we removed among-field differences in the analysis by including categorical variables for a fixed effect of field identity on *C. maculata* and pea aphid numbers. Therefore, the analyses identify relationships between dandelion number (independent variable) and either *C. maculata* or pea aphid numbers (dependent variables) within fields. Poisson regression involves maximum likelihood estimation, and statistical inference is based on asymptotic 95% confidence intervals for the parameter estimates. If the confidence intervals do not include zero, then the parameters are statistically significantly different from zero ($P<0.05$).

To test for an association between *C. maculata* and pea aphid numbers within quadrats, we used Spearman's rank correlation (Sokal and Rohlf 1981). In the analyses for the effects of dandelion density on *C. maculata* and pea aphid numbers that use Poisson regression, we used dandelion density as an independent variable because it is not effected by either *C. maculata* or pea aphid numbers. In contrast, *C. maculata* and pea aphid numbers may affect each other if *C. maculata* are attracted to pea aphids and pea aphids are consumed by *C. maculata*. Therefore, correlation, rather than regression, is the appropriate tool to determine the relationship between *C. maculata* and pea aphid numbers.

Laboratory cage experiment

A laboratory cage experiment was conducted to determine (1) whether dandelions influenced aphids through predation by *C. maculata*, and (2) how the presence of dandelions influenced the foraging behavior of *C. maculata*. In 2×1×1 m mesh cages we simulated two adjacent patches of alfalfa, one with dandelions and one without. On one side of each cage, 12 alfalfa stems were alternated with 12 dandelion flowers placed in vials. On the opposite side, 12 alfalfa stems were alternated with 12 control vials. The side of the cage with alfalfa and dandelions was first determined by a coin toss and was thereafter alternated between each side. Alfalfa and dandelion stems were cut and placed in 7×2.5 cm clear plastic vials filled with tap water. A plastic lid with a hole for the stem covered the opening of the vial, and plastocine was placed around the stem to seal the vial. Alfalfa stems were cut so that 15–25 cm of alfalfa was above the lid, and dandelion stems were cut so that only the flower was above the vial. The vials were fixed onto the center of small plastic dishes that contained fluon (a slippery substance) on the inside edges. The fluon ensured that any aphids that dropped from the alfalfa could only climb back up the alfalfa or remain in the dish. Control vials were prepared the same manner as those containing alfalfa and dandelions, but without any vegetation.

All alfalfa stems were inoculated with ten apterous adult pea aphids that were reared from a laboratory colony on fava beans. Neither the dandelion nor control vials contained any aphids. Increased plant density has been found to reduce the foraging rates of *C. maculata* (Risch et al. 1982), so to minimize the possibly extraneous effects of plant density or surface area, we spaced vials evenly on both sides of the cage and cut dandelions so that only the flower head was accessible.

C. maculata adults were collected from alfalfa fields and kept in the laboratory less than 1 week before the experiment. They were satiated and then starved for 24 h to maximize foraging activity (Frazer and Gill 1981), and then eight were released in the middle of each cage and allowed to forage for 11 h. Every 30 min, the location of each coccinellid was recorded. We identified *C. maculata* location using three categories. The “alfalfa only” category included beetles on the dishes, alfalfa, or cage screen up to the height of the alfalfa on the side of the cage without dandelions. Similarly, the “dandelion and alfalfa” category included beetles on the other side of the cage that were on dandelions, alfalfa, dishes, or the cage screen up to the height of the alfalfa. We also created an “off” category for beetles that were on the cage either above the height of the alfalfa or in the middle of the cage between the two sides. At the end of the experiment, the number of aphids consumed was determined by subtracting the number of aphids remaining on the alfalfa or in the dish from the ten original aphids. We replicated the experiment ten times. Data comparing *C. maculata* predation on aphids, predation rate per unit time, and time spent on a side were analyzed using paired *t*-tests.

Results

Field observations

The results of a Poisson regression model showed that there was a significant positive correlation between the number of dandelion flowers per quadrat and the number of *C. maculata* per quadrat (Table 1, Fig. 2). There was also a significant negative correlation between the number of dandelion flowers per quadrat and the number of aphids per quadrat (Table 2, Fig. 3). The number of *C. maculata* per quadrat was negatively correlated with the

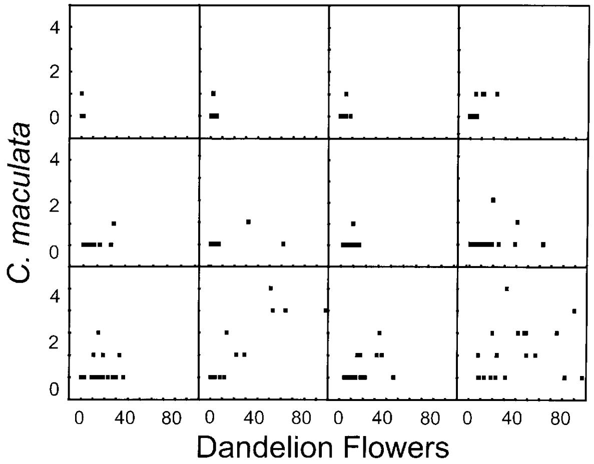

Fig. 2 The number of *Coleomegilla maculata* per plot versus the number of dandelions per plot for each of the fields sampled

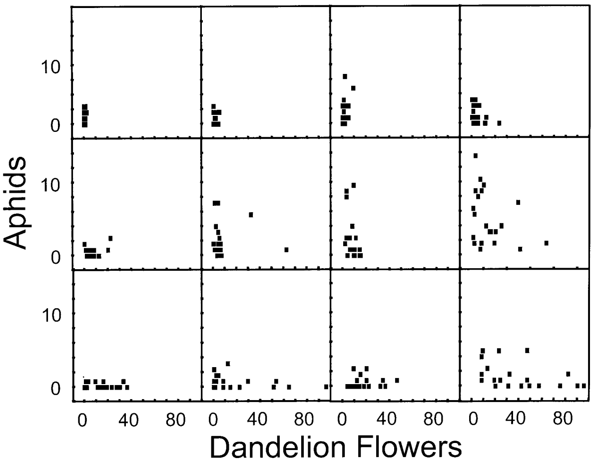

Fig. 3 The number of pea aphids per plot versus the number of dandelions per plot for each of the fields sampled

Table 1 Poisson regression model for number of *Coleomegilla maculata* per quadrat

Source	*df*	SS		
Regression	13	67.00		
Residual	239	233.06		
Uncorrected total	252	300.06		
Parameter	Estimate	SE	95% Confidence interval	
Intercept	–3.053	1.000	–5.02	–1.08
Dandelion	0.025	0.005	0.0157	0.0337
Field[a]	–0.27 to 2.11			

[a] “Field” represents 11 categorical variables to distinguish among the 12 fields in the study. Because the focus of the analysis is on the effect of dandelion abundance, the separate coefficients for each field are not presented

Table 2 Poisson regression model for number of aphids per quadrat

Source	*df*	SS		
Regression	13	447.00		
Residual	239	482.40		
Uncorrected total	252	929.40		
Parameter	Estimate	SE	95% Confidence interval	
Intercept	–0.093	0.229	–0.545	–0.359
Dandelion	–0.020	0.005	–0.029	–0.011
Field[a]	0.35–1.00			

[a] “Field” represents 11 categorical variables to distinguish among the 12 fields in the study. Because the focus of the analysis is on the effect of dandelion abundance, the separate coefficients for each field are not presented

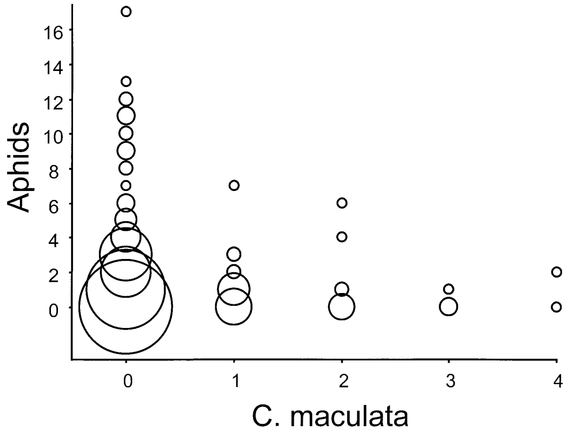

Fig. 4 The number of *C. maculata* per plot versus the number of pea aphids per plot over all sampled fields. *Data points* are weighted to show the number of times they occurred, and the *smallest dot* represents a single data point (n=252)

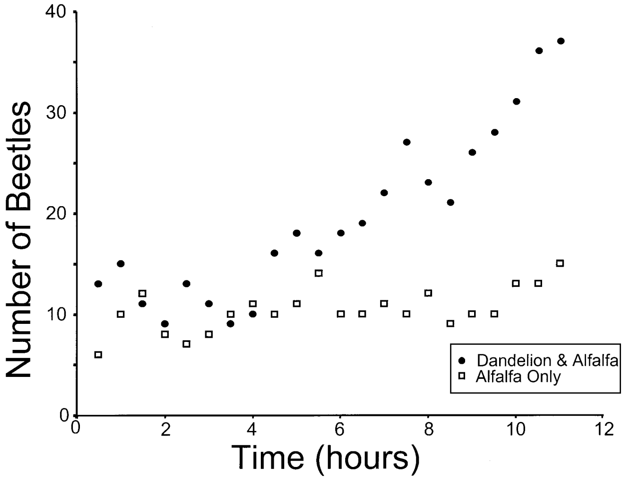

Fig. 5 Number of beetles observed on each side of the laboratory cages through time averaged over all 10 replicate cages

number of aphids (Spearman rank correlation, r_s=–0.161, n=252, P=0.010, Fig. 4).

Laboratory experiments

The average number of aphids consumed on the alfalfa-only side of a cage (12.30±1.58, mean±SE) was significantly less than the average number of aphids consumed on the side with dandelions and alfalfa (25.00±3.62) (two-tailed paired t-test, n=10, P=0.004). From the observation data, we approximated the total time beetles spent on each side of the cage. We assumed that one observation of a beetle on a side represented 0.5 beetle-hours on that side. The total beetle-hours per side were summed to calculate the approximate amount of time *C. maculata* spent on each side. Overall, the time spent on the alfalfa-only side (11.68±3.36 h) was significantly less than the time spent per beetle on the dandelion side (22.96±1.76 h) (two-tailed paired t-test, n=10, P=0.048). To obtain a measure of predation efficiency, the number of aphids eaten per beetle was divided by the time spent per beetle for each side in each cage. The average number of aphids eaten per beetle per hour was greater on the alfalfa only side (4.86±2.39 aphids eaten h^{-1}) than on the dandelion plus alfalfa side (2.08±1.02 aphids eaten h^{-1}), though the results were not statistically significant (two-tailed paired t-test, n=10, P=0.097).

Observational data showed a change in beetle location over time (Fig. 5). During the first 5 h of the experiment, there was little difference between the amount of time all eight beetles in a cage spent on the alfalfa only side (4.05±1.06 h) compared to the time spent on the dandelion side (5.40±0.79 h) (two-tailed paired t-test, n=10, P=0.228). After 5 h the average time all beetles in a cage spent on the alfalfa only side (7.4±2.52 h) was less than the time spent on the dandelion side (16.25±1.85 h) (two-tailed paired t-test, n=10, P=0.035), and in eight of the ten replications more time was spent on the dandelion side than on the alfalfa only side (sign-test, n=10, P=0.109).

Discussion

Our field observations revealed a negative relationship between the density of dandelion flowers in a patch and the number of aphids. One of the possible explanations for this is an indirect interaction through the predator, *C. maculata*. This explanation has two components. First, dandelions must have a positive effect on *C. maculata* density within patches. Our field observations showed a positive relationship between the density of dandelion flowers in a patch of alfalfa and the density of *C. maculata*. Second, there must be a negative correlation between the density of *C. maculata* and the density of aphids. Our field observations supported this relationship as well. Therefore, we have field evidence to support the possibility of an indirect interaction between dandelions and pea aphids through *C. maculata*.

While our field observations suggest that dandelions could be promoting *C. maculata* predation on aphids, it does not rule out other potential mechanisms that could be facilitating the negative relationship between dandelion and pea aphid densities. Our laboratory experiment tested whether the presence of dandelions could reduce aphid numbers exclusively by increasing *C. maculata* predation. The results showed that aphids on alfalfa intermixed with dandelions suffered twice as much predation of aphids on alfalfa intermixed with control dishes. This demonstrates that increased predation by *C. maculata* caused by the presence of dandelions has the potential to explain the patterns we observed in the field. This does not exclude the possibility of other mechanisms explaining the field observations. For example, dandelions could have a negative impact on alfalfa through competition which then discourages aphid immigration or population growth. The magnitude of the effect in the cage experiment, however, appears to be sufficient to explain the field observation in the absence of other mechanisms.

The final objective of our study was to determine how dandelions might be influencing *C. maculata* behavior to promote aphid predation. Dandelions could lead to increased predation on aphids in two ways: by causing increased predator efficiency in dandelion patches, or by influencing the number of *C. maculata* through increased immigration or increased tenure time within patches with dandelions. In the laboratory experiment, dandelions could be influencing the foraging of *C. maculata* as measured by the number of aphids eaten per unit of foraging time. Structural complexity within plants (Elsey 1974; Quilici and Iperti 1986; Kareiva and Sahakian 1990) and between plants (Risch et al. 1982) can influence the foraging behavior of predators, making it easier or harder for them to find prey in particular habitats. Our results, however, do not suggest that individual beetles forage more efficiently for aphids in the side with dandelions compared to the side without dandelions. In fact, the average number of aphids eaten per time spent foraging is slightly lower in the side with dandelions compared to the side without. This is the opposite of what would be needed to explain the observed difference in total predation.

Although predation efficiency was lower in the presence of dandelions, overall predation was higher in the presence of dandelions; the increased time beetles spent in the presence of dandelions compensated for and exceeded the effect of reduced predation efficiency. Preferential immigration to the dandelion side could explain the higher beetle numbers on that side; however, there was no significant difference in the number of beetles that moved to either alfalfa patch during the initial period of the experiments. This suggests that neither side is initially more attractive to the beetles, and therefore preferential immigration is not a principal mechanism for increased beetle densities in the presence of dandelions.

After 5 h the number of beetles found on both sides of the cage increased, with the increase on the side with dandelions being greater than on the side without dandelions. Since there was no difference in accumulation at the beginning of the experiment, we suspect that dandelions influence *C. maculata* behavior primarily through an increase in local tenure time. This shift in behavior after 5 h could have been influenced by a variety of behavioral or methodological factors. There is evidence for periodicity in the foraging of some coccinellid species (Nakamuta 1987), and changes in hunger level have also been found to affect foraging behavior (Frazer and Gill 1981; Carter and Dixon 1982; Quilici and Iperti 1986). Additionally, individuals could have been influenced by an accumulation of experience. Numerous studies have shown a positive correlation between the numbers of *C. maculata* and food resources (Ewert and Chiang 1966; Radcliffe et al. 1976; Wright and Laing 1980; Andow and Risch 1985; Gross et al. 1985; Arpaia et al. 1997). In our cages, the assemblage of pollen and aphids may act to accumulate beetles more effectively on the side with dandelions than on the side without. Holt (1984; Holt and Kotler 1987) has previously predicted that this type of short-term, local, numerical response to an increase in prey density can lead to “apparent competition” between prey species within a patch.

The “enemies hypothesis” states that natural enemies should be more effective in more vegetationally diverse ecosystems (Root 1973). While some studies have supported this idea, there have been a number of counter-examples and inconsistencies which make it difficult to predict the effects of increased vegetation diversity in a given system (reviewed by Andow 1991). The increased availability of nectar and pollen sources is one of the possible mechanisms for increased herbivore control by natural enemies in more vegetationally complex habitats (Root 1973; reviewed by Russell 1989). Pollen as an individual food item is suitable for *C. maculata* development and may help facilitate egg development (Smith 1960; Hemptinne and Desprets 1986). Therefore, habitats with pollen could theoretically lower coccinellid mortality and increase reproduction, leading to a greater potential for herbivore control across multiple generations. Thus, the presence of dandelions or other pollen sources could not only cause local increases in predation on aphids (as demonstrated in this study), but could also increase the production of coccinellids from one generation to the next.

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References

Abrams PA (1987a) Indirect interactions between species that share a predator: varieties of indirect effects. In: Kerfoot WC, Sih A (eds) Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, pp 38–54

Abrams PA (1987b) On classifying interactions between populations. Oecologia 73:272–281

Andow DA (1991) Vegetational diversity and arthropod population response. Annu Rev Entomol 36:561–586

Andow DA, Risch SJ (1985) Predation in diversified agroecosystems: relations between a coccinellid predator *Coleomegilla maculata* and its food. J Appl Ecol 22:357–372

Arpaia S, Gould F, Kennedy G (1997) Potential impact of *Coleomegilla maculata* predation of *Leptinotarsa decemlineata* to Bt-transgenic potatoes. Entomol Exp Appl 82:91–100

Carter MC, Dixon AFG (1982) Habitat quality and the foraging behaviour of coccinellid larvae. J Anim Ecol 51:865–878

Clausen CP (1978) Introduced parasites and predators of arthropod pests and weeds: a world review. In: Clausen CP (ed) Agricultural handbook 480. USDA, Washington, DC

Elsey KD (1974) Influence of plant host on searching speed of two predators. Entomophaga 19:3–6

Ewert MA, Chiang HC (1966) Dispersal of three species of coccinellids in corn fields. Can Entomol 98:999–1003

Frazer BD, Gill B (1981) Hunger, movement, and predation of *Coccinella californica* on pea aphids in the laboratory and in the field. Can Entomol 113:1025–1033

Gordon RD (1985) The Coccinellidae (Coleoptera) of America north of Mexico. J NY Entomol Soc 93:1–912

Gross HR Jr, Pair SD, Jackson D (1985) Behavioral responses of primary entomophagous predators to larval homogenates of *Heliothis zea* and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in whorl-stage corn. Environ Entomol 14:360–364

Hemptinne JL, Desprets A (1986) Pollen as a spring food for *Adalia bipunctata*. In: Hodek I (ed) Ecology of Aphidophaga. Academia, Prague, pp 29–35

Hodek I (1973) Biology of Coccinellidae. Junk, The Hague

Hodek I, Honek A (1996) Ecology of Coccinellidae. Kluwer, Dordrecht

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theor Popul Biol 12:197–229

Holt RD (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am Nat 124:377–406

Holt RD, Kotler BP (1987) Short-term apparent competition. Am Nat 130:412–430

Holt RD, Lawton JH (1994) The ecological consequences of shared natural enemies. Annu Rev Ecol Syst 25:495–520

Huang C, Sih A (1990) Experimental studies on behaviorally mediated, indirect interactions through a shared predator. Ecology 71:1515–1522

Kareiva P, Sahakian R (1990) Tritrophic effects of a simple architectural mutation in pea plants. Nature 345:433–434

Kotler BP, Brown JS, Slotow RH, Goodfriend WL, Strauss M (1993) The influence of snakes on the foraging behavior of gerbils. Oikos 67:309–316

Letourneau DK, Dyer LA (1998) Experimental test in lowland tropical forest shows top-down effects through four trophic levels. Ecology 79:1678–1687

Levins R (1973) The qualitative analysis of partially specified systems. Ann NY Acad Sci 231:123–138

Losey JE, Denno RF (1998) Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. Ecology 79:2143–2152

Losey JE, Ives AR, Harmon J, Ballantyne F, Brown C (1997) A polymorphism maintained by opposite patterns of parasitism and predation. Nature 388:269–272

Mareida KM, Gage SH, Landis DA, Wirth TM (1992) Ecological observation on predatory Coccinellidae (Coleoptera) in southwestern Michigan. Great Lakes Entomol 25:265–270

Mueller SC, Fick GW (1987) Weed and insect effects on alfalfa development and quality. Proceedings of the forage and grassland conference. American Forage and Grassland Council, Lexington, pp 96–100

Murdoch WW (1969) Switching in general predators: experiments of predator specificity and stability of prey populations. Ecol Monogr. 39:335–354

Murdoch WW, Oaten A (1975) Predation and population stability. Adv Ecol Res 9:2–132

Nakamuta K (1987) Diel rhythmicity of prey-search activity and its predominance over starvation in the lady beetle, *Coccinella septempunctata bruckii*. Physiol Entomol 12:91–98

Putnam WL (1964) Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. Can Entomol 96: 1149–1155

Quilici S, Iperti G (1986) The influence of host-plant on the searching ability of first instar larvae of *Propylea quatuordecimpunctata*. In Hodek I (ed) Ecology of Aphidophaga. Academia, Prague, pp 99–106

Radcliffe EB, Weires, RW, Stucker RE, Barnes DK (1976) Influence of cultivars and pesticides on pea aphids, spotted alfalfa aphid, and associated arthropod taxa in a Minnesota alfalfa ecosystem. Environ Entomol 5:1195–1207

Risch SJ, Wrubel R, Andow D (1982) Foraging by a predaceous beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae), in a polyculture; effects of plant diversity and density. Environ Entomol 11:949–950

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monogr 43:94–125

Rosenheim JA, Wilhoit LR, Armer CA (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96:439–449

Russell EP (1989) Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ Entomol 18:590–599

SAS Institute (1990) SAS/STAT user's guide, vol 2, GLM-VARCOMP. SAS Institute, Cary

Schellhorn NA, Andow DA (1999) Cannibalism and interspecific predation: role of oviposition behavior. Ecol Appl 9:418–428

Sheaffer CC, Wyse DL (1982) Common dandelion (*Taraxacum officinale*) control in alfalfa (*Medicago sativata*). Weed Sci 30:216–220

Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. Trends Ecol Evol 13:350–355

Smith BC (1960) A technique for rearing coccinellid beetles on dry foods, and influence of various pollens on the development of *Coleomegilla maculata* Timb. (Coleoptera: Coccinellidae). Can J Zool 38:1047–1049

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, New York

Solbrig OT, Simpson BB (1974) Components of regulation of a population of dandelions in Michigan. J Ecol 62:473–486

Soluk DA (1993) Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. Ecology 74:219–225

Strauss SY (1991) Indirect effects in community ecology: their definition, study and importance. Trends Ecol Evol 6:206–210

Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. Annu Rev Ecol Syst 25: 443–466

Wright EJ, Laing JE (1980) Numerical response of coccinellids to aphids in corn in Southern Ontario. Can Entomol 112:977–988