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Aggregation of polyphagous predators in response to multiple prey: ladybirds (Coleoptera: Coccinellidae) foraging in alfalfa

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Abstract The spatial distribution of polyphagous predators may often reflect the integration of aggregative responses to local densities of multiple species of prey, and as such may have consequences for the indirect linkages among the prey sharing these predators. In a factorial field experiment in which we manipulated local prey densities within a field of alfalfa in Utah (USA), we tested whether aphidophagous ladybirds would aggregate not only in response to their primary aphid prey, but also in response to an abundant alternative prey, the alfalfa weevil (*Hypera postica* [Gyllenhal]). Native North American ladybirds (primarily *Hippodamia convergens* Guerin and *H. quinquesignata quinquesignata* [Kirby]) responded only to spatial variation in aphid density. In contrast, the introduced ladybird, *Coccinella septempunctata* L., aggregated also at local concentrations of the weevil late in the experiment when weevil density was high and aphid density was relatively low throughout all experimental plots. The results support the hypothesis that *C. septempunctata* is more responsive than are native ladybirds to the availability of alternative prey in alfalfa, which may account in part for the displacement of native ladybirds from alfalfa by the introduced species as aphid numbers have declined. The differing responses of the native and introduced ladybirds to spatial patterns of the alternative prey underscore the importance of extending the study of predator aggregation to understand better how polyphagous predators distribute themselves in response to spatial patterns of multiple species of potential prey.

Keywords Alternative prey · Biological control · *Coccinella septempunctata* · *Hippodamia* · Invasive species · Numerical response

Introduction

The response of natural enemies to spatial variation in the density of their prey is a long-standing issue of great interest, with implications for pest control (e.g., Murdoch and Briggs 1996; Bonsall et al. 2004). Arthropod predators frequently aggregate in patches of high prey density (e.g., Morris 1972; Huffaker et al. 1976; Bryan and Wratten 1984; Harwood et al. 2001, 2003; Horvath et al. 2005). Given that most of these predators are polyphagous and attack diverse prey (Hagen et al. 1999), and given the potential for indirect interactions among prey from sharing these predators (e.g., Holt and Lawton 1994; Evans and England 1996; Cardinale et al. 2003; Musser and Shelton 2003; Harmon and Andow 2004; Koss et al. 2004; Koch et al. 2005), it is of interest to determine how arthropod predators respond to varying local densities of multiple species of prey as they forage within and among habitats.

In this light, it is noteworthy that even broadly generalist predators may show distinct prey preferences that influence where they forage (e.g., Ostman and Ives 2003). Aphidophagous ladybirds (Coleoptera: Coccinellidae) are an interesting example, in that their apparent prey preference for aphids is often

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accompanied by generalist tendencies to feed on a variety of alternative prey as well (Hodek and Honěk 1996; Dixon 2000). Adults of these predators are well-known to aggregate in response to their aphid prey at a variety of spatial scales (Ives et al. 1993), ranging from among individual plants and patches within habitats (e.g., Frazer et al. 1981; Sakuratani et al. 1983; Turchin and Kareiva 1989; Obata and Johki 1990; Elliott and Kieckhefer 2000; With et al. 2002; Schellhorn and Andow 2005) to among large-scale habitat units (e.g., agricultural fields and orchards) scattered across the landscape (e.g., Honěk 1982; Evans and Youssef 1992; Giles et al. 1994; Elliott et al. 2002; Brown 2004). In general, however, the tendencies of aphidophagous ladybirds to aggregate also in response to availability of alternative prey are unknown (but see, e.g., Evans and Youssef 1992; Giles et al. 1994; Harmon et al. 2000).

Here we assess the aggregative responses of adult ladybirds to primary versus alternative prey in alfalfa in the intermountain west of North America. Differences among species in these responses may play an important role in the recent replacement of native ladybirds by the introduced species, *Coccinella septempunctata* L., in this habitat (Evans 2000, 2004). Aided by USDA redistribution efforts following its establishment in eastern North America in the 1970s (Angalet et al. 1979; Schaefer et al. 1987), *C. septempunctata* rapidly dispersed westward and arrived in alfalfa fields of Utah in the early 1990s (Evans and Swallow 1993). Historically, these alfalfa fields have harbored many native ladybirds (e.g., Parks 1913; Evans and Richards 1997). Upon its arrival, *C. septempunctata* rose rapidly in numbers, while numbers of native ladybirds declined. Thus, in recent years, *C. septempunctata* has become consistently the most common ladybird occupying this habitat (Evans 2004; see also Turnock et al. 2003).

Both *C. septempunctata* and native ladybirds feed primarily on the pea aphid (*Acyrthosiphon pisum* [Harris]) in Utah's alfalfa fields, although they also consume other prey as well (Hussain 1975; Ouayogode and Davis 1981). Pea aphids occurred in high numbers in these fields at the time of *C. septempunctata*'s arrival in the early 1990s, but they have occurred only in low (economically insignificant) numbers since that time (Evans 2004). A frequent alternative prey of ladybirds is the larva of the alfalfa weevil (*Hypera postica* [Gyllenhal]); this is the most important pest insect of alfalfa in Utah, and it continues to occur every year in very large numbers in most fields (Evans and England 1996).

Native adult ladybirds aggregate strongly in response to locally high densities of the pea aphid in alfalfa fields in Utah (Evans 2004). The decline in numbers of native ladybirds in recent years in this habitat may hence reflect that these species have abandoned alfalfa fields to forage and reproduce elsewhere as aphid numbers have dropped. In contrast, the newly dominant *C. septempunctata* may continue to persist in this habitat, even in the presence now of only low numbers of aphids, because it is more responsive to the availability of alternative prey such as weevils. An initial set of field experiments, in which local aphid (but not weevil) densities within alfalfa fields were manipulated intentionally, supported this general hypothesis (Evans 2004). In these experiments, intentional alterations of aphid numbers (achieved by caging) were confounded with unintentional alterations of weevil numbers. Therefore, to assess ladybird foraging patterns further, here we have manipulated independently the local densities of alfalfa weevil larvae and pea aphids within an alfalfa field, and measured the aggregative responses of the introduced and native ladybird adults. The central question addressed in the field experiment presented here is the degree to which these predators (especially *C. septempunctata*) may respond to spatial variation in density not only of their primary prey (i.e., aphids), but also to that of the abundant alternative prey, alfalfa weevils.

Materials and methods

A field experiment was conducted by creating thirty-two square plots, each 2 m^2, in a grid in an alfalfa field near Logan, Utah, in spring 2002, with 15 m between adjacent plots. Numbers of weevil larvae or aphids were manipulated in these plots, in a 2 × 2 factorial, completely randomized design, such that there were eight plots each of the following four treatments: high numbers of both aphids and weevils (HaHw), high numbers of aphids and low numbers of weevils (HaLw), low numbers of aphids and high numbers of weevils (LaHw), and low numbers of both aphids and weevils (LaLw).

The field was naturally infested with high numbers of weevils and low numbers of aphids (see Results below). Low numbers of weevil larvae hatching and maturing in the plots were achieved by placing screened cages ($1.4 \times 1.4 \times 0.75$ m^3) over plots for 3 weeks (from mid April through early May) to protect the plots, thereby reducing the number of ovipositing females of the weevils during this time period (some females had migrated into plots before the plots were caged). Although such caging also prevented aphid predators from colonizing the plots, any reduction in the low numbers of aphids present in the plots at this time was temporary, and by the start of the experiment (in late May) aphid numbers in these plots were similar to those that had remained uncaged (see Results below). High numbers of aphids were achieved in plots by rearing aphids in the greenhouse and adding them to plots in large numbers on May 23 (approximately 7,500 aphids of mixed ages were added per plot). The alfalfa stood 40–50 cm tall and was nearly mature at this time; it was cut for hay in early June at the conclusion of the experiment.

Upon the addition of aphids, all 32 plots were censused over the next 8 days for weevils, aphids, and ladybird adults. To assess prey densities, samples of 25 alfalfa stems were taken from each plot twice during the experiment. On May 24, the stems were cut at the base and inverted and shaken in a large plastic bucket; the aphids and weevils shaken from the stems were collected and frozen for later counting. On May 31, similarly cut stems were placed into a plastic bag and frozen. Subsequently, aphids and weevils were counted from these frozen samples. On the mornings of May 24, 25, 29, 30, and 31, each of the 32 plots was searched visually for ladybirds in systematic fashion for 2 min. All adults observed were identified to species and recorded, but otherwise the ladybirds and the plots were left undisturbed.

Densities of aphids, weevils, and adults of *C. septempunctata* and native ladybirds were each compared among treatments by two-way analysis of variance (ANOVA), both early (i.e., May 24 for prey, and May 24–25 [combined censuses] for ladybirds) and late in the experiment (May 31 for prey, and May 29–31 [combined censuses] for ladybirds). Because only modest numbers of native ladybirds occurred in the plots, and because patterns for individual native species were similar, the collective response to treatments of native ladybirds (i.e., of all native species combined) was analyzed statistically along with the responses of sufficiently abundant individual native species. To equalize variances among treatment combinations (as tested by the $F_{\max}$ test), densities (i.e., count data) were square-root transformed prior to analysis (Sokal and Rohlf 1981). Densities are expressed below as the number of prey per stem or the number of adult ladybirds per m^2.

Results

Overall, adults of the introduced species, *C. septempunctata*, outnumbered adults of all native ladybird species combined in the plots throughout the experiment (Figs. 1, 2). Individuals of *Hippodamia convergens* Guerin and *H. quinquesignata quinquesignata* (Kirby) represented 64% and 28% of all native adults recorded in plot censuses (other, less abundant species included *H. sinuata crotchi* Casey, *Coccinella transversoguttata richardsoni* Brown, and *H. apicalis* Casey/*H. expurgata* Casey [these two sibling species can only be distinguished by examination of male genitalia; Gordon 1985]).

At the outset of the experiment, plots with aphids added harbored 13× more aphids than the low numbers of aphids occurring naturally in plots to which aphids had not been added, and plots that had been unprotected from ovipositing weevil females earlier in the spring harbored more than twice as many weevil larvae as did protected plots (there was no significant

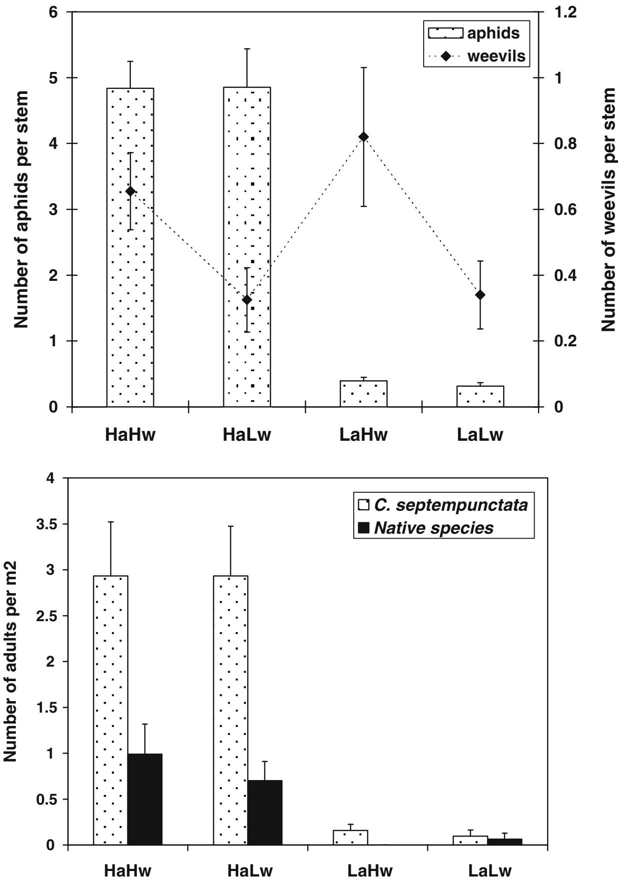

Fig. 1 *Top* The mean number (±1 standard error) of pea aphids and alfalfa weevil larvae per stem at the outset (24 May) of a field experiment in which plots of alfalfa were manipulated to have high numbers of both aphids and weevils (*HaHw*), high numbers of aphids and low numbers of weevils (*HaLw*), low numbers of aphids and high numbers of weevils (*LaHw*), or low numbers of both aphids and weevils (*LaLw*). *Bottom* The mean number (+1 standard error) of adults per m^2 of the introduced ladybird, *C. septempunctata*, and of native ladybirds (all species combined) in these same plots (on 24–25 May)

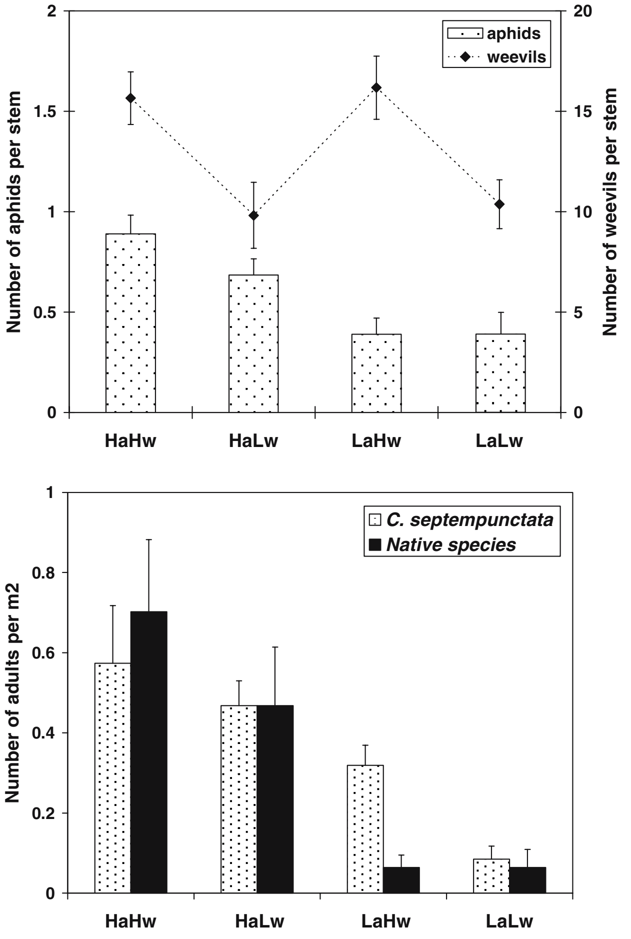

Fig. 2 *Top* The mean number (±1 standard error) of pea aphids and alfalfa weevil larvae per stem at the conclusion (31 May) of the field experiment in which plots of alfalfa were manipulated to have high numbers of both aphids and weevils (*HaHw*), high numbers of aphids and low numbers of weevils (*HaLw*), low numbers of aphids and high numbers of weevils (*LaHw*), or low numbers of both aphids and weevils (*LaLw*). *Bottom* The mean number (+1 standard error) of adults of the introduced ladybird, *C. septempunctata*, and of native ladybirds (all species combined) in these same plots (on 29–31 May)

interaction among treatments for either aphids or weevils; Fig. 1 and Table 1). Adults of both *C. septempunctata* and native ladybirds responded very strongly to experimentally increased numbers of aphids at this time, but did not respond to differences in local weevil density (Fig. 1; Table 1). Thus, most ladybirds occurred in plots with aphids added.

By the conclusion of the experiment a week later, the ladybirds and other predators had reduced greatly the number of aphids present in plots to which aphids had previously been added. Nonetheless, significantly more aphids remained in these plots than in plots to which aphids had not been added (Table 1). Overall, plots with aphids added harbored twice as many aphids as plots to which aphids had not been added (and in which little change in density had occurred from one week earlier; Fig. 2).

During the course of the experiment, populations of larval weevils in the plots increased greatly (Fig. 2). While much of the increase apparent in Fig. 2 resulted from large numbers of eggs hatching, the increase also reflected in part the more thorough assessment of stem samples late versus early in the experiment. Thus, whereas all instars were censused fully by examining frozen stems in the laboratory late in the experiment, very young weevil larvae were not censused well early in the experiment, when stems were sampled by shaking them in a bucket in the field (young larvae fed in protected locations on the plant from which they were not dislodged readily by shaking). More importantly, however, the sampling effort did not vary among plots on either occasion. Weevil densities increased in all plots, and plots unprotected from weevil adults earlier in the spring continued to harbor significantly more (1.6× as many) weevil larvae as plots that had been protected (Table 1; Fig. 2).

Again, native ladybirds responded very strongly to aphid numbers but not to weevil numbers (Fig. 2; Table 1). In contrast, a significant interaction occurred in the response of *C. septempunctata* adults to aphid and weevil density (Table 1). Overall, adults of *C. septempunctata* responded positively to aphid numbers in the plots, but they also responded positively to weevil numbers in plots with low (but not high) numbers of aphids (Fig. 2). Thus, relatively large numbers of *C. septempunctata* adults were found in plots with low aphid numbers but high weevil numbers.

Discussion

It is important to determine how polyphagous predators respond to individually varying local densities of multiple prey species, as such may have consequences for the interlinking of population dynamics of the individual prey species sharing the predators (Holt and Lawton 1994). Predator aggregations in response to local prey densities develop from the collective actions of individual predators, whose foraging behavior typically is strongly influenced by the rate and nature of prey encounter (e.g., Nakamuta 1982, 1991; Kareiva and Odell 1987; Kareiva 1990; Yasuda and Ishikawa 1999; but note also Hemptinne et al. 1992; Kindlmann and Dixon 1993; Dixon 1997). Adult ladybirds foraging in alfalfa fields readily consume larvae of alfalfa weevils as well as pea aphids (Essig and Michelbacher 1933; Yakhontov 1934; Evans and England 1996).

Table 1 *P* values (for associated $F_{1,\ 28}$ values for effects of aphid or weevil density manipulation and their interaction) in two-way analyses of variance for square-root transformed counts of prey (pea aphids and alfalfa weevil larvae) and predators (adults of *C. septempunctata* and native ladybirds) in experimental plots of alfalfa

Date(s)	Species	Effect		
		Aphid	Weevil	Interaction
Early				
May 24	Pea aphid	<0.0001	NS	NS
May 24	Alfalfa weevil	NS	0.003	NS
May 24–25	*C. septempunctata*	<0.0001	NS	NS
May 24–45	Native ladybirds	<0.0001	NS	NS
May 24–25	*H. convergens*	<0.0001	NS	NS
May 24–25	*H. quinquesignata*	<0.01	NS	NS
Late				
May 31	Pea aphid	<0.001	NS	NS
May 31	Alfalfa weevil	NS	0.0006	NS
May 29–31	*C. septempunctata*	<0.001	0.031	0.043
May 29–31	Native ladybirds	<0.0001	NS	NS
May 29–31	*H. convergens*	<0.0001	NS	NS
May 29–31	*H. quinquesignata*	<0.005	NS	NS

Analyses are presented both for all individuals of native ladybirds combined, and for numbers of individuals of the two most common native species, *H. convergens* and *H. quinquesignata*

NS not significant ($P > 0.05$)

Local densities of these two major ladybird prey in this habitat vary independently of each other (Evans and Youssef 1992; E.W. Evans, unpublished results). The field experiment presented here was conducted to determine the extent of aggregation of adult ladybirds in response to manipulation of local densities of these prey species.

The experimental results reveal that native ladybirds (primarily *H. convergens* and *H. quinquesignata*), and the introduced ladybird, *C. septempunctata*, aggregated strongly in response to high aphid density within alfalfa plots. This was true both at the outset (when aphids numbers were vastly higher in plots to which they had been added than in control plots with background levels of aphids reflective of the field at large), and at the conclusion of the experiment (when the difference in aphid density between treatments had narrowed considerably, such that relatively low numbers of aphids occurred even in "high density" plots). The ladybirds' strong aggregative response to aphids is similar to results in previous studies (e.g., Frazer et al. 1981; Honěk 1982; Sakuratani et al. 1983; Elliot and Kieckhefer 2000).

Native ladybird adults did not respond to spatial variation in alfalfa weevil density throughout the experiment. Adults of *C. septempunctata* similarly did not respond when densities of their primary prey, pea aphids, were high in treated plots at the outset. However, as overall densities for all plots combined declined for aphids and increased for weevils as the experiment proceeded, adults of the introduced predator occurred in relatively high numbers in plots with high weevil numbers but low aphid numbers. Thus, it appears that the introduced predator was distinctive in its responsiveness to high local availability of the alternative prey, alfalfa weevil larvae, when the availability of the primary prey, pea aphids, was low throughout the habitat. It is not clear why *C. septempunctata* differs from native ladybirds in its response to weevils. Native ladybirds may be especially dependent upon aphid-specific cues in choosing where to forage (e.g., Evans and Richards 1997). The difference between the ladybirds may also reflect the long history of association of *C. septempunctata* and the alfalfa weevil in the Old World (e.g., Yakhontov 1934; Honěk 1985).

These results are consistent with previous results of experiments in which only the local abundance of aphids (and not that of weevils) was manipulated in alfalfa fields, and from which it appeared that adults of the native ladybirds are more responsive than is *C. septempunctata* to spatial variation in aphid numbers (Evans 2004). In those experiments, native ladybirds aggregated strongly at high aphid density plots, but dispersed rapidly when aphid densities dropped to the same low levels characteristic of the fields at large (see also Ives 1981). Adults of *C. septempunctata* persisted in the alfalfa fields, but shifted their attentions from local areas formerly harboring large densities of aphids to local areas in which alfalfa weevils occurred in high numbers. However, as an inadvertent consequence of the experimental design (initial caging in experimental plots to protect aphid populations), these local areas with high weevil density were the control (i.e., uncaged) plots with low numbers of aphids throughout the experiment, and thus the interpretation of the experimental results was not fully clear (Evans 2004). The consistency of the results of the present experiment (in which a two-way factorial design was used to separate the effects of varying aphid and weevil density) with those of the previous experiments supports the hypothesis that *C. septempunctata* has replaced native species as the dominant ladybird in alfalfa at least in part because it is relatively responsive to the availability of alternative prey such as weevils in the absence of high aphid numbers in this habitat. Native ladybirds, in contrast, appear to have largely abandoned alfalfa fields in recent years as the numbers of aphids in these fields have declined (Evans 2004).

The results reveal relatively subtle differences among closely related predators (i.e., among species of aphidophagous Coccinellini) in their aggregative responses to primary versus alternative prey. Such may have interesting consequences for the population dynamics of the prey. In the case of native ladybirds, the vulnerability of the alternative prey, alfalfa weevil larvae, appears to be strongly influenced by the co-occurrence of these larvae with individuals of the primary prey, pea aphids. Thus, adult native ladybirds appear to concentrate their foraging especially where aphids occur in high numbers, and may eat alternative prey incidentally as they encounter them (see also Evans and England 1996; Ostman and Ives 2003). On the other hand, adults of *C. septempunctata* may at times (e.g., early in the season in alfalfa) be influenced in where they forage by the local density of the alternative prey (alfalfa weevil larvae), thereby contributing through predation of co-occurring aphids to keeping numbers of the primary prey in such areas at low density. In this way, these introduced predators may act in alfalfa fields more as generalist predators that contribute to preventing initially small populations of aphids from growing to economically significant levels (e.g., Flaherty 1969; Ehler and Miller 1978; Edwards et al. 1979; Riechert and Bishop 1990; Settle et al. 1996; Ives and Settle 1997; Chang and Kareiva 1999; Symondson et al. 2002; Harwood et al. 2004). In contrast, native ladybirds may act more nearly as specialist predators that track their primary prey populations more closely across space and time. Introduced and native species therefore may interact synergistically in influencing the population dynamics of alfalfa insect pests (e.g., Pimentel 1961; Murdoch et al. 1985). Such possibilities underscore the importance of expanding the study of predator aggregation to better understand how polyphagous arthropod predators respond to individually varying local densities of the multiple prey species that they attack.

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References

Angalet GW, Tropp JM, Eggert AN (1979) *Coccinella septempunctata* in the United States: recolonizations and notes on its ecology. Environ Entomol 8:896–901

Bonsall MB, Hassell MP, Reader PM, Hefin Jones T (2004) Coexistence of natural enemies in a multitrophic host-parastoid system. Ecol Entomol 29:639–647

Brown MW (2004) Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA. Biol Control 29:189–198

Bryan KM, Wratten SD (1984) The responses of polyphagous predators to prey spatial heterogeneity: aggregation by carabid and staphylinid beetles to their cereal aphid prey. Ecol Entomol 9:251–259

Cardinale BJ, Harvey CT, Gross K, Ives AR (2003) Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. Ecol Lett 6:857–865

Chang GC, Kareiva P (1999) The case for indigenous generalists in biological control. In: Hawkins BA, Cornell HV (eds) Theoretical approaches to biological control. Cambridge University Press, Cambridge, pp 103–115

Dixon AFG (1997) Patch quality and fitness in predatory ladybirds. Ecol Stud Anal Synth 130:205–233

Dixon AFG (2000) Insect predator-prey dynamics. Ladybird beetles and biological control. Cambridge University Press, Cambridge, p 257

Edwards CA, Sunderland KD, George KS (1979) Studies on polyphagous predators of cereal aphids. J Appl Ecol 16:811–823

Ehler LE, Miller JC (1978) Biological control in temporary agroecosystems. Entomophaga 23:207–212

Elliott NC, Kieckhefer RW (2000) Response of coccinellids to spatial variation in cereal aphid density. Popul Ecol 42:81–90

Elliott NC, Kieckhefer RW, Michels GJ Jr, Giles KL (2002) Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. Environ Entomol 31:253–260

Essig EO, Michelbacher AE (1933) The alfalfa weevil. Calif Agric Exp Stn Bull 567:3–99

Evans EW (2000) Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* in western North America. Eur J Entomol 97:469–474

Evans EW (2004) Habitat displacement of North American ladybirds by an introduced species. Ecology 85:637–647

Evans EW, England S (1996) Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. Ecol Appl 6:920–930

Evans EW, Richards DR (1997) Managing the dispersal of ladybird beetles (Col.: Coccinellidae): use of artificial honeydew to manipulate spatial distributions. Entomophaga 42:93–102

Evans EW, Swallow JG (1993) Numerical responses of natural enemies to artificial honeydew in Utah alfalfa. Environ Entomol 22:1392–1401

Evans EW, Youssef NN (1992) Numerical responses of aphid predators to varying prey density among Utah alfalfa fields. J Kans Entomol Soc 65:30–38

Flaherty DL (1969) Ecosystem trophic complexity and densities of the Williamette mite, *Eotetranychus williamettei* Ewing (Acarina: Tetranychidae). Ecology 50:911–916

Frazer BD, Gilbert N, Nealis V, Raworth DA (1981) Control of aphid density by a complex of predators. Can Entomol 113:1035–1041

Giles KL, Obrycki JJ, Degooyer TA (1994) Prevalence of predators associated with *Acyrthosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. Biol Control 4:170–177

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

Hagen KS, Mills NJ, Gordh G, McMurtry JA (1999) Terrestrial arthropod predators of insect and mite pests. In: Bellows TS, Fisher TW (eds) Handbook of biological control. Principles and applications of biological control. Academic, San Diego, pp 383–503

Harmon JP, Andow DA (2004) Indirect effects between shared prey: predictions for biological control. BioControl 49:605–626

Harmon JP, Ives AR, Losey JE, Olson AC, Rauwald KS (2000) *Colemegilla maculata* (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions. Oecologia 125:543–548

Harwood JD, Sunderland KD, Symondson WOC (2001) Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. J Appl Ecol 38:88–99

Harwood JD, Sunderland KD, Symondson WOC (2003) Web-location by linyphiid spiders: prey-specific aggregation and foraging strategies. J Anim Ecol 72:745–756

Harwood JD, Sunderland KD, Symondson WOC (2004) Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. Mol Ecol 13:3549–3560

Hemptinne J-L, Dixon AFG, Coffin J (1992) Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. Oecologia 90:238–245

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

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

Honěk A (1982) Factors which determine the composition of field communities of adult aphidophagous coccinellids (Coleoptera). Z Ang Entomol 94:157–168

Honěk A (1985) Habitat preferences of aphidophagous coccinellids (Coleoptera). Entomophaga 30:253–264

Horvath R, Lengyel S, Szinetar C, Jakab L (2005) The effect of prey availability on spider assemblages on European black pine (*Pinus nigra*) bark: spatial patterns and guild structure. Can J Zool 83:324–335

Huffaker CB, Simmonds FJ, Laing JE (1976) The theoretical and empirical basis of biological control. In: Huffaker CB, Messenger PS (eds) Theory and practice of biological control. Academic, New York, pp 41–78

Hussain M (1975) Predators of the alfalfa weevil, *Hypera postica*, in western Nevada—a greenhouse study. (Coleoptera Curculionidae). J N Y Entomol Soc 83:226–228

Ives AR, Kareiva P, Perry R (1993) Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. Ecology 74:1929–1938

Ives AR, Settle WH (1997) Metapopulation dynamics and pest control in agricultural systems. Am Nat 149:220–246

Ives PM (1981) Estimation of coccinellid numbers and movement in the field. Can Entomol 113:981–997

Kareiva P (1990) The spatial dimension in pest-enemy interactions. In: Mackauer M, Ehler LE, Roland J (eds) Critical issues in biological control. Intercept, Andover, Hants, pp 213–227

Kareiva P, Odell G (1987) Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. Am Nat 130:233–270

Kindlmann P, Dixon AFG (1993) Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. Eur J Entomol 90:443–450

Koch RL, Venette RC, Hutchison WD (2005) Influence of alternate prey on predation of Monarch butterfly (Lepidoptera: Nymphalidae) larvae by the multicolored Asian lady beetle (Coleoptera: Coccinellidae). Environ Entomol 34:410–416

Koss AM, Chang GC, Snyder WE (2004) Predation of green peach aphids by generalist predators in the presence of alternative, Colorado potato beetle egg prey. Biol Control 31:237–244

Morris RF (1972) Predation by insects and spiders inhabiting colonial webs of *Hyphantria cunea*. Can Entomol 104:1197–1207

Murdoch WW, Briggs CJ (1996) Theory for biological control: recent developments. Ecology 77:2001–2013

Murdoch WW, Chesson J, Chesson PL (1985) Biological control in theory and practice. Am Nat 125:344–366

Musser FR, Shelton AM (2003) Predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. Environ Entomol 32:1131–1138

Nakamuta K (1982) Switchover in searching behavior of *Coccinella septempunctata* L. (Coleoptera Coccinellidae) caused by prey consumption. Appl Entomol Zool 17:501–506

Nakamuta K (1991) Aphid alarm pheromone component, (E)-B-farnesene, and local search by a predatory lady beetle, *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae). Appl Entomol Zool 26:1–7

Obata S, Johki Y (1990) Distribution and behaviour of adult ladybird, *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae), around aphid colonies. Jpn J Entomol 58:839–845

Ostman O, Ives AR (2003) Scale-dependent indirect interactions between two prey species through a shared predator. Oikos 102:505–514

Ouayogode BV, Davis DW (1981) Feeding by selected predators on alfalfa weevil larvae. Environ Entomol 10:62–64

Pimentel D (1961) Species diversity and insect population outbreaks. Ann Entomol Soc Am 54:76–86

Parks TH (1913) The alfalfa weevil. Extension Bulletin Number 7, Agricultural Experiment Station. University of Idaho, Moscow, Idaho, USA

Riechert SE, Bishop L (1990) Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology 71:1441–1450

Sakuratani Y, Sugiura Y, Isida M, Kuwahara S, Sugimoto T (1983) Aggregative response of adults of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) to aphid population density. Mem Fac Agric Kinki Univ 16:49–54

Schaefer PW, Dysart RJ, Specht HB (1987) North American distribution of *Coccinella septempunctata* (Coleoptera: Coccinellidae) and its mass appearance in coastal Delaware. Environ Entomol 16:368–373

Schellhorn NA, Andow DA (2005) Response of coccinellids to their aphid prey at different spatial scales. Popul Ecol 47:71–76

Settle WH, Ariawan H, Astuti ET, Cahyana W, Hakim AL, Hindayana D, Lestari AS, Pajarningsih, Sartanto (1996) Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77:1975–1988

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. WH Freeman, San Francisco

Symondson WOC, Sunderland KD, Greenstone MH (2002) Can generalist predators be effective biocontrol agents? Annu Rev Entomol 47:561–594

Turchin P, Kareiva P (1989) Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. Ecology 70:1008–1016

Turnock WL, Wise IL, Matheson FO (2003) Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. Can Entomol 135:391–404

With KA, Pavuk DM, Worchuck JL, Oates RK, Fisher JL (2002) Threshold effects of landscape structure on biological control in agroecosystems. Ecol Appl 12:52–65

Yakhontov VV (1934) The alfalfa weevil *Phytonomus* (*Phytonomus variabilis* Hbst.). Rev Appl Entomol Ser A 22:334–336

Yasuda H, Ishikawa H (1999) Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle. J Appl Entomol 123:585–589