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INTERACTIONS BETWEEN SPECIALIST AND GENERALIST NATURAL ENEMIES: PARASITOIDS, PREDATORS, AND PEA APHID BIOCONTROL

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Abstract. Most biological control systems involve a diverse community of natural enemies. We investigated how specialist and generalist natural enemies differ as biological control agents of pea aphids (*Acyrthosiphon pisum*), and how interactions among natural enemies affect successful control. In alfalfa, pea aphids are attacked by a specialist parasitoid wasp, *Aphidius ervi*, and a guild of generalist predators primarily made up of *Nabis* and *Orius* bugs, coccinellid and carabid beetles, and web-building spiders. In three field experiments, we manipulated the parasitoid, then the generalist predator guild, and finally both classes of natural enemy, and recorded resulting impacts on pea aphid population control. The parasitoid caused little immediate reduction in aphid population growth but caused a large decline after a delay corresponding to the generation time of the parasitoid. In contrast, the generalist guild caused an immediate decline in the aphid population growth rate. However, the generalists did not exert density-dependent control, so aphid densities continued to increase throughout the experiment. The third field experiment in which we simultaneously manipulated parasitoids and predators investigated the possibility of ''nonadditive effects'' on aphid control. Densities of parasitoid pupae were 50% lower in the presence of generalist predators, indicating intraguild predation. Nonetheless, the ratio of parasitoids to aphids was not changed, and the impact of the two types of natural enemies was additive.

We constructed a stage-structured model of aphid, parasitoid, and predator dynamics and fit the model to data from our field experiments. The model supports the additivity of parasitoid and predator effects on aphid suppression but suggests that longer-term experiments (32 d rather than 20 d) would likely reveal nonadditive effects as predation removes parasitoids whose response to aphid densities occurs with a delay. The model allowed us to explore additional factors that could influence the additivity of parasitoid and predator effects. Aphid density-dependent population growth and predator immigration in response to aphid density would likely have little influence on the additivity between parasitism and predation. However, if a parasitoid were to show a strong Type II functional response, in contrast to *A. ervi* whose functional response is nearly Type I, interactions with predators would likely be synergistic. These analyses reveal factors that should be investigated in other systems to address whether parasitism and predation act additively on host densities.

Key words: Acyrthosiphon pisum; *additive effect;* Aphidius ervi; *biocontrol; coccinellid beetle; entomopathogen; fungus spp.; generalist predator guild; intraguild predation; nabid bug; parasitoid wasp; specialist natural enemy; spider.*

INTRODUCTION

Ecologists interested in biological control have suggested several characteristics of a natural enemy that are likely to make it an effective control agent. These characteristics include a high degree of prey specificity, short development time relative to prey, and high reproductive potential (e.g., Wardle and Buckle 1923, Huffaker and Messenger 1976, Debach and Rosen 1991). Among entomophagous arthropods, parasitoid Hymenoptera and Diptera exemplify these characteristics, since parasitoids generally attack only a few prey species, develop within their prey and thus must have a generation time comparable to that of the host, and generally have highly fecund adult females that can attack many hosts in their lifetime. These characteristics can allow parasitoids to mount a strong numerical response when prey outbreaks occur, perhaps leading to outbreak suppression (Hassell 1980, Hassell and May 1986, Berryman 1992, Murdoch 1994, Turchin et al. 1999). Intentional parasitoid introductions have often led to successful biological control of accidentally introduced agricultural pests, clearly demonstrating the ability of these specialists to regulate densities of their hosts (Debach and Rosen 1991), and examinations of compiled life tables appear to verify the importance of parasitoids as natural enemies of herbivorous insects (Cornell and Hawkins 1995, Hawkins et al. 1997).

In contrast, generalist predators often possess none of the traits believed to confer effectiveness in biolog-

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ical control. Predatory arthropods often have catholic feeding habits and long generation times relative to herbivores, so that even if there is a numerical response to changes in the density of a single herbivore species (e.g., Symondson et al. 2002*a*), the response is unlikely to occur quickly enough to lead to outbreak suppression (Hassell and May 1986, DeBach and Rosen 1991). Indeed, where predator introductions have led to successful biological control, the predators have usually been specialists with life histories more closely resembling parasitoids than typical predators (DeBach and Rosen 1991). Generalists also commonly engage in intraguild predation (Polis et al. 1989, Polis and Holt 1992, Rosenheim et al. 1993, 1995, Rosenheim 1998), feeding not only on other predators but also on parasitoids (Brodeur and Rosenheim 2000, Snyder and Ives 2001). Through strong intraguild predation, predators can exacerbate prey outbreaks (Rosenheim et al. 1993, Snyder and Ives 2001, Snyder and Wise 2001) and thus indirectly increase herbivore damage to plants (Snyder and Wise 2001). Despite these limitations, generalist predators have been reported to be successful control agents in cropping systems as different as vegetable gardens (Riechert and Bishop 1990, Snyder and Wise 2001) and rice (Settle et al. 1996, Fagan et al. 1998), leading some authors to question the superiority of specialist natural enemies (Riechert and Lockley 1984, Murdoch et al. 1985, Sunderland 1999, Symondson et al. 2002*b*). Progress in understanding the relative merits of specialists vs. generalists in biological control has been hampered by the paucity of field studies that compare the impact of these two classes of natural enemies in the same agroecosystem (Chang and Kareiva 1999).

The experiments reported here were designed to examine the relative impacts of a specialist parasitoid and a guild of predators on herbivore population dynamics. We specifically asked whether different types of natural enemies act additively to control herbivore populations, or whether they negatively impact each other, such that the combined effect of multiple types of natural enemies is less than the sum of effects that each would achieve by itself. We have been working with the community of natural enemies that attack pea aphids (*Acyrthosiphon pisum*) in alfalfa (*Medicago sativa*) fields in Wisconsin. A specialist parasitoid wasp, *Aphidius ervi*, frequently reaches high levels of percent parasitism of pea aphids (Rauwald and Ives 2001), and a diverse guild of generalist predators attack pea aphids both in the foliage and on the ground. In a previous study (Snyder and Ives 2001), we found that predatory carabid beetles (primarily *Pterostichus melanarius*) diminished pea aphid biological control by feeding on parasitoid pupae. However, in that earlier study we did not examine the impact of other predators, so we could not determine whether predation on herbivores by other predators in the community might compensate for the negative effects of carabids.

Of the three field experiments we report here, the first manipulates parasitoid and aphid densities, the second manipulates the entire generalist predator guild in the absence of parasitoids, and the third simultaneously manipulates both parasitoids and generalist predators. The first and third experiments also experienced a fungal epizootic. All experiments were conducted for time periods corresponding to 2–4 aphid generations, thereby allowing us to investigate both aphid suppression and potential nonadditive interactions among natural enemies on time scales appropriate to observe population dynamics. We also developed a stage-structured population model for aphids, parasitoids, and generalist predators. By fitting the model to the data from all experiments, we were able to examine in more detail the importance of intraguild interactions on pea aphid control.

Materials and Methods

Pea aphids and their specialist parasitoid

Pea aphids, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), are phloem-feeders that attack a variety of legumes. Pea aphids were introduced into North America from Europe sometime in the last century (Hagen et al. 1976, Mackauer and Kambhampati 1986). Pea aphids develop quickly, with development from first instar to reproducing adults occurring in as little as 10 d (Hutchinson and Hogg 1984, 1985, Thiboldeaux 1986). During the summer, reproduction is asexual (Blackman and Eastop 1984). The parthenogenic females produce as many as four nymphs per day, and nymphs go through four juvenile instars in ~7 d at normal summer temperatures (Hutchinson and Hogg 1984, 1985, Thiboldeaux 1986).

Aphidius ervi

The parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae), also native to Europe, was released in North America in the 1960s in an attempt to control pea aphids (Gonzalez et al. 1978). *Aphidius ervi* populations are tightly coupled to those of their host. Female wasps deposit a single egg into an early instar aphid. The *A. ervi* develops within the host for ~8 d, then kills the aphid and pupates within its former host's exoskeleton, the mummy, for ~6 d. In Wisconsin alfalfa fields, pea aphids are *A. ervi*'s only host. Estimates of the egg load for female *A. ervi* range from 96.4 (Thiboldeaux 1986) to 567 eggs (Mackauer 1971), leading to high potential lifetime fecundity. Thus, *A. ervi* possesses the traits believed to characterize a good biological control agent, with generations of similar duration to the pest, strong prey specificity, and a high reproductive potential. However, although pea aphid outbreaks have become less common following the introduction of *A. ervi*, densities of the aphids still can reach damaging levels in alfalfa and pea crops (Harvey et al. 1972, Harper and Kaldy 1982, Maiteki and Lamb

1985, Soroka and MacKay 1990, White and Eigenbrode 2000).

The generalist predator guild

Alfalfa fields in Wisconsin also contain a diverse community of predators that vary in their degree of prey specificity. We will discuss these predators in order of their prey specificity, with the more specialized generalists considered first. Ladybird beetles, lacewings, and syrphid flies all have larvae (and, in the case of ladybirds, adults) that prey largely on aphids. However, all of these predators also feed opportunistically on other prey. For example, the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), one of the most abundant predators during our field experiments (Table 1), feeds not only on aphids (LaMana and Miller 1996) but also on other herbivores (Cottrell and Yeargan 1998*a*, *b*) and other predators (Cottrell and Yeargan 1999), including conspecifics (Wagner et al. 1999, Snyder et al. 2000). Indeed, these beetles can complete larval development on a diet of intraguild prey (Phoofolo and Obrycki 1998).

Also common in our fields are *Nabis* spp. (Hemiptera: Nabidae) and *Orius* spp. (Hemiptera: Anthocoridae), and a diverse group of spiders (primarily Linyphiidae and Tetragnathidae). These polyphagous predators feed on aphids (Sunderland 1975, Wheeler 1977, Sunderland and Vickerman 1980, Frazer et al. 1981, Flinn et al. 1985, Ekbom 1994, Giles et al. 1994) and also attack a wide variety of other insects, including other predators (Wheeler et al. 1968, Braman and Yeargan 1989). Even more broadly polyphagous are the carabid beetles. *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae), the most common carabid at our site (Snyder and Ives 2001), feeds not only on insects (Hagley et al. 1982) but also small vertebrates (Ovaska and Smith 1987), mollusks (Symondson et al. 1996), and seeds (Hagley et al. 1982). All of the most common predators at our study site have been reported to feed on pupae of the parasitoid *A. ervi* (Wheeler et al. 1968, Snyder and Ives 2001).

The predators have egg-to-adult development times 5 (coccinelids, lacewings, syrphids) to 20 times (many spiders, carabid beetles) longer than pea aphids. Thus, the community of predators in alfalfa share the traits thought to yield ineffective biological control agents, with moderate to very high degrees of polyphagy and long developmental times relative to aphids.

Fungal pathogen

Pea aphids are episodically attacked by fungal pathogens. Fungal epizootics require a combination of high host density and favorable moisture and temperature conditions that allow spore germination (Latge and Papierok 1988, Pickering and Gutierrez 1991, Milner 1997). In the final stages of fungal infection the aphid is killed, and a mass of fungal hyphae forms within the hosts' exoskeleton (a ''cadaver''). In Wisconsin, when aphid density is high, fungal infection of pea aphids can reach >50% (Hutchinson and Hogg 1985). Hutchinson and Hogg (1985) identified *Erynia* sp. as the main fungal pathogen attacking pea aphids in Wisconsin.

Field experiments

We conducted three field experiments in which we manipulated natural enemies to determine their impact on pea aphid population dynamics. Our field experiments were conducted in alfalfa fields located on the University of Wisconsin's Arlington Research Farm in south-central Wisconsin. Our experimental units were twelve $2 \times 2 \times 2$ m cages, covered on all sides but the bottom with 32×32 mesh Lumite screening (opening size 530 μm; Bioquip, Gardena, California, USA). The bottom edges of the cages were buried beneath 10 cm of soil to block movement of arthropods. Cages were randomly assigned to treatments. Each experiment also included three 2×2 m open reference areas where no arthropod manipulations were made.

Field experiment 1: aphid and parasitoid manipulation.—In the first experiment, we manipulated aphid and parasitoid abundances within cages in a 2×2 factorial design of ambient vs. supplemented aphid density, and ambient vs. supplemented parasitoid density, leading to four treatments: ambient aphids and parasitoids (treatment Control); aphids added, ambient parasitoids (+Aphid); ambient aphids, parasitoids added (+Para); and aphids and parasitoids added (+Aphid+Para). The alfalfa field was harvested on 11 June 1993, and cages were set up on 15 June when the alfalfa was just beginning to develop new leaves. Care was taken not to disturb the sites, so the cages contained ambient densities of aphids and natural enemies. Three randomly selected 2×2 m sites were marked as open references. The experiment was started on 16 June. Aphid densities were supplemented by distributing ~1000 aphids evenly throughout the cage. These aphids had been reared in the field in sleeve cages that were inoculated with unparasitized aphids on 16 May, so they were acclimated to field conditions. Parasitoid densities were supplemented in six cages by adding 10, 10, 10, and 8 mated females to cages on days 2, 5, 8, and 12 of the experiment (16 June is day 0). These female parasitoids were raised in a greenhouse and mated before release.

Aphid and parasitoid densities were monitored by counting the number of aphids and mummies on 50–200 haphazardly selected stems on days 0, 8, 14,18, 22, and 26 of the experiment in both cages and open reference plots. In most samples 200 stems were counted, but 100 and 50 stems were counted if there were >5 and 10 aphids per stem, respectively. In one cage in the +Aphid treatment, a female ladybird *Coccinella septempunctata* laid eggs, and we removed >100 coccinellid larvae. Despite removing larvae, high aphid mortality occurred, and this cage differed markedly

from the other two cages in the same treatment. Therefore, we excluded the cage from analysis. Cadavers caused by fungal infections were counted, and in cages that reached high aphid densities, these cadavers made up 10–18% of the total aphid population. In the open reference plots where aphid densities remained low, cadavers from fungal infection made up 0.5% of the aphid population. No assessment of other natural enemies was made.

Field experiment 2: predator manipulation.—In the second experiment, we manipulated the entire generalist predator guild, both ground- and foliar-dwelling predators, by removing predators from all 12 cages and then re-introducing predators to just six of the cages (Control), and not the other six (−Pred). The experiment was conducted in a field where parasitoids were naturally at low densities (a total of one aphid was parasitized in two collections of 25 aphids each), allowing us to isolate the impact of the generalists. Manipulations (described below) were initiated 2 wk after cutting, when alfalfa plants were about ~10 cm tall.

We manipulated predators in the foliage using a D-vac suction sampler (D-vac Company, Ventura, California, USA). We suctioned each cage twice, with each suction period lasting ~4 min. We used a separate collection bag for each suction period for each cage. After collection, we placed collection bags in a cooler, and returned all samples to the laboratory for sorting. We carefully hand-searched each D-vac bag three times, collecting all predators into individual plastic 33.3-mL (9-dram) vials (Bioquip, Gardena, California, USA). We then pooled the predators collected from all cages, returned to the field, and released these predators into the Control treatment cages. After predators were removed, all nonpredatory insects (including aphids) in the D-vac samples from each cage were also returned to the field and released into the cage from which they had been collected. Thus, we standardized the number and species composition of foliage predators released into each predator addition cage, but did not alter densities or species composition of other foliage arthropods.

We manipulated ground predators using pitfall traps made out of plastic cups (see Snyder and Wise 1999 for design). We placed one pitfall trap in each corner of each cage. Traps were covered with plastic plates suspended on a piece of wire; these plates block aphids from falling into the traps and also prevent traps from filling with rainwater (Snyder and Ives 2001). In predator removal cages, pitfall traps were left open for the duration of the experiment, and predators were collected from traps every 2 d. In the other cages traps were opened for 24 h to census ground predator densities at the beginning and end of each experiment. Nonpredatory arthropods were immediately released back into the cages.

We sampled aphids by counting the number of aphids and mummies on 200 haphazardly selected alfalfa stems in each cage and in the open reference plots. We counted aphids and mummies on days 5, 8, and 12 (day 0 was 28 June 2000). We terminated the experiment after 13 d, at which time we measured densities of foliage predators by suctioning each cage, as before, and thrice hand-searching each D-vac sample for predators.

Field experiment 3: predator and parasitoid manipulation.—In the third experiment we manipulated predators and parasitoids within the same experiment. This allowed us to compare directly the dynamical impact of each natural enemy on pea aphids, and also to look for interactions between generalists and the parasitoid. Our 2 × 2 factorial design yielded the following treatments: both predators and parasitoids removed (−Pred−Para); predators present, parasitoids removed (−Para); parasitoids present, predators removed (−Pred); and predators and parasitoids both present (Control). Each cage treatment was replicated three times. We also established three open reference plots.

Our methodology for manipulating ground and foliage predators was the same as in experiment 2. However, unlike in experiment 2, we standardized the number of aphids added to all cages. We placed all aphids collected from the D-vac samples (the same samples from which we removed predators) into a single plastic tray and allowed them to intermingle for ~10 min. We removed 12 groups of 200 aphids from this pooled collection and added one allotment to each field cage. At the time of the experiment, aphid densities in the field were high, and these allotments of 200 aphids/cage represented ~20% of the original aphid density. Adult parasitoids were not added to the cages, but rather parasitoids were manipulated by removing any observed mummy from the parasitoid removal cages during 5-min searches conducted every other day throughout the experiment. Percentage parasitism of the aphids we released in the cages was 8.0 ± 2.7% (N = two collections of 50 aphids each), so that each cage received about 16 parasitoids as larvae within aphids.

Arthropod densities were measured as in experiment 2. We counted aphids and mummies on day 3, 7, 10, 14, 17, and 21 (day 0 was 17 July 2000). We measured activity densities of ground-dwelling predators on days-3 and 21. We terminated the experiment on day 21 by suctioning to collect foliage-dwelling predators.

Laboratory experiments

We conducted a laboratory feeding trial designed to test whether the two most common foliage-dwelling predators, ladybird beetle larvae and nabid bugs, preferentially fed on aphids or mummies. In previous work we found that selective predation on mummies allowed carabid beetles to diminish biological control by *A. ervi* (Snyder and Ives 2001), and we wanted to test whether the foliage-dwelling predators acted similarly. We transplanted ~10 cm tall alfalfa plants collected at our study site into 18 cm diameter × 15 cm tall pots. The

arenas were housed in a glasshouse (14:10 L:D, temperature 22°–27°C) for 2 wk to allow the plants to acclimate. Plants were enclosed with 18 cm diameter × 30 cm tall Mylar plastic tubes, covered on top with fine mesh and with the bottom twisted into the soil until the lower edge fit snugly against the sides of the pot.

We glued five field-collected mummies onto the alfalfa plants using small drops of Elmer's glue (Borden, Columbus, Ohio, USA). The glue drops are entirely covered by the mummies and do not affect predator choice (Snyder and Ives 2001; W. E. Snyder and A. R. Ives, *unpublished data*). We then released 10 field-collected aphids into each arena. We gave the aphids 24 h to acclimate, and then recounted aphids and mummies. We added a single fourth-instar larva of the ladybird beetle *Harmonia axyridis* or an adult of the hemipteran *Nabis* spp. We established 12 replicates for each predator, and also 12 control arenas without a predator. After 24 h of exposure to predation we counted aphids and mummies. *Nabis* spp. feed with piercing–sucking mouthparts that do not always leave a clear sign of mummy predation. Therefore, we collected the mummies from all arenas, placed them in petri dishes, and allowed 2 wk for parasitoid emergence to verify that mummies we initially scored as alive after the 24-h predator exposure period indeed contained a viable parasitoid larva.

Statistics

We analyzed dynamical data for aphids and parasitoid mummies from field experiments 1–3 using multivariate repeated measures analysis in SYSTAT (SPSS 1999) or SAS (SAS 1996). The data from experiment 1 were more complicated, because there were differences among treatments in the dynamics of aphids and parasitism. Therefore, we performed a profile analysis that compares the effects of treatments on changes in the dependent variables between successive samples (von Ende 1993). Aphid densities were log-transformed, and the proportions of parasitoids parasitized and infected were arcsine square-root transformed before analysis to reduce heterogeneity of variances. The aphid-mummy choice experiments were analyzed using paired *t* tests.

RESULTS

Field experiments

Experiment 1: aphid and parasitoid manipulation.—This experiment manipulated initial aphid and parasitoid abundances within cages in a 2 × 2 factorial design, leading to four treatments: ambient aphids and parasitoids (treatment Control); aphids added, ambient parasitoids (+Aphid); ambient aphids, parasitoids added (+Para); and aphids and parasitoids added (+Aphid+Para). There was a highly significant effect of aphid addition on aphid densities ($F_{1,7} = 63.3$, $P < 0.001$), with aphid densities in cages initially supplemented with 1000 aphids reaching much higher densities than in cages without supplemental aphids (Fig. 1A). Conversely, initial supplementation with parasitoids reduced aphid densities, although this effect was weaker ($F_{1,7} = 3.82$, $P < 0.10$). Analysis of the contrasts between consecutive samples shows a significant effect of parasitoid addition on changes in aphid density between the samples at day 14 and 18 ($F_{1,7} = 6.91$, $P < 0.05$); this timing corresponds to the emergence of the first generation of parasitoids that would have been produced by the experimentally added adults. Cages with ambient aphid densities and supplemented parasitoid densities matched closely the densities observed in the open references.

By the end of the experiment, parasitoid densities (as measured by mummies) were higher in the treatments with supplemental aphids (+Aphid and +Aphid+Para treatments) than in treatments with ambient initial aphid densities (Control and +Para treatments) ($F_{1,7} = 27.4$, $P < 0.002$, Fig. 1B), even though parasitoids did not appreciably suppress aphid densities in the treatments with supplemental aphids. This is because, even though parasitoid densities at the end of the supplemental aphid treatments were higher, the numbers of parasitoids relative to aphids were lower than in treatments with ambient aphid densities. This is shown in Fig. 1C where we use the ratio mummy/(mummy + aphid density) as a measure of the severity of parasitism. This measure is related to % parasitism (i.e., the probability an aphid is parasitized over its lifetime), although it differs because mummies represent only the pupal stage of the parasitoid's life cycle. There was a significant negative main effect of experimental aphid addition on parasitism ($F_{1,7} = 7.18$, $P < 0.05$). Profile analysis revealed significant increases in parasitism between samples on days 14 and 18 ($F_{1,7} = 6.32$, $P < 0.05$), when treatments receiving additional aphids had relatively lower increases in parasitism. Nonetheless, the main effect of parasitoid addition was not significant ($F_{1,7} = 1.63$, $P > 0.20$).

The severity of fungal infection, measured by the ratio cadaver/(cadaver + aphid density), differed among treatments, being highest in the Control treatment and lowest in the +Aphid+Para treatment and in the open reference plots (Fig. 1D); the main effects of aphid supplementation and parasitoid supplementation on the proportion of cadavers were both not statistically significant. Unlike parasitism, there was no consistent relationship between the severity of fungal infection and the maximum aphid density in treatments. Furthermore, there was high heterogeneity in the prevalence of fungal infection within treatments. For example, in the Control treatment, the ratios of cadaver/(cadaver + aphid density) calculated by summing cadaver and aphid densities across all samples were 0.04, 0.082, and 0.20 in the three replicates.

Although the experimental parasitoid addition did not have a strong effect on aphid densities, parasitism is still implicated in aphid suppression. Lack of a strong

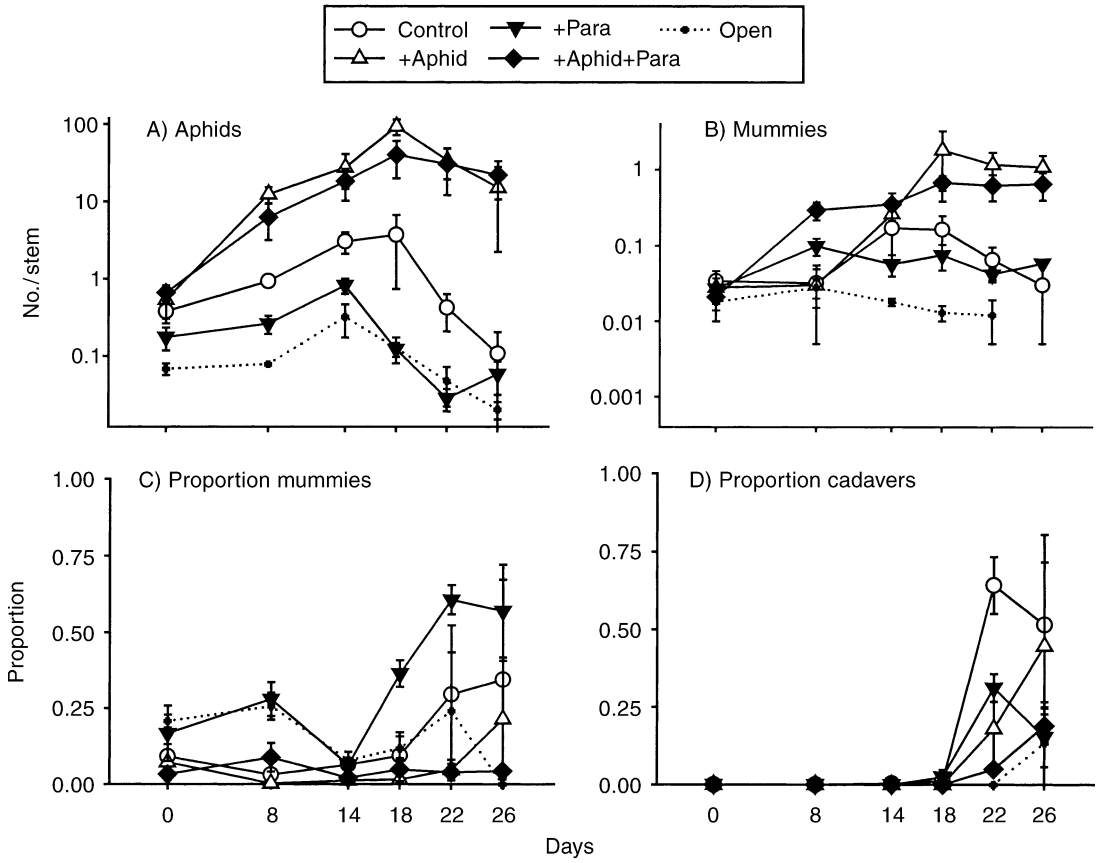

FIG. 1. (A) Aphid and (B) mummy densities, and proportions of (C) parasitism (mummy/(mummy + aphid density)) and (D) fungal infection (cadaver/(cadaver + aphid density)) through time for experiment 1. Initial aphid and parasitoid densities were manipulated to yield the following treatments: ambient aphids and parasitoids (Control); aphids added, ambient parasitoids (+Aphid); ambient aphids, parasitoids added (+Para); aphids and parasitoids added (+Aphid+Para); and uncaged plots where aphids and parasitoids were not manipulated (Open).

parasitoid treatment effect was caused by heterogeneity among replicates within treatments and high background levels of parasitism (e.g., more mummies occurred in the Control treatment than in the +Para treatment, Fig. 1B). The most compelling argument for the importance of parasitism in suppressing aphid populations can be made from the effect of parasitism on aphid population growth rates. The per capita aphid population growth rate between days 0 and 18 (Fig. 2A) and between days 14 and 26 (Fig. 2B) of the experiment against parasitism on days 18 and 26 of the experiment, respectively, as measured by the ratio mummy/(mummy + aphid density), are shown in Fig. 2. Using mummy densities at the end of these periods rather than the beginning is appropriate, because mummies form roughly 8 d after aphids are parasitized. Therefore, mummy densities at the end of the periods measure parasitism of still-living aphids over the periods. Fig. 2 shows a strong relationship between mummy/(mummy + aphid density) and aphid population growth and decline, particularly in the second half of the experiment.

Field Experiment 2: predator manipulation.—Orius spp., *Nabis* spp., and spiders were the most abundant foliage-dwelling predators, each making up 20–30% of the total D-vac catch at the beginning of each experiment (Table 1). As we found previously (Snyder and Ives 2001), carabid beetles dominated the community of ground-dwelling predators, representing almost 90% of total pitfall trap catch (Table 1).

Densities of ground and foliage predators did not differ between treatments before predator manipulation ($F_{1,10} = 0.466$, $P > 0.5$, $F_{1,10} = 1.40$, $P > 0.2$, for ground- and foliage-dwelling predators, respectively, Fig. 3A, C), but at the end of the experiment ground predator densities were 75% lower ($F_{1,10} = 105.31$, $P < 0.001$; Fig. 3C), and foliage predator densities were 60% lower ($F_{1,10} = 22.89$, $P < 0.001$; Fig. 3A) in removal cages. Final ground predator densities were lower in predator cages than in open controls ($F_{1,7} = 14.91$, $P < 0.007$), while final foliage predators in predator cages and open controls could not be distinguished ($F_{1,7} = 0.50$, $P > 0.5$).

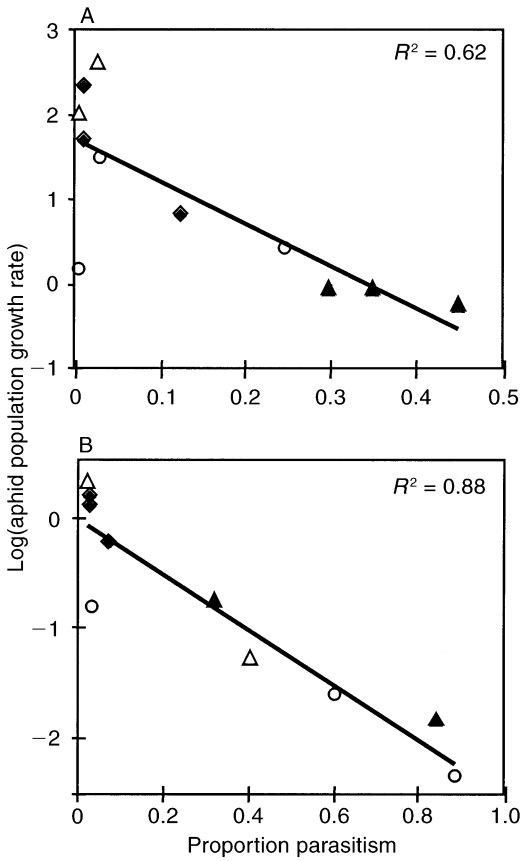

FIG. 2. Per capita aphid population growth vs. proportion parasitism (mummy/[mummy + aphid density]) in field cages from experiment 1. Per capita aphid population growth was calculated as the difference in log aphid abundance between (A) days 0 and 18 (samples 1 and 4) and (B) days 14 and 26 (samples 3 and 6) of the experiment. Proportion parasitism was calculated for the last sample in each of the panels. Symbols denote treatments as in Fig. 1.

Aphid densities increased through time in both treatments (Wilks' lambda = 0.061, $F_{2,9} = 69.7$, $P < 0.001$; Fig. 4). The impact of predators was consistent through time, so that the treatment × time interaction was not significant (Wilks' lambda = 0.699, $F_{2,9} = 1.942$, $P > 0.2$). Generalist predators significantly reduced mean aphid densities ($F_{1,10} = 5.037$, $P < 0.05$).

Field Experiment 3: predator and parasitoid manipulation.—In experiment 3 we manipulated both predators and parasitoids yielding four treatments: both predators and parasitoids removed (−Pred−Para); predators present, parasitoids removed (−Para); parasitoids present, predators removed (−Pred); predators and parasitoids both present (Control). The composition of foliage-dwelling predators was similar to that found in experiment 2, although coccinellid beetles were more common, equaling 22% of the predators collected (Table 1). The community of ground-dwelling predators was similar to that in experiment 2 (Table 1).

Densities of ground and foliage predators did not differ between treatments before predator manipulation ($F_{1,8} = 0.960$, $P > 0.35$ for both ground and foliage predators; Fig. 3B, D). At the end of the experiment ground predator densities were significantly reduced by our predator removal ($F_{1,8} = 20.331$, $P = 0.002$; Fig. 3D), but were not impacted by parasitoid manipulation ($F_{1,8} = 0.27$, $P > 0.6$; Fig. 3D). Similarly, final foliage-dwelling predator densities were lowered by our predator removal procedure ($F_{1,8} = 23.515$, $P = 0.001$; Fig. 3B), but densities were not impacted by parasitoid manipulation ($F_{1,8} = 1.156$, $P > 0.3$). Final ground- and foliage-dwelling predator densities did not differ between open plots and treatments without predator removal (−Para and Control) ($F_{1,7} = 1.086$, $P = 0.332$; $F_{1,7} = 0.10$, $P = 0.761$ for ground- and foliage-dwelling predators, respectively).

Pea aphid dynamics were affected by both predators and parasitoids. Predators had an immediate but apparently density-independent impact, while parasitoids had a delayed impact on aphids (Fig. 5A). Aphid densities changed through time, first increasing and later decreasing after 14 d (Wilks' lambda = 0.003, $F = 285.79$; $P < 0.001$). Predators significantly reduced pea aphid densities ($F_{1,8} = 34.12$, $P < 0.001$), and this effect was consistent through time, resulting in a nonsignificant predator × time interaction (Wilks' lambda = 0.129; $F_{5,4} = 0.64$, $P = 0.064$). The generalist predator guild immediately lowered the rate of aphid increase, with this impact nearing statistical significance at day 3 (two-way ANOVA at 3 d; predator effect; $F_{1,8} = 3.79$, $P < 0.09$), and then remaining statistically significant through the end of the experiment ($P < 0.03$ for all subsequent sample dates). Parasitoids also reduced aphid densities ($F_{1,8} = 96.411$, $P < 0.001$), but the strength of the parasitoid effect increased through time, leading to a significant treatment × time inter-

TABLE 1. Proportion of different predator taxa collected by either D-vac (foliage predators) or pitfall traps (ground predators) at day 0 for experiments 2 and 3.

Category	Taxon	Experiment 2	Experiment 3
Foliage	*Nabis* spp.	0.342	0.299
	Orius spp.	0.208	0.225
	Coccinellidae	0.033	0.222
	Araneae	0.325	0.196
	Chrysopidae	0.033	0.012
	Opiliones	0.000	0.016
	Staphylinidae	0.033	0.016
	Syrphidae	0.021	0.009
	Geocoris spp.	0.000	0.003
Ground	Carabidae	0.879	0.870
	Araneae	0.013	0.010
	Staphylinidae	0.081	0.000
	Opiliones	0.027	0.109
	Chilopoda	0.000	0.010

Note: Total number of predators collected: Foliage, 240 in experiment 2, 311 in experiment 3; Ground, 223 in experiment 2, 193 in experiment 3.

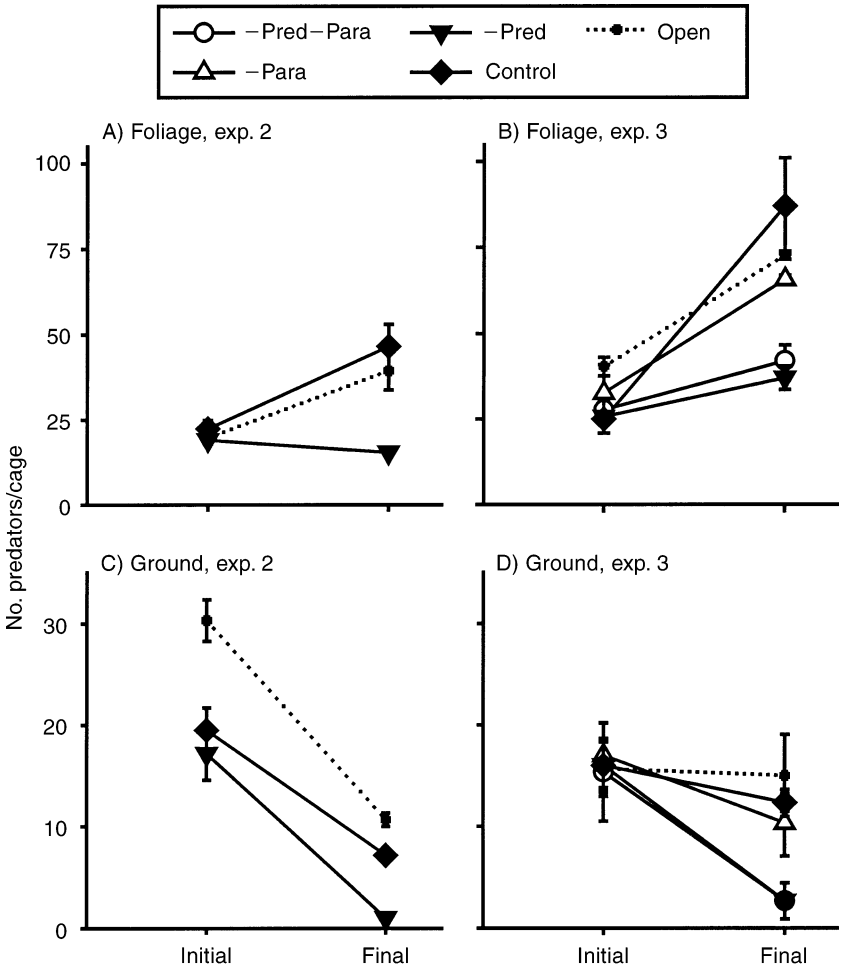

FIG. 3. Generalist predator densities at the beginning (''Initial'') and at the end (''Final'') of field experiments 2 and 3: (A) foliage predators in experiment 2, (B) foliage predators in experiment 3, (C) ground predators in experiment 2, and (D) ground predators in experiment 3. Foliage-dwelling predators were collected with a D-vac suction sampler; ground-dwelling predators were collected using pitfall traps. Experiment 2 treatments: predators reduced (−Pred); predators present (Control); and uncaged open reference areas (Open). Experiment 3 treatments: both predators and parasitoids removed (−Pred−Para); predators present, parasitoids removed (−Para); parasitoids present, predators removed (−Pred); predators and parasitoids both present (Control); and uncaged open reference areas (Open).

action (Wilks' lambda = 0.019, $F_{5,4}$= 42.39, $P <$ 0.001). Parasitoids only weakly depressed aphid population growth early on, but later exerted strong depression of aphids. Parasitoids significantly reduced aphid densities from day 7 through the end of the experiment ($P < 0.001$ for samples on days 7–21). The impacts of the two classes of natural enemy were additive throughout, as indicated by the absence of either a significant predator × parasitoid interaction ($F_{1,8}$ = 0.003, $P = 0.956$) or a predator × parasitoid × time interaction in profile analysis (Wilks' lambda = 0.556, $F_{5,4} = 0.64$, $P = 0.686$). Our analyses were conducted on log-transformed data, but interaction effects also were not statistically significant with untransformed data (i.e., both multiplicative and additive interactions were not significant [Wooton 1994, Sih et al. 1998]).

Experimental removal of mummies reduced mummy densities by more than an order of magnitude by the end of the experiment ($F_{3,8} = 90.53$, $P < 0.001$; Fig. 5B). Comparing the treatments without mummy removal (treatments Control and −Pred), predators caused a twofold decrease in mummy density ($F_{1,4}$ = 23.33, $P < 0.008$; Fig. 5B). This could be due to predators feeding directly on either mummies or parasitized aphids. Despite the reduction in the density of mummies, there was no effect of predators on parasitism, measured by the ratio mummy/(mummy + aphid density) ($F_{1,4} = 4.91$, $P > 0.09$, Fig. 5C). This suggests that predators did not disrupt parasitism.

Finally, even in the −Pred−Para treatment, aphid densities declined at the end of the experiment (Fig. 5A). This was caused by a fungal epizootic that caused

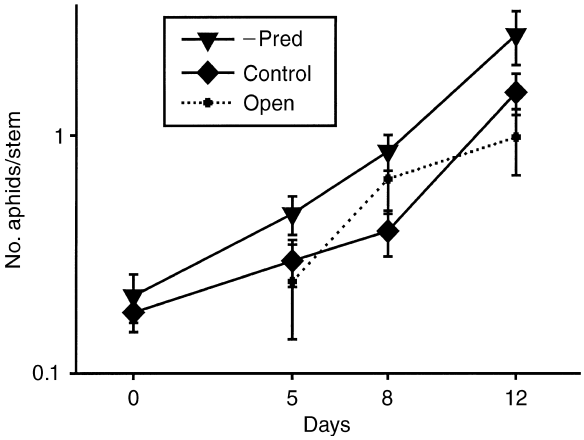

FIG. 4. Aphid densities through time from experiment 2, predator manipulation. Treatments: predators removed (−Pred); predators added (Control); and uncaged open reference areas (Open).

a similar decline is aphid density in the surrounding field (open treatment). The decline in the surrounding field occurred before that observed in the cages. This is probably because we reduced aphid densities in the cages at the start of the experiment relative to the surrounding field. Since fungal infection is density dependent, reducing initial aphid density delayed the onset of the epizootic. An additional factor that could have led to aphid decline is the phenology of the plants. In contrast to experiment 1, which was initiated immediately following harvesting, experiment 3 was initiated 14 d following harvest, and by the end of the experiment the plants were close to the onset of flowering. The maturity of the plants could thus have lowered aphid population growth rates (e.g., White and Eigenbrode 2000).

Laboratory experiment

In the controls, 0.25 ± 0.31 aphids and 0.33 ± 0.14 mummies disappeared, and the mummy–aphid ratio did not change (0.413 ± 0.022 and 0.411 ± 0.029 at 0 and 24 h, respectively; $t_{1,11} = 0.140$, $P = 0.891$; paired t test), over 24 h. In cages containing larvae of the ladybird beetle *Harmonia axyridis*, 4.8 ± 0.81 aphids and 1.0 ± 0.19 mummies disappeared. This differential effect on aphids and mummies significantly increased the ratio of mummies to aphids after 24 h (0.436 ± 0.019 and 0.738 ± 0.068 at 0 and 24 h, respectively; $t_{1,10} = -4.255$, $P < 0.002$). Nabids had a similar, although weaker, impact, reducing the numbers by 3.8 ± 0.61 aphids and 1.9 ± 0.43 mummies, respectively, and increasing the ratio of mummies to aphids (0.452 ± 0.016 and 0.649 ± 0.082 at 0 and 24 h, respectively; $t_{1,9} = -2.597$, $P < 0.03$; not significant with Bonferroni correction for three comparisons).

THE MODEL

We constructed a model to investigate the interactions between parasitoids and predators, and how these interactions affect pea aphid control. We have four interrelated objectives. First, field experiment 3 demonstrated additivity between the effects of parasitoid and predators. Nonetheless, mortality from the fungal epizootic was high. In the absence of the fungus, would parasitism and predation be additive? Second, field experiment 3 was run for 21 d, at which time the aphid densities within cages had peaked. The duration of the experiment was therefore appropriate for determining the effect of biological control on peak aphid densities within a harvesting cycle. Nonetheless, the average in-

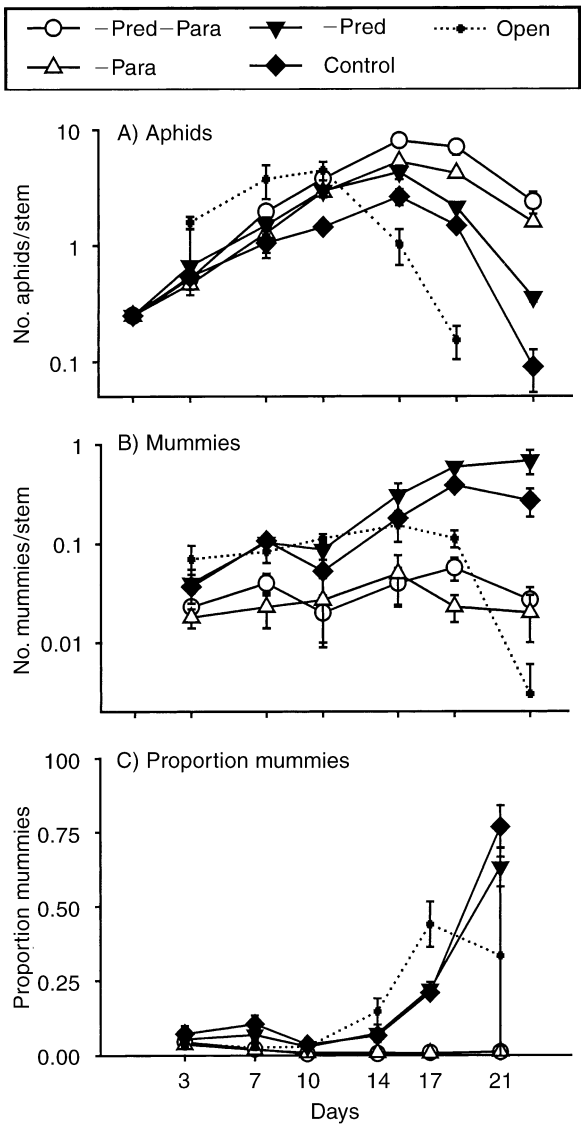

FIG. 5. (A) Aphid and (B) mummy population dynamics, and (C) parasitism (mummy/[mummy + aphid density]) through time from field experiment 3, where we manipulated both predators and parasitoids. Treatments: both predators and parasitoids removed (−Pred−Para); predators present, parasitoids removed (−Para); parasitoids present, predators removed (−Pred); predators and parasitoids both present (Control); and uncaged open reference areas (Open).

terval between harvests is longer (roughly 32 d), and the population size of aphids at the end of the harvesting cycle will influence both the dispersal of aphids to other fields and the number of aphids at the start of the following harvest cycle. How did the duration of experiment 3 affect our conclusion about the additivity of parasitism and predation? Third, the cages excluded movement of predators in response to aphid densities that is likely to occur in open field conditions (Evans and Youssef 1992). Would aphid-density-dependent migration of predators affect the additivity between parasitism and predation? Fourth, although our experiments involved the specific system of pea aphids in alfalfa, we are interested in the broader question of whether additive interactions should be expected in other host–parasitoid–predator systems. This requires understanding the underlying processes leading to additivity. What potential processes could lead to nonadditivity in our aphid–parasitoid–predator system and other similar systems?

To address these four objectives, we designed a system-specific model, striking a balance between including enough detail to describe the dynamics of the system, and excluding enough detail to limit the number of parameters that need to be estimated. We first estimated parameter values for aphid and parasitoid dynamics using data from the first two experiments. Using these values, we then fit the model to the data from experiment 3. This allowed us to determine whether the model could correctly describe the dynamics of experiment 3, in particular, the additivity of parasitoid–predator effects on pea aphid control, when parameterized using independent data. The full model and fitting procedure are presented in the Appendix, while we give a brief description below.

We restricted the model by not including movement of aphids and parasitoids. Movement of aphids or adult parasitoids could reduce any nonadditive effects of predation if movement decoupled the dynamics of aphids and parasitoids. For example, if adult parasitoids moved readily among fields, then any decline in parasitoids caused by predation could be replenished by immigration. However, this would require a pool of parasitoids outside the field to provide immigrants. If fields were harvested asynchronously, such a pool might exist, but if fields were harvested synchronously, such that all fields had roughly equal abundances of adult parasitoids, a pool of immigrants would not necessarily be available. This example illustrates that incorporating aphid and parasitoid movement would introduce a suite of issues involving the metapopulation dynamics of dispersal-connected subpopulations (fields), making the problem quite complex (e.g., Ives 1992, Murdoch et al. 1992). Furthermore, although we have measured the movement rate of *A. ervi* within fields (Olson et al. 2000), we have no information about movement at larger, among-field scales. Therefore, we do not explicitly consider aphid and parasitoid movement in the model.

Model structure.—The model explicitly includes stage structure of the aphid population, dividing the population into five instars. Aphid dynamics are modeled using a Leslie matrix (Caswell 1989) in which density-independent survivorship of all aphid stages is given by the parameter s_a, and adult fecundity is f. Because generalist predators acted in a density-independent manner, we do not model predator dynamics explicitly, but instead implicitly incorporate predation by decreasing the stage-specific survival of aphids (and larval parasitoids within still-living aphids). Because we have no information about the mechanisms of transmission and infection of the fungal pathogen from our experiments, we treat the epizootic as a delayed density-dependent source of mortality on aphids. Delayed density-dependent aphid population growth could also be caused by aphid-density-dependent declines in plant quality, and we make no attempt to separate this from the effects of the fungal pathogen on aphid dynamics. We performed preliminary analyses investigating density-dependent time delays of 0, 2, 4, and 6 d, and the best-fitting model with a 4-d time delay fit the data better than the best-fitting models with other delays. Thus, we let the overall survivorship of aphids be $s_a(1 + kx(t - 4))^{-1}$, where $x(t - 4)$ is the density of all aphid instars 4 d previously, and k measures the strength of density dependence, with larger k corresponding to stronger density dependence.

Parasitoids are assumed to have a Type II functional response and show a preference for different aphid instars according to the experimental results of Ives et al. (1999); these experiments showed that *A. ervi* preferentially attacks second- and third-instar pea aphids. Letting y denote the density of parasitoid adults, the proportion of aphids in instar i that are parasitized is given by $1 - \exp(-ar_i y(t)/(1 + gax(t)))$, where a is the overall attack rate (searching efficiency), r_i is the relative preference for aphids in instar i, and g governs the rate of deceleration of parasitism, with $g = 0$ giving a Type I functional response, and the functional response becoming more strongly Type II as g increases. Parasitoid larvae kill their hosts and form mummies in 8 d, during which time they suffer density-dependent survivorship equal to that of unparasitized aphids (Rauwald and Ives 2001). Mummies remain for 6 d, during which time they experience survivorship s_m, and they then emerge as adults and experience survivorship s_w.

Parameter estimation.—We first estimated parameter values using the data from experiments 1 and 2. Using the values of the parameters governing parasitism rates (a and g) from experiment 1, we then estimated the remainder of the model parameters for data from experiment 3 (Table 2). Fig. 6 shows the fit of the model to data for one randomly selected cage from each of the four experimental treatments in experiment 3. For model fitting, we assumed that all differences between model and data were due to measurement error, thereby allowing a total least-squares fitting pro-

TABLE 2. Parameters for the model investigating how interactions between parasitoids and predators affect pea aphid control.

Parameter	Description	Values		
		Experiment 1	Experiment 2	Experiment 3
a	parasitoid searching efficiency	146†	⋯	146
g	type of functional response	0.0011†	⋯	0.0011
f	aphid fecundity	8	8	8
s_a	density-independent aphid survival	0.94†	no pred: 093† pred: 0.85†	no pred: 1.0† pred: 0.95†
k	density-dependent aphid survival	0.01†	0.00†	0.16†
s_m	mummy-stage parasitoid survival	0.62†	⋯	no pred: 0.96† pred: 1.0† removal: 0.57†
s_w	adult parasitoid survival	0.8	⋯	0.8

† Parameters estimated from the data; other values were fixed inputs into the model (see *The model: Model structure*).

cedure (Ludwig and Walters 1989, Hilborn and Walters 1992, Ives et al. 1999). We calculated least-squares differences between observed and predicted log densities rather than absolute densities, thereby making the assumption that the coefficient of variation of the measurement error is independent of mean aphid and parasitoid densities.

Two sets of parameters were difficult to fit simultaneously. First, estimates of aphid fecundity, f, and aphid survival, s_a, strongly covaried, with the statistical fitting procedure poorly distinguishing between the cases of high fecundity and low survival vs. low fecundity and high survival. This is a common problem in fitting stage-structured models (Wood 1994). Therefore, we fixed fecundity at $f = 8$, which is the maximum 2-d fecundity for pea aphids obtained in laboratory experiments (Thiboldeaux 1986). Second, estimates of adult parasitoid survival, parasitoid searching efficiency, and mummy survival all covaried. Therefore, we set adult parasitoid survival, s_w, to 0.8, and then fit the other two parameters.

Model analysis.—The analyses of the model are summarized in Fig. 7. Each panel gives the aphid density at the end of a simulated experiment vs. the predation rate measured by $(1 - s_a)$. The thin line corresponds to the case in which there are no parasitoids. There are three lines for the case when parasitoids are present. The generalist predators in our study range from those that attack mummies rarely compared to aphids (see *Laboratory experiment*) to those that attack mummies similar to aphids (carabids; Snyder and Ives 2001). These two cases are bounded by the thick solid and thick dashed lines in Fig. 7. The thick solid line is calculated assuming that predators attack parasitized aphids at the same rate they attack unparasitized aphids, but they do not attack mummies. The thick dashed line assumes that predators attack mummies at the same rate as they attack unparasitized and parasitized aphids. We have added the third case in which predators do not attack parasitized aphids (thick long-and-short dashed lines), because for this case there is no direct intraguild predation. Experiment 3 was initiated 14 d following alfalfa harvesting. Previous

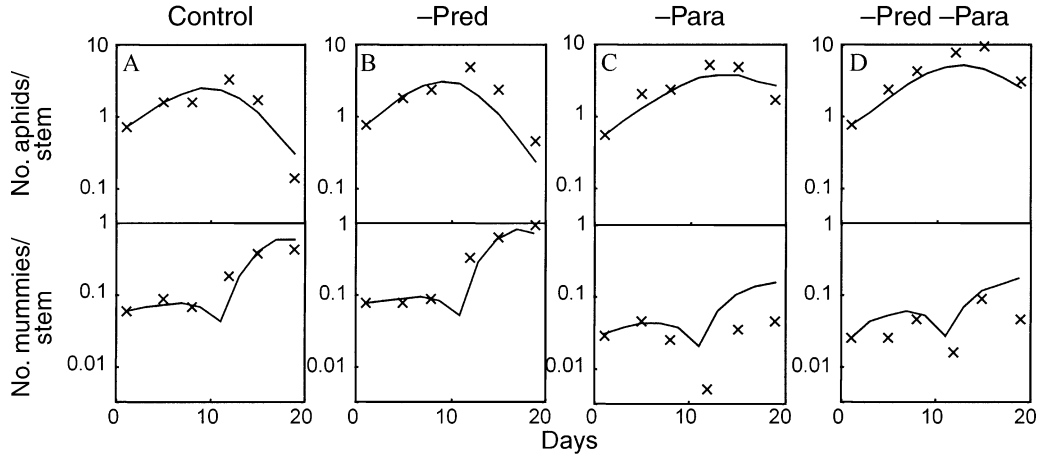

FIG. 6. For field experiment 3, fit of the model to aphid (upper panels) and mummy (lower panels) densities in four cages randomly selected from each of the four experimental treatments: (A) predators and parasitoids both present (Control), (B) parasitoids present, predators removed (−Pred), (C) predators present, parasitoids removed (−Para), and (D) both predators and parasitoids removed (−Pred−Para). Data are shown as ×'s, and model output is shown as solid lines. Parameter values of the fitted model are given in Table 2.

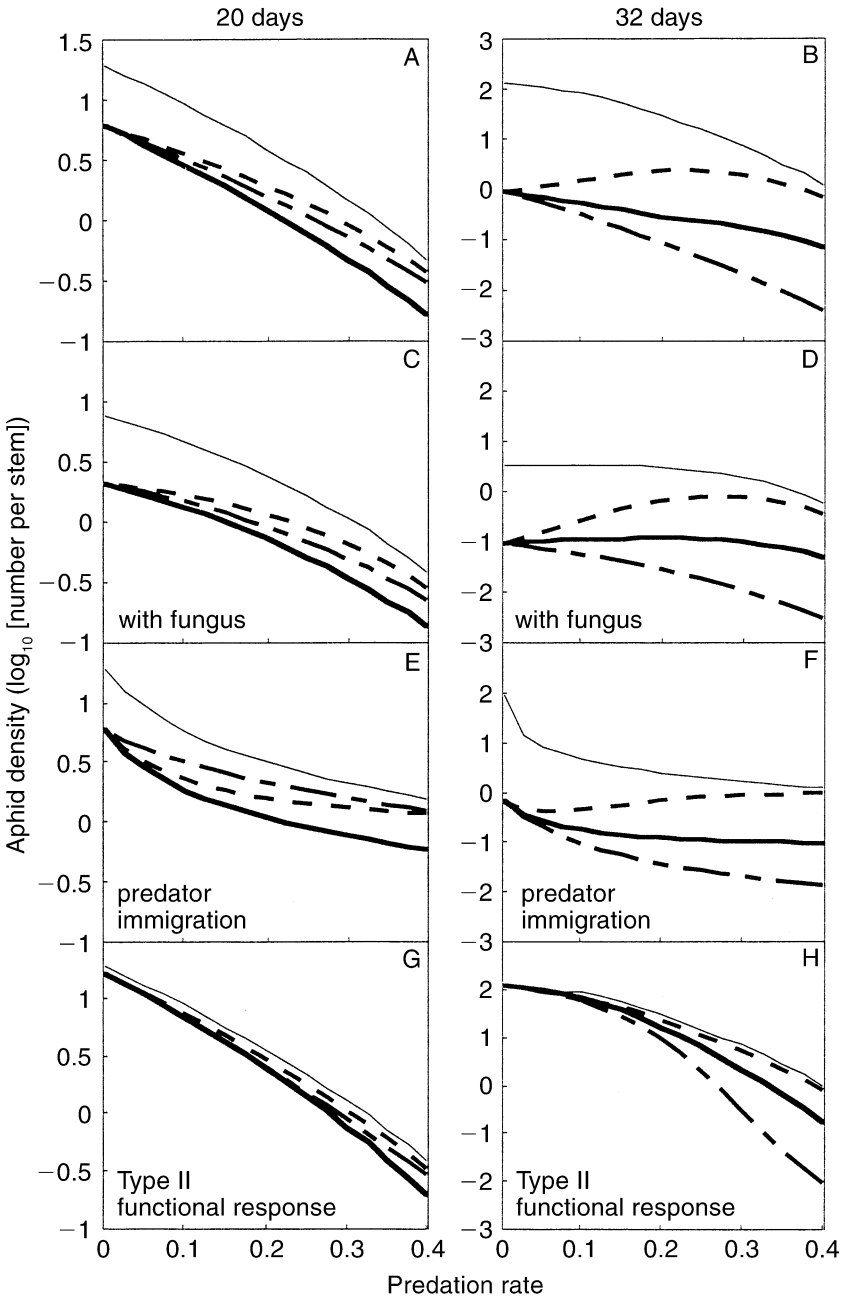

FIG. 7. Log aphid densities at the end of simulated experiments (20 or 32 d) demonstrating the intraguild effects of parasitoids and predators on aphids (see *The model*: *Model analysis*). The horizontal axis gives the predation rate on aphids, measured by $1 - s_a$ (aphid survivorship). The thick solid line gives the case in which unparasitized and parasitized aphids have the same survivals; the thick dashed line gives the case in which mummies and aphids have the same survivals; and the thick long-and-short dashed line gives the case in which only unparasitized aphids are depredated, and survivals of parasitized aphids and mummies are 1. The thin line gives the case of no parasitoids present. For (A) and (B), parameter values are $a = 146$, $g = 0.0011$, $f = 8$, $k = 0.01$, and $s_w = 0.8$ (see Table 2). Parameter values are the same for (C) and (D), but a fungal epizootic is included by increasing the delayed aphid-density dependence to $k = 0.16$, as estimated in experiment 3 (Table 2). In (E) and (F) aphid-density-dependent immigration by predators is simulated by assuming that aphid mortality is given by $\exp[-(1 - s_a)x(t)]$, with other parameter values as in (A) and (B). In (G) and (H) the functional response of parasitoids is more strongly Type II, with $g = 0.11$ and other parameter values as in (A) and (B).

work (Snyder and Ives 2001) showed that carabids become less effective mummy predators on taller alfalfa stems (Snyder and Ives 2001), and hence the foliar predators are likely to be more important in this experiment. Therefore, we consider the case of predators attacking aphids but not mummies as closest to the reality of experiment 3.

Additive effects on log aphid density are equivalent to additive mortality rates imposed by different natural enemies (Wooton 1994, Sih et al. 1998). Because aphid densities are graphed on a log scale, additivity occurs when the lines generated with (thin line) and without (thick lines) parasitoids are parallel. Panels on the left give cases of simulated experiments lasting 20 d (corresponding to experiment 3), while the right panels give cases of experiments lasting 32 d (roughly the average interval between harvesting).

The first objective of the model is to determine how the additivity of parasitism and predation on aphid control observed in experiment 3 could have been influenced by fungal pathogens. Fig. 7A shows the simulation corresponding to experiment 3 assuming there are no strong fungal epizootics, in which the parameter governing the delayed density dependence in aphid dynamics is $k = 0.01$. Fig. 7C shows the case with an epizootic, with $k = 0.16$ as estimated from experiment 3. In both cases, parasitism and predation are additive, provided predators attack parasitized and unparasitized aphids, but not mummies (thick solid line). Thus, the model increases our confidence in the result of experiment 3, because the model shows that additivity of parasitism and predation occurs regardless of delayed density dependence in aphid population dynamics.

The second objective of the model is to ask whether the additivity of parasitism and predation depend upon when aphid densities are measured. Fig. 7B is the same as 7A, except the simulated experiment is 32 d long rather than 20 d. In Fig. 7B, if predators attack parasitized and unparasitized aphids, but not mummies (thick solid line), the interaction between parasitism and predation is no longer additive; as predation increases, parasitoids become relatively less effective in reducing aphid density. This is not surprising, because intraguild predation occurs as predators consume parasitized aphids. If predators only attacked unparasitized aphids (long-and-short dashed line), then parasitism and predation would be additive. This begs the question of why in the 20-d simulated experiment (Fig. 7A) parasitism and predation are additive when predators attack parasitized and unparasitized aphids (thick solid line). At the 20-d time point, percentage parasitism is increasing rapidly, yet the effect of predation on parasitized aphids only affects the aphid dynamics in the following parasitoid generation. Therefore, there is a delay of roughly two parasitoid generations before the effects of predation on parasitized aphids (and the attendant nonadditivity) are observed in the aphid dynamics. We conclude that, while additivity was observed at the time scale of experiment 3, at the longer time scale of harvest intervals, nonadditivity is likely. Note that at these longer time periods, however, aphid densities have already peaked (e.g., experiment 1 Control, Fig. 1A), and therefore the nonadditive effects do not influence peak aphid densities.

Our third objective was to address the consequences of predator migration in response to aphid density. Predators such as ladybird beetles and nabids respond strongly to aphid densities, with aphid density a strong predictor of predator density at the scale of whole fields (Hagen 1976, Ives 1981, Evans and Youssef 1992; A. R. Ives, *unpublished data*). Our enclosure cages contained fixed densities of predators and hence did not allow for aphid-density-dependent predator immigration. To incorporate this into the model, we assumed that predator abundance was proportional to aphid density, $x(t)$, and therefore that the predator-dependent survivorship of aphids was governed by $\exp[-(1 - s_a)x(t)]$. Although predator immigration changes the shape of the relationship between aphid density and predation (measured by $1 - s_a$), it does not change our previous conclusions about the additivity of parasitism and predation (Fig. 7E and F).

The fourth objective of the model is to explore what potential factors could break down the additivity between parasitoids and predators on pea aphid control. As discussed above, predation on parasitized aphids will lead to nonadditivity, but only at longer time scales (compare Fig. 7A and B). Conversely, delayed aphid density dependence does not affect the pattern of additivity (compare Fig. 7C and D with A and B); the same is true for direct (rather than delayed) aphid density dependence (results not shown). Also, aphid-density-dependent movement of predators into fields does not affect additivity (compare Fig. 7E and F with A and B). We have assumed that there is not a time delay in the movement response of predators to aphid density; however, a delayed response also does not affect additivity (results not shown), as found for the case of delayed aphid density dependence.

A final key property is the parasitoid's functional response (Fig. 7G and H). The estimated functional response for *A. ervi* was very weakly Type II. The estimated value of $g = 0.0011$ implies that the reduction in parasitoid attack rate at the maximum aphid density observed in experiment 3 is $<10\%$. To determine the importance of this weak Type II functional response, we simulated experiment 3 with $g = 0.11$, which gives a reduction in the parasitoid attack rate by $\sim 50\%$ at the maximum aphid density observed in experiment 3. Fig. 7G and H show that a strong Type II functional response leads to strong nonadditivity. When there is a strong Type II functional response, parasitoids are more effective on a per capita basis when aphid density is low. Therefore, predators and parasitoid act synergistically to control aphid density, as predators help to keep aphids at low densities where

the parasitoids are more effective. This result suggests that in systems in which parasitoids show strong Type II functional responses, synergistic interactions with predators are expected.

Discussion

The specialist parasitoid *Aphidius ervi* and generalist predators both reduced pea aphid densities in our experiments, although the dynamics they created differed. *A. ervi* exerted only weak suppression of pea aphid population growth early, with stronger suppression becoming visible after ~21–28 d. In contrast, the generalist predator guild caused an immediate decrease in the aphid population growth rate that remained constant throughout the experiments. When both specialist and generalist natural enemies were present, aphid population dynamics reflected the impacts of both types of natural enemy; initial aphid increase was slowed, and aphid densities then peaked and decreased. When present together, generalist predators decreased parasitoid densities by 50%. However, despite evidence of intraguild predation, the impacts of the predators and parasitoids on pea aphid densities were additive.

To disentangle the joint effects of the natural enemies on aphid suppression, we fit a stage-structured model to the data from our field experiments. The model reproduced the additivity between parasitism and predation that we observed in experiment 3 when parameters for aphid–parasitoid interactions were independently estimated. We then used the model to ask what factors could potentially lead to nonadditivity either in our system or in other host–parasitoid–predator systems. In the model, detecting nonadditive interactions depended strongly on the time scale. Nonadditive effects occurred after longer periods (32 d), except in cases in which predators attacked unparasitized, but not parasitized aphids. Because peak densities in experiment 3 were reached by 21 d, our model results about additivity at longer time intervals does not affect the success of biological control within a harvesting cycle. Nonetheless, the longer term success of biological control will depend on the density of aphids throughout the harvesting cycle, since the number of aphids at the end of the harvesting cycle influences the number of aphids and parasitoids at the start of the following cycle (Rauwald and Ives 2001). Our results provide a caution for other experiments on nonadditive effects among natural enemies. If one or more natural enemies have dynamics tightly coupled to the prey, nonadditive effects may only become visible after several generations.

The model demonstrated that additivity between parasitism and predation was relatively insensitive to either delayed density dependence in the aphid dynamics (such as occurred due to the fungal epizootic), or aphid-density-dependent immigration of predators. In contrast, additivity was affected by the type of functional response of the parasitoid, with a strong Type II functional response leading to a synergistic effect of parasitoids and predators. The functional response estimated for *A. ervi* in our experiments was only weakly Type II, as was also found using direct observations of *A. ervi* foraging (Ives et al. 1999). Nonetheless, many parasitoid species exhibit pronounced Type II functional responses (Hassell 1978), and these will likely be strong candidates for synergistic effects with predators.

Our model could be faulted for being either too simple to capture all processes involved in aphid–parasitoid–predator interactions, or too complex to allow general conclusions about additivity in parasitoid–predator systems. We selected a level of detail for the model so that it had few parameters that needed to be estimated, yet included enough detail to successfully capture the dynamics of our experiments (Fig. 6). Although many factors were left out, and the model represents only a caricature of the real system, it nonetheless gives a tool with which we can probe the aphid–parasitoid–predator interactions to tell us how informative our experiments were likely to be. As we showed, although the model also demonstrated additivity between parasitoid and predators under the conditions of experiment 3, under other conditions additivity should not be expected. This simultaneously gives us greater confidence in our results and cautions against claiming that parasitoid–predator effects on pea aphids are likely to be additive under all conditions.

Conversely, we have not tried to use the model to make broad conclusions about the additivity of all host–parasitoid–predator systems, because we do not think it is possible to derive any rules that have no exceptions. When addressing the additivity of natural enemies in a particular system, researchers can specify what natural enemies they are interested in, what time scale is appropriate, what spatial scales are important for the interactions, etc. Because these factors will influence whether parasitoid–predator effects are additive, there is no single answer to the question of additivity. Rather than try to make broad conclusions about additivity of parasitoid–predator effects, instead we have used the model to illustrate what types of factors might be important.

Intraguild predation and biocontrol by predator guilds

Snyder and Ives (2001) examined the impact of the carabid beetle *Pterostichus melanarius* on pea aphid population dynamics. Carabids had little direct impact on pea aphids, apparently because aphids actively avoided carabids climbing in foliage. However, carabids could capture the immobile parasitoid mummies, so that the net effect of carabids was to disrupt aphid biological control by parasitoids. If other predators in alfalfa also had a stronger indirect impact on aphids through mummy predation, then the predator guild should act together to disrupt biological control. Con-

sistent with this, the predator guild reduced parasitoid abundance. Nonetheless, the high rate of intraguild predation by generalists on the specialist parasitoid did not reduce the impact of the complete complex of natural enemies on pea aphids. Furthermore, even under conditions simulated with the model that lead to nonadditive interference between parasitoid and predators, control by both types of natural enemies together was more effective than either alone, except in cases in which predators strongly attacked mummies (Fig. 7).

Conclusions

Based on the experiments presented here, it is difficult to single out one class of natural enemy as the most effective biological control agent. Parasitoids were able to suppress aphid densities, but the effect occurred with a time delay so that aphids still reached high densities before the decline initiated. The generalist predator guild had an immediate effect on aphid population dynamics, but only reduced the rate of aphid increase. Thus, aphids still reached high densities when generalists were the only abundant natural enemy. Because specialists and generalists contributed additively to aphid biological control over the time scale of our experiments, biological control was the most effective when both types of natural enemy were present.

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Literature Cited

Berryman, A. A. 1992. The origins and evolution of predator–prey theory. Ecology **73**:1530–1535.

Blackman, R. L., and V. G. Eastop. 1984. Aphids on the world's crops: an identification and information guide. John Wiley and Sons, New York, New York, USA.

Braman, S. K., and K. V. Yeargan. 1989. Intraplant distribution of three *Nabis* species (Hemiptera: Nabidae), and impact of *N. roseipennis* on green cloverworm populations in soybean. Environmental Entomology **18**:240–244.

Brodeur, J., and J. A. Rosenheim. 2000. Intraguild interactions in aphid parasitoids. Entomologia Experimentalis et Applicata **97**:93–108.

Caswell, H. 1989. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Chang, G. C. 1996. Comparison of single versus multiple species of generalist predators for biological control. Environmental Entomology **25**:207–212.

Chang, G. C., and P. Kareiva. 1999. The case for indigenous generalists in biological control. Pages 103–115 *in* B. A. Hawkins and H. V. Cornell, editors. Theoretical approaches to biological control. Cambridge University Press, New York, New York, USA.

Cornell, H. V., and B. A. Hawkins. 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. American Naturalist **145**:563–593.

Cottrell, T. E., and K. V. Yeargan. 1998*a*. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environmental Entomology **27**:1402–1410.

Cottrell, T. E., and K. V. Yeargan. 1998*b*. Influence of a native weed, *Acalypha oestryaefolia* (Euphorbiacaeae) on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. Environmental Entomology **27**:1375–1385.

Cottrell, T. E., and K. V. Yeargan. 1999. Intraguild predation between an introduced lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and a native lady beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae). Journal of the Kansas Entomological Society **71**:159–163.

Debach, P., and D. Rosen. 1991. Biological control by natural enemies. Cambridge University Press, New York, New York, USA.

Ekbom, B. 1994. Arthropod predators of the pea aphid, *Acyrthosiphon pisum* Harr. (Hom., Aphididae) in peas (*Pisum sativum* L.), clover (*Trifolium pratense* L.) and alfalfa (*Medicago sativa* L.). Journal of Applied Entomology **117**: 469–476.

Evans, E. W., and N. N. Youssef. 1992. Numerical responses of aphid predators to varying prey density among Utah alfalfa fields. Journal of the Kansas Entomological Society **65**:30–38.

Fagan, W. F., A. L. Hakim, H. Ariawan, and S. Yuliyantiningsih. 1998. Interactions between biological control efforts and insecticide applications in tropical rice agroecosystems: the potential role of intraguild predation. Biological Control **13**:121–126.

Flinn, P. W., A. A. Hower, and R. A. J. Taylor. 1985. Preference of *Reduviolus americoferus* (Hemiptera: Nabidae) for potato leafhopper nymphs and pea aphids. Canadian Entomologist **117**:1503–1508.

Frazer, B. D., N. Gilbert, V. Nealis, and D. A. Raworth. 1981. Control of pea aphid density by a complex of predators. Canadian Entomologist **113**:1035–1041.

Giles, K. L., J. J. Obrycki, and T. A. Degooyer. 1994. Prevalence of predators associated with *Acyrthosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. Biological Control **4**:170–177.

Gonzalez, D., W. White, J. Hall, and R. C. Dickson. 1978. Geographical distribution of Aphiidae (Hym.) imported to California for biological control of *Acyrthosiphon kondoi* and *Acyrthosiphon pisum* (Hom.: Aphididae). Entomophaga **23**:239–248.

Hagen, K. S. 1976. Role of nutrition in insect management. Proceedings of the Tall Timbers Conference on Ecological Animal Control **6**:221–261.

Hagen, K. S., G. A. Viktrorov, K. Yasumatsu, and M. F. Shuster. 1976. Biological control of pests of range, forage, and grain crops. Pages 397–442 *in* C. B. Huffaker and P. S. Messenger, editors. Theory and practice of biological control. Academic Press, New York, New York, USA.

Hagley, E. A. C., N. J. Holliday, and D. R. Barber. 1982. Laboratory studies of the food preferences of some orchard carabids (Coleoptera: Carabidae). Canadian Entomologist **114**:431–437.

Harper, A. M., and M. S. Kaldy. 1982. Effect of the pea aphid *Acyrthosiphon pisum* (Hemiptera: Aphididae), on yield and quality of forage alfalfa. Canadian Entomologist **114**:485–489.

Harvey, T. L., H. L. Hackerott, and E. L. Sorensen. 1972. Pea aphid resistant alfalfa selected in the field. Journal of Economic Entomology **65**:1661–1663.

Hassell, M. P. 1978. The dynamics of arthropod predator–prey systems. Princeton University Press, Princeton, New Jersey, USA.

Hassell, M. P. 1980. Foraging strategies, population models and biological control: a case study. Journal of Animal Ecology **49**:603–628.
Hassell, M. P., and R. M. May. 1986. Generalist and specialist natural enemies in insect predator–prey interactions. Journal of Animal Ecology **55**:923–940.
Hawkins, B. A., H. V. Cornell, and M. E. Hochberg. 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. Ecology **78**:2145–2152.
Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment. Chapman and Hall, New York, New York, USA.
Huffaker, C. B., and P. S. Messenger, editors. 1976. Theory and practice of biological control. Academic Press, New York, New York, USA.
Hutchinson, W. D., and D. B. Hogg. 1984. Demographic statistics for the pea aphid (Homoptera: Aphididae) in Wisconsin and a comparison with other populations. Environmental Entomology **13**:1173–1181.
Hutchinson, W. D., and D. B. Hogg. 1985. Time-specific life tables for the pea aphid, *Acyrthosiphon pisum* (Harris), on alfalfa. Researches on Population Ecology **27**:231–253.
Ives, A. R. 1992. Continuous-time models of host–parasitoid interactions. American Naturalist **140**:1–29.
Ives, A. R., S. S. Schooler, V. J. Jagar, S. E. Knuteson, M. Grbic, and W. H. Settle. 1999. Variability and parasitoid foraging efficiency: a case study of pea aphids and *Aphidius ervi*. American Naturalist **154**:652–673.
Ives, P. M. 1981. Estimation of coccinellid numbers and movement in the field. Canadian Entomologist **113**:981–997.
LaMana, M. L., and J. C. Miller. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. Biological Control **6**:232–237.
Latge, J. P., and B. Papierok. 1988. Aphid pathogens. Pages 323–335 *in* A. K. Minks and P. Harrewijn, editors. Aphids: their biology, natural enemies and control. Elsevier, Amsterdam, The Netherlands.
Ludwig, D., and C. J. Walters. 1989. A robust method for parameter estimation from catch and effort data. Canadian Journal of Fisheries and Aquatic Sciences **46**:137–144.
Mackauer, M. 1971. *Acyrthosiphon pisum* (Harris), pea aphid. Pages 3–10 *in* C. A. Bureau, editor. Biological control programmes against insects and weeds in Canada 1959–1968. Lamport Gilbert Printers, Reading, UK.
Mackauer, M., and S. Kambhampati. 1986. Structural changes in the parasite guild attacking the pea aphid in North America. Pages 347–356 *in* I. Hodek, editor. Ecology of aphidophaga. Academia, Prague, Czechoslovakia.
Maiteki, G. A., and R. J. Lamb. 1985. Spray timing and economic threshold for the pea aphid, *Acyrthosiphon pisum* (Homoptera: Aphididae), on field peas in Manitoba. Journal of Economic Entomology **78**:1449–1454.
Milner, R. J. 1997. Prospects for biopesticides for aphid control. Entomophaga **42**:227–239.
Murdoch, W. W. 1994. Population regulation in theory and practice. Ecology **75**:271–287.
Murdoch, W. W., C. J. Briggs, R. M. Nisbet, and W. S. C. Gurney. 1992. Aggregation and stability in metapopulation models. American Naturalist **140**:41–58.
Murdoch, W. W., J. Chesson, and P. L. Chesson. 1985. Biological control in theory and practice. American Naturalist **125**:344–366.
Olson, A. C., A. R. Ives, and K. Gross. 2000. Spatially aggregated parasitism on pea aphids, *Acyrthosiphon pisum*, caused by random foraging behavior of the parasitoid *Aphidius ervi*. Oikos **91**:66–76.
Ovaska, K., and M. A. Smith. 1987. Predatory behavior of two species of ground beetles (Coleoptera: Carabidae) towards juvenile salamanders (*Plethodon vehiculum*). Canadian Journal of Zoology **66**:599–604.
Phoofolo, M. W., and J. J. Obrycki. 1998. Potential for intraguild predation and competition among predatory coccinellidae and chrysopidae. Entomologia Experimentalis et Applicata **89**:47–55.
Pickering, J., and A. P. Gutierrez. 1991. Differential impact of the pathogen *Pandora neoaphidis* (R. and H.) Humber (Zygomycetes: Entomophthorales) on the species composition of *Acyrthosiphon* aphids in alfalfa. Canadian Entomologist **123**:315.
Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution **7**:151–154.
Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology and Systematics **20**:297–330.
Rauwald, K. S., and A. R. Ives. 2001. Biological control in disturbed agricultural systems and the rapid re-establishment of parasitoids. Ecological Applications **11**:1224–1234.
Riechert, S. E., and L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. Ecology **71**:1441–1450.
Riechert, S. E., and T. Lockley. 1984. Spiders as biological control agents. Annual Review of Entomology **29**:299–320.
Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. Annual Review of Entomology **43**:421–447.
Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois, and B. A. Jaffee. 1995. Intraguild predation among biological-control agents: theory and practice. Biological Control **5**:303–335.
Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia **96**:439–449.
SAS. 1996. SAS. Version 6.12. SAS Institute, Cary, North Carolina, USA.
Settle, W. H., H. Ariawan, E. T. Astuti, W. Cahyana, A. L. Hakim, D. Hindayana, A. S. Lestari, Pajarningsih, and Sartanto. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology **77**:1975–1988.
Sih, A., G. England, and D. Wooster. 1998. Emergent impacts of multiple predators on multiple prey. Trends in Ecology and Evolution **13**:350–355.
Snyder, W. E., and A. R. Ives. 2001. Generalist predators disrupt biological control by a specialist parasitoid. Ecology **82**:705–716.
Snyder, W. E., S. B. Joseph, R. F. Preziosi, and A. J. Moore. 2000. Nutritional benefits of cannibalism for the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. Environmental Entomology **29**:1173–1179.
Snyder, W. E., and D. H. Wise. 1999. Predator interference and the establishment of generalist predator populations for biocontrol. Biological Control **15**:283–292.
Snyder, W. E., and D. H. Wise. 2001. Contrasting trophic cascades generated by a community of generalist predators. Ecology **82**:1571–1583.
Soroka, J. J., and P. A. MacKay. 1990. Seasonal occurrence of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae), on cultivars of field peas in Manitoba and its effects on pea growth and yield. Canadian Entomologist **122**:503–513.
SPSS. 1999. Systat. Version 9. SPSS, Chicago, Illinois, USA.

Sunderland, K. D. 1975. The diets of some predatory arthropods in cereal crops. Journal of Applied Ecology **12**: 507–515.
Sunderland, K. D. 1999. Mechanisms underlying the effects of spiders on pest populations. Journal of Arachnology **27**: 308–316.
Sunderland, K. D., and P. Vickerman. 1980. Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. Journal of Applied Ecology **17**:389–396.
Symondson, W. O. C., D. M. Glen, A. R. Ives, C. J. Langdon, and C. W. Wiltshire. 2002*a*. Dynamics of the relationship between a generalist predator and slugs over five years. Ecology **83**:137–147.
Symondson, W. O. C., D. M. Glen, C. W. Wiltshire, C. J. Langdon, and J. E. Liddell. 1996. Effects of cultivation techniques and methods of straw disposal on predation by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable land. Journal of Applied Ecology **33**:741–753.
Symondson, W. O. C., K. D. Sunderland, and M. H. Greenstone. 2002*b*. Can generalist predators be effective biocontrol agents? Annual Review of Entomology **47**:561–594.
Thiboldeaux, R. 1986. The effect of temperature on population level interactions between the pea aphid, *Acyrthosiphon pisum*, and its primary parasitoid, *Aphidius ervi*. Thesis. University of Wisconsin, Madison, Wisconsin, USA.
Turchin, P., A. D. Taylor, and J. D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. Science **285**:1068–1071.
von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 *in* S. M. Scheiner and J. Gurevitch, editors. The design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.
Wagner, J. D., M. D. Glover, J. B. Mosely, and A. J. Moore. 1999. Heritability and fitness consequences of cannibalism in larvae of the ladybird beetle *Harmonia axyridis*. Evolutionary Ecology Research **1**:375–388.
Wardle, R. A., and P. Buckle. 1923. The principles of insect control. University of Manchester Press, New York, New York, USA.
Wheeler, A. G. 1977. Studies on the arthropod fauna of alfalfa. VII. Predaceous insects. Canadian Entomologist **109**: 423–427.
Wheeler, A. G., J. T. Hayes, and J. L. Stephens. 1968. Insect predators of mummified pea aphids. Canadian Entomologist **100**:221–222.
White, C., and S. D. Eigenbrode. 2000. Effects of surface wax variation in *Pisum sativum* on herbivorous and entomophagous insects in the field. Environmental Entomology **29**:773–780.
Wood, S. N. 1994. Obtaining birth and mortality patterns from structured population trajectories. Ecological Monographs **62**:23–44.
Wooton, J. T. 1994. Putting the pieces together: testing the independence of interactions among organisms. Ecology **75**:1544–1551.

APPENDIX

A detailed description of the model for interactions between specialist and generalist natural enemies: parasitoids, predators, pathogens, and pea aphid (*Acyrthosiphon pisum*) biocontrol is available in ESA's Electronic Data Archive: *Ecological Archives* E084-002-A1.