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GENERALIST PREDATORS DISRUPT BIOLOGICAL CONTROL BY A SPECIALIST PARASITOID

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Abstract. Two broad classes of arthropod natural enemies attack insect herbivores: specialists and generalists. The tight dynamical linkage of specialist natural enemies and their prey may make the specialists able to respond numerically to, and perhaps suppress, herbivore outbreaks. Because generalist predators may attack not only herbivores, but also the herbivores' specialist natural enemies, generalist predators may disrupt control of herbivore populations rather than contribute to it.

We examined interactions between pea aphids (*Acyrthosiphon pisum*), a specialist parasitoid wasp (*Aphidius ervi*) that attacks the aphids, and a common generalist predator, carabid beetles (primarily *Pterostichus melanarius*). In two field experiments in alfalfa, we manipulated carabid densities to measure their direct (through predation) and indirect (through intraguild predation on *A. ervi*) impact on aphid population dynamics. The first experiment was initiated when plants were short (following cutting), and carabid predation of aphids led to an immediate reduction in aphid densities. This reduction was short-lived, however, because carabids reduced parasitism, leading to higher aphid population growth rates. Therefore, although the immediate direct effect of carabids was a reduction in aphid densities, this was offset in the longer term by the indirect effect of carabids disrupting the control of aphids by parasitoids. The second experiment was initiated after plants had regrown following cutting. When plants were tall, carabids had no direct impact on aphid densities. Nonetheless, the slow indirect effect of carabids on aphid densities through reduction in parasitism still occurred, leading to higher aphid population growth rates in the presence of carabids. Additional laboratory experiments demonstrated that carabids are able to climb into plants and prey upon the immobile parasitoid pupae ("mummies"), whereas antipredator behaviors of the aphids protect them from predation by carabids when plants are tall.

Overall, carabid predation caused an immediate but ephemeral decrease in aphid density. In contrast, the indirect positive effect on aphid density caused by reducing parasitism developed later but persisted longer. Thus the generalist carabid primarily acted as an intraguild predator, interrupting aphid population control by the specialist parasitoid.

Key words: Acyrthosiphon pisum; *aphid;* Aphidius ervi; *biological control; carabid beetle; indirect effects; intraguild predation; parasitoid wasp;* Pterostichus melanarius; *Wisconsin, USA.*

INTRODUCTION

The entomophagous arthropods that attack insect herbivores can be divided broadly into specialists and generalists. Specialists feed on one or a few prey species, and their dynamics are thus tightly linked to those of their prey. This close relationship with a prey species may allow specialists to mount a strong numerical response and thereby control the prey population (Hassell 1980, Hassell and May 1986, Murdoch 1994, Turchin et al. 1999). The tight dynamical link between specialist natural enemies and prey populations has focused attention on specialists as potential biological control agents (Debach and Rosen 1991). In contrast, generalists feed on many species and thus respond less strongly to density fluctuations of any single prey spe-

cies. The lack of a close relationship with any single prey species may limit the ability of generalists to respond to and control herbivore population growth (Hassell and May 1986, DeBach and Rosen 1991; but see Riechert and Lockley 1984, Murdoch et al. 1985, Chang and Kareiva 1999).

The catholic feeding habits of generalists may also limit their effectiveness at controlling herbivore populations for another reason: generalists feed not only on herbivores, but potentially on other natural enemies. Predation on other natural enemies, an interaction known as intraguild predation, appears to be common among generalist predators in both natural (Polis et al. 1989, Polis and Holt 1992) and agricultural (Rosenheim et al. 1993, 1995; Rosenheim 1998, Snyder and Wise 1999) systems. Intraguild predation might limit the ability of generalist predators to control herbivore populations (Sih et al. 1985, Polis 1991, Strong 1992, Rosenheim et al. 1993, Polis and Strong 1996). If intraguild predation is intense, a given generalist predator
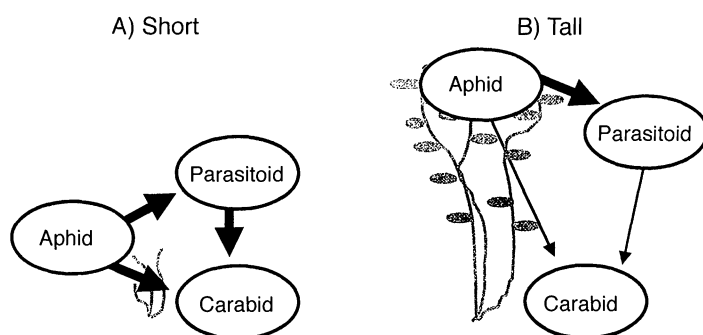
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A) Short   B) Tall

FIG. 1. Hypothesized impact of plant height on pea aphid–parasitoid–carabid interactions. Arrows denote the direction of energy flow, with line thickness scaled to denote the intensity of the pairwise interaction. (A) Diagram of possible interactions among aphids, parasitoids, and carabid beetles. Because carabids primarily forage on or near the ground, they might interact more strongly with aphids and parasitoids after cutting, when alfalfa plants are short. (B) Interactions may weaken as the plants regrow, and as spatial separation between carabids and aphids and between carabids and parasitoids increases.

species can release herbivores from control by other natural enemies, and through a trophic cascade reduce plant productivity (Snyder and Wise 2001).

Since specialist natural enemies attack a narrow range of prey, they are more likely to be the victims than perpetrators of intraguild predation (Lucas et al. 1998). Empirical studies have found that generalist predators can reduce (Tostowaryk 1971, Press et al. 1974, Rees and Onsager 1982, 1985, Jones 1987, Abramson et al. 1989, Völkl 1992, Evans and England 1996, Müller and Godfray 1997, Taylor et al. 1998), increase (Roland 1988, 1995, Kindlmann and Ruzicka 1992, Völkl 1992, Hoelmer et al. 1994), or have no effect on (Stark and Hopper 1988, Harizanova and Ekbom 1997) the proportion of herbivores parasitized by parasitoid Hymenoptera and Diptera, two commonly studied groups of specialists. However, these empirical studies have not tracked herbivore population dynamics through multiple generations, so the long-term (i.e., >1 generation) impact of intraguild predation on parasitoid–host dynamics is unclear.

The experiments reported here were designed to investigate how a generalist predator may affect the longer term population dynamics of parasitoid–prey interactions over the course of one or more host and parasitoid generations. Specifically, we ask whether a short-term suppression of prey densities by a generalist predator may be erased in the longer term by the negative impact of the generalist predator on specialist parasitoids. We have been working with a group of insects in alfalfa: pea aphids, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae); a specialist parasitoid wasp, *Aphidius ervi* (Haliday) (Hymenoptera: Braconidae), that attacks the aphids; and generalist predators, carabid beetles (Coleoptera: Carabidae), which might attack both aphids and parasitoids. In field and laboratory experiments, we manipulated densities of carabids and recorded the impact of these manipulations on pea aphid–parasitoid dynamics both in the short term and over multiple aphid and parasitoid generations.

Our experiments both document and take advantage of the effect of plant architecture on aphid–parasitoid–predator interactions. The most common carabid species that we found in alfalfa fields in Wisconsin, *Pter-*

ostichus melanarius (Illiger), generally forages on the ground and is an awkward climber. Pea aphids feed high in alfalfa plants, and parasitoid mummies (the exoskeletons of aphids in which the parasitoid pupates) occur high in plants. We hypothesized that when alfalfa plants are short immediately after cutting and harvesting, carabid predation on both aphids and mummies would be high. Therefore, both direct and indirect effects of carabids on aphids should be strong (Fig. 1A). When alfalfa has regrown, however, carabid predation on aphids and mummies might be weaker (Fig. 1B). By conducting separate experiments using both short and tall alfalfa, we manipulated the strengths of direct and indirect interactions between carabids and aphids, thereby giving a more detailed picture of the dynamical outcome of aphid–parasitoid–predator interactions.

MATERIALS AND METHODS

Study organisms

Pea aphids, *Acyrthosiphon pisum*, are phloem-feeding homopterans that attack a variety of legumes, including alfalfa, in their native range in Europe. They were accidentally introduced into North America sometime in the last century (Blackman and Eastop 1984). Pea aphids reproduce rapidly, with a total development time from first instar to adult of ~5 d at summer temperatures (Hutchinson and Hogg 1984, 1985, Thiboldeaux 1986). Alfalfa is cut and harvested two to four times per year. The period immediately following cutting is critical for aphid population dynamics, because cutting causes high aphid mortality and consequently decreases aphid density by two to three orders of magnitude (Rauwald and Ives 2001). The aphids that survive cutting, and those that immigrate shortly after cutting, contribute to an exponentially growing population. Therefore, small numbers of aphids consumed by carabids immediately following cutting could greatly reduce the number of aphids later in the cutting cycle.

The hymenopterous parasitoid *Aphidius ervi* was collected in France and released in the U.S. for biological control of pea aphids in the 1960s (Gonzalez et al. 1978). The parasitoid is now widely sympatric with these aphids in North America, but pea aphid outbreaks still regularly occur (Harvey et al. 1972, Harper and

Kaldy 1982, Maiteki and Lamb 1985, Soroka and MacKay 1990). Female *A. ervi* prefer to oviposit in second- and third-instar aphids (Ives et al. 1999). Development of the aphid then continues, with the parasitoid developing within its host. After ~8 d at summer temperatures (Thiboldeaux 1986), the *A. ervi* completes its larval development, and the parasitoid causes its host to move to an apical leaf, usually near the top of the host plant. The parasitoid then kills the host and pupates in a cocoon within the host's exoskeleton to create a mummy. In the field *A. ervi* development (egg to adult) is completed in ~12 d (Thiboldeaux 1986). *A. ervi* is the only common parasitoid that attacks pea aphids in Wisconsin, and pea aphids are *A. ervi*'s only host that occurs in alfalfa fields.

Pterostichus melanarius is the most abundant carabid species in alfalfa at our site, comprising >95% of pitfall-trap catches (see *Results: Field experiments: Carabid manipulations*). This carabid was accidentally introduced into North America from Europe and is now widespread (Niemela et al. 1997). Thus, the pea aphid, its parasitoid *A. ervi,* and *P. melanarius* are widely sympatric both in their native range in Europe and now in North America. *P. melanarius* is a relatively carnivorous carabid, feeding on a variety of insects (Hagley et al. 1982), other invertebrates (Symondson et al. 1996), and even small vertebrates (Ovaska and Smith 1987), although seeds may also be eaten (Hagley et al. 1982). *P. melanarius* has been found to feed on several species of aphids (Edwards et al. 1979, Hamon et al. 1990, Helenius 1990), including pea aphids (Ekbom 1994). *P. melanarius,* then, is a typical generalist predator, probably opportunistically feeding on many types of prey it encounters but not relying on any particular prey species.

Field experiments

Experimental design.—Our field site was a 4-ha alfalfa (*Medicago sativa*) field on the University of Wisconsin Arlington Research Farm, near Madison, Wisconsin. Our experimental units were 2 × 2 × 2-m cages, covered on all sides but the bottom with 32 × 32 mesh Lumite screening (BioQuip, Gardena, California, USA, catalog number 1412C). A zipper on one side allowed entry into the cages. The bottom edge of each cage was buried ~20 cm into the ground to ensure that aphids and parasitoids could not move in and out of the cages, and to hamper movement of carabid beetles. Cages were arranged in a single row and randomly assigned to treatment. Each experiment also included 2 × 2-m reference areas, with pitfall traps in the corners but not enclosed by a cage. These open plots were used to measure carabid activity-densities in the surrounding field, so that we could determine if caging altered carabid activity-densities.

We conducted two field experiments, each with two aphid manipulations (high or low aphid density) and two carabid manipulations (natural carabid density or carabids removed) in a 2 × 2 factorial design. Thus our treatments were (A) high aphid density, carabids removed; (A + C) high aphid density, carabids present; (a) low aphid density, carabids removed; and (a + C) low aphid density, carabids present. In both experiments, each of these four treatments was replicated three times (total of 12 cages), and three open reference plots were monitored for carabid activity. In both experiments, we installed cages, then made the initial aphid manipulation and began carabid removals within 24 h. We considered the time when aphid addition and carabid removal were begun as day 0. While the two experiments shared the same treatments, each was conducted during a different stage of plant growth. The first experiment was started immediately after the plants were cut, reproducing conditions during initial regrowth following alfalfa harvest. The second experiment was initiated 2 wk after cutting, so that the plants were ~8–20 cm tall at the start of the experiment. This second experiment reproduced conditions later in regrowth.

The first experiment was continued for 15 d and the second for 17 d. The potential population doubling time for pea aphids is roughly 3 d, so the experiments could potentially involve a 32× increase in aphid abundance from initiation to termination. The generation time (egg to adult) of *A. ervi* is ~12 d, so that both of our experiments included an entire parasitoid generation within the cages. However, since we added parasitoids as larvae within field-collected aphids, parasitoids were added across a range of larval development stages. Thus, parasitoids that began development in the field were eclosing throughout the duration of each experiment.

Aphid and parasitoid manipulation.—The aphid manipulations were established 24 h after cage installation. The aphids used in each experiment were collected from nearby alfalfa fields on the Arlington Research Farm. Subsamples of the aphids used in the experiments were returned to the laboratory and dissected to determine percentage parasitism. Parasitoids were not directly manipulated; parasitoids were added to the cages within parasitized aphids. Because we expected that carabids might interact most strongly with the aphids after cutting, we added relatively large numbers of aphids to the cages in experiment 1; high aphid density cages received 1000 aphids each, and low aphid density cages received 100 aphids each. While these aphid densities were higher than in experiment 2, they are still well below maximum aphid densities observed in the field (e.g., Hutchinson and Hogg 1985). For experiment 2 we added fewer aphids for two reasons. First, we expected the impact of carabids to be weaker when the plants were taller, and second, aphid populations had already started to recover during the 2 wk following cutting, providing a moderate ambient aphid density (mean densities were 32.0 ± 6.2 aphids per cage). For experiment 2, high aphid density cages re-

ceived 100 aphids, and low aphid density cages were not supplemented with aphids.

Carabid manipulation.—We installed one pitfall trap (see Snyder and Wise [1999] for trap design) into each corner of each cage (4 traps per cage). These traps were used to estimate carabid activity-densities in all cages, and to remove carabids in carabid-removal treatments. Carabids captured in the removal plots were released into nearby alfalfa fields or were used for laboratory experiments; carabids captured in the nonremoval plots were rereleased into the cages. In all cages, trapped arthropods other than carabids were immediately released into each cage. Removal traps were left open throughout each experiment. To exclude rain, traps were covered with 23 cm diameter plastic plates, suspended ~4 cm from the ground with a piece of wire.

Plates suspended in this way also helped to make the traps more selective for carabids by intercepting aphids that dropped from the foliage; aphids were rarely found in the pitfall traps. After cages and pitfall traps were installed, the traps were opened in carabid-removal plots.

Sampling.—Carabid activity-densities in the cages and the open reference areas were measured by running the four pitfall traps in each cage for 24 h. Carabid densities were sampled at -1, 8, and 13 d (16 June, 25 June, and 30 June 1999) after aphid manipulation in experiment 1, and 1, 8, 12, and 14 d (10 July, 17 July, 21 July, and 23 July 1999) after aphid manipulation in experiment 2.

Aphid densities were measured by counting the aphids on each of 200 haphazardly chosen alfalfa stems in each cage. Each cage enclosed ~800 alfalfa stems (792 ± 20.46 alfalfa stems; experiment 1), so ~25% of all stems in each cage were censused on each sample date. During these counts we also recorded numbers of mummies and foliar-dwelling predators we encountered (e.g., nabid bugs, coccinellid beetles). These counts were taken 7, 12, and 15 d (24 June, 29 June, and 2 July 1999) after aphid manipulation in experiment 1, and 0, 6, 10, 13, and 17 d (9, 15, 19, 22, and 26 July 1999) after aphid manipulation in experiment 2.

At the end of both experiments, we collected aphids from each cage using a sweep net. These aphids were returned to the laboratory and dissected to determine percentage parasitism.

Laboratory experiments

Simultaneous plant height and carabid manipulation.—The objective of this experiment was to examine the direct effects of carabids on aphids and mummies, and how these interactions are modified by plant height. We simultaneously manipulated both factors in laboratory microcosms containing alfalfa plants and aphids with a known percentage parasitism. Because we were interested in direct effects, we terminated the experiment after 7 d. This time allowed parasitoids to form mummies, and for mummies to be subject to carabid

predation, but was not enough time for a second generation of parasitoids to complete development in situ.

We collected alfalfa plants from our field site, brought them back to the laboratory, and transplanted them into 18 cm diameter × 15 cm tall plastic pots. The plants were allowed to acclimate for 2 wk, during which time they were housed in a greenhouse (14:10 L:D, temperature 22–27°C) and watered regularly. We selected 32 plants that were most similar in size for use in the experiment. Plants were covered with an 18 cm diameter × 30 cm tall, transparent Mylar plastic tube, with the bottom of the tube twisted into the soil to form a seal with the edge of the pot. We cut half of the plants to a height of ~4 cm; the remaining plants were left uncut at ~20 cm tall. To each microcosm we then added 30 pea aphids. As in the field experiments, some of these aphids were parasitized by *A. ervi*; this was the only route for *A. ervi* to enter the microcosms. Before aphid additions we removed a subsample of the aphids and dissected these 10–20 individuals to determine initial percentage parasitism. The top of each tube was covered with a fine mesh lid to prevent the escape of parasitoids and carabids, and to prevent other arthropods from entering the microcosms.

We added one adult female *Pterostichus melanarius* to half of the microcosms, to achieve eight replicates of each of the following treatments, in a 2 × 2 factorial design: (T + C) tall alfalfa, a carabid present; (T) tall alfalfa, no carabid; (S + C) short alfalfa, one carabid individual present; and (S) short alfalfa, no carabid. We visually counted the number of aphids in each microcosm each day for 7 d, starting on the same day as the carabids were added to the microcosms. Seven days is approximately the larval development time of *A. ervi* under these conditions, and parasitoids formed mummies on the plants throughout the week. On day 7 we terminated the experiment and counted the number of mummies in each microcosm. Mummies from which adult parasitoids had already emerged (emergence is clearly indicated by the emergence hole made by the parasitoids) were included as survivors.

Carabid predation on mummies.—The results of the laboratory microcosm and field experiments suggested that carabids might be altering percentage parasitism by feeding on mummies more heavily than on aphids. Many parasitoids, including *A. ervi,* alter host behavior just before parasitoid pupation (Brodeur and McNeil 1989). Parasitized pea aphids walk to the apical leaf of the plant they are on, where mummies are then formed. This behavior has been interpreted as a strategy to avoid hyperparasitism (Brodeur and McNeil 1992, Brodeur and Vet 1994), although this location might also be less accessible to ground-foraging predators like carabids. To measure the ability of *P. melanarius* to prey upon *A. ervi* mummies at varying heights on alfalfa plants, we glued field-collected mummies to alfalfa plants in laboratory microcosms like those described in the section just above (see *Simultaneous*

FIG. 2. Activity-densities of carabids in (A) field experiment 1 and (B) field experiment 2. Data are the mean catch per trap in a 24-h period, averaged over three sampling dates in experiment 1, and four sampling dates in experiment 2. Treatments: A = high aphid density, carabids removed; A + C = high aphid density, carabids unmanipulated; a = low aphid density, carabids removed; a + C = low aphid density, carabids unmanipulated; open = uncaged reference areas. Data are presented as mean and 1 SE.
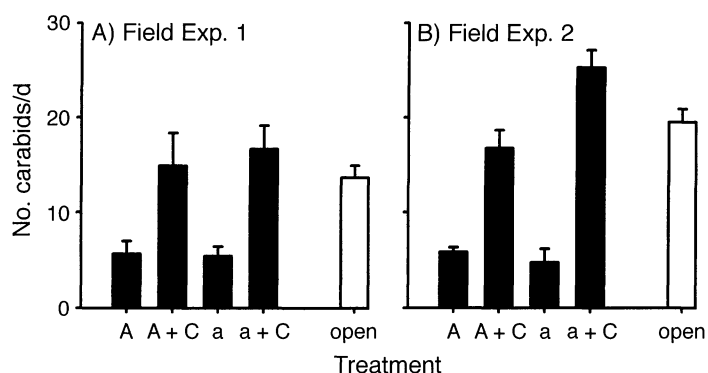
plant height and carabid manipulation). Mummies were attached to alfalfa plants using a small drop of Elmer's glue (Borden, Columbus, Ohio, USA). In the first of these experiments, we attached two mummies at each of four heights (5, 10, 15, and 20 cm from the soil surface) in each of 10 microcosms. To measure the ability of carabids to reach mummies that were both high in the plants and on stems far from the central core of the plant, we conducted a second experiment. In this experiment we attached four mummies in each microcosm with all mummies 20 cm from the soil surface, but with two mummies within 5 cm of the core of the plant and two on stems >10 cm from the core of the plant. In each experiment we then added a single female *P. melanarius* to each microcosm at 1700 in the late afternoon, left the microcosms undisturbed until 1200 on the following day, and then recorded the number of mummies (zero, one, or two) remaining at each height or location in each microcosm.

Statistics.—The two field experiments and the laboratory microcosm experiment were first analyzed using multivariate repeated-measures analysis in SYSTAT (SPSS, Chicago, Illinois, USA). Where we found significant treatment × time interactions, we also separately analyzed data from each sample date using two-way ANOVA. The feeding behavior trials were analyzed using randomized block design, with individual microcosms considered blocks and mummy location as the independent variable. For all analyses, data were log transformed to meet the assumptions of ANOVA when necessary.

RESULTS

Field experiments

The two field experiments both used a 2 × 2 factorial design to manipulate carabid and aphid abundances, with experiment 1 conducted immediately following alfalfa cutting and experiment 2 conducted after allowing 2 wk for plant regrowth.

Carabid manipulation.—One carabid species, *Pterostichus melanarius*, made up 96% and 97% of carabids trapped in experiments 1 and 2, respectively. The remaining 3–4% of the carabids trapped were a mix, in roughly equal proportions, of *Bembidion quadrimaculatum*, *Poecilus chalcites*, *Agonum placidus*, *Cyclotrachelus seximpressus*, *Chlaenius emarginatus*, and *Harpalus pennsylvanicus*. *P. melanarius* is larger than these other species (with the exception of *H. pennsylvanicus*), so that *P. melanarius* represented >96% of carabid biomass.

In both experiments, carabid removals were effective in reducing carabid densities (Fig. 2A, B). In experiment 1, carabids were reduced ~66% in the carabid-removal cages ($F_{1,8} = 32.259$, $P < 0.001$); carabid densities were not affected by the aphid manipulation ($F_{1,8} = 0.044$, $P = 0.839$) or by the interaction between the treatments ($F_{1,8} = 0.040$, $P = 0.846$). In experiment 2, carabids were again reduced ~66% in the carabid removal cages ($F_{1,8} = 81.959$, $P < 0.001$); the aphid manipulation ($F_{1,8} = 0.888$, $P = 0.374$) and the interaction between the treatments ($F_{1,8} = 1.173$, $P = 0.310$) did not significantly affect carabid activity-densities.

In both experiments, carabid densities were similar in the caged and open plots [$F_{1,7} = 0.02$, $P = 0.891$, $F_{1,7} = 2.051$, $P = 0.195$, for experiments 1 and 2 respectively; contrast of carabid activity-densities in open to pooled (A + C and a + C)].

Experiment 1: Short plants.—Carabids initially depressed aphid densities, but this effect diminished through time, with aphid densities in all treatments eventually converging. The ephemeral carabid effect led to a significant treatment × time interaction (Wilks' lambda = 0.201, $F_{2,9} = 2.771$, $P = 0.035$; Fig. 3A). At day 7, carabids reduced aphid densities 66% ($F_{1,8} = 13.05$, $P = 0.007$), although aphid density was still affected by our initial aphid manipulation ($F_{1,8} = 19.221$, $P = 0.002$); the carabid × aphid interaction term was non-significant ($F_{1,8} = 3.064$, $P = 0.118$). By the end of the experiment aphid densities in all treatments converged, so that carabid, aphid manipulation, and the carabid by aphid manipulation effects were nonsignificant ($P > 0.10$ for all effects) on days 12 and 15.

Percentage parasitism of aphids added to the cages was 26.8 ± 4.5% (eight subsamples of 10–20 aphids each were dissected; total $N = 107$ aphids). At the end
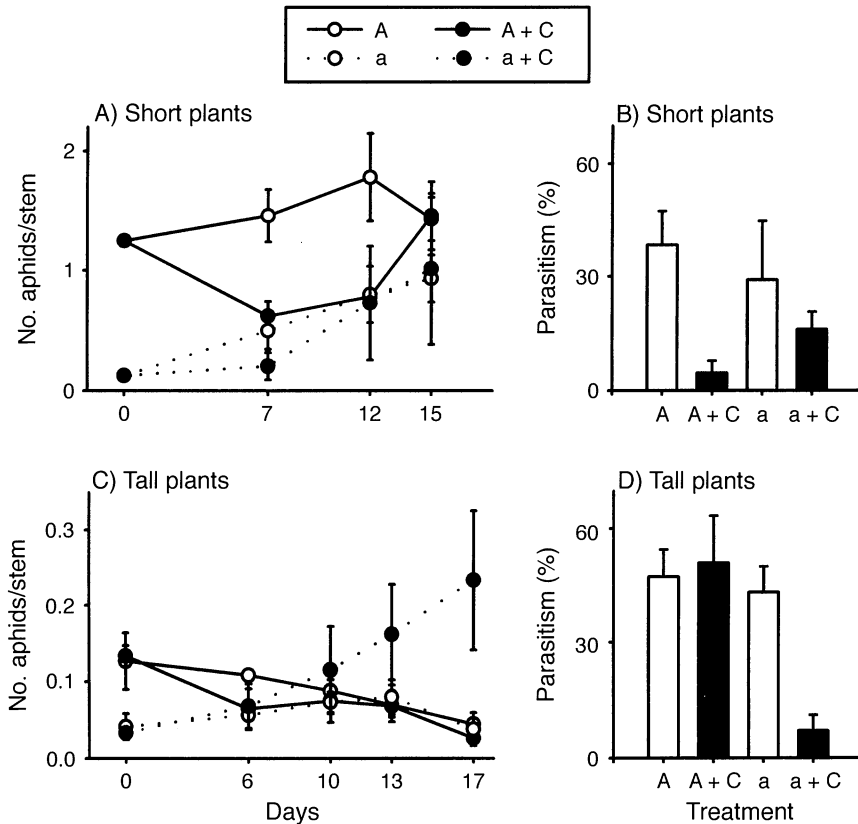
FIG. 3. Aphid densities through time and final percentage parasitism in experiment 1 (parts A and B), which was initiated just after alfalfa cutting, and experiment 2 (parts C and D), which was initiated when plants were taller. Carabid manipulation began after the aphid census on day 0. Treatment descriptions are the same as in Fig. 2.

of the experiment, in cages without carabids, percentage parasitism increased to ~30%, while in cages with carabids percentage parasitism was ~10% (Fig. 3B). Thus, carabids caused a threefold decrease in percentage parasitism by the end of the experiment ($F_{1,8}$ = 6.151, P = 0.038). Final percentage parasitism was not affected by aphid manipulation ($F_{1,8}$ = 0.012, P = 0.917) or by the interaction between predator and aphid manipulations ($F_{1,8}$ = 1.20, P = 0.305).

Experiment 2: Tall plants.—Aphid densities were similar in all treatments through day 10. After day 10, aphid populations grew in the carabid and low-aphid-density treatment (a + C) for the remainder of the experiment, but declined in the other three treatments (Fig. 3C), leading to a statistically significant time × treatment interaction (Wilks' lambda = 0.010, $F_{12,13}$ = 5.292, P = 0.002). Analysis of each sample date reveals no statistically significant effect of carabid or aphid manipulation on days 6, 10, or 13 (P > 0.10; for carabid, aphid, and carabid × aphid effects, respectively, on each date). However, the increase in aphid densities in the a + C treatment led to a statistically significant carabid × aphid effect ($F_{1,8}$ = 7.958, P = 0.022) on the final sample date (day 17).

Percentage parasitism for aphids added to the cages

was 34.1 ± 2.8% (four subsamples of 10–20 aphids each were dissected; total N = 58 aphids). In carabid-removal cages, percentage parasitism increased to ~40% (treatments A and a, Fig. 3D), as it did in the high-aphid cage without carabid removal (treatment A + C, Fig. 3D). In contrast, percentage parasitism was three times lower in the a + C treatment (Fig. 3D). Thus, there was a significant interaction between carabid and aphid manipulations ($F_{1,8}$ = 5.790, P = 0.043). The carabid main effect approached statistical significance ($F_{1,8}$ = 3.835, P = 0.086), and the aphid main effect was significant ($F_{1,8}$ = 8.413, P = 0.020).

Laboratory experiments

The laboratory experiments were designed to look at the direct effects of carabids on aphids and parasitoids, and thus were run for less than one parasitoid generation.

Simultaneous plant height and carabid manipulation.—Aphid densities increased through time in all treatments (Wilks' lambda = 0.263, $F_{5,24}$ = 13.473, P < 0.001; Fig. 4A). Aphids increased more slowly in the treatment with short alfalfa and carabids (S + C) than in the other treatments that had similar aphid densities, and these treatment differences were maintained

FIG. 4. (A) Aphid densities through time and (B) mummy survivorship through the 7-d experimental period for the laboratory microcosm experiment. Carabids were added to the microcosms on day 0 after the aphid count. Treatments: T + C = tall alfalfa, carabid present; T = tall alfalfa, no carabid; S + C = short alfalfa, carabid present; S = short alfalfa, no carabid.
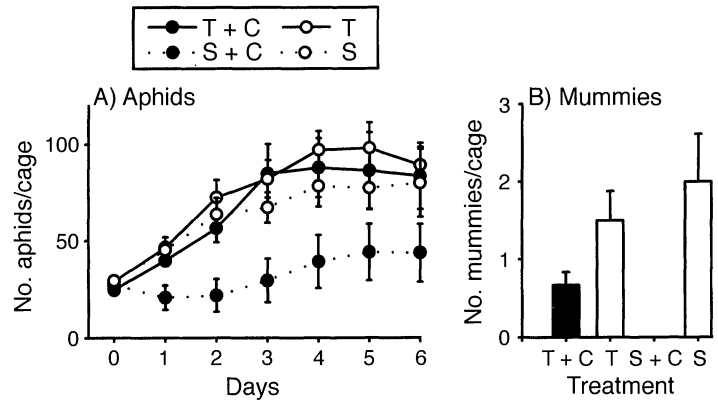
through time (Wilks' lambda = 0.505, $F_{15,66}$ = 1.248, P = 0.260; treatment × time interaction). Carabid addition led to reduced mean aphid densities over the course of the experiment, but only when plants were short ($F_{1,28}$ = 4.29, P = 0.048; carabid × plant height interaction). Both the carabid ($F_{1,28}$ = 7.331, P = 0.011) and plant height ($F_{1,28}$ = 6.679, P = 0.015) main effects on mean aphid densities were significant.

No mummy survived until the end of the experiment when carabids were present and plants were short (S + C; Fig. 4B). Some mummies survived in the presence of carabids when plants were tall, but the number of mummies surviving was significantly lower than when carabids were absent [$F_{1,22}$ = 5.228, P = 0.032; contrast of mummies surviving in T + C treatment to pooled T and S treatments].

Mummy location and carabid predation.—The first experiment on mummy location examined how the height of mummies in alfalfa plants affected carabid predation. Individual carabids significantly differed in their total consumption of mummies ($F_{11,33}$ = 9.60, P < 0.001; blocking by individual). Nonetheless, there was a strong pattern, with mummies lower on plants eaten more frequently than those higher on plants ($F_{3,33}$

= 8.067, P < 0.001; Fig. 5A). However, even at the greatest height we examined (20 cm), carabids ate ~50% of the mummies during the 17-h experiment.

The second experiment examined the relationship between carabid predation and the distance of mummies from the central core of the alfalfa plant. Individual carabids differed marginally in their total mummy consumption ($F_{11,11}$ = 2.735, P = 0.055; blocking by individual), but there was no significant difference between predation rates on mummies near the core of the plant and those on exterior leaves ($F_{1,11}$ = 3.313, P = 0.096; Fig. 5B).

DISCUSSION

As we hypothesized, carabids interacted strongly with aphids and parasitoids when plants were short, and interactions were weaker when plants were tall (Fig. 1). Carabids reduced aphid densities by >50% within 7 d on short plants, but this direct effect was not evident on tall plants. However, the indirect effect of carabids, mediated by intraguild predation, occurred regardless of plant height. Carabids caused a threefold decrease in percentage parasitism when plants were short, and caused a similar reduction in percentage parasitism at low aphid densities when plants were tall. Laboratory studies showed that carabids were able to climb into plants and consume the immobile mummies, while the mobile aphids are apparently more effective at escaping in tall plants. Thus, plant architecture determined the presence vs. absence of a direct effect of carabids on pea aphids, but not the presence vs. absence of the indirect effect of carabids acting through intraguild predation on parasitoids.

The direct and indirect effects of carabids became apparent at different times, scaled to the generation time of parasitoids. Direct predation led to an immediate, but temporary, decrease in aphid populations, but the indirect effect via intraguild predation did not appear until one or more parasitoid generation later.

The indirect effect is slower to develop because intraguild predation occurs most strongly during the
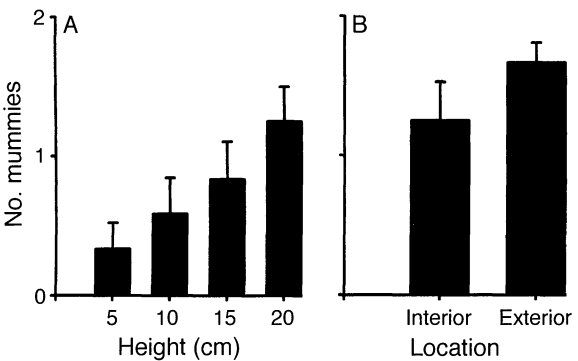

FIG. 5. Number of mummies surviving (A) at increasing height in plant foliage, and (B) with increasing distance from the central core of the plant. Mummies were exposed to predation by a single carabid for 17 h.

mummy stage of the parasitoid, thereby reducing the numerical response of parasitoids to aphid densities. This generates a time lag in the indirect effect of intraguild predation of roughly a parasitoid generation. This time lag is short relative to the cutting cycle (roughly 25% of the time interval between cuttings), but it might still strongly impact aphid densities throughout plant regrowth. Relative densities of aphids and parasitoids immediately after cutting, in part, determine aphid population growth trajectories (Rauwald and Ives 2001). Thus, by releasing aphids from control by parasitoids early in alfalfa regrowth, carabids can establish biotic conditions likely to lead to higher aphid densities later in the cutting cycle.

Results from experiments conducted in cages must always be viewed cautiously, because caging may increase or decrease the likelihood of species interactions relative to the open field. However, in many respects conditions in our cages closely approximated those in open alfalfa fields. Aphid densities within our cages, which ranged from 0.02 to 2.25 aphids/stem, are typical of those seen in alfalfa fields in Wisconsin (Ives et al. 2000; A. R. Ives, *unpublished data*). Similarly, both of our field experiments were initiated with a percentage parasitism of ~30%, a typical level of parasitoid attack in Wisconsin (Ives et al. 2000; A. R. Ives, *unpublished data*). It is difficult to compare carabid activity-densities inside cages with those measured in the open reference areas. This comparison only approximately reflects actual relative densities, because traps in open plots have a larger effective sampling area, inflating estimates of relative population size in the open vs. caged plots (Wise 1981). However, counteracting this bias, in our experiments the cage edge probably acted as a drift fence, making the traps relatively more effective inside the cages (Holland and Smith 1999). With these caveats in mind, carabid densities inside the cages and in the open field appeared similar (Fig. 2), suggesting that the carabid impacts we recorded were similar in intensity to those likely to occur outside of cages.

Direct effect of carabids

In the field, carabids were only able to decrease aphid populations directly when plants were short (experiment 1). Immediately after cutting, carabids reduced aphid densities by 66% (Fig. 3A). When plants were taller (experiment 2), we could not detect any reduction in aphid densities by direct carabid predation (Fig. 3C). These results from the field experiments were confirmed in a laboratory experiment where we simultaneously manipulated plant height and carabid presence; in the laboratory, carabids only reduced aphid densities when plants were short (Fig. 4A). It appears that taller plants provide a spatial refuge from carabid predation, but this refuge is periodically lost when alfalfa is cut.

Indirect effect of carabids

While carabid predation sometimes led to initially lower aphid densities, carabids eventually increased the rate of aphid population growth. In the field experiment with short alfalfa (experiment 1), aphid densities increased more rapidly in the presence of carabids after the initial reduction, so that aphid densities in all treatments eventually converged (Fig. 3A). There was no initial reduction in aphid densities in the field experiment with tall alfalfa (experiment 2), but carabid presence did lead to increased aphid population growth when aphid densities were initially low (Fig. 3C). In both experiments, accelerated aphid population growth corresponded to decreased percentage parasitism. In experiment 1, where aphids eventually increased more rapidly in both treatments containing carabids, percentage parasitism was reduced in both of these treatments (Fig. 3B). In experiment 2 carabids reduced percentage parasitism only when initial aphid density was low, which was also the only treatment that exhibited increased aphid population growth (Fig. 3C). Thus the results of the field experiments support the hypothesis that carabids increase aphid population growth through intraguild predation on parasitoids.

In experiment 2, with tall alfalfa, carabids only had a strong indirect effect on aphid population growth when initial aphid densities were low; when initial aphid densities were high, percentage parasitism was not reduced by carabids. This result, that disruption of aphid population control occurs more readily at low aphid and parasitoid densities, was found in similar field experiments in which carabids were not manipulated (Rauwald and Ives 2001). There are two possible explanations for this. First, carabids could remove a greater fraction of mummies when mummy densities are low, thereby causing a greater disruption in aphid population control. Second, even if carabids remove the same fraction of mummies regardless of mummy density, the subsequent effect of mummy removal on aphid population control could depend on aphid density. At high aphid densities, any parasitoid that survives carabid predation will likely have high success in finding aphids, thereby allowing the recovery of the parasitoid population. In contrast, at low aphid density the parasitoid population may not recover. This second explanation assumes that parasitoid success in finding aphids, and hence their per capita effect on aphid population control, depends on the density of aphids rather than the ratio of parasitoid to aphid density; in other words, parasitism is density dependent rather than ratio dependent (Abrams 1994, Arditi and Saiah 1992, Berryman 1992).

Increasing plant structural complexity has been proposed as a strategy to reduce negative interactions between generalist predators in agro-ecosystems, thereby favoring biological control (Riechert and Bishop 1990, Snyder and Wise 1999). Indeed, we found that intra-

guild predation was less common when plants were taller. However, direct predation on the herbivore disappeared when the environment became structurally more complex. Therefore, even though increasing plant structural complexity did reduce intraguild predation, its net effect was to disrupt biological control, at least over the time scale of our experiments.

Carabid predation on mummies

The results from both field and laboratory experiments suggest that carabids are reducing percentage parasitism by preying on mummies. In the first laboratory microcosm experiment, carabids consumed all mummies when plants were short (Fig. 4B). Carabids also preyed upon mummies when plants were taller, but some mummies survived until the end of the experiment. In the second laboratory microcosm experiment, we found that carabids could effectively prey upon mummies at the greatest height we examined (20 cm), but their effectiveness as mummy predators declined with increasing mummy height (Fig. 5A). Together, the pattern of mummy predation in the laboratory was consistent with the results of the field experiments, where intraguild predation weakened, but did not disappear, when plants were tall.

Pea aphids have a variety of antipredator behaviors, including the release of alarm pheromones, kicking, running, and dropping from plants (McAllister and Roitberg 1987, McAllister et al. 1990). Aphids appear to be able to differentiate between enemies, and deploy the most effective behaviors against each predator (Losey and Denno 1998a, b). The dropping behavior is usually used against larger predators, such as coccinellid beetles. If aphids also drop to escape from carabids moving in the foliage, this may explain the inability of carabids to capture aphids when plants are taller. When plants are short, dropping behavior will only move aphids a short distance from a foraging carabid, but the displacement will be much greater when plants are taller. If the aphids' dropping behavior is indeed less effective when plants are short, this might explain the greater reduction of aphid density by carabids on short plants.

Unlike unparasitized aphids, or parasitized aphids that are still active, mummies are immobile and remain susceptible to carabid predation when plants are tall. In laboratory microcosms, we found that carabids were most effective at preying upon mummies that were lower in the foliage. It is unclear whether this is due to the poor climbing ability of carabids, so that mummies higher in the foliage are more difficult for the beetles to reach, or because carabids become satiated on the first mummies they encounter as they climb up the plant. The latter seems unlikely, however. *P. melanarius* can consume ≥20 adult pea aphids in 24 h (W. E. Snyder, *personal observation*); assuming mummies are similar nutritionally to adult aphids, carabids

should have easily been able to consume the eight mummies in each microcosm.

Many carabids are primarily ground-foraging predators (Thiele 1977, Lovei and Sunderland 1996), although otherwise terrestrial carabids have been reported moving through the foliage (e.g., Barney and Pass 1986). Our results suggest that *P. melanarius* is unable to capture active prey in the foliage but remains an effective predator of immobile prey. Indeed, it has been proposed that inactive stages may generally experience the highest rates of intraguild predation (Lucas et al. 1998), since they are unable to escape predators once located.

There are several other routes through which carabids might alter percentage parasitism. Carabids could also reduce percentage parasitism if they preferred to prey upon parasitized vs. unparasitized aphids. In other laboratory feeding trials, we have found that carabids do not selectively prey upon parasitized, but still active, aphids, and will consume aphids and mummies roughly in proportion to the abundance of each when both prey are provided (W. E. Snyder, *personal observation*). Thus, a feeding preference for mummies or parasitized aphids does not appear to contribute to the disproportionate impact of carabids on parasitoids. Pea aphids have been reported to exhibit "adaptive suicide," with parasitized aphids more likely to drop in response to predator attack than unparasitized aphids (McAllister and Roitberg 1987, McAllister et al. 1990). Increased rates of dropping by parasitized aphids would subject them to disproportionately high rates of carabid predation (Losey and Denno 1998b, c). Such a mechanism could be contributing to selective mortality of parasitized aphids in our study.

Carabids as biological control agents

Many studies have demonstrated that carabids prey upon agricultural pests (Thiele 1977, Lovei and Sutherland 1996). However, evidence of direct predation on a given pest does not by itself indicate that a generalist predator is an effective biological control agent, since the predator may be simultaneously disrupting biological control by other natural enemies (e.g., Rosenheim et al. 1993, Snyder and Wise 2001). Two recent studies that explicitly examined carabid interactions with both herbivores and other predators have reached the conclusion that carabids contribute to, rather than detract from, pest population control (Losey and Denno 1998c, Snyder and Wise 2001). This is in contrast to the work we report here, where the net impact of carabids was a disruption of biological control. We discuss both of these studies in turn, and suggest possible explanations of why these studies reached conclusions opposite from ours.

Working in vegetable gardens, Snyder and Wise (2001) found that carabid beetles significantly reduced a major herbivore of squash, the squash bug (*Anasa tristis*). The reduction in squash bugs was sufficiently

strong to increase squash productivity (Snyder and Wise 2001). While the community impact of carabids may have been different in Snyder and Wise's study than in ours, carabids seemed to be acting through a similar type of predation. Squash bug eggs are sessile and located near the ground, where they can be easily reached by carabids (Snyder 1999). In contrast, the other major natural enemies in the system (wolf spiders and nabid bugs) are mobile and appear largely immune from carabid predation (Snyder 1999, Snyder and Wise 2001). Thus, in both studies carabids had the greatest impact on immobile insect stages, in one case a herbivore's eggs (Snyder and Wise 2001) and the other a parasitoid's pupae (Snyder and Ives 2001).

Working in the pea aphid/alfalfa system, Losey and Denno (1998c) found that ground beetles (primarily the carabid *Harpalus pennsylvanicus*) contributed to the control of pea aphid densities. They found that carabids encountered and consumed aphids that dropped to escape coccinellid beetles foraging in the foliage. Losey and Denno's experiments, however, were not designed to investigate possible effects on parasitism. Losey and Denno established aphid populations from a laboratory colony, so that no aphids were initially parasitized. Furthermore, the duration of their experiments (1, 7, or 14 d) was too short to allow parasitoids to locate aphid populations and instigate population control. Thus, negative interactions between carabids and parasitoids could not have been detected, because the possibility of parasitoid control of aphids was not allowed.

Interactions between generalists and specialists

It has been proposed that guilds of generalist predators may be more effective than individual species at regulating herbivore populations, by attacking many prey stages and by being present during herbivore colonization (Riechert and Lockley 1984, Riechert and Bishop 1990). However, negative interactions between generalist predators appear to be common (Polis et al. 1989, Polis and Holt 1992, Rosenheim et al. 1993, 1995, Rosenheim 1998, Snyder and Wise 1999, 2001), making it difficult to predict the net impact of generalist predator guilds on herbivores. Pairs of predators might act additively or synergistically to increase or decrease the impact of any one predator by itself (Wooton 1994, Chang 1996, Ferguson and Stiling 1996, Sih et al. 1998). However, intraguild predation of parasitoids by generalist predators may be particularly likely to reduce control of herbivore populations. Specialists are dynamically linked to one or a few prey species, so that they can respond in a density-dependent fashion to changes in herbivore population density and thus control population densities. Generalists often lack the ability to respond numerically to changes in the density of any single prey species. Furthermore, generalists will often be intraguild predators of specialists, while the reverse will seldom be true (Lucas et al. 1998). This sets up a scenario that will typically be detrimental

for overall population control: generalists, ineffective at regulating populations themselves, will often prey on the more-effective specialists.

There has been recent debate about whether direct and indirect effects are likely to occur on the same temporal scale (Schoener 1993, Bender et al. 1984, Brown et al. 1986, Dungan 1986, Menge 1997). The type of indirect effect we have documented, mediated by intraguild predation on specialist natural enemies, may be particularly likely to occur at a slower time scale than any direct effects. Direct predation by carabids on herbivores resulted in an immediate change in aphid densities. In contrast, the indirect effect of carabids on aphids via intraguild predation had an inherent time lag of roughly a parasitoid generation. This is because intraguild predation occurs on parasitoid pupae, and the indirect effect on aphids manifests itself as a reduction in the number of aphids parasitized by the following generation of parasitoids. This time lag of indirect effects has important implications for studies of intraguild predators where specialists are important components of a natural enemy guild: short-term experiments run the risk of revealing only direct effects of generalists on population control, while potentially more important indirect effects mediated by specialists are invisible.

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