

*Ecological Applications*, 9(2), 1999, pp. 378–386  
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## FACTORS FACILITATING SYNERGISTIC PREDATION: THE CENTRAL ROLE OF SYNCHRONY

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**Abstract.** Determining the phenological and diel concurrence of potentially overlapping predator guilds in a given system provides a gauge of the potential prevalence and importance of synergistic prey suppression. The phenology of pea aphids (*Acyrtosiphon pisum*) and ground- and foliar-foraging predators was determined through a combination of pitfall and sweep-net sampling in alfalfa. These results revealed diverse guilds of ground- and foliar-foraging predators with a high degree of phenological overlap among individual species. One of the most common ground-foraging predators, *Harpalus pennsylvanicus*, was found to be significantly more active at night, but also to maintain moderate activity levels during the day. When tested individually in simple arenas with full access to aphids, the aphid-consumption rates of five common ground-foraging predators (*H. aeneus*, *H. pennsylvanicus*, *Amara familiaris*, *A. octopunctatum*, and *Philonthus* spp.) were not significantly different from that of *Coccinella septempunctata*, a foliar-foraging predator that is held to be one of the most important aphid consumers in alfalfa. Thus, both the seasonal occurrence and daily activity levels of these two aphid predator guilds overlap, and the ground-foraging predators, which are often overlooked as sources of aphid predation, were shown to be effective aphid consumers.

Three key elements emerge from the alfalfa–aphid–predator system as general predictors of the probability for the synergistic predation on pests by members of a predator complex: (1) synchrony of predator species in the complex, (2) predator-induced escape behavior of prey resulting in habitat switching and encounter with a new predator guild, and (3) minimal negative interaction (intraguild predation or interference) between the predator species. These elements can aid in identifying systems where the conservation or augmentation of ground-foraging predators or other interactive predator guilds will be most effective.

**Key words:** *Acyrtosiphon pisum*; agroecosystem management; alfalfa–aphid–predator system; aphids; biological control; carabids; coccinellids; ground-foraging predators; predator–guild overlap; predator–predator interactions; predator–prey interaction; synergistic predation.

### INTRODUCTION

One of the major obstacles to the wider utilization of biological control is variability in the level of pest suppression achieved. One reason why both basic population dynamics and biological-control models have failed to accurately predict the impact of natural enemies on pest populations is that these models have traditionally focused almost exclusively on interactions between individual prey and predator species (Kareiva 1994). The incorporation of interactions between predators into ecological theory (Polis et al. 1989, Strauss 1991, Soluk 1993, Kareiva 1994, Losey and Denno 1998b, Sih et al. 1998) shows great promise for increasing the effectiveness of biological control (Rosenheim et al. 1993, 1995)

The predator interactions that have so far been considered in biological control are antagonistic, in that fewer prey than expected are killed by the combined action of the predators (Polis et al. 1989, Rosenheim et al. 1993, Döbel and Denno 1994). In contrast, predator species can also interact synergistically, resulting in the complex of predator species killing more prey in combination than the sum of their individual impacts (Soluk 1993). Such synergistic predation usually occurs when the foraging activity of one predator species alters the behavior (e.g., by increasing prey movement on the plant) or feeding niche (e.g., by inducing prey to leave the plant) of the herbivore, making it more susceptible to attack by another predator species (Charnov et al. 1976, Soluk and Collins 1988, Soluk 1993). This type of synergism, also termed “predator facilitation” (Charnov et al. 1976), is well documented in several systems (Moynihan 1962, Willis 1966, Hobson 1968). However, there are very few studies that actually demonstrate the impact of synergistic predation on prey-population dynamics and only one case that dem-

Manuscript received 6 June 1997; revised 17 September 1998; accepted 23 September 1998. For reprints of this Invited Feature, see footnote 1, p. 363.

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onstrates the impact of synergistic predation on the dynamics of an agricultural pest (Losey and Denno 1998b).

A first step to incorporating synergistic predation into biological control would be the ability to predict how likely it is to occur in any given system. The three key elements for synergistic predation—(1) predator-induced escape behavior of the prey, resulting in habitat switching; (2) synchrony of predators in both habitats; and (3) minimal negative interaction (intraguild predation or interference) between the predator species—are prevalent in most arthropod predator systems (Soluk and Collins 1988, Soluk 1993, Döbel and Denno 1994). Quantifying the relative prevalence and magnitude of these elements across systems will facilitate the prediction of systems where synergistic predation is likely to occur.

The exact mechanisms driving synergistic predation may vary widely based on the predator and prey species involved. Based on the three elements outlined above we believe a specific type of synergistic predation involving herbivorous insects and foliar- and ground-foraging predators should be particularly prevalent. One of the most common defensive behaviors of herbivorous insects is to drop or jump from their host plant in response to the activities of a foliar-foraging predator (Gross 1993). Such dropping behavior results in a habitat shift whereby the herbivore falls from the plant to the ground, and consequently becomes susceptible to ground-foraging predators (Roitberg and Myers 1979, Gross 1993). Both foliar-foraging and ground-foraging predators are abundant in a wide diversity of natural and agricultural habitats and are thus likely to exhibit some temporal overlap (Pimentel and Wheeler 1973, Frazer et al. 1981, Döbel and Denno 1994). Although there are exceptions, most ground-foraging predators seldom climb plants, and most foliar-foraging predators forage only occasionally on the ground. This minimizes the occurrence of intraguild predation or interference phenomena that may offset any effects of altered prey behavior and increased risk of predation (see Wissinger and McGrady 1993). Hence, we predict that this specific type of synergistic predation is likely to be fairly prevalent among arthropods and has probably been underestimated. This prediction is supported by recent theoretical work that points to the probable underestimation of positive interactions (Dodds 1997).

Previous work on the pea aphid, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphidae), in alfalfa has documented synergistic predation by ground- and foliar-foraging predators in alfalfa (Losey and Denno 1998b). The combined impact of ground- and foliar-foraging predators is nearly double the impact that would be predicted if they were acting additively. Across a wide range of ecological conditions, foliar-foraging predators take on the “driver” role in predator facilitation when aphids respond to them by dropping off the plant

and onto the ground (Losey and Denno 1998a). The results of that study suggested that by examining the intensity of the dropping response of various pests to predators across a range of conditions we may be able to predict systems in which synergistic predation is likely to be important. In this paper we examine another factor that may aid in predicting the importance of synergistic predation, the ability of ground-foraging predators to take on the “hunter” role by consuming aphids once they have been driven from the plant. We focus on three questions concerning the potential effectiveness of ground-foraging predators in this role: (1) Are ground-foraging predators present at those portions of the alfalfa growing season when aphids are being driven from plants? (2) Are ground-foraging predators present and active during the portions of the diel cycle when aphids are being driven from the plant? and (3) If ground-foraging predators are present and active will they actually consume aphids? Based on the results of these findings we explore the potential prevalence and importance of synergistic predation in the alfalfa system and the general implications for the conservation of ground-foraging predators and the biological control of pest populations.

## METHODS

### *Phenology of aphids and predators in alfalfa*

The phenology of pea aphids and predators was determined in a large, conventionally managed, alfalfa field (3 ha) located at the U.S. Department of Agriculture (USDA)'s Beltsville Agricultural Research Center in Beltsville, Maryland, USA. No insecticides were applied to the field during the entire 1994 growing season, but it was cut on a normal cycle (approximately every 4 wk).

The seasonal phenologies of pea aphids and foliar-foraging predators in alfalfa were determined by sweep-net sampling. Five sweep-net samples were taken on 12 dates during 1994: 11 and 17 May, 9 and 19 June, 10 and 19 July, 21 and 31 August, 10 and 19 September, and 9 and 17 October. Each sample consisted of 10 sweeps with a standard (92-cm diameter) canvas sweep net at randomly selected locations within the alfalfa field. Each sample of arthropods was emptied into a plastic bag and frozen for future counting.

The seasonal phenology of fallen aphids and ground-foraging predators was determined using pitfall traps under the alfalfa canopy. Twenty pitfall traps were sunk into the field on 8 May in a four-row array with five traps per row. Each row was separated by 11 m and the five traps within each row were placed 30 m apart. Each pitfall trap consisted of an 8-ounce (240 mL) plastic cup fit into a sleeve of polyvinyl chloride pipe (15 cm in height and 10 cm in diameter) buried so that its top edge was flush with the surface of the ground. Traps were kept half full of an aqueous solution of 5% formaldehyde with a trace (<1 mL) of liquid dish soap

to break the surface tension. Traps were emptied and the contents returned to the laboratory for identification on each of the 12 dates shown above for sweep-net sampling.

*Phenological overlap between aphids, foliar-foraging predators, and ground-foraging predators*

The seasonal overlap between pair-wise combinations of aphids, foliar-foraging predators, and ground-foraging predators was quantified following published protocols (Schoener 1970, Colwell and Futuyma 1971). Since this technique is based on proportions, it is not necessary for data (i.e., for ground- and foliar-foraging predators) to be in the same units. Overlap values ( $O$ ) range from 0 to 1 with "0" representing no seasonal overlap and "1" representing complete seasonal overlap between a given pair of species.

Because pea aphids and certain predator taxa are very seasonal in their occurrence (e.g., spring and/or fall season appearance), seasonal overlap values were calculated from sweep-net and pitfall-trap data in three ways: (1) using their proportional occurrence across all 12 sample dates to determine total seasonal overlap, (2) using their proportional occurrence across the first 6 samples to determine early season concurrence, and (3) using their proportional occurrence across the last 6 samples to determine late-season overlap.

*Diel activity of *Harpalus pennsylvanicus**

Because the interaction between two predator taxa depends not only on their seasonal concurrence but also on their diel overlap, the day–night activity cycle of the dominant ground-foraging predator *Harpalus pennsylvanicus* was determined. The activity of *H. pennsylvanicus* was assessed using pitfall traps placed into a small, weedy alfalfa field with an unusually high density of *H. pennsylvanicus* (see Hokkanen and Holopainen 1986, Holopainen 1992). The field was located near our main study field in the USDA complex of alfalfa fields at Beltsville, Maryland. Ten pitfall traps (as described above) were sunk into the field at random locations at least 10 m apart. Traps were monitored continuously for three 24-h periods in 1995 (10–11, 11–12, and 12–13 August). The diel activity of *H. pennsylvanicus* was determined by tallying the number of individuals captured during the night (1900–0700) and day (0700–1900). Data were analyzed using a one-way analysis of variance (SAS Institute 1990). Although no heteroscedascity was found, means in Fig. 2 are presented with unpooled standard errors to illustrate variance patterns.

*Comparative consumption rate of aphids by foliar-foraging and ground-foraging predators*

The aphid consumption rates of the major foliar-foraging predator, *Coccinella septempunctata*, and five ground-foraging predators, the rove beetle *Philonthus*

sp., and the carabid beetles *H. pennsylvanicus*, *H. aeneus*, *Amara familiaris*, and *Agonum octopunctatum*, were compared. One adult of each predator species was offered 30 pea aphids (4th- and 5th-instar nymphs) in a 5-cm-diameter petri dish for 1 h. Each predator's aphid consumption rate was calculated as the difference between the number of aphids offered and the number remaining at the end of the experiment. Each predator species treatment was replicated 10 times except for *H. pennsylvanicus*, which was replicated 6 times. All predators were collected from alfalfa and starved for 24 h prior to the experiment. Consumption rates of predators were analyzed using ANOVA, and treatment means were compared with  $F$  tests on the pooled error variances (SAS Institute 1990). Means are presented with unpooled standard errors to illustrate trends in variance.

RESULTS

*Phenology of aphids and predators in alfalfa*

*Acyrtosiphon pisum* showed a typical seasonal phenology for aphids in this region, with peaks of abundance (>250 individuals/sample) in May and September (Fig. 1A). The most abundant foliar-foraging predators in the alfalfa canopy were heteropterans, followed by arachnids and coccinellids. Several of these predator taxa showed a bimodal phenology, which paralleled that for aphids with peaks of abundance in May–June and September and a marked reduction in numbers during summer. Overall, the seasonal phenology of foliar-foraging predators (pooled total of all taxa) mirrored the bimodal pattern seen for aphids, with a major peak in June (>50 individuals/sample) and a smaller flux in September (>20 individuals/sample) (Fig. 1A cf. B).

The phenology of aphids captured on the ground mirrored their pattern of seasonal abundance in the alfalfa canopy; both phenologies were bimodal, with peaks of abundance in May and again in September (Fig. 1A and B). The low numbers of aphids caught in pitfall traps may not indicate low aphid densities on the ground since pitfall-trap catches are a function of both density and activity. The most abundant ground-foraging predators were ants followed by spiders (mostly the spiderlings and adults of Lycosidae), and Coleoptera (Carabidae and Staphylinidae). In contrast to the foliar-foraging predators, most of the major ground predators did not show a bimodal, spring–fall phenology as did aphids. Rather, most taxa occurred abundantly in either spring/early summer or fall, but not both. Although the total of all carabid species did exhibit a bimodal phenology, this pattern resulted from the pooling of species that were abundant in fall with those that occurred primarily in spring and early summer.

*Phenological overlap between aphids, foliar-foraging predators, and ground-foraging predators*

Patterns of phenological concurrence among aphids, foliar-foraging predators, and ground-foraging preda-

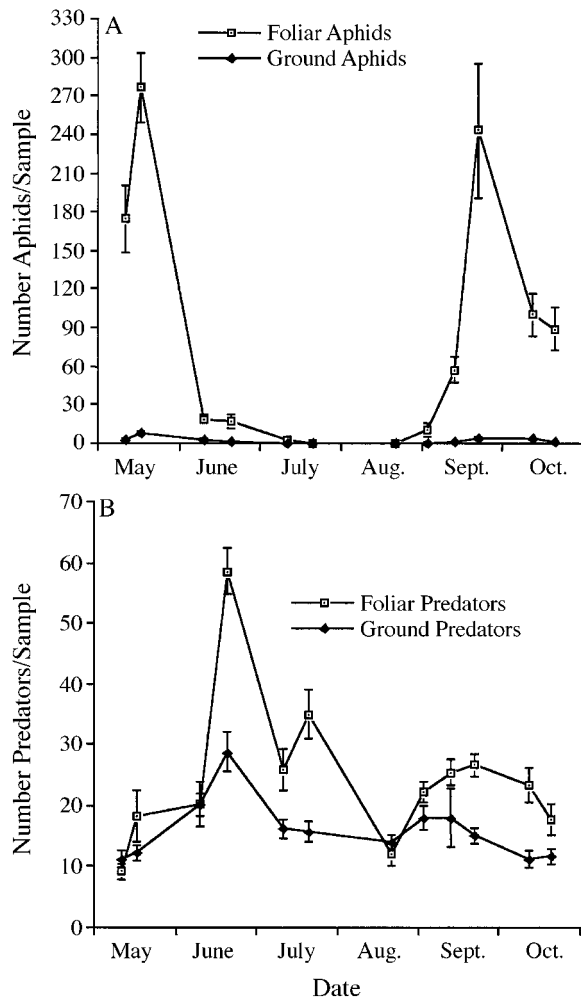


FIG. 1. (A) Seasonal abundance of pea aphids (*Acyrtosiphon pisum*) sampled in the foliage of alfalfa (no. individuals per sweep sample) and on the ground (no. individuals per pitfall). (B) Seasonal abundance of the pooled total of foliar-foraging predators (e.g., coccinellids and heteropterans) sampled in the canopy of alfalfa (no. individuals per sweep sample) and ground-foraging predators (e.g., carabids and staphylinids) trapped on the ground (no. individuals per pitfall). All samples were taken in an alfalfa field at Beltsville, Maryland (USA), during 1994.

tors were quantified in order to assess rigorously the probability for aphid predation and possible interactions among predators. The proportional overlap ( $O$ ) of aphids in the foliage and aphids on the ground was extremely high ( $O > 0.8$ ) when assessed over the course of the entire alfalfa growing season (Table 1), during the early part of the season (Table 2), or during the later part of the season (Table 2). These data suggest that the phenological distribution of aphids on the ground can be effectively predicted by their seasonal occurrence in the canopy.

Foliar-foraging predators showed moderate levels of concurrence with aphids (0.43) over the course of the

entire season, with greater phenological congruence in the late season (0.67) than the early season (0.24).

The guild of ground-foraging predators also exhibited moderate levels of seasonal overlap with aphids (both in the foliage and on the ground) (0.37–0.57), but synchrony was slightly higher during the later part of the season (0.55–0.57) than it was in the early season (0.30–0.48) (Tables 1 and 2). Carabid beetles and spiders overlapped substantially with aphids (0.28–0.47) and exhibited this same seasonal trend (Tables 1 and 2). *H. pennsylvanicus*, a fall-occurring species, overlapped moderately with aphids (0.25) during the later part of the season, but did not overlap with aphids at all during spring and early summer (0).

Phenological overlap was very high (0.87–0.90) between the foliar-foraging and ground-foraging predator guilds (pooled taxa), whether it was assessed over the entire growing season, during the early season, or during the late growing season (Tables 1 and 2). Overall, the potential for interaction between the foliar-foraging and ground-foraging predator guilds in alfalfa is very high.

#### *Diel activity of Harpalus pennsylvanicus*

Significantly more *H. pennsylvanicus* were caught in pitfall traps at night than were trapped during the day ( $F_{1,2} = 175.73$ ,  $P = 0.0001$ ; Fig. 2). However, daytime catches were significantly different from zero on all three trapping dates, suggesting that this carabid exhibits measurable daytime activity. The difference between day and night catches varied significantly across the three dates, as indicated by the significant interaction between the effects of trapping date and diel period on the catch ( $F_{2,132} = 17.68$ ,  $P = 0.0001$ , Fig. 2). These data suggest that although *H. pennsylvanicus* forages actively primarily during the night, there is significant diurnal activity and, in general, activity as measured by trap catches is highly variable.

#### *Comparative consumption rate of aphids by foliar-foraging and ground-foraging predators*

All species of ground-foraging predators consumed aphids, but there was significant variation among these predators in their hourly consumption rates ( $F_{5,50} = 2.84$ ,  $P = 0.025$ ) (Fig. 3). None of the predation rates of the ground-foraging predators, including the abundant *H. pennsylvanicus* ( $12.3 \pm 1.6$  aphids/h) and *Philonthus* spp. ( $9.0 \pm 1.6$  aphids/h), differed significantly from the predation rate of the dominant foliage-foraging predator *C. septempunctata* ( $8.1 \pm 1.6$  aphids/h). Thus, although they are not often cited as important aphid predators, the voraciousness of the ground-foraging predators we tested equaled that of *C. septempunctata*, which is reported to be one of the most important aphid predators (Frazer et al. 1981).

TABLE 1. Proportional overlap ( $O_{ij}$ ) in the temporal occurrence of aphids, foliar-foraging predators, and ground-foraging predators throughout the entire alfalfa growing season at Beltsville, Maryland, USA. Pairwise comparisons values were calculated on the basis of samples taken on 12 dates during 1994 (11 May–17 October).

Occurrence	Aphids on foliage	Aphids on ground	<i>C. septempunctata</i>	<i>C. maculata</i>	<i>N. americanoferus</i>	<i>O. insidiosus</i>	Total foliar predators	<i>H. pennsylvanicus</i>	Total carabids	<i>Philonthus</i> spp.	Ground spiders
Aphids on foliage	...										
Aphids on ground	0.80										
<i>C. septempunctata</i>	0.44	0.56									
<i>C. maculata</i>	0.41	0.41	0.57								
<i>N. americanoferus</i>	0.42	0.48	0.50	0.58							
<i>O. insidiosus</i>	0.18	0.23	0.36	0.58	0.50						
Total foliar predators	0.43	0.47	0.58	0.67	0.76	0.63					
<i>H. pennsylvanicus</i>	0.17	0.16	0.26	0.18	0.34	0.32	0.38				
Total carabids	0.20	0.30	0.59	0.50	0.49	0.51	0.61	0.41			
<i>Philonthus</i> spp.	0.13	0.24	0.48	0.48	0.34	0.66	0.39	0.07	0.42		
Ground spiders	0.42	0.49	0.57	0.62	0.67	0.60	0.78	0.43	0.63	0.35	
Total ground predators	0.43	0.50	0.62	0.67	0.76	0.61	0.88	0.41	0.66	0.37	0.82

Notes: The major foliar-foraging predator was *Coccinella septempunctata*; other foliar-foraging predators were *Colemazilla maculata*, and *Nabis americanoferus*. The major ground-foraging predator was *Harpalus pennsylvanicus*; the other ground-foraging predator was *Philonus* spp.

#### DISCUSSION

We found substantial temporal overlap among aphids, foliar-foraging predators, and ground-foraging predators, a requisite for synergistic predation. Specifically, the seasonal phenology of pea aphids in our study showed a classic pattern for aphids in alfalfa, with peaks of abundance during periods of milder weather in spring and fall (Fig. 1). The density of pea aphids dropped below measurable levels in August. This characteristic summer decline of aphids has been attributed to a combination of hot temperatures and the diminished nutritional quality of their host plant (Dixon 1985). Under these conditions, the survival and fecundity of aphids are dramatically reduced and population growth is very adversely affected (Dixon 1985). The seasonal phenology of dislodged aphids on the ground mirrored their pattern of temporal abundance in the foliage. Thus, ground-foraging predators experienced

the same phenology of aphids as did foliar-foraging predators.

Although heteropterans and spiders were more abundant than coccinellids in this study, coccinellids are generally regarded as more important predators of aphids due to their high consumption rates and ability to suppress aphid populations (Frazer et al. 1981, Gutierrez et al. 1990, Losey and Denno 1998a, b). The pooled total of foliar-foraging predators, and several major members of this guild (the coccinellids *Coccinella septempunctata* and *Colemegilla maculata* and the nabid *Nabis americanoferus*) showed a bimodal phenology that roughly paralleled that for aphids. In general, however, the peaks of foliar-predator abundance lagged behind the peaks of aphid abundance by ~1–4 wk, a delay that was more apparent in spring than fall. This difference in predator lag time between the spring and fall generations of aphids is confirmed by a much

TABLE 2. Proportional overlap ( $O_{ij}$ ) in the temporal occurrence of aphids, foliar-foraging predators, and ground-foraging predators during the 1994 alfalfa growing season at Beltsville, MD. Pairwise comparisons values below the diagonal were calculated on the basis of samples taken on six dates during spring/summer (11 May–19 July), and those above the diagonal were calculated from six dates during summer/fall (21 August–17 October).

Occurrence	Aphids on foliage	Aphids on ground	<i>C. septempunctata</i>	<i>C. maculata</i>	<i>N. americanoferus</i>	<i>O. insidiosus</i>	Total foliar predators	<i>H. pennsylvanicus</i>	Total carabids	<i>Philonthus</i> spp.	Ground spiders	Total ground predators
Aphids on foliage	...	0.83	0.34	0.51	0.69	0.43	0.67	0.22	0.38	0.59	0.47	0.57
Aphids on ground	0.82	...	0.47	0.45	0.63	0.41	0.65	0.25	0.39	0.53	0.47	0.55
<i>C. septempunctata</i>	0.44	0.62	...	0.53	0.43	0.46	0.56	0.51	0.54	0.45	0.52	0.53
<i>C. maculata</i>	0.33	0.39	0.58	...	0.73	0.56	0.71	0.30	0.45	0.84	0.62	0.71
<i>N. americanoferus</i>	0.13	0.31	0.57	0.45	...	0.59	0.82	0.38	0.53	0.82	0.68	0.78
<i>O. insidiosus</i>	0.11	0.15	0.36	0.64	0.48	...	0.65	0.74	0.85	0.63	0.83	0.74
Total foliar predators	0.24	0.35	0.56	0.65	0.72	0.65	...	0.47	0.62	0.81	0.77	0.90
<i>H. pennsylvanicus</i>	0.01	0.00	0.00	0.10	0.30	0.22	0.25	...	0.84	0.37	0.68	0.57
Total carabids	0.28	0.46	0.77	0.62	0.73	0.59	0.76	0.19	...	0.52	0.83	0.72
<i>Philonthus</i> spp.	0.12	0.30	0.66	0.68	0.58	0.68	0.54	0.03	0.67	...	0.69	0.78
Ground spiders	0.37	0.49	0.60	0.62	0.74	0.48	0.80	0.31	0.71	0.38	...	0.87
Total ground predators	0.30	0.48	0.69	0.63	0.73	0.58	0.87	0.26	0.85	0.54	0.84	...

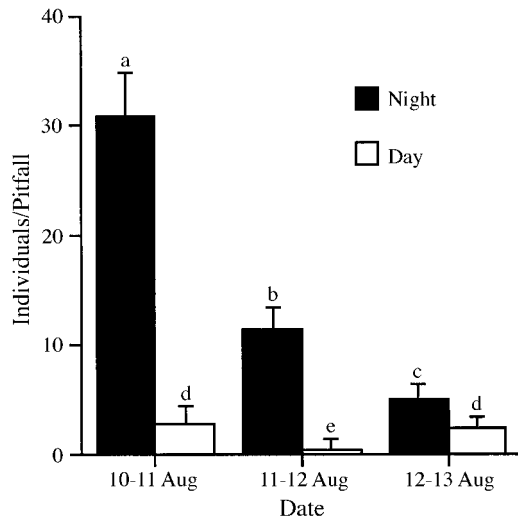


FIG. 2. The diel activity of the dominant ground-foraging predator *Harpalus pennsylvanicus* as measured by the number of individuals captured per pitfall trap (means and 1 SE) in alfalfa at Beltsville, Maryland (USA). The number of individuals trapped during the night (1900–0700; black bars) and day (0700–1900; white bars) is shown for three trapping periods in 1995. Bars with the same lowercase letters are not significantly different ( $P < 0.05$ ).

higher value of seasonal overlap in fall (0.67) compared to spring (0.24). Such time lags in numerical response are commonly observed in invertebrate predators and are usually attributed to delays in immigration or reproduction (Hassell 1978, Murdoch 1990, Döbel and Denno 1994).

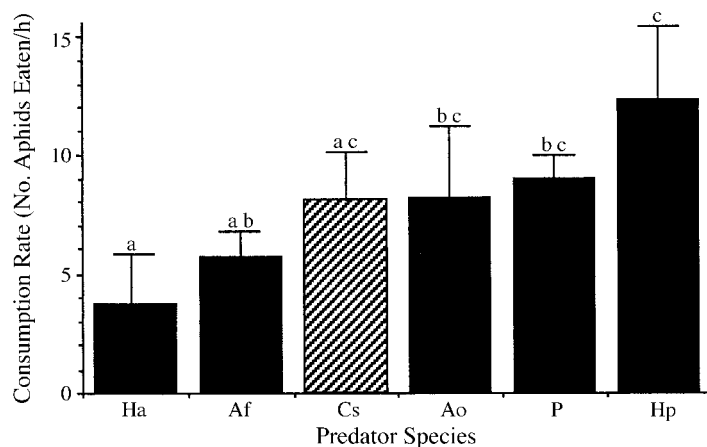
Despite the temporal lag, there was considerable seasonal overlap between aphids and their foliar-foraging predators in general (0.43) (Table 1). In particular, there was substantial seasonal overlap, both early in the season (0.44) and late (0.34), between aphids and *Coccinella septempunctata* (Table 2). The coccinellid *Coleomegilla maculata* and the nabid *Nabis americanoferus* also showed very high values of concurrence with

aphids during the late part of the season (Table 2: 0.51 and 0.69, respectively). Thus, there is substantial opportunity for coccinellids in particular, and foliar predators in general, to promote dropping behavior in aphids. The constant appearance of aphids in our pitfall traps is consistent with this notion. Additional studies in alfalfa and other agricultural crops have also documented that a substantial proportion of the local aphid population falls to the ground where they are readily consumed by ground-foraging predators (Loughbridge and Luff 1983, Bryan and Wratten 1984, Winder 1990, Losey and Denno 1998a).

The consumption of fallen aphids by ground-foraging predators depends on the presence of ground predators at a time when aphids are abundant. Important ground-foraging predators in this study were carabid and rove beetles as well as spiders, a taxonomic composition that reflects results of other surveys in alfalfa (Pimentel and Wheeler 1973, Barney et al. 1984). In particular, carabids and staphylinids are potentially important predators of aphids due to their high consumption rates (Losey and Denno 1998b). Overall, there was substantial seasonal congruence (0.43) between aphids and ground-foraging predators. From this enemy complex, two species emerged as the most abundant beetle predators. The rove beetle *Philonthus* spp. occurred predominantly in spring and early summer, whereas the carabid *Harpalus pennsylvanicus* dominated the community in fall, a phenology reported by other investigators (Riddick and Mills 1995). Thus, *Philonthus* spp. co-occurred primarily with the spring peak of pea aphids and *H. pennsylvanicus* overlapped for the most part with the fall peak. Because these two ground predators consume aphids at a rate equal to that for the coccinellids (8–12 aphids/h, Fig. 3), and because their seasonal phenologies overlap substantially with aphids, both predators have the potential to decimate that portion of the aphid population that falls to the ground.

The number of fallen aphids on the ground, however,

FIG. 3. Comparative consumption rates (no. pea aphids eaten/h) of foliar-foraging (hatched bar) and ground-foraging (black bars) predators (means and 1 SE). Bars with the same lowercase letter are not significantly different ( $P < 0.05$ ). Predator species: Ha = *Harpalus aeneus*, Af = *Amara familiaris*, Cs = *Coccinella septempunctata*, Ao = *A. octopunctatum*, P = *Philonthus* spp., and Hp = *H. pennsylvanicus*.



depends in part on there being foliar-foraging predators in the canopy of alfalfa (Losey and Denno 1998a). Consequently, for there to be a significant interactive effect of foliar-foraging and ground-foraging predators on aphid-population suppression, these two guilds of predators must co-occur. Our investigations in alfalfa demonstrate high seasonal overlap between the foliar-foraging and ground-foraging predator guilds, with different species becoming prominent in each of the guilds at different times of the season. Thus, there is great potential for interaction between the foliar-foraging and ground-foraging guilds in general and between particular pairs of predators in both spring and fall.

The mere seasonal congruence of foliar-foraging and ground-foraging predators may not be sufficient to promote interactions if the guild members are active at different times of the day. This would be particularly true if dislodged aphids quickly relocate their host, as is the case for *Acyrtosiphon pisum* (Losey and Denno 1998c). Indeed, the major late-season ground predator in Maryland alfalfa, *H. pennsylvanicus*, is active primarily at night (Fig. 2), a rhythm shown for other carabid species (Thiele 1977, Luff 1978). This apparent diurnal asynchrony might make it seem unlikely that *H. pennsylvanicus* would have a strong interaction with foliar-foraging predators. However, significant synergistic predation on aphids has been demonstrated (Losey and Denno 1998b, c). There are several possible explanations for this apparent paradox. First, although the major ground-foraging predator activity is at night, there is also measurable activity during the day (Fig. 2). Also, the major foliar-foraging predator in alfalfa, *Coccinella septempunctata*, dislodges aphids with equal frequency during both the day and night (Losey and Denno 1998a). Thus although there are clearly differences in diurnal activity patterns, data indicate that at least *C. septempunctata* will cause aphid dropping at a time when *H. pennsylvanicus* is foraging on the ground. The seasonal synchrony and contemporaneous diel activity of foliar-foraging and ground-foraging predators in alfalfa contribute significantly to the observed synergistic predation of aphid populations in the field (Losey and Denno 1998b).

Using this alfalfa system as a model, we can now ask what key elements can be extracted to predict the likelihood for synergistic predation in other systems. A necessary requisite for synergistic predation is habitat switching by the herbivore, with significant predation in both habitats. Thus, of primary importance is the behavioral response of the prey to an approaching predator. It follows that herbivores such as aphids, planthoppers, and some caterpillars that drop, jump, or release on a silken thread from the plant with the approach of a foliar-foraging predator (Stamp and Wilkins 1993, Döbel and Denno 1994, Losey and Denno 1998a, c) are more likely to incur synergistic predation. Prey species that do not exhibit habitat shifting in the pres-

ence of a predator, such as very sessile herbivores (scale insects, miners, borers, and gallers), aposematic caterpillars, and some cryptic species that rely on specific backgrounds for defense (Bowers 1993, Stamp and Wilkins 1993), are much less apt to incur synergistic mortality from predators. Synergistic predation may be most important when the habitat shift is substantial enough that a different guild of predator species is encountered, as was the case with pea aphids falling into the foraging ambit of ground predators that they do not encounter in the canopy. Furthermore, a drastic habitat shift on the part of the prey is more likely to involve predators that infrequently meet (e.g., canopy-foraging coccinellids and ground-foraging carabids), thereby minimizing intraguild predation. In contrast, intraguild predation appears to be commonplace for different predators within the same habitat on the plant (Rosenheim et al. 1995).

Another essential requisite of synergistic prey suppression by predators is the simultaneous occurrence of the prey along with both guilds of predators. It is important to note, however, that synchrony among predators in the same habitat can enhance intraguild predation (Rosenheim et al. 1993). Thus, it is the combination of predator-induced habitat shifting in the prey with increased risk from a newly encountered predator guild, minimal intraguild predation, and the synchrony of prey and predators that together promote synergistic predation. Canopy-inhabiting herbivores that are mobile and exhibit strong behavioral escape responses that distance them temporarily from foliar-foraging predators (both arthropod and vertebrate) appear to be the best candidates for synergistic suppression from natural enemies.

The tightly linked system of predator facilitation we have described here is only one example of how ground- and foliar-foraging predators can interact to enhance overall suppression of pest populations. Ground- and foliar-foraging predators can impact pest populations additively in the following situations: (1) a portion of the pest's life cycle is spent on the ground and another portion aboveground on plants (e.g., the corn rootworm, *Diabrotica virgifera virgifera*); (2) the pest alternates each day between time on plants and time on the ground, (e.g., the gypsy moth, *Lymantria dispar*); (3) the pest crawls on the ground to disperse from one plant to another (e.g., the stalk borer, *Papaipema nebris*). For all of these common scenarios, pests are susceptible to attack from both ground- and foliar-foraging predators at some point in their life cycle. However, it is important to distinguish these cases of additive predation from actual synergistic predation. Because the susceptibility of pests to ground-foraging predators in these instances does not depend on the presence of foliar-foraging predators, synergistic predation does not occur. Regardless of the exact mechanism, the intensity of the interaction between the pred-

ator guilds will be heavily influenced by the synchrony of pest susceptibility and ground-foraging predator presence.

The contribution of ground-foraging predators to pest suppression is particularly interesting because it is highly variable and can potentially be manipulated. The density of ground-foraging predators is known to be affected by both plant diversity and the use of insecticides (Los and Allen 1983, Barney et al. 1984, Barney and Pass 1986). Predictions of the temporal and spatial patterns of ground-foraging predators in relation to the period of pest susceptibility could be used as a guide for choosing systems for focusing efforts on conserving or even augmenting ground-foraging predators.

There are some special considerations that apply in cases of synergistic predation such as between the ground- and foliar-foraging predators we examined. Since the ground-foraging predators will not climb plants, they will only have a substantial impact on aphids and many other foliar pests when foliar-foraging predators are present. Thus, the effectiveness of augmentation of ground-foraging predators through releases or conservation via habitat manipulation or pesticide management will be dependent on the density and phenology of foliar-foraging predators. This does not imply that efforts to enhance ground-foraging predator populations would be ineffective in biological control programs. When pest densities are low and few foliar pests drop from plants, many ground-foraging predator species will not disperse but turn to other prey sources including other pests that are accessible at that time. When pest densities are high, foliar predators will migrate into the field (Losey et al. 1997) and many pests will drop from plants and be consumed on the ground. Thus, enhancing ground-foraging predator populations provides density-dependent "reserve" protection against foliar pest outbreaks.

In conclusion, the synergistic predation by ground-foraging predators in the presence of foliar-foraging predators represents an additional process by which ground-foraging predators can contribute to the suppression of foliar pests. Our results add to the growing evidence that enhancement of ground-foraging predators can be an effective strategy for the biological control of these pests. The more general implications are that a full understanding of the interactions between predators can lead to the design of more effective biological control strategies.

#### ACKNOWLEDGMENTS

The authors would like to thank Warren Steiner for identifying carabids and Kevin Conover and the staff at Central Maryland Research and Education Center for their assistance with field research. This work could not have been completed without a dedicated band of technicians including Ting-Yuan Chu, John McAllister, John Steffy, and Gregory Ose. This manuscript was greatly improved by helpful comments from Marina Caillaud, Michele Hamill, and Erin Cudney. This work has been supported in part by a Doctoral Dissertation

Improvement grant from the National Science Foundation and by a graduate assistantship from the Department of Entomology, University of Maryland.

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