REVIEW

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Multitrophic interactions among plants, aphids, alternate prey and shared natural enemies – a review

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Abstract. Given the generalist tendencies of most predatory arthropods, it is widely thought that their impact on a particular prey species in a given habitat (e.g., an insect pest in a crop) will depend frequently on the local availability of other prey (which for omnivorous predators, can include plant resources, such as fruit and pollen). Thus, from a slightly different perspective, aphids, other herbivorous insects, and plants often may interact indirectly by sharing natural enemies. Such interactions may be either negative or positive, as in the concepts of apparent competition and apparent mutualism, and may therefore have variable impact on the herbivores' host plants as well. I examine the different mechanisms for such indirect effects among herbivores as explored in the experimental literature. An impressive collective effort by numerous researchers recently has expanded considerably our empirical base of support for a variety of hypothesized mechanisms; aphids stand out as the most commonly studied subjects in research on these mechanisms. I therefore focus especially on the recent literature of cases involving aphids interacting indirectly with other prey for generalist predators. My remarks are organized by considering how the availability of alternate prey may alter functional and numerical (aggregative and reproductive) responses of predators to focal prey density. Although the distinctions among these different classes of predator responses and the associated indirect effects are often blurred and scale-dependent, this classification remains useful for organizing the diverse ways in which aphids have been found to participate in indirect interactions among prey as mediated by predators. Collectively, the results of the numerous studies reviewed here suggest that many such indirect interactions likely occur frequently in natural settings, with consequences ultimately for host plant performance.

INTRODUCTION

Most predatory arthropods, including aphidophagous insects, are generalists that attack a variety of prey and other foods (Hagen et al., 1999), although most are restricted also to some degree in their choice of prey (Symondson et al., 2002). The generalist tendencies of these predators may arise from low food availability (e.g., O'Neil & Wiedenmann, 1987; Bilde & Toft, 1998; Beckman & Hurd, 2003; Wise, 2006). In addition, the predators may benefit from balancing their nutritional requirements through a mixed diet (e.g., Greenstone, 1979; Soares et al., 2004; Mayntz et al., 2005). Given the generalist tendencies of most predatory arthropods, it is generally thought that their impact on a particular prey species in a given habitat (e.g., an insect pest in a crop) will depend frequently on the local availability of alternate prey (with "prey" broadly including plant resources such as fruit and pollen in the case of omnivorous predators) (e.g., van Emden, 1965; Symondson et al., 2002). Similarly, the impact of parasitoids may also depend on the availability of alternate hosts (e.g., Doutt & Nakata, 1973; Settle & Wilson, 1990; Müller & Godfray, 1999a; Langer & Hance, 2004), or non-hosts or plants that provide key nutrition for parasitoid females (e.g., honeydew-producing aphids; Evans, 1994 and references therein). Thus, from a slightly different perspective, aphids, other herbivorous insects, and plants often may interact indirectly through shared natural enemies. Such interactions may be either negative or positive, as in the concepts of apparent competition and apparent mutualism (Holt & Lawton, 1994; van Veen et al., 2006), and may have important consequences as well for the herbivores' host plants.

Here I review different mechanisms as explored in the experimental literature, by which two or more species of prey may interact with each other indirectly through natural enemies. An impressive collective effort by numerous researchers recently has expanded considerably our empirical base of support for a variety of hypothesized mechanisms of indirect interactions among herbivores. Aphids stand out as most commonly studied. I therefore focus especially on cases involving aphids interacting indirectly with other prey for generalist predators (Müller & Godfray, 1999a have provided an excellent review for aphid parasitoids). I consider how the availability of alternate prey may alter the functional and numerical (aggregative and reproductive) responses of predators to focal prey density (Symondson et al., 2002; Kean et al., 2003; Harmon & Andow, 2004). These different classes of effects in turn determine, often in complex fashion, the degree to which indirect interactions among herbivores are trait and density mediated (Bolker et al., 2003; Křivan & Schmitz, 2004). The distinctions among the different classes of predator responses (and associated indirect effects) are often blurred and scale-dependent (e.g., Müller & Godfray, 1997; Ostman & Ives, 2003). Nonetheless, this classification is useful for organizing the diverse means of indirect interaction among herbivores as mediated by predators. I seek here especially to highlight recent empirical examples in the peer-review literature concerning the applicability of these different mechanisms to aphid predator-prey interactions.

FUNCTIONAL RESPONSE

An earlier generation (e.g., Solomon, 1949; Holling, 1966) set the stage for much of the research reviewed here, by defining the basic functional response of a natural enemy as the number of individuals of the prey attacked by an individual predator, as a function of prey density. From the beginning, it was well recognized that in natural settings this response would depend on many factors, likely often including for generalist predators the availability of alternate prey. Hence herbivores may interact indirectly by occurring together as potential prey for a single predator foraging within a local habitat. Such indirect interactions are likely to vary considerably depending on characteristics of the interacting herbivores as matched against prey preference and selection of different predators (e.g., Bilde & Toft, 1997; Eubanks & Denno, 2000a; Provost et al., 2006). With such variability in mind, a number of researchers recently have quantified carefully how the feeding behavior and rate of consumption of particular prey species by an individual predator may depend on the presence of alternate prey.

Reduced consumption of focal prey (dilution/distraction effects of alternate prey)

In considering functional responses, most researchers have focused on whether the availability of alternate prey weakens predation on a focal prey. Thus, from the perspective of the herbivores themselves and as explored earlier with predator switching behavior (e.g., Murdoch & Marks, 1973), co-occurring prey species may affect each other indirectly in positive fashion (apparent mutualism) by influencing the foraging behavior that underlies a predator's functional response. For example, Bergeson & Messina (1998) report that lacewing larvae [*Chrysoperla plorabunda* (Fitch)] consume fewer Russian wheat aphids [*Diuraphis noxia* (Mordvilko)] when bird cherry-oat aphids [*Rhopalosiphum padi* (L.)] are also present on the host plant (wheat). Although the lacewing larvae appear to have no innate preference for one aphid over the other, they most readily encounter and consume the more exposed bird cherry-oat aphids, which feed on leaf sheaths and open blades. Consequently, the lacewings are less likely to encounter Russian wheat aphids, which feed inside rolled leaves on the same plant. The predator's capacity to dampen population growth of Russian wheat aphids hence may be reduced when bird cherry-oat aphids are present also, as these two aphid species otherwise interact only weakly over a broad range of densities through feeding effects on the host plant itself (Bergeson & Messina, 1997).

Petersen & Hunter (2001), in contrast, found only weak evidence overall for reduced effects of a predator on one aphid species in the presence of another. In field and greenhouse experiments, two species of pecan aphids, *Melanocallis caryaefoliae* (Davis) and *Monellia caryella* (Fitch), were caged on pecan foliage either together or alone. Thereafter a lacewing larva [*Chrysoperla comanche* (Banks) or *Chrysopa nigricornis* Burmeister] was added for 2–5 days to half of the experimental enclosures. In only one of six comparisons with the predator present, did one of the aphid species benefit by having a higher population growth rate in the presence (versus absence) of the second aphid (overall, the aphids tended to have much stronger, negative effects on each other through interactions mediated by the host plant).

Aphids may interact indirectly with other kinds of insect herbivores as well. For example, researchers have investigated predator response to the co-occurrence of green peach aphids (*Myzus persicae* Sulzer) and Colorado potato beetles (*Leptinotarsa decemlineata* Say) on potatoes. In eastern North America, field populations of the lady beetle *Coleomegilla maculata* (DeGeer) consume many Colorado potato beetle eggs. Hazzard & Ferro (1991), however, found in laboratory trials that the predator's per capita rate of consumption of Colorado potato beetle eggs declined when green peach aphids were present as an alternate (and preferred) prey. Field cage trials yielded similar results; interestingly, simulation studies suggested that such reduced predation might speed the evolution of Bt resistance by the Colorado potato beetle (Mallampalli et al., 2005).

Koss & Snyder (2005) conducted field cage experiments in potato fields of eastern Washington to assess predation of Colorado potato beetle eggs and green peach aphids by the generalist arthropod fauna (primarily hemipterans, carabids, and spiders). The predators reduced initial densities of Colorado potato beetle eggs (set experimentally) when aphid numbers were low early in the season, but not when aphid numbers were high later on. In greenhouse microcosms with potato plants, both *Geocoris* spp. and *Nabis* spp. (Hemiptera) ate fewer Colorado potato beetle eggs when more aphids were present but not vice versa (Koss et al., 2004; Koss & Snyder, 2005). Especially the nabids appeared to prefer aphids over beetle eggs as prey, although both groups of predators readily consumed beetle eggs in the absence of aphids. Overall, the studies from both eastern and western North America suggest that the presence of green peach aphids reduces predation rates of individual predators on Colorado potato beetle eggs.

Eubanks & Denno (2000b) addressed a similar theme, but from an additional perspective: could the host plant (lima bean) also serve as an alternate food (prey) in indirect interactions between pea aphids [*Acyrthosiphon pisum* (Harris)] and eggs of the corn earworm [*Helicoverpa zea* (Boddie)]? The mediating predator is the big-eyed bug *Geocoris punctipes* (Say), an omnivore that consumes both insect species and the plant (particularly pods). In the laboratory, individual bugs ate fewer aphids and corn earworm eggs when the host bean plant had pods. Individual bugs ate fewer corn earworm eggs when aphids also occurred on a bean, but not vice versa. Similarly, in field cages, the capacity of individual bugs to reduce aphid population size on bean plants was weakened in the presence of pods, but not in the presence of corn earworm eggs. It appeared that the bug met much of its food needs by feeding on pods when available, and preferentially attacked mobile aphids over immobile eggs even though the latter were nutritionally superior (Eubanks & Denno, 2000a).

Additional field and greenhouse studies also suggest that individual predators often consume fewer non-aphid prey when aphids are available. Examples include lady beetles attacking fewer eggs of the European corn borer [*Ostrinia nubilalis* (Hubner)] when corn leaf aphids [*Rhopalosiphum maidis* (Fitch)] were present (Musser & Shelton, 2003); lady beetles (*H. axyridis*) attacking fewer larvae of the oblique banded leaf roller [*Choristoneura rosaceana* (Harris); Tortricidae] when apple aphids (*Aphis pomi* DeGeer) were present (Lucas et al., 2004), or fewer larvae of the monarch butterfly (*Danaus plexippus* L.) when the aphid *Aphis nerii* Boyer de Fonscolombe was present (Koch et al., 2005); and carabids attacking fewer fly eggs when green peach aphids (*Myzus persicae*) were present (Prasad & Snyder, 2006a).

In greenhouse cage experiments, Ostman and Ives (2003) explored the behavioral mechanisms underlying reduced predation of alternate prey in the presence of aphids. *Nabis* spp. ate fewer of the less preferred potato leafhopper [*Empoasca fabae* (Harris)] on alfalfa when pea aphids were present but not vice versa. Interestingly, this result was observed when nabids foraged within a mixture of individual plants harboring only leafhoppers or aphids, versus within a mixture of plants with only leafhoppers or without insects altogether. It was not observed, however, when nabids foraged on small clusters of plants on which the two prey species occurred together. Aphid presence did not influence the tendency of nabids to attack leafhoppers upon encounter. The nabids, however, spent less time foraging on plants with only leafhoppers and were less active on these plants, when they also encountered and consumed aphids on adjacent plants with aphids.

The influence of non-aphid prey on aphid consumption has also been studied. In some cases but not in others, the presence of alternate prey may weaken the functional response of predators to aphids. Madsen et al. (2004) compared the capacity of single individuals of several generalist predators (four spider species, a harvestman, and a carabid) to reduce population growth of the cereal aphid *R. padi* on potted plants. Tests were conducted over a ten-day period in the presence versus absence of alternate prey [adult *Drosophila melanogaster* (Meigen) with vestigial wings]. All of the predators attacked the aphid, but the aphid is a poor food for them and was consumed at low rates. Nonetheless, in the absence of alternate prey, all of these predators were able to slow significantly aphid population growth. Availability of the alternate prey had a strong negative effect on aphid predation by individuals of only one predator, the Tetragnathid spider *Pachygnatha degeeri* Sundevall.

Field studies also have revealed variable effects of alternate prey (especially Collembola) on rates of aphid consumption by broadly generalist predators. Harwood et al. (2004) related the local abundance of cereal aphids [*Sitobion avenae* (F.)] and Collembola at microsites occupied by Lyniphiid spider webs within a wheat field, to aphid consumption by the web owners. Individual spiders (both Erigoninae and Lyniphiinae) ate more aphids when more were present. As predicted by relative preferences for aphids versus collembolans, individuals of Erigoninae, but not of Lyniphiinae, ate fewer aphids when more Collembola were present. Adults of the carabid *Pterostichus cupreus* L. searched wheat plants less (and the soil surface more), and consequently ate fewer cereal aphids (*R. padi* and *Metopolophium dirhodum* Walker) when soil-dwelling Collembola (*Heteromurus nitidus* Templeton) were added to field arenas (Mundy et al., 2000). In contrast, the wolf spider *Hogna hellua* did not deviate from feeding especially on foliage-dwelling insect herbivores in stands of cucurbits, when Collembolan densities in field plots were increased by adding mulch to the soil (Wise et al., 2006). Ostman (2004) studied predation of sentinel aphids (*A. pisum*) attached to the ground in wheat fields. The abundance of alternate prey (Homoptera, Thysanoptera, Diptera and Collembola combined) had at most a very weak negative effect on per capita predation rates by generalist arthropod predators (such rates were inferred from the directly measured overall rates of predation, which also reflected numerical responses of the predators to varying densities of alternate prey among fields).

Greater consumption of focal prey (stimulatory effects of alternate prey)

The presence of alternate prey may sometimes strengthen rather than weaken predators' per capita consumption rates of aphids. From the perspective of the herbivores, such a response by a predator yields a negative rather than the more typically hypothesized positive indirect effect of one herbivore on the other. Both *H. axyridis* and *C. septempunctata* ate more rather than fewer apple aphids when leafroller larvae were present (Lucas et al., 2004). When also provided with fruit flies, the carabid *Bembidion lampros* (Herbst) ate more cereal aphids (*R. padi*) (Madsen et al., 2004). Nabids consumed more green peach aphids on potatoes when many Colorado potato beetle eggs were also present, perhaps because encounters with eggs as well as aphids increased the time spent searching by these predators (Koss et al., 2004). Prasad & Snyder (2006b) added either aphids and/or individuals of the intraguild predator *Pterostichus melanarius* (Carabidae) to field cages of radish stocked with a given number of smaller carabids. Carabid consumption of fly eggs declined when only aphids were added, presumably because the carabids were distracted by the alternate prey. But when the intraguild predator was present, egg predation increased when aphids were added. Behavioral and activity-density data suggest that the intraguild predator foraged more actively in the presence of aphids, leading to its increased opportunistic consumption of less preferred fly eggs (Prasad & Snyder, 2006b).

Rates of parasitism as influenced by predators attacking alternate prey

Functional responses of predators in the presence of alternate prey can have intriguing indirect effects by influencing rates of parasitism. Cardinale et al. (2003) report that pea aphid parasitism by *Aphidius erv*i Haliday (Braconidae) in experimental field cages in an alfalfa field was negatively related to the ratio of cowpea aphids (*Aphis craccivora* Koch) to pea aphids. Thus, the wasp was less likely to parasitize pea aphids as cowpea aphids increasingly outnumbered them (for another interesting example in which this parasitoid is distracted from pea aphids by a second aphid, with consequences for interspecific competition with a second parasitoid species, see Meisner et al., 2007). When adults of the lady beetle *H. axyridis* were added to cages with both aphid species present, the lady beetle succeeded in reducing numbers particularly of the cowpea aphid. Consequently, in those cages in which the parasitoid was also present, pea aphid parasitism was enhanced, pea aphid population growth was correspondingly reduced, and alfalfa yield was increased. In contrast, the direct mortality of pea aphids inflicted by the predator itself was a relatively weak factor that did not result in a significant reduction in population growth of the pea aphids (or an increase in alfalfa yield).

Because many parasitoids (and other natural enemies) consume aphid honeydew, the presence of aphids may enhance parasitism of other herbivores. Consumption of aphids by predators may therefore also influence mortality rates (through parasitism) of these other herbivores. Evans & England (1996), for example, found increased levels of parasitism of the alfalfa weevil [*Hypera postica* (Gyllenhal), Curculionidae] by the ichneumonid wasp *Bathyplectes curculionis* (Thomson), in field cages of alfalfa when pea aphids were also present (access to pea aphid honeydew significantly increased fecundity as well as adult lifespan of the wasps; England & Evans, 1997). Addition of lady beetles (adults of *C. septempunctata*) to cages with aphids, however, resulted in reduced parasitism of the alfalfa weevil, as the predator fed especially on aphids (and less so on alfalfa weevils) and thereby reduced the availability of honeydew for the wasp.

AGGREGATIVE RESPONSE

Negative interactions among herbivores (apparent competition)

Predators and parasitoids typically accumulate (aggregate) where prey are abundant (e.g., Huffaker et al., 1976). Short-lived, locally abundant populations of aphids can support temporary aggregations not only of aphidophagous predators such as lady beetles (e.g., see references in Evans & Toler, 2007) but also of other, more generalist predators such as carabids (e.g., Bryan & Wratten, 1984; see also Monsrud & Toft, 1999). Similarly, spiders may place their webs in areas of elevated aphid density (Harwood et al., 2001, 2003). Such aggregations of natural enemies may foster high rates of predation on co-occurring alternate prey as well as on the aphids (an example of short-term apparent competition among the herbivores; Holt & Kotler, 1987).

Several field experiments have tested this hypothesis of short-term apparent competition. Müller & Godfray (1997) placed populations of the nettle aphid *Microlophium carnosum* Buckton on potted nettles adjacent to grass plots infested by few or many aphids of a second species (*R. padi*). Populations of the nettle aphid declined much more rapidly and produced fewer alates when many *R. padi* were nearby. Coccinellids colonized the highly infested grass plots in large numbers and soon reduced numbers of *R. padi* to low levels. The predators, many now swollen with eggs, shifted next to the nearby potted nettles where they laid their eggs, and where they and their offspring fed on large numbers of *M. carnosum*. In a related field experiment, pea aphid populations on potted broom declined more rapidly when surrounded by potted nettles with versus without colonies of the nettle aphid (Rott et al., 1998). Pea aphid parasitism differed little in the presence versus absence of nettle aphids. Rott et al. (1998) instead attributed the increase in pea aphid mortality to greater predator aggregation in the presence of nettle aphids (such presumptive predation pressure is particularly arresting, as all predators encountered were removed at each census). In contrast, apparent competition seemingly does not account for the local rarity of another nettle aphid, *Aphis urtica* Gmelin, at a meadow site where *M. carnosum* was common (Kean & Müller, 2004). Despite the presence of numerous predators, the colony dynamics of the rare aphid were not different on potted nettles when a colony of the common aphid occurred on the same plant or on a plant nearby (or when the common aphid was altogether absent).

Ostman & Ives (2003) report that within alfalfa fields throughout the growing season, the local abundance of nabids was not related to that of leafhoppers, but was strongly positively correlated with abundance of aphids (most likely primarily through aggregation of predator adults versus their subsequent reproduction). It was not possible to measure directly nabid predation rates on leafhoppers in the field. An intriguing negative correlation between nabid abundance and growth rates of leafhopper populations from one sampling occasion to the next, however, suggested that aggregation of nabids in response to local aphid density resulted in increased mortality of leafhoppers. A similar negative indirect (i.e., short-term apparent competitive) effect of pea aphids on alfalfa weevils through aggregation of lady beetles in response to high aphid densities is suggested by field experimental results (Evans, 1994; Evans & England, 1996).

Apparent competition involving aphids may also be diffuse. The pressure exerted by predators on other herbivores may sometimes be associated with a community of aphid species rather than a single, highly abundant species. Müller & Godfray (1999b), for example, tested whether two aphid species that were absent from an English meadow [*Aphis jacobaeae* Schrank and *Brachycaudus cardui* (L.)] could establish when introduced. Founder colonies of the aphids were placed on their host plant (*Senecio jacobaea* L.) in the meadow but failed to persist unless the diverse resident community of predators was prevented from attacking them (either mechanically or by aphid-tending ants). The authors suggest that *A. jacobaeae* and *B. cardui* were excluded from the meadow by these predators occurring in abundance in response to the numerous species of other aphids that occurred naturally at the site.

Similarly, high densities of alternate prey may promote predator aggregation and thereby lead to greater predation of aphids in a local area. Interestingly, in two of the best field examples of such, the key alternate "prey" is food of plant origin. Thus, Harmon et al. (2000) found that local densities of the coccinellid *C. maculata* within alfalfa fields were positively correlated with local densities of dandelions (the pollen of which is fed upon by the lady beetles). Local densities of aphids were negatively correlated with local densities of both dandelions and *C. maculata*. One interpretation is that lady beetles accumulated in areas with high dandelion density, and consequently depressed aphid populations. In support, laboratory cage experiments demonstrated that individual lady beetles spent more time foraging in alfalfa patches with versus without dandelions. Overall predation rates of pea aphids were highest in patches with dandelions even though foraging efficiency (number of prey consumed per predator per unit time) was reduced slightly in such patches. Given that decreased aphid density results in increased alfalfa yield (Cardinale et al., 2003), the two species of plants (dandelion and alfalfa) also interacted indirectly in this example.

In a second, similar example, Eubanks & Denno (2000b) used a fruit thinner to reduce the number of pods in experimental field plots of lima beans. Over a six-week study, many more omnivorous bugs (*G. punctipes*) occurred in plots with many versus few pods. At the same time, populations of aphids (and other herbivorous insects) increased to much higher levels in the plots with few versus many pods (of note here is that the presence of pods alone, without predators, would likely promote population growth of these herbivores). Thus, even though individual predators probably consumed fewer aphids in plots with many pods (see discussion above), the predators as a population inflicted much greater mortality on aphids when high numbers of the predator were sustained by the availability of the alternate food (pods).

Given that many generalist predators are highly vagile and responsive to landscape pattern (e.g., Elliott et al., 2002), it is intriguing to consider how indirect interactions among herbivores sharing predators may occur over large spatial scales (e.g., Duelli et al., 1990; Rand et al., 2006). Rand & Louda (2006), for example, recorded spillover effects of lady beetles moving from agricultural crops and associated prey populations into adjacent grassland habitats where they heavily attacked an aphid species (*Bipersona* sp.) on a native thistle. In other instances, however, aggregation of mobile generalist predators in response to high densities of herbivores in one habitat may lessen predation pressure on other herbivores in other habitats. Frere et al. (2007) report, for example, that cereal aphid populations were especially high in wheat plots that were close to strips of rose bush, perhaps because predators and parasitoids aggregated instead to attack aphid populations infesting the roses.

Over the long-term, large numbers of predators may be maintained within a habitat by the presence of alternate prey, thereby preventing individual prey species from obtaining high densities (e.g., Flaherty, 1969; Settle et al., 1996; Chang & Kareiva, 1999; Gratton & Denno, 2003). Perhaps the most thoroughly investigated such case involving aphids is that of cereal fields of northern Europe. An impressive variety of field experimental, observational, and modeling (simulation) results support the conclusion that generalist arthropod predators (especially carabids and spiders) at times can slow significantly the population growth of aphids, particularly early in the growing season (e.g., Edwards et al., 1979; Chiverton 1986, 1987; Ekbom et al., 1992; Ostman et al., 2001; Lang, 2003; Toft, 2005; Winder et al., 2005; Bommarco et al., 2007). These predators overwinter in large numbers especially at field margins, and repopulate the fields each spring (Petersen, 1999a; Oberg & Ekbom, 2006). When cereal aphids colonize the crop a few weeks later in early summer, these predators are present in large numbers. Cereal aphids are poor food for which many of these predators have low tolerance (Toft, 2005). The aphids may also be of limited availability for predators that forage principally on the ground (Winder et al., 1994). Even so, these generalist predators by sheer number appear capable in some cases of inflicting sufficient mortality early in the season (when aphid abundance is low) to dampen substantially the exponential growth of cereal aphid populations.

Such high numbers of these predators in cereal fields presumably are promoted by alternate prey, as identified from diet analysis (e.g., Sunderland, 1975; Symondson, 2002). For example, Collembola appear to support high numbers of spiders early in the season (Harwood et al., 2004). As these prey dwindle in number in late spring, the spiders feed more frequently on cereal aphids (now building in numbers). Similarly, more generalist predators occurred with more alternate prey (Homoptera, Thysanoptera, Diptera and Collembola combined) among barley fields, and the rate of predation of sentinel aphids correspondingly increased with abundance of these generalist predators (Ostman, 2004). But at least some generalist predators survive well with few or no prey early in the season (Petersen, 1999b). So how critical are alternate prey in early spring, ultimately, in determining predator impact on aphid numbers? A fertile area of field experimentation seemingly would be to address further not only the direct link between the generalist predators and aphids, but also the direct link between these predators and alternate prey (e.g., Halaj & Wise, 2002).

Promoting large populations of aphidophagous as well as of more generalist predators early in the season can slow significantly the exponential growth of pest aphid populations (e.g., Hagen et al., 1971), with knock-on effects such as reducing the spread of aphid-vectored plant diseases (e.g., Landis & van der Werf, 1997). An interesting case involving indirect interactions of aphids comes from the Great Plains of North America. The presence of the non-damaging corn leaf aphid (*R. maidis*) on grain sorghum early in the season maintains relatively high numbers of lady beetles that feed as well on the few greenbugs [*Schizaphis graminum* (Rondani)] also present, thereby slowing greenbug population growth. It may further contribute to long-term greenbug suppression as well, by enhancing the impact of the braconid parasitoid *Lysiphlebus testaceipes* (Cresson) that arrives late in the season (Kring & Gilstrap, 1986; Gilstrap, 1997). [See also discussion below of the predators' reproductive response (Michels & Burd, 2007)].

At least some aphidophagous predators may be responsive also to the availability of non-aphid prey within a habitat. The recently introduced *C. septempunctata* has become the most common aphidophagous lady beetle in alfalfa fields of the intermountain west of North America. In contrast to the indigenous lady beetles, this generalist predator colonizes and persists in alfalfa fields even when aphid densities are low, presumably because alternate prey such as the abundant larvae of the alfalfa weevil are also available (Evans & Toler, 2007). The presence of significant numbers of *C. septempunctata* early in the growing season may be a key factor now in dampening pea aphid population growth, with one consequence being that native lady beetles have largely abandoned alfalfa fields in recent years in the absence of sufficient numbers of aphids to retain them (Evans, 2004).

Positive interactions among herbivores: numbers of generalist predators decreased by presence of aphids (and ants that tend them)?

Honeydew-producing aphids are frequently tended by ants that drive away natural enemies. Thus, the presence of aphids, when associated with ants, may drive down local numbers of generalist predators and thereby reduce their predation rates on other, co-occurring herbivores. But the ants may also attack other herbivores (e.g., Harvey & Eubanks, 2004). Kaplan & Eubanks (2005) explored such interactions in cotton fields where the invasive fire ant *Solenopsis invicta* Buren tends cotton aphids, *Aphis gossypii*. These researchers found a positive correlation between ant and aphid numbers on cotton plants, and documented many adverse effects of ants on other arthropods. Overall, predators more than herbivores suffered adverse consequences, suggesting that at least some other herbivores may benefit from reduced predation in the presence of aphids and their ant mutualists (but see also Eubanks, 2001). The majority of studies, however, suggest that plants benefit from reduced damage from other herbivores when infested by honeydew-producing homopterans that are tended by ants (Styrsky & Eubanks, 2007).

REPRODUCTIVE RESPONSE

Alternate prey may enhance the reproductive capacity of generalist predators in several ways, thereby leading to an increase in the number of predators attacking a focal prey. The general importance of alternate prey and other foods in promoting predator reproduction has long been a central theme in biological control (e.g., Hagen et al., 1971). Consequently, many laboratory studies (but fewer field studies) have explored this topic.

In contrast to essential prey sensu Hodek (1973, 1996), other (alternative) prey may not contribute directly to reproduction itself, but may better maintain a predator such that it can more readily reproduce if and when essential prey become available. Such prey thus may serve to sustain foraging adults, in contrast to the essential prey that permit maturation of the adult predator as well as the full development of the larval predator (Hodek, 1962). For example, adult *Coccinella* spp. maintain themselves by eating coleopteran or lepidopteran larvae but do not reproduce (e.g., Richards & Evans, 1998; Evans, 2000). Females of *H. axyridis* females failed to reproduce when they fed on alfalfa weevils alone. But when they were placed on a diet of aphids, the females began laying eggs earlier, and laid more eggs altogether, when they had fed previously on weevils versus only sugar (Evans & Gunther, 2005). Similarly, egg production of *C. septempunctata* depended primarily on aphid consumption but was slightly increased by addition of weevils to the diet, apparently because reproducing females were able to rely on weevil (versus aphid) consumption to meet the competing demands of self-maintenance (Evans et al., 1999, 2004). Dixon (2000) and Michaud (2005) expand further on the topic of varying prey suitability for lady beetle reproduction.

Interestingly, for more generalist predators such as many carabids and spiders, aphids are often very poor food, apparently because these predators are not well-adapted to their chemical defenses (Toft, 2005). Consumption of aphids therefore appears often to serve primarily to maintain the more generalist predators, with other, non-aphid prey much more strongly supporting predator reproduction [even so, there is substantial variability in suitability among prey supporting reproduction for more generalist predators (Bilde et al., 2000) as well as for aphidophagous predators (Michaud, 2005)].

Most feeding tests of generalist predators have involved cereal aphids (especially *R. padi*). Many generalist predators consume few of these aphids even when starved, and reproductive measures (fecundity, egg volume, hatching success) as well as measures of immature growth and development are typically reduced on a diet of aphids versus more suitable prey (Toft, 2005). Spiders appear especially reluctant to consume cereal aphids, and some may quickly develop an aversion to doing so (Toft, 1997). Even the generalist predator *Calathus melanocephalus* L. (Carabidae), which consumes aphids as readily as more suitable food (*Drosophila*), has greatly reduced fecundity on a diet of aphids (Bilde & Toft, 1999).

The negative effect of aphids on reproductive responses of generalist predators sometimes is also apparent in studies of mixed diets (e.g., Bilde & Toft, 2001). Such may result from aphid toxins interfering with assimilation of nutrients obtained from other prey (Toft, 2005). Consequently, the presence of aphids or other toxic prey in a habitat may indirectly benefit other herbivores if generalist predators consume the toxic prey upon encounter. For example, in laboratory studies of the wolf spider *Pardosa lugubris*, Rickers et al. (2006a) found that females did not develop aversions to feeding on the toxic Collembolan *Folsomia candida*. As suggested by stable isotope analysis, ingestion of this prey appeared to interfere with nutrient uptake from other ingested prey, and females maintained on mixed diets including the collembolan died prematurely without reproducing.

Equally thought-provoking is the phenomenon wherein a mixed diet of two or more prey species best supports reproduction. When food was provided only intermittently, the carabid *B. lampros* Herbst produced more and larger eggs when feeding on a mixed diet of aphids (*R. padi*) and cat food than on either food type alone (Wallin et al., 1992). Furthermore, two other carabids, *Pterostichus cupreus* L. and *P. melanarius* Illiger, had highest rates of egg-laying when their diets were shifted regularly between aphids, cat food, and maggots (Wallin et al., 1992). Bilde & Toft (1994) found that the carabid *Agonum dorsale* (Pont.) consumed fruit flies [*Drosophila melanogaster* (Meig.)] much more readily than aphids (*R. padi*) or earthworms and produced eggs at rates commensurate with consumption, when reared in the laboratory on monotypic diets of these prey. Egg production was highest, however, when the predator was provided with a mixed diet of all three prey types. Toft (1995) found that hatching success was higher, and consequently more offspring were produced, when females of the spider *Erigone atra* (Bl.) were provided with aphids (*R. padi*) as well as a limited number of fruit flies, than when the spiders were provided with large numbers of fruit flies alone. Although provision of fruit flies alone sustained a high level of spider reproduction, provision of aphids alone resulted in greatly reduced reproduction (and consumption of prey). Soares et al. (2004) recorded significantly higher fecundity and fertility of *H. axyridis* when females fed on a mixed diet of *Aphis fabae* Scopoli and *M. persicae* rather than on a diet of either aphid alone. Thus by serving together in a mixed diet that enhances predator reproduction, prey species may indirectly interact with each other in negative fashion.

I have focused here on how alternate prey may affect female predators' production of fertile eggs. The suitability of a given prey may be quite different for the development of immature stages than for reproducing adults of a generalist predator (e.g., Michaud, 2005; Rickers et al., 2006a). Thus, an additional issue is how alternate prey may affect the survivorship and development of immature offspring that will provide the next generation of reproducing adults. For example, late maturing lady beetle larvae may complete development even after a local aphid population has collapsed by feeding on other, non-aphid prey (e.g., Kalaskar & Evans, 2001), including other lady beetle larvae (e.g., Yasuda & Shinya, 1997; Schellhorn & Andow, 1999). Alternatively, as suggested by laboratory feeding studies especially of spiders (Toft, 1999; Oelbermann & Sheu, 2002), mixed diets of two or more prey might promote predator development by providing particularly well-balanced nutrition (e.g., Greenstone, 1979; Mayntz et al., 2005). The presence of alternate prey may also boost predator survivorship through reduction of cannibalism and intraguild predation (Rickers et al., 2006b).

Interestingly, laboratory studies also suggest that immature generalist predators may suffer sometimes from feeding on multiple species of prey, if their broad diet includes toxic prey. Toft & Wise (1999a, b) found that immature wolf spiders failed to develop aversions to consuming the chemically well-defended aphid *Aphis nerii*, even though inclusion of this prey to an otherwise highly suitable diet resulted in reduced growth and survivorship. Similarly, Snyder & Clevenger (2004) found that four species of lady beetles were unable to complete larval development on a pure diet of Colorado potato beetle eggs. Larvae consumed the eggs even when green peach aphids were provided ad libitum, and generally suffered lower rates of development and survivorship on a mixed egg-aphid diet than on a pure diet of aphids.

Laboratory studies raise intriguing possibilities for both negative and positive effects of prey species on each other via predator reproductive (and developmental) responses in natural settings. There are few examples, however, to illustrate how these possibilities may be realized in the field. Among the clearest is that of Müller & Godfray (1997) in their study of lady beetle predation of aphids on potted nettles placed next to grass plots (see above). Much of the early population decline of nettle aphids near grass plots heavily infested by other aphids was attributed by these researchers to lady beetle larvae hatching from eggs laid on the nettles. Lady beetle adults laid these eggs after gaining the necessary nutrients from feeding on the abundant grass aphids before moving to the nettles. That such an indirect interaction among aphid species may occur in agricultural settings at large spatial and temporal scales is illustrated well by long-term studies in sorghum fields of the Texas High Plains (Michels & Burd, 2007). Lady beetle (*Hippodamia* spp.) larvae in these fields hatch from eggs produced by adults that feed on the corn leaf aphids infesting the sorghum early in the season. The larvae in turn feed heavily on the greenbugs that appear later. Indeed, when corn leaf aphids are sufficiently abundant early on, the numerical (reproductive as well as aggregative) response of lady beetles prevents greenbugs from causing economic damage (Michels & Burd, 2007).

In a similar example, early spring feeding on pollen as an alternate food enables females of the lady beetle *Adalia bipunctata* (L.) to lay eggs as soon as aphids later become available (Hemptinne & Desprets, 1986). Chiverton & Sotherton (1991) collected females of the carabids *Agonum dorsale* (Pontoppidan) and *P. mela-*

narius from herbicide-treated and untreated plots in an English grain field. Untreated plots had many more weeds than treated plots. The carabids fed on many alternate prey associated with the abundant weeds in the untreated plots, whereas they fed most commonly on cereal aphids in the herbicide-treated plots. Females from untreated plots also had higher numbers of eggs in their ovaries than females from herbicide-treated plots. Similarly, Zangger et al. (1994) found that females of the carabid *Poecilus cupreus* L. occurring in or near a weed strip had more food in their crops and more eggs in their ovaries than females collected far from weed strips in a cereal (rye) field. These authors suggest that the availability of diverse prey associated with the weeds enhanced carabid reproduction, but the foods eaten near and far from the weed strip were not identified.

PUTTING IT ALL TOGETHER

The numerous studies cited above illustrate many ways in which aphids, other herbivores, and even plants (e.g. by providing fruit or pollen) may interact indirectly by sharing predators. Collectively, these studies suggest that such indirect interactions are likely to occur frequently in natural settings. Ultimately, however, the challenge remains to determine how differing mechanisms of indirect interaction reinforce or negate each other when combined to yield an overall, long-term relationship between two or more prey species and their predators. The challenge is heightened because the relative strengths of these differing mechanisms may vary with spatial and temporal scales (e.g., Ostman & Ives, 2003). For example, as noted by many researchers, the presence of an alternate prey may promote predator aggregation (perhaps leading to negative indirect interaction between prey), but may also serve to reduce consumption rates of focal prey by individual predators (thereby yielding a positive indirect interaction between prey). Similarly, enhancement of predator reproductive success in the presence of alternate prey may lead to reduced numbers of focal prey in future generations (a negative indirect interaction between prey) even as over the short-term, individual predators consume fewer focal prey (a positive indirect interaction between prey). On the other hand, the aggregative, functional, and reproductive responses of predators in the presence of alternate prey may act synergistically (e.g., Müller & Godfray, 1997), with resultant strong suppression of focal prey numbers (i.e., strong negative indirect interaction between the prey species).

Perhaps most progress has been made so far in understanding how alternate prey may influence the population dynamics of cereal aphids of northern Europe through effects on generalist predators. For example, Ostman (2004) found that these predators' numerical responses outweighed their functional responses as they responded to variable numbers of alternate prey among fields, thereby leading to higher overall rates of aphid predation in fields with high numbers of alternate prey. The relatively stable, high numbers of generalist predators from year to year in these fields (e.g., Wallin, 1985) suggests also that reproductive as well as aggregative responses lead to significant effects of alternate prey on cereal aphid populations over the long-run. But clearly even in this case, much remains to learn about the importance and specific mechanisms of indirect effects. It is of much interest, for example, to determine how often a single alternate prey species (e.g., Gilstrap, 1997; Michels & Burd, 2007), versus a diffuse collection of multiple prey species (e.g., Müller & Godfray, 1999b, Ostman, 2004), may critically affect a focal prey species indirectly by interactions with shared predators. In general, we now have the strong experimental foundation to support our ecological intuition that predator-mediated, indirect interactions among aphids and other prey are likely to occur widely, and that they are likely to be multifaceted. It remains for us to determine how often such indirect interactions are strong enough to significantly influence the long-term population dynamics of phytophagous insects such as aphids, and consequently the impact of the herbivores on the fitness and productivity of their host plants.

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