

## Intraguild Predation among Biological-Control Agents: Theory and Evidence

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Received June 30, 1994; accepted March 27, 1995

Theoretical and empirical evidence developed in four subdisciplines of biological control (biocontrol of plant pathogens, weeds, nematodes, and arthropods) is brought to bear upon a shared question: the significance of intraguild predation. Intraguild predation ("IGP") occurs when two species that share a host or prey (and therefore may compete) also engage in a trophic interaction with each other (parasitism or predation). We describe the prevalence of IGP and its role in the population dynamics of biological-control agents and target pests. IGP is a widespread interaction within many, but not all, communities of biological-control agents. IGP appears to be pervasive among communities of control agents associated with nematode or arthropod pests. Common forms of IGP include pathogens that infect both herbivores and parasitoids of the herbivore; facultative hyperparasitoids, which can parasitize either an herbivore or a primary parasitoid of the herbivore; predators that attack herbivores that harbor a developing parasitoid; and predators that attack each other. In contrast, IGP appears to be relatively uncommon among biological-control agents of plant pathogens because trophic interactions are less important than competition or antibiosis. Likewise, biological-control agents of weeds interact primarily through competition alone because host ranges are mostly restricted to plant taxa. Empirically based simulation models and general analytical models of interactions involving arthropod pathogens or facultative hyperparasitoids yield variable and often conflicting predictions for the influence of IGP on the success of biological control. Models for predator-predator interactions, however, consistently predict that IGP disrupts biological control. All the field-documented cases of IGP leading to disruption of biological control stem from studies of predators, including mites, insects, and predatory fishes. IGP between two predators or between a predator and an adult parasitoid does not require mortality of the shared prey/host (i.e., the target pest); thus, IGP can be intense, resulting in high levels of mortality for one or both of the natural enemies, while the total mortality imposed

on the target pest population is minimal. For this reason, we hypothesize that IGP by predators is particularly likely to influence the efficacy of biological control. Our ability to develop successful programs of biological control will be enhanced by field studies that address the complexity of trophic interactions occurring in agroecosystems. There is a critical need for additional manipulative experiments conducted in the field that test not only population ecology theory for two-species interactions, but also community ecology theory for multispecies interactions. © 1995 Academic Press, Inc.

**KEY WORDS:** biological control; intraguild predation; parasitism; insects; nematodes; weeds; plant pathogens.

### INTRODUCTION

The ecological processes underlying successful biological control are often complex. Simple verbal and mathematical models of the suppression of pest populations by predators, parasitoids, pathogens, and antagonists have increasingly given way to more complex models (Murdoch *et al.*, 1985; May and Hassell, 1988; Hochberg, 1989; Luck, 1990). The development of general theory for biological control is made difficult also by the diversity of organisms that are the usual targets of control: arthropods, nematodes, plant pathogens, and weeds. Workers in each of these taxonomically defined branches of biological control have, in large part, developed theory in isolation from each other and in response to perceived or actual taxon-specific aspects of ecology.

Different branches of biological control have varied in their adoption of principles from population ecology versus community ecology to build theory (Fig. 1). At one extreme is the theory for biological control by predatory arthropods, where simple two-species interactions, as represented in Lotka–Volterra and Nicholson–Bailey models (reviewed by Berryman, 1992), have dominated theoretical developments. At the other

2-species interactions		Interactions in groups of a few species		Complex interactions in speciose communities
Population Ecology		Community Ecology		
<i>Simplest arthropod predator-prey, parasitoid-host, and pathogen-host models</i>	<i>Hyperparasitoid-primary parasitoid-host models</i>	<i>Biological control of weeds by herbivore complexes</i>	<i>Biological control of plant pathogens</i>	<i>Soil communities of plant pathogens and nematodes</i>

**FIG. 1.** Historical contribution of population and community ecology to the development of biological control theory in different subdisciplines.

extreme is the theory for biological control of pathogens and nematodes in soil ecosystems, where diverse communities of organisms are thought to interact through complex networks of competition, parasitism, and predation that create strong “buffering” effects, limiting epidemics (Wilhelm, 1965; Cook and Baker, 1983). Theorists working with other taxa, such as insect parasitoids, have adopted intermediate positions in which interactions of up to three species at different trophic levels in the community (host, primary parasitoid, hyperparasitoid) are recognized as potentially important (Luck *et al.*, 1981).

In this review we attempt to bring these different theoretical backgrounds to bear upon a shared question in biological control theory: the significance of intraguild predation. Intraguild predation occurs when two heterospecific organisms share a given host or prey (and therefore may compete for that host or prey) and also engage in some sort of trophic interaction (parasitism or predation). Our hope is that our understanding of intraguild predation will be strengthened through a diversity of theoretical approaches. Secondarily, we will argue that perspectives from population ecology and community ecology can contribute to the understanding of biological control and that the cross-fertilization of different subdisciplines of biological control can lead to important insights.

Our review of empirical studies is organized along taxonomic lines and proceeds from the less to the more intensively studied groups. We address intraguild predation among biological-control agents of plant pathogens, weeds, nematodes, and arthropods. In each case we attempt to describe the prevalence of intraguild predation, its role in the population dynamics of biological-control agents, and its impact on the success of biological control. We then review simulation and analytical models that have been used to build theory for intraguild predation. We conclude with a general hypothesis for when intraguild predation is most likely to have a strong influence on the efficacy of biological control and with a plea for additional experimental work.

Given the limited attention devoted by biological control workers to multispecies interactions, this review’s

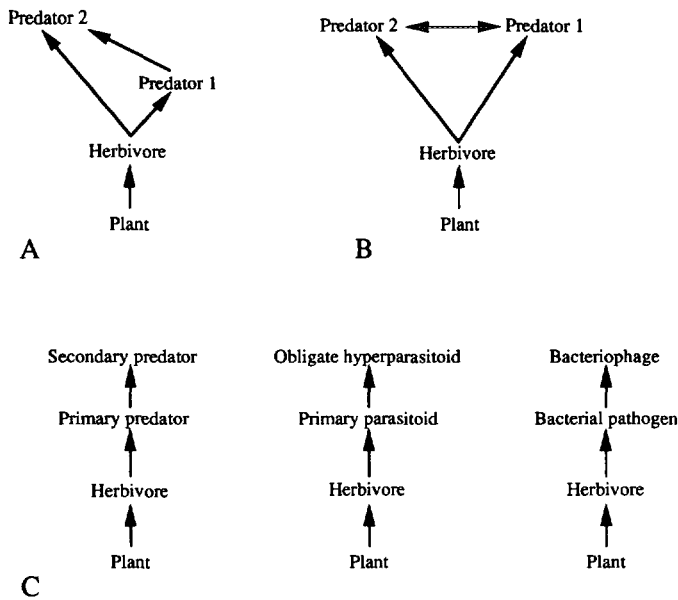
aim is not to develop a final conclusion regarding the importance of intraguild predation. Rather, we hope to stimulate the needed research by (i) synthesizing a diffuse literature, most of which has never been reviewed, and (ii) identifying critical empirical and theoretical questions.

### Terminology

Both parts of the term “intraguild predation” need some explanation. First, we use “guild” in the broadest sense, to include all organisms that share a common food resource. Thus, we follow Polis *et al.* (1989) in lumping organisms that use a resource in different ways (e.g., via predation or parasitism). This usage of the term “guild” is much broader than that used by some previous authors (Ehler, 1994; Mills, 1994). We use “predation” also in the broadest sense to include any trophic interaction between biological-control agents. Intraguild predation may be unidirectional, in which one of the interacting species may be called the intraguild predator (henceforth “IG predator”) and the other the intraguild prey (henceforth “IG prey”), or may be bidirectional (or “mutual”), with each species preying upon the other.

### Intraguild Predation and Obligate Secondary Predators

In restricting our discussion to intraguild predation (henceforth “IGP”), we exclude consideration of similar ecological relationships involving (i) intraspecific predation (“cannibalism”) or (ii) obligate secondary predation (Fig. 2). Interactions between biological-control agents and obligate secondary consumers differ from IGP in that the secondary consumer does not compete with the primary consumer (the biological-control agent) for a common resource (in this case, the target of the biological control effort). Thus, the competition leg of IGP is absent. Obligate secondary consumers are known in many biological control settings and include such organisms as insect hyperparasitoids (e.g., *Alloxysta* spp.; Sullivan, 1987), arthropod predators (e.g., spiders in the family Mimetidae; Foelix, 1982), and par-



**FIG. 2.** Trophic webs demonstrating the distinction between intraguild predation and obligate secondary predation. (A) Unidirectional intraguild predation. Predators 1 and 2 share a common prey (the herbivore), and predator 2 eats predator 1. (B) Bidirectional intraguild predation. Same as (A), except that predators 1 and 2 eat each other. (C) Obligate secondary predation. The secondary consumer (which is shown as a secondary predator, an obligate hyperparasitoid, or a bacteriophage) attacks the primary consumer, but does not attack the herbivore. Thus the primary and secondary consumers can not compete for a common resource.

asitic microbes (e.g., bacteriophages associated with insect pathogenic bacteria; O'Callaghan and Jackson, 1993). We also exclude cases of strict competition, in which two organisms compete for a given food resource but do not themselves engage in trophic interactions.

#### BIOLOGICAL CONTROL OF PLANT PATHOGENS

Biological control of plant pathogens is dependent upon competition, antibiosis, and parasitism/predation (Campbell, 1989). Although in the recent past most emphasis has been on the role of antibiosis in disease control, the mechanism first identified was hyperparasitism by the soil fungus *Trichoderma* spp. observed by Weindling (1932) in petri plate cultures. Many other hyperparasites of plant pathogens have been studied since this original observation, including *Pythium oligandrum* Drechsler, which is the major inhibitor of *Pythium ultimum* Trow (Martin and Hancock, 1987); *Sporidesmium sclerotivorum* Uecker, Ayers & Adams, which parasitizes *Sclerotinia minor* Jagger (Ayers and Adams, 1979; Adams *et al.*, 1984); and *Sphaerellopsis filum* (Biv.-Bern. ex Fr.) Sutton and *Ampelomyces quisualis* Ces. ex Schlecht, which parasitize rust and mildew colonies (Jeffries and Young, 1994). Several spe-

cies of mycoparasitic fungi often occur together naturally in agricultural soils, and some commercial formulations of mycoparasitic fungi employ combinations of species (Jeffries and Young, 1994). While some mycoparasites have very narrow host ranges, others have extremely broad host ranges; for example, the mycoparasitic fungus *Verticillium lecanii* (Zimm.) Viegas parasitizes hosts in at least two kingdoms (arthropods and fungi) (Jeffries and Young, 1994). This combination of mycoparasite species diversity and broad host range should provide ample opportunities for IGP. Other mycophagous organisms with potential roles in biological control include soil-dwelling amoebae and ciliate protozoa (Campbell, 1989). One area of recent research is the use of a nonobligate predatory bacterium, *Pseudomonas* Strain 679-2, to control bacterial plant pathogens (Casida, 1992; Casida and Lukezic, 1992).

The potential for IGP among biocontrol agents of plant pathogens has not been explored. This is due in part to the undefined assumption that microbial communities are bottom-up ecosystems with little control exerted from the typical top-down predatory forces. For example, most soil microbes are dormant in the soil most of the time and reproduce only when ephemeral substrates become available. Microorganisms can respond to the appearance of substrate with extremely rapid population growth. When the substrates are depleted, populations may rapidly crash. Thus, potential for feedback systems normally associated with predator/prey relationships and IGP may have very little opportunity to develop.

If IGP is an important influence on microbial hyperparasites, it may explain the difficulty of introducing and establishing mycoparasites and other beneficial microorganisms into many soils. Despite the use of practices designed to enhance mycoparasite establishment, such as the prior treatment of soil with a broad-spectrum biocide or the addition of large amounts of nutrients to soils when the mycoparasite is released, it is still very difficult to obtain efficient, long-term establishment of desired organisms. One of the few cases where this has been accomplished is with *S. sclerotivorum*.

Before the role of IGP can be investigated, more information on the biology of mycoparasites must be obtained. Although many fungi appear to be mycoparasites in defined laboratory conditions, it is difficult to determine if they are actual parasites under field conditions and if they have any potential of affecting the population dynamics of their hosts. Problems of isolation, identification, and quantification are extreme. Just 1 g of soil may contain a speciose community of millions of bacteria and thousands of fungi. Typically, only half of the organisms isolated from soil samples have been taxonomically described, and a high level of

expertise is needed to achieve precise identifications. Because organisms have been identified that appear to be mycoparasites on a large number of species, it is possible that IGP is taking place. However, we are far from being able to quantify and assess the role of IGP in the development and implementation of the biological control of plant pathogens.

### BIOLOGICAL CONTROL OF WEEDS

Because most introduced weed-control agents are highly host specific and strictly herbivorous, IGP is probably uncommon. Nevertheless, even relatively host-specific phytophagous insects can be omnivorous under certain circumstances, creating possibilities for IGP. The geometrid *Prochoerodes truxaliata* (Guenée) is a case in point. This insect is native to California where its larvae feed on *Baccharis pilularis* DC. It has a sufficiently narrow host range that it has been cleared for release against a related host (*Baccharis halimifolia* L.) in Australia (Palmer and Tilden, 1987; Ehler *et al.*, 1990). However, in both the laboratory and field, larvae of *P. truxaliata* (which are normally defoliators) also readily feed on developing terminal galls containing young larvae of the native midge *Rhopalomyia californica* Felt (G. English-Loeb and M. G. Kinsey, personal communication). Because the gall midge is already established in Australia and shows considerable potential as a biological-control agent for *B. halimifolia*, the importation of *P. truxaliata* could establish IGP among the biological-control agents of this weed.

Zwölfer (1994) described another example of IGP among the herbivorous insects associated with flower heads of thistles (Asteraceae: Cardueae) in Europe. Three types of herbivores exploit the flower heads: (1) gall inducers and species that feed on callus tissue in the flower head, (2) those that feed on achenes and receptacle tissues, and (3) omnivorous species that may be cannibalistic or predatory if they encounter another herbivore. Omnivorous species are thus IG predators, and IGP may be common in endophytic guilds where there is no escape from interspecific competitors.

Story *et al.* (1991) assessed the impact of an IG predator within just such a guild of three endophytic herbivores imported to North America as biological-control agents of the spotted knapweed *Centaurea maculosa* Lamarck. The seed head moth *Metzneria paucipunctella* Zeller feeds on seeds and also attacks and consumes the larvae of two species of seed-destroying gall flies (*Urophora affinis* Frauenfeld and *Urophora quadrifasciata* [Meigen]) occupying the same seed head. In field cages, moths killed from 67 to 69% of gall fly larvae in the seed heads that they occupied. In seed heads attacked by moths, only 4.7 seeds survived on average, whereas in seed heads without moths (some of which

were attacked by flies) 9.8 seeds survived. Story *et al.* (1991) concluded that the seed head moth was contributing to the overall suppression of spotted knapweed, despite its status as an IG predator. However, other results that they present suggest that this conclusion may warrant further examination. A survey of field sites in British Columbia revealed that the density of the fly *U. affinis* was more than twice as great at sites where *M. paucipunctella* was absent than where the two co-occurred (a substantial although not statistically significant difference), and other studies have suggested that *U. affinis* may be the most important control agent in the guild (Harris, 1980; Story *et al.*, 1991). Experiments comparing the population dynamics of spotted knapweed in the presence of flies alone versus flies plus moths would be very valuable in resolving the role of the IG predator *M. paucipunctella*.

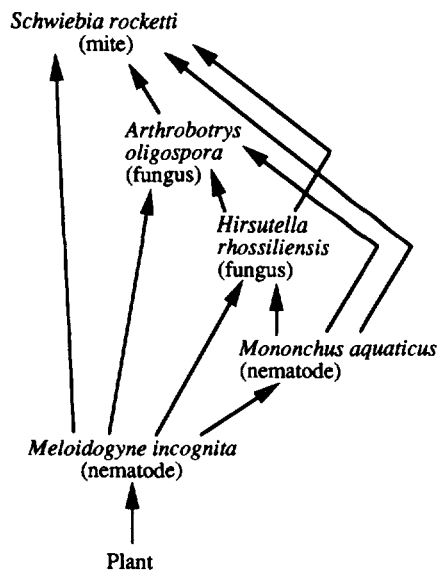
In summary, field observations suggest that IGP does occur among weed biological-control agents. The significance of this IGP for the success of weed biological control is unclear, and experimental work is clearly needed before its importance can be assessed.

### BIOLOGICAL CONTROL OF NEMATODES

Plant-parasitic nematodes and their predators and parasites often are abundant in soil (Stirling, 1991). Predators include other nematodes, mites, Collembola, tardigrades, and amoebae, whereas parasites include bacteria and fungi. Some consumers of nematodes are host specific and therefore unlikely to act as IG predators. Other consumers, however, may have a diverse range of prey or hosts and may even attack species in more than one phylum. A broad selection of prey and hosts makes IGP likely, but no case of IGP has been quantitatively documented in the field.

Consider the following possible examples of IGP involving a plant-parasitic nematode, *Meloidogyne incognita* (Kofoid & White) Chitwood; the nematophagous fungi *Arthrobotrys oligospora* Fres. and *Hirsutiella rhossiliensis* Minter & Brady; a predacious nematode, *Mononchus aquaticus* Coetzee; and a predacious mite, *Schwiebia rocketti* Woodring (Fig. 3). First, the nematode-trapping fungus *A. oligospora* is common in soil (Barron, 1977) and attacks many species of nematodes, perhaps including predacious species like *M. aquaticus* and plant-parasitic species like *M. incognita*. In addition, the hyphae of *A. oligospora* coil around, kill, and presumably consume hyphae of other fungi in dual culture on agar plates (Tzean and Estey, 1978; Persson and Bååth, 1992). If this interaction occurs in soil and involves a second species of nematophagous fungus, such as *H. rhossiliensis*, then IGP would again be occurring.

Although prey selection by predacious nematodes, such as *M. aquaticus*, may change with developmental



**FIG. 3.** Intraguild predation among biological-control agents of nematodes in soil ecosystems. The nematode-trapping fungus *Arthrobotrys oligospora* has a broad host range and may attack both plant-parasitic nematodes, like *Meloidogyne incognita*, and predacious nematodes, like *Mononchus aquaticus*. *Arthrobotrys oligospora* also may be mycoparasitic, i.e., it may parasitize other fungi, such as *Hirsutella rhossiliensis*. *Hirsutella rhossiliensis* does not attack other fungi but may parasitize both plant-parasitic and predacious nematodes. Predacious nematodes may consume plant-parasitic or other predacious nematodes. Finally, the mite *Schwiebia rocketti* eats both nematodes and nematophagous fungi.

stage of the predator (Yeates, 1987), prey often encompass a range of nematode species, including predacious species (Small, 1987). The potential for IGP exists because two predacious species may attack each other as well as plant-parasitic nematodes. Moreover, some predacious nematodes are omnivorous, feeding on fungi, mites, tardigrades, and other potentially nematophagous organisms.

Omnivory also is common among soil mites, which could consume both plant-parasitic nematodes and all of the other organisms considered above. For example, the mite *S. rocketti* eats nematodes and the nematode-trapping fungus *A. oligospora* (Walter and Kaplan, 1990).

A primary concern is "Does IGP interfere with biological control of plant-parasitic nematodes?" In fact, biological control of nematodes has rarely been enhanced through active intervention (Stirling, 1991), and for the most part we do not understand the bases of the failures.

Recommending a preferred approach to study IGP with respect to plant-parasitic nematodes and their enemies is difficult. Clearly, we need quantitative data on their interactions in the soil. Because soil is opaque, such data are difficult to collect. Quantitative ecological studies may be facilitated by using soil microcosms, which provide the researcher with enhanced control

of the soil environment and adequate replication. Soil microcosms are not overly artificial given the small size and limited motility of the organisms. Community ecologists may prefer to study fully complex soil systems, whereas population biologists may prefer to study specific interactions within systems. Both approaches will be useful, should be combined, and should involve observation, experimentation, and theory.

### BIOLOGICAL CONTROL OF ARTHROPODS

Biological-control agents of arthropod pests may be grouped into three classes: parasitoids, predators, and pathogens. Here we consider the most widespread and important forms of IGP among these classes of natural enemies.

#### *Parasitoid-Parasitoid Interactions*

There is a general tendency to view insect parasitoids as being either primary (parasitizing nonparasitic hosts) or secondary (parasitizing primary parasitoids). Yet, in many parasitoid guilds there are "facultative secondary parasitoids," whose larvae can develop either as primary or secondary parasitoids. For example, if the searching female discovers a healthy, nonparasitic (e.g., phytophagous) host and oviposits in or on it, the parasitoid's larva develops as a primary parasitoid. If the female discovers a host that is already parasitized by a primary parasitoid, she may oviposit in or on this host also, but her progeny will develop as a secondary parasitoid on the incumbent parasitoid. This is quite distinct from interspecific competition (because one parasitoid consumes the other), and thus qualifies as IGP. Although some consider this phenomenon to be common in parasitoid guilds (see Hawkins, 1992), data on the prevalence of IGP among parasitoids are limited. Tertiary parasitism occurs in some guilds and may be facultative as well. Both secondary and tertiary parasitism are forms of hyperparasitism.

Ehler (1990) suggested that there is a continuum of feeding strategies in parasitoids; the two extremes are obligate primary parasitism and obligate secondary parasitism. A facultative secondary parasite can then be placed within this continuum at an intermediate position, determined by its propensity to develop as a primary vs a secondary parasitoid. This propensity is relevant to biological control. Although there is relatively little information on this question in the literature, there are at least two studies that warrant our attention. Weseloh *et al.* (1979) assessed the egg parasitoid *Anastatus kashmirensis* Mathur for possible importation against the gypsy moth *Lymantria dispar* (L.). Their analysis indicated that this facultative secondary parasitoid poses considerable risk to other parasitoids already established, leading to the recommen-

dation that it not be released in North America. More recently, Kfir *et al.* (1993) considered the release of *Tetrastichus howardi* (Olliff) (Eulophidae), a facultative hyperparasitoid associated with lepidopterous stem borers. Preference tests showed that *T. howardi* prefers to parasitize phytophagous insects rather than their associated parasitoids. Nevertheless, *T. howardi* was not released because of its broad host range. Although a few facultative secondary parasitoids have been released for classical biological control (Bennett, 1981; Kfir *et al.*, 1993), Ehler (1979) suggested that such introductions should be considered only as a last resort, and Rosen and Kfir (1983) argued that such species should never be introduced.

The wasp family Aphelinidae, widely used in biological control programs, contains a group of facultative secondary parasitoids known as "heteronomous hyperparasitoids." These species have a unique biology: male and female offspring are produced on different hosts. In many cases, females are produced as primary parasitoids of scale insects or whitefly, while males are produced as secondary parasitoids of parasitoids developing in scale insects or whitefly. In "facultative autoparasitoids" the hyperparasitic males develop either on conspecific parasitoid females ("autoparasitism") or on other species of primary parasitoids (Walter, 1983; Viggiani, 1984). A model recently developed by Mills and Gutierrez (in press) has predicted that facultative autoparasitoids can disrupt biological control exerted by primary parasitoids (see the discussion below under "Empirically Based Models").

Studies of two parasitoid communities provide tests of the Mills and Gutierrez (in press) prediction. First, field observations made during the course of biological control introductions against the citrus blackfly *Aleurocanthus woglumi* Ashby may be consistent with the prediction, at least in part (Nguyen *et al.*, 1983; Thompson *et al.*, 1987). Three parasitoids were released for citrus blackfly control: *Amitus hesperidum* Silvestri, a primary parasitoid; *Encarsia opulenta* (Silvestri), which develops on citrus blackfly but for which the details of larval development are not known; and *Encarsia smithi* (Silvestri), a facultative autoparasitoid whose males develop as secondary parasitoids on conspecific females or on *E. opulenta* (Nguyen *et al.*, 1983; Nguyen and Sailer, 1987; Thompson *et al.*, 1987). Citrus blackfly was strongly suppressed at three release sites by *A. hesperidum* alone or in combination with *E. opulenta*. At the one site where the facultative autoparasitoid *E. smithi* was abundant, *E. opulenta* appeared to be suppressed, and the establishment of effective biological control (by *A. hesperidum*) was delayed. It is unclear why *A. hesperidum* also appeared to have reduced efficacy at this site. The hypothesized suppression of *E. opulenta* was at most transitory; however, within 3 years of the initial releases *E. opulenta* had

become the dominant parasitoid (Thompson *et al.*, 1987). Further studies of this system would be particularly valuable.

A second test of the hypothesis that facultative autoparasitoids can disrupt biological control is provided by an experimental study conducted by Heinz and Nelson (in press) with two parasitoids of the silverleaf whitefly *Bemisia argentifolii* Bellows & Perring. The parasitoid *Encarsia formosa* Gahan develops as a primary parasitoid of *Bemisia* attacking poinsettias in greenhouses, whereas the parasitoid *Encarsia pergandiella* Howard develops as a facultative autoparasitoid (males are hyperparasitic on either *Encarsia* species). In large cages maintained in a greenhouse, the addition of *E. pergandiella* (an IG predator) to cages containing whitefly and *E. formosa* led to significant decreases in whitefly densities. Thus, contrary to the prediction of Mills and Gutierrez (in press), the addition of a facultative autoparasitoid led to enhanced biological control.

An alternative means of analyzing the ecological impact of facultative secondary parasitoids is to employ naturally occurring parasitoid guilds as model systems. The parasitoid guild associated with larvae of the gall midge *R. californica* provides an example. This guild consists of seven species, three of which are facultative secondary parasitoids (Doutt, 1961; Force, 1974; Ehler, 1992). Two of the facultative secondary parasitoids appear to be guild specific, are relatively abundant in the field, and can have a considerable impact on both the midge population and the structure of the parasitoid guild. In a laboratory experiment, Force (1974) observed that one of these facultative secondary parasitoids (*Zatropis capitis* Burks) dominated a key primary parasitoid (*Tetrastichus* sp.); the latter species usually is rare in the field. Ehler (1979) analyzed field-collected galls and found that total percentage parasitism of midge larvae per gall is greatest in galls where primary parasitoids occur with the dominant facultative secondary parasitoid. This suggests that facultative hyperparasitoids may increase the overall suppression of *R. californica*; however, the analysis was based on a spatial "snapshot" of a dynamic system rather than a long-term, temporal investigation. Furthermore, the study was observational rather than manipulative. Field experimentation with facultative hyperparasitoids, perhaps employing relatively well-understood systems like this one, are needed to advance our understanding of IGP among insect parasitoids.

Finally, we note that many insect parasitoids also engage in predatory feeding behavior as adults when they feed on the hemolymph or tissues of insects during "host feeding" (Jervis and Kidd, 1986). In a very few cases, host feeding may constitute IGP. One example is provided by the obligate hyperparasitoid *Tetrastichus* sp., which develops on primary parasitoids of cockroach oothecae and may host feed on cockroach

eggs housed in oothecae (Narasimham, 1984); these trophic interactions constitute IGP. No experimental work has been conducted to assess the importance of IGP involving host feeding.

### *Predator-Parasitoid Interactions*

We recognize two types of unidirectional IGP by arthropod predators on parasitoids. First, predators may prey directly on parasitoids, feeding either on immature stages developing externally on the host or on free-living parasitoid adults. While direct predation on adult parasitoids may be common, only when the predator also attacks the host of the parasitoid can the interaction be described as IGP. Second, predators may prey on parasitized hosts, consuming both the host and, indirectly, an associated immature parasitoid.

Rees and Onsager (1982) reported field observations and a manipulative field cage experiment examining interactions between predators and adult parasitoids of the migratory grasshopper *Melanoplus sanguinipes* (F.). Dissections of field-collected grasshoppers demonstrated 1–7% parasitism by three fly species in the genus *Blaesoxipha* (Diptera: Sarcophagidae). Field observations revealed that several species of predatory flies in the family Asilidae that feed on grasshoppers were also preying on adult *Blaesoxipha*. Furthermore, field samples of adult female *Blaesoxipha* taken across two field seasons (with 2–3 parasitoid generations per year) revealed that only 5–15% were gravid at any time. With the knowledge that parasitoids require 8–9 days to become gravid, Rees and Onsager (1982) were able to calculate mean longevities in the field of only 3.0–4.8 days, which differed dramatically from laboratory-based estimates of mean longevities of  $\geq 30$  days. Grasshoppers were introduced into large field cages with either (i) parasitoids alone or (ii) parasitoids plus predators (insect densities and species compositions varied across trials, with one replicate of each treatment conducted per trial). Survivorship of adult parasitoids across the 13-day experiment ranged from 25 to 67% in the parasitoids only treatment, while no parasitoids survived in the parasitoids plus predators treatment. Total parasitism rates ranged from 5 to 31% in the parasitoids only treatment and were consistently  $< 1\%$  in the parasitoids plus predators treatment. Finally, the overall percentage reduction in grasshopper numbers across the experiment (considering parasitized grasshoppers as killed) averaged 41.3% in the parasitoids only treatment and 20.7% in the parasitoids plus predators treatment. Thus, biological control was substantially disrupted by the addition of the IG predators (the asilid flies). Direct predation by asilid flies on grasshoppers was not sufficiently strong to compensate for the decreased parasitism caused by asilid predation on *Blaesoxipha*.

Because of the paucity of studies exploring mortality

factors acting on adult parasitoids in the field, it is difficult to assess whether interactions like those observed by Rees and Onsager (1982) are common. Wheeler (1977) observed predation on adult *Aphidius* spp. parasitoids by *Nabis* spp. Because *Nabis* spp. also fed on the likely host of these parasitoids (the pea aphid *Acyrtosiphon pisum* [Harris]), this interaction probably represents IGP. Two studies have documented predation on parasitoids developing externally on their host. Press *et al.* (1974) reported that the anthocorid predator *Xylocoris flavipes* (Reuter) feeds not only on the stored products pest *Plodia interpunctella* (Hübner), but also on the larvae of its ectoparasitoid, *Bracon hebetor* Say. In laboratory assays, suppression of *P. interpunctella* was more effective with *B. hebetor* present alone than with both *B. hebetor* and *X. flavipes* present (Press *et al.*, 1974). Nevertheless, more recent larger-scale studies with a complete community of stored products pests have led to recommendations for combined augmentative releases of both these and other natural enemies (Brower and Press, 1992). In a second example of direct predation on developing parasitoids, Jackson and Kester (1995) showed in the field and laboratory that the predatory stilt bug *Jalysus wickhami* Van Duzee preys on eggs of the hornworm *Manduca sexta* (L.) and on cocoons of the parasitoid *Cotesia congregata* (Say) that are spun on the dorsum of *M. sexta* larvae. Immature parasitoids in cocoons became less vulnerable to predation as they developed.

Most insects are attacked both by parasitoids and predators, creating abundant opportunities for IGP when predators consume parasitized hosts (Kot, 1971). Several food webs implicitly or explicitly represent this type of interaction (Nowierski, 1979; van den Bosch *et al.*, 1982; Gutierrez *et al.*, 1988b, 1990; Gutierrez, 1992), and some models of insect population dynamics have incorporated this form of IGP (Frazer and Gilbert, 1976; Gutierrez *et al.*, 1984, 1988a, 1990; Gutierrez, 1992; Kindlmann and Ruzicka, 1992). In some cases, the impact of predators may be greater on parasitized hosts than on unparasitized hosts, as demonstrated for predation by ants in the genus *Iridomyrmex* on caterpillars of the cabbage butterfly *Artogeia rapae* (L.) parasitized by *Apanteles glomeratus* L. (Jones, 1987). Several factors may modulate the importance of predation on parasitized hosts. First, predators may have different probabilities of encountering parasitized and unparasitized hosts. Differential encounter probabilities may be less likely when hosts are immobile. For instance, Ruberson and Kring (1991) demonstrated through laboratory assays that the predatory anthocorid *Orius insidiosus* Say is equally likely to encounter parasitized or unparasitized eggs of *Helicoverpa zea* (Boddie). In contrast, Tostowaryk (1971) demonstrated that the pentatomid *Podisus modestus* (Dallas) is more likely to attack sawfly larvae parasitized by tachinid



or ichneumonid parasitoids than unparasitized sawfly larvae. This pattern of predation was generated by the group defense behavior of sawflies, which provided opportunities for attack by both parasitoids and predators primarily at the periphery of sawfly colonies, creating a large overlap of attacked hosts.

In some cases, the impact of predators on parasitized hosts has been sufficiently strong to favor parasitoids that have evolved an ability to manipulate the behavior of their hosts. Brodeur and McNeil (1992) demonstrated that potato aphids, *Macrosiphum euphorbiae* (Thomas), parasitized by *Aphidius nigripes* Ashmead change their microhabitat selection just prior to death. Parasitized aphids die and form "mummies" higher in the plant canopy and primarily on the upper surfaces of leaves, thereby reducing the incidence of predation in the field. Potato aphids harboring diapausing parasitoid larvae exhibit yet another type of microhabitat selection, leaving the host plant to seek concealed locations (Brodeur and McNeil, 1989). Frazer and Gilbert (1976) similarly hypothesized that microhabitat selection in parasitized pea aphids may be manipulated by their parasitoid, *Aphidius ervi* Haliday, to minimize predation by coccinellids.

Once a host is encountered, predators may have different probabilities of attacking unparasitized versus parasitized hosts. Fritz (1982) reviewed predation on parasitized arthropods by birds and small mammals, including several examples where unparasitized hosts are preferred, and at least one in which parasitized hosts are preferred. Stark and Hopper (1988) showed that *Chrysoperla carnea* (Stephens) is equally likely to attack unparasitized *Heliothis virescens* (F.) larvae and larvae harboring 1- to 3-day-old immature braconid parasitoids. It is not surprising that generalist predators do not distinguish between unparasitized hosts and hosts harboring parasitoid eggs or young larvae, because parasitoids may need to reach more advanced developmental stages before they have an important influence on the behavior, morphology, or physiology of their hosts. For example, Kindlmann and Ruzicka (1992) stated that the larvae of the syrphid fly *Metasyrphus corollae* (Fabr.) eat recently parasitized aphids but avoid parasitized aphids that have become partially or completely mummified. Studies of two predatory coccinellid beetles have shown that the acceptability of herbivorous prey harboring developing endoparasitoids changes as the parasitoid develops. First, the vedalia beetle *Rodolia cardinalis* (Mulsant) attacks cottony-cushion scales, *Icerya purchasi* Maskell, harboring the eggs or young larvae of the parasitoid *Cryptochaetum iceryae* (Williston) but does not attack scales harboring mature larval or pupal parasitoids (Quezada and DeBach, 1973). Second, *Delphastus pusillus* (LeConte) does not discriminate between whitefly prey that are unparasitized versus those that are newly parasitized by aphelinid wasps, but in-

creasingly avoids parasitized hosts as immature parasitoids consume the host (Hoelmer *et al.*, 1994; Heinz *et al.*, 1994). Hosts harboring parasitoid pupae are largely free from attack. While the possibility of different rates of encounter with unparasitized and parasitized hosts was not formally excluded for either *R. cardinalis* or *D. pusillus*, in both cases it appears likely that differential attack is due at least in part to differences in prey acceptance and/or physical defenses of the host or parasitoid cuticles (Quezada and DeBach, 1973; Hoelmer *et al.*, 1994; J. M. Nelson and K. M. Heinz, personal communication).

Not all parasitized hosts become increasingly unacceptable prey as internal parasitoids develop, however. Ruberson and Kring (1991) found that *O. insidiosus* accepts unparasitized eggs of *H. zea* nearly twice as often as eggs harboring either young larvae or pupae of the parasitoid *Trichogramma pretiosum* Riley, but that *O. insidiosus* does not appear to discriminate between the two classes of parasitized hosts. Furthermore, there are many examples in the literature of parasitized aphids being consumed by a diverse group of aphid predators even after the aphid has been completely consumed and transformed into a mummy by an internal parasitoid (Wheeler *et al.*, 1968; Frazer and van den Bosch, 1973; Frazer and Gilbert, 1976; Wheeler, 1977; Nowierski, 1979; Brodeur and McNeil, 1992; Ferguson, 1994; Colfer and Rosenheim, 1995; Rosenheim, 1995). For example, predation by lacewings, assassin bugs, and coccinellid beetles on mummies of the walnut aphid *Chromaphis juglandicola* (Kaltenbach) harboring *Trioxys pallidus* (Haliday) increased continuously across a growing season, peaking at 81% (Nowierski, 1979). Studies of predation on aphid mummies hold particular promise for future analysis of IGP on parasitized hosts because the damaged mummy often remains after the predator attack, providing a record of predation.

A well-characterized example of predation on parasitized hosts is that of the winter moth *Operophtera brumata* (L.) in England and Canada. Winter moth larvae defoliate broad-leaf trees. Mature larvae drop to the soil and pupate, and there is only one generation per year. In England, the larval-pupal parasitoid *Cyzenis albicans* (Fall.) (Tachinidae) is not a major mortality factor. This is apparently due to hyperparasitism and predation by beetles and a shrew on parasitized pupae in the soil (Hassell, 1969a,b; East, 1974). However, when *Cyzenis* and another parasitoid (*Agrypon flaveolatum* [Grav.]) were introduced into eastern Canada, they provided outstanding biological control of the winter moth (Embree, 1971; Hassell, 1980). The success of *Cyzenis* in eastern Canada was presumed to be due at least in part to a reduction in pupal mortality.

Some years later, the winter moth invaded western Canada. Following introduction of the same parasitoids



released in eastern Canada, winter moth populations declined to ca. one-tenth of their previous peak densities (Roland, 1990). Roland (1990) observed that following the initial peak in parasitism, pupal predation by staphylinid beetles increased to very high levels; he also suggested that a similar trend had occurred in eastern Canada. Unparasitized winter moth pupae spend about 5 months in the soil compared with 10 months for pupae containing *Cyzenis*. Roland (1988, 1990) suggested that predator buildup may have been a direct result of the introduction of *Cyzenis*—i.e., as parasitism increased, there was a commensurate increase in the proportion of pupae available to ground predators for 10 (instead of 5) months. Following the collapse of winter moth populations in both eastern and western Canada, pupal predation has remained relatively high and is believed responsible for maintaining populations at low levels (Roland and Embree, 1995). Thus, the successful biological control of winter moth in Canada may have resulted from an interaction between an introduced parasitoid and an incumbent guild of predators. This provocative hypothesis raises a number of new issues for biological control and should serve as a reminder that preintroductory investigations in classical biological control should consider the ecological structure of the targeted system as well as the natural-enemy complex in pest's native range. It also suggests that an introduced parasitoid may enhance or "synergize" a guild of predators.

The influence of adding a predator to a system comprising a host and its endoparasitoid, when the predator consumes some parasitized hosts, has been experimentally tested in three systems (see also Kindlmann and Ruzicka, 1992). First, Ferguson (1994) demonstrated in field cage experiments that mean densities of the saltmarsh aphid *Dactynotus* sp. were not significantly different in the presence of either (i) the endoparasitoid *Aphidius floridaensis* Smith alone or (ii) combinations of *A. floridaensis* and the predator *Cycloneda sanguinea* L. Second, Colfer and Rosenheim (1995) demonstrated that suppression of field populations of the cotton aphid *Aphis gossypii* Glover on seedling cotton is enhanced by adding *Hippodamia convergens* Guerin, despite the fact that *Hippodamia* consumes both healthy aphids and aphids mummified by the endoparasitoid *Lysiphlebus testaceipes* (Cresson). Third, Heinz and Nelson (in press) demonstrated in greenhouse cage trials that suppression of the whitefly *B. argentifolii* is consistently improved by adding the predator *D. pusillus* to any of three host + parasitoid combinations, despite the fact that *D. pusillus* consumes many whitefly harboring first and second instar parasitoid larvae (see above).

#### Predator–Predator Interactions

Biological control textbooks and general treatments of arthropod predators have usually emphasized the

consumption of herbivorous arthropod prey (Clausen, 1940; Hagen *et al.*, 1976; Tanigoshi, 1982; van den Bosch *et al.*, 1982; University of California, 1984; DeBach and Rosen, 1991). Such an emphasis is perhaps natural, as it is herbivorous species that usually are the targets of biological control projects. This emphasis has created the impression that predator diets are comprised either entirely of herbivores or that predator–predator interactions are uncommon and unimportant.

Many predators are generalists and may consume a broad array of prey. The inclusion of a given prey species in a predator's diet may reflect the relative size of predator and prey (Warren and Lawton, 1987; Polis and McCormick, 1987; Nyffeler *et al.*, 1992; Wissinger, 1992), the interplay of prey behavioral and structural defenses with the predator's foraging behavior (McCaffrey and Horsburgh, 1982; McPeck, 1990; Power *et al.*, 1992), and predator preference, which may be rigid or flexible. In many cases, there appears to be little reason to expect predators to discriminate between prey on the basis of their being herbivores, saprovores, or carnivores. Although some predators may orient to herbivorous prey by responding to chemical cues ("kairomones") liberated from damaged plants (Vet and Dicke, 1992), upon reaching a microhabitat supporting herbivores, predators may often encounter both the herbivores that liberated the kairomones and other predators associated with the herbivores.

A growing number of studies conducted in both the field and laboratory have demonstrated that IGP among predators is widespread (Table 1). Both unidirectional and bidirectional IGP appear to be common; bidirectional IGP often takes the form of late instars or adults of two species feeding on each other's earlier developmental stages (Polis *et al.*, 1989). Species in a broad array of taxa engage in IGP; generalist predators in the Acari, Araneae, and Hemiptera are especially well-represented, but species in the Pseudoscorpiones, Diptera, Coleoptera, Neuroptera, Odonata, Orthoptera, and Thysanoptera also are included. IGP has been recorded in diverse agroecosystems, including greenhouse vegetables, animal manure, stored grains, highly disturbed annual cropping systems (cassava, cotton, potato, and soybean), and more stable perennial cropping systems (alfalfa, apple, and walnut). IGP also has been studied in communities of medically important mosquitoes that breed in ricefields or treeholes (Lounibos, 1985).

It is important to note that many instances of predators eating other predators do not constitute IGP (although they might have important implications for biological control). For instance, some predators may feed only on other predators (i.e., obligate secondary predators; discussed above), in which case the competition component of IGP is absent. In addition, two predators that prey on different herbivores cannot engage in IGP

**TABLE 1**  
Intraguild Predation Involving Predators of Arthropods: A Selective Review

Study type	Agricultural ecosystem	IGP species (E = exploiter; V = victim)	Biological control target	Effect on target pest density <sup>a</sup>	Reference
Field observation	Cotton	Many predators	Many	na	Whitcomb & Bell 1964
Field observation	Soybeans	Predatory insects and mites	Several	na	Mayse & Price 1978
Field observation	Soybeans	<i>Nabis americanoferus</i> (Hemiptera: Nabidae) (E) <i>Orius</i> sp. (Hemiptera: Anthoridae) (V)	na	na	Braman & Yeargan 1989
Field observation	Alfalfa	<i>Podisus</i> spp. (Hemiptera: Pentatomidae) (E) <i>Chrysoperla carnea</i> (Neuroptera: Chrysopidae) (E) <i>Coleomegilla maculata</i> (Coleoptera: Coccinellidae) (V)	<i>Hypera postica</i>	na	Wheeler 1977
Field observation	Cotton	<i>Oxyopes salticus</i> (Araneae: Oxyopidae) (E) Several predatory insects and spiders (V)	Several	na	Nyffeler et al. 1987a, 1992
Field observation	Cotton	<i>Peucetia viridans</i> (Araneae: Oxyopidae) (E) Several predatory insects and spiders (V)	Several	na	Nyffeler et al. 1987b, 1992
Field observation	Cotton, soybeans, clover	<i>Geocoris</i> spp. (Hemiptera: Lygaeidae) (E) <i>Orius tristicolor</i> (Hemiptera: Anthoridae) (V)	na	na	van den Bosch et al. 1956; Crocker & Whitcomb 1980
Field observation	Cotton	<i>Geocoris pallens</i> (Hemiptera: Lygaeidae) (E) <i>Orius tristicolor</i> (Hemiptera: Anthoridae) (E) <i>Frankliniella occidentalis</i> (Thysanoptera: Thripidae) (V)	<i>Tetranychus</i> spp. (Acari: Tetranychidae)	na	González and Wilson 1982; Trichilo & Leigh 1986
Field observation	Cassava	<i>Geocoris amabilis</i> (Hemiptera: Lygaeidae) (E) <i>Nephus</i> sp. (Coleoptera: Coccinellidae) (V)	Complex of mealybugs	na	Neuenschwander et al. 1987
Field observation	Potato	<i>Podisus maculiventris</i> (Hemiptera: Pentatomidae) (E) <i>Perillus bioculatus</i> (Hemiptera: Pentatomidae) (V)	<i>Leptinotarsa decemlineata</i> (Coleoptera: Chrysomelidae)	na	J. Hough-Goldstein (pers. comm.)
Field observation	Walnut	<i>Sinea</i> sp. (Hemiptera: Reduviidae) (E) <i>Zelus renardii</i> (Hemiptera: Reduviidae) (E) coccinellid larvae (V)	<i>Chromaphis juglandicola</i> (Homoptera: Aphididae)	na	Sluss (1967), Nowierski (1979)
Laboratory observations	Animal manure	<i>Parasitus coleoptratorum</i> (Acari: Parasitidae) (E) <i>Macrocheles glaber</i> (Acari: Macrochelidae) (V)	<i>Musca domestica</i> (Diptera: Muscidae)	na	Ignatowicz 1974
Laboratory observations	Apple	<i>Balaustium putmani</i> (Acari: Erythraeidae) (E) <i>Zetzellia mali</i> (Acari: Stigmaeidae) (V) <i>Amblyseius fallacis</i> (Acari: Phytoseiidae) (V)	<i>Panonychus ulmi</i> (Acari: Tetranychidae) <i>Aculus schlechtendali</i> (Acari: Eriophyidae) <i>Tetranychus urticae</i> (Acari: Tetranychidae)	na	Cadogan & Laing 1977

<sup>a</sup> Abbreviations used: na, not addressed; addition of the intraguild predator caused significant decreases in the density of the pest targeted for biological control (–), had no effect (0), or caused significant increases in the density of the target pest (+).

<sup>b</sup> Experiments used only older stages of the herbivore (thrips), which are not eaten by the IGP prey (*A. cucumeris*); these experiments cannot, therefore, be used to test the influence of IGP on the efficacy of biological control.

<sup>c</sup> Hoy et al. (1972) consider their interpretation of the mosquito outbreak as a result of predation by *G. affinis* on notonectid predators to be speculative.

<sup>d</sup> Experiments should be interpreted cautiously because of a confounding effect of insecticide applications.

even if one (or both) preys on the other; again, competition is absent.

In a seminal study, Whitcomb and Bell (1964) spent hundreds of hours observing predaceous arthropods in Arkansas cotton fields. Although the published summary of their observations included “only a few cases involving major predators of the cotton field,” it remains the most detailed record of predator–predator interactions and IGP in an agroecosystem. We have attempted to translate the prose of Whitcomb and Bell (1964) into a graphical trophic web, including only pri-

mary predators of the cotton bollworm *H. zea* and their higher-order predators (Fig. 4); parasitoids have been omitted. We have included only those trophic links that are supported by their direct field observations. Some subjective decisions regarding how taxa should be grouped in the diagram are unavoidable, as a full web using species names would have become intractable. Whitcomb and Bell (1964) reported similar instances of IGP among predators of the cotton fleahopper *Psallus seriatus* (Reuter), tarnished plant bug, *Lygus lineolaris* (Beauvois), cotton leafworm, *Alabama argillacea*

TABLE 1—Continued

Study type	Agricultural ecosystem	IGP species (E = exploiter; V = victim)	Biological control target	Effect on target pest density <sup>a</sup>	Reference
Laboratory observations	Apple	<i>Zetzellia mali</i> (Acari: Stigmaeidae) (E) <i>Amblyseius fallacis</i> (Acari: Phytoseiidae) (V)	<i>Panonychus ulmi</i> (Acari: Tetranychidae) <i>Aculus schlechtendali</i> (Acari: Eriophyidae)	na	Santos 1976
Laboratory experiment	Treeholes	<i>Toxorhynchites rutilus</i> (Diptera: Culicidae) (E) <i>Corethrella appendiculata</i> (Diptera: Culicidae) (V)	<i>Aedes triseriatus</i> (Diptera: Culicidae) <i>Orthopodomyia signifera</i> (Diptera: Culicidae)	na	Lounibos (1985)
Laboratory experiment	Apple	<i>Zetzellia mali</i> (Acari: Stigmaeidae) (E) <i>Typhlodromus caudiglans</i> (Acari: Phytoseiidae) (V)	<i>Panonychus ulmi</i> (Acari: Tetranychidae)	na	Clements & Harmsen 1990
Laboratory experiment	Stored corn	<i>Xylocoris flavipes</i> (Hemiptera: Anthocoridae) (E) Several predatory beetles (E,V)	Several	- or 0	Brower & Press 1992
Laboratory experiment	Greenhouse vegetables	<i>Orius tristicolor</i> (Hemiptera: Anthocoridae) (E) <i>Amblyseius cucumeris</i> (Acari: Phytoseiidae) (V)	<i>Frankliniella occidentalis</i> (Thysanoptera: Thripidae)	na <sup>b</sup>	Gillespie & Quiring 1992
Laboratory experiment	Greenhouse cucumbers	<i>Orius tristicolor</i> (Hemiptera: Anthocoridae) (E) <i>Phytoseiulus persimilis</i> (Acari: Phytoseiidae) (V)	<i>Tetranychus urticae</i> (Acari: Tetranychidae)	na	Cloutier & Johnson 1993
Laboratory experiment and field observation	Greenhouse cucumbers	<i>Chernes cimicoides</i> (Pseudoscorpiones) (E) <i>Phytoseiulus persimilis</i> (Acari: Phytoseiidae) (V)	<i>Tetranychus urticae</i> (Acari: Tetranychidae)	+	Markkula & Tiihtanen 1982 Hokkanen 1982
Laboratory experiment	--	<i>Phytoseiulus persimilis</i> (Acari: Phytoseiidae) (E,V) <i>Amblyseius degenerans</i> (Acari: Phytoseiidae) (E,V)	<i>Tetranychus pacificus</i> (Acari: Tetranychidae)	na	Yao & Chant 1989
Laboratory experiment	Apple	<i>Orius insidiosus</i> (Hemiptera: Anthocoridae) (E) <i>Leptothrips mali</i> (Thysanoptera: Phlaeothripidae) (V)	<i>Panonychus ulmi</i> (Acari: Tetranychidae)	0	Parrella et al. 1980, McCaffrey & Horsburgh 1982
Laboratory experiment and field observation	Grapes	<i>Scolothrips sexmaculatus</i> (Thysanoptera: Thripidae) (E) <i>Metaseiulus occidentalis</i> (Acari: Phytoseiidae) (V)	<i>Tetranychus pacificus</i> (Acari: Tetranychidae)	na	R. Hanna, (pers. comm.)
Laboratory experiment	Cotton	<i>Geocoris uliginosus</i> (Hemiptera: Lygaeidae) (E,V) <i>Oxyopes salicus</i> (Araneae: Oxyopidae) (E,V)	<i>Heliothis</i> spp. (Lepidoptera: Noctuidae)	na	Guillebeau & All 1989
Laboratory experiment	Alfalfa	Nine species of spiders (Araneae) (E) <i>Nabis</i> sp. (Hemiptera: Nabidae) (V) <i>Chrysopa</i> sp. (Neuroptera: Chrysopidae) (V) <i>Hippodamia parenthesis</i> (Coleoptera: Coccinellidae) (V)	Several	na	Howell & Pienkowski 1971
Laboratory experiment	Alfalfa	<i>Geocoris punctipes</i> (Hemiptera: Lygaeidae) (E,V) <i>Nabis alternatus</i> (Hemiptera: Nabidae) (E,V)	Several	na	Atim & Graham 1984

(Hübner), cabbage looper, *Trichoplusia ni* (Hübner), and cotton aphid, *A. gossypii*. They suggested that "Many predators are general feeders; it is not surprising that they destroy a few beneficial insects. Others, however, specialize in feeding on certain predaceous arthropods." They concluded, "The most spectacular foes of predaceous insects, spiders, and mites are other predators" (see also Whitcomb, 1974).

We have tabulated a number of laboratory studies (Table 1), and some comments on their interpretation are in order. Experimental studies have demonstrated that the presence of alternate prey is often critical in modulating the occurrence or severity of IGP (Cadogan and Laing, 1977; McCaffrey and Horsburgh, 1982; Atim and Graham, 1984; Bence, 1988; Polis *et al.*, 1989; Gillespie and Quiring, 1992; Jackson and Kester, 1995). Because laboratory studies are often conducted without any alternate prey or with only a small subset

of naturally occurring alternate prey, predators may be faced with a choice of attacking another predator, attacking a nonpreferred prey, or starving. In addition, an artificial laboratory environment may eliminate important spatial heterogeneity, including potential refuges from predators (Ignatowicz, 1974; Parrella *et al.*, 1980). We therefore join a number of authors (Howell and Pienkowski, 1971; Frazer and Gilbert, 1976; Atim and Graham, 1984; Lounibos, 1985; Yao and Chant, 1989) in noting that results from laboratory studies may not be directly applicable to field conditions.

### Ants

Ants often are dominant predators in arthropod communities. In contrast to the limited attention that has been afforded most predator-predator interactions in biological control research, the role of ants as potential

TABLE 1—Continued

Study type	Agricultural ecosystem	IGP species (E = exploiter; V = victim)	Biological control target	Effect on target pest density <sup>a</sup>	Reference
Laboratory experiment	--	<i>Adalia bipunctata</i> (Coleoptera: Coccinellidae) (E, V) <i>Adalia decempunctata</i> (Coleoptera: Coccinellidae) (E, V) <i>Coccinella septempunctata</i> (Coleoptera: Coccinellidae) (E, V) <i>Coccinella undecimpunctata</i> (Coleoptera: Coccinellidae) (E, V)	Aphids	na	Agarwala & Dixon 1992
Field observation and non-manipulative experiment	Poultry manure	<i>Carcinops pumilio</i> (Erichson) (Coleoptera: Histeridae) (E, V) <i>Macrocheles muscaedomesticae</i> (Scopoli) (Acari: Macrochelidae) (E, V)	<i>Musca domestica</i> (Diptera: Muscidae)	-	Geden et al. 1988, Wilhoit et al. 1991
Field experiment	Soybeans	<i>Nabis roseipennis</i> (Hemiptera: Nabidae) (E, V) <i>Geocoris punctipes</i> (Hemiptera: Lygaeidae) (V) Several predatory insects (E)	Lepidoptera spp. (Noctuidae)	na	McCarty et al. 1980
Field observations and semi-field experiment	Apple	<i>Metaseiulus occidentalis</i> (Acari: Phytoseiidae) (E, V) <i>Typhlodromus pyri</i> (Acari: Phytoseiidae) (E, V) <i>Zeizellia mali</i> (Acari: Stigmaeidae) (E)	<i>Panonychus ulmi</i> (Acari: Tetranychidae) <i>Aculus schlechtendali</i> (Acari: Eriophyidae) <i>Tetranychus urticae</i> (Acari: Tetranychidae)	Mostly - or 0 Rarely +	Croft & MacRae 1992a,b; Croft et al. 1992
Field observation and experiment	Cotton	<i>Zelus renardii</i> (Hemiptera: Reduviidae) (E) <i>Geocoris</i> spp. (Hemiptera: Lygaeidae) (E) <i>Nabis</i> spp. (Hemiptera: Nabidae) (E) <i>Chrysoperla carnea</i> (Neuroptera: Chrysopidae) (V)	<i>Aphis gossypii</i> (Homoptera: Aphididae)	+ or 0	Rosenheim et al. 1993
Field experiment	Rice	<i>Gambusia affinis</i> (fish) (E) Invertebrate predators, including species in the Notonectidae (V)	<i>Culex tarsalis</i> (Diptera: Culicidae) <i>Anopheles freeborni</i> (Diptera: Culicidae)	-, 0, or +	Hoy and Reed 1971; Hoy et al. 1972 <sup>c</sup>
Field experiment	Rice	<i>Gambusia affinis</i> (fish) (E) A complex of predatory insects, including <i>Tropisternus lateralis</i> , <i>Ischnura</i> spp., and <i>Enallagma</i> spp. (V)	<i>Culex tarsalis</i> (Diptera: Culicidae)	-	Bence 1988
Field experiment	Rice	<i>Lepomis cyanellus</i> (fish) (E, V) <i>Gambusia affinis</i> (fish) (E, V) notonectids (V)	<i>Culex tarsalis</i> (Diptera: Culicidae) <i>Anopheles freeborni</i> (Diptera: Culicidae) <i>Psorophora columbiana</i> (Diptera: Culicidae)	-, 0, or +	Davey and Meisch 1977; Blaustein 1988, 1992
Field experiment	Rice	<i>Gambusia affinis</i> (fish) (E) A complex of predatory insects, including notonectids, damselflies, and dragonflies (V)	<i>Culex tarsalis</i> (Diptera: Culicidae)	-, 0, or +	Farley and Younce 1977a, b <sup>d</sup>

disrupters of otherwise effective biological control has been the subject of extensive study (Way, 1963; Buckley, 1987; Way and Khoo, 1992). For this reason, we devote detailed attention to interactions between ants and other natural enemies. We conclude that many (indeed most) examples of ant interference are not examples of IGP, and that the degree to which ants engage in IGP remains unclear.

Although some ants are highly specialized predators or strict herbivores, many are generalized feeders (Hölldobler and Wilson, 1990). Generalists may consume both living and dead arthropods, other carrion, honeydew produced by Homoptera, plant material (seeds, sap), and fungi. Because ants can act both as predators and carrion feeders, observations of foraging ants returning to a nest with arthropods do not constitute proof of a predator-prey relationship; other observations are needed to distinguish predation from scavenging dead arthropods. (The same is true for some

hemipteran predators, which may also feed on dead arthropods [Crocker and Whitcomb, 1980].)

Three types of interactions are common between ants and herbivores: mutualism, commensalism, and predation.

*Mutualism (ants+; herbivore+).* Ants often engage in mutualistic interactions with honeydew producing Homoptera. Ants benefit primarily by receiving honeydew, and secondarily in some cases by consuming the homopteran after it dies (carrion feeding) or through limited direct predation on the homopteran (Way, 1954, 1963). Homopterans derive diverse benefits from ant attendance, including protection from natural enemies. Three kinds of protection are well-documented (Way, 1963): (i) the normal foraging activity of ants may inadvertently disrupt foraging by natural enemies (Way, 1954); (ii) ants may actively defend Homoptera, attacking and driving off natural enemies without killing them; and (iii) ants may attack, capture, and consume

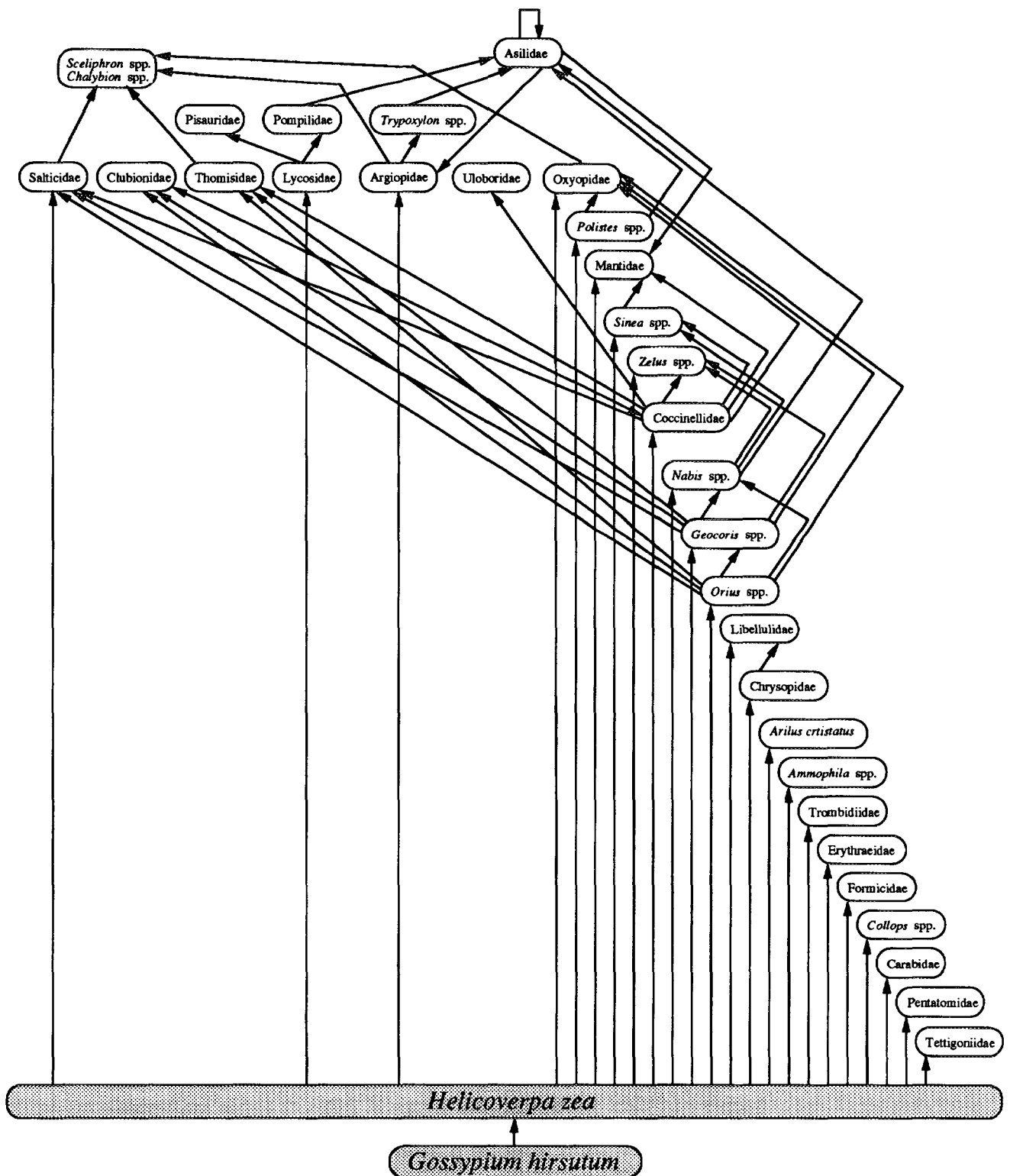


FIG. 4. Trophic web of arthropod predators feeding on the cotton bollworm, *Helicoverpa zea*, on Arkansas cotton; extracted from the direct field observations reported by Whitcomb and Bell (1964). Arrows point from prey to predator. Vertical arrows indicate predation on *H. zea*; all other arrows indicate predator-predator trophic interactions.

natural enemies, including predators (Adlung, 1966; Reimer *et al.*, 1993) and parasitoids (Adlung, 1966; Quezada and DeBach, 1973; Völkl, 1992; Völkl and Mackauer, 1993). That ants can and frequently do interfere with otherwise effective biological control of homopteran pests has been repeatedly demonstrated in manipulative field experiments (Flanders, 1945; Bartlett, 1961; Quezada and DeBach, 1973; Haney *et al.*, 1987; Moreno *et al.*, 1987). Ant interference forms the basis for one of the earliest means of evaluating the efficacy of biological-control agents—i.e., the “biological check method,” in which ants are used experimentally to produce a treatment in which natural enemies are excluded (DeBach *et al.*, 1951).

Frazer and van den Bosch (1973) documented what may be a fourth type of protection provided by mutualistic ants. The Argentine ant *Linepithema humile* (Mayr) preys upon walnut aphids, *C. juglandicola*, that are alive and those that have been killed and transformed into mummies by the parasitoid *T. pallidus*. Dissections revealed that all living aphids captured by ants were parasitized, whereas only 45% of the living aphids on the same trees were parasitized. Frazer and van den Bosch (1973) suggested that selective predation by ants on parasitized aphids may threaten the efficacy of biological control by *T. pallidus*. However, this has not been realized, and the walnut aphid remains under effective biological control.

Regardless of the nature of the interaction between ants and other predators, ant–homopteran interactions are best viewed as mutualisms (rather than IGP) because the ants rarely if ever prey upon the homopterans and generally have a net positive influence on homopteran densities.

**Commensalism (ants 0; herbivore+).** Commensalism occurs when two conditions are met: (i) ants co-occur with nonhoneydew producing herbivores without preying on them, and (ii) ants inadvertently protect the herbivores from their natural enemies. This has been demonstrated in field experiments with the Argentine ant foraging on citrus trees harboring armored scales (Flanders, 1945; DeBach *et al.*, 1951; Moreno *et al.*, 1987; Murdoch *et al.*, 1995) and an herbivorous mite (Haney *et al.*, 1987). Once again, IGP cannot occur under commensalistic relationships because the ants are not preying upon the herbivore.

**Predation (ants+; herbivore–).** It is as predators, rather than as mutualists or commensals, that ants have the potential to engage in IGP. Ants are important predators of herbivorous arthropods in many agroecosystems (reviewed by Way and Khoo, 1992). Although it seems likely that ants must frequently prey upon both an herbivore and the herbivore's natural enemies, we know of no published investigations of IGP by ants in agroecosystems; IGP between different species of

ants in natural ecosystems is reviewed by Polis *et al.* (1989). Risch and Carroll (1982) demonstrated that the fire ant *Solenopsis geminata* (F.) suppressed a group of herbivores in a corn/squash polyculture, apparently via direct predation. Ants also suppressed predator abundance, but whether via competition, nonlethal interference, or predation is unclear.

Ants clearly play a number of ecological roles in agroecosystems. As dominant generalist predators, ants are likely to engage in IGP. Because the impact of ants on arthropod communities is often strong, ants may provide excellent systems for future work on the significance and dynamics of IGP.

#### *Influence of Intraguild Predation on the Efficacy of Biological Control: Empirical Evidence*

The question of greatest significance to the applied ecologist may be: Does IGP among arthropod predators influence the suppression of pest species? Unfortunately, few studies have addressed this question under field conditions (Table 1). One reason for the paucity of empirical work may be the technical challenges associated with conducting the needed experiments. Formidable difficulties may be anticipated in attempts to manipulate different components of a predator guild independently under field conditions, especially while maintaining realistic spatial and temporal scales for the experiment (see Wise, 1993). Here we review three experimental studies conducted with arthropod predators, noting in each case the limitations inherent in the experimental design.

Geden *et al.* (1988) reported a nonmanipulative evaluation of predation on house fly larvae in poultry manure by three co-occurring predators; two of the predators, the beetle *Carcinops pumilio* (Erichson) and the mite *Macrocheles muscaedomesticae* (Scopoli), engaged in mutual IGP, while the third predator, the fly *Ophyra aenescens* (Weidemann), was not described as being engaged in IGP. The study employed small experimental units (250 cm<sup>3</sup> of manure in plastic dishes imbedded in manure rows in poultry houses) that were experimentally stocked with a fixed density of prey (fly eggs) and subjected to natural predation for 3 days. The influence of naturally occurring variation in the abundance of each of the three predators (quantified at the end of the experiment) on overall predation on fly eggs was assessed with multiple regression, employing a model for independent and additive action of each predator. An analysis supported the additive action model, although significance levels for *Macrocheles* and *Ophyra* were not reported. A possible negative effect of IGP might, however, have gone undetected in this experiment for two reasons. First, IGP involves *Macrocheles* feeding on *Carcinops* eggs (a nonpredatory stage of the beetle) and *Carcinops* feeding on *Mac-*

*rocheles* in its early life stages, rather than on its deutonymphs and adults, which are responsible for most of the predation (Wilhoit *et al.*, 1991). Thus, IGP might have minimal effects on levels of total predation on house fly larvae observed in the short term (e.g., the 3-day experiment), even if it had substantial longer-term effects on reproductive recruitment by either *Macrocheles* or *Carcinops*. Second, predator counts were made only at the close of the experiment, so that the influence of IGP on predator mortality rates could not be assessed. We should recognize that the primary intent of the experiment by Geden *et al.* (1988) was not to evaluate IGP; thus, we discuss this study not to criticize it, but rather to learn from it.

Croft and MacRae (1992a,b) and Croft *et al.* (1992) reported a manipulative experiment assessing predation by different combinations of three predatory mites on three species of phytophagous mites on apple. The experiment employed potted apple trees placed in the field and monitored for two years. Trees were treated with insecticides regularly throughout the experiment to eliminate insect populations. Although some insecticides are used in commercial management practices, the experimental results should be interpreted against the backdrop of a strong simplification of the arthropod community. Predator treatments included releases of *Metaseiulus occidentalis* (Nesbitt) and *Typhlodromus pyri* Scheuten alone and in combination; in addition, each of the treatments was evaluated with a third predator, *Zetzellia mali* (Ewing), present or absent as a result of acaricide applications. In both years of the study, mixed releases of *Metaseiulus* and *Typhlodromus* resulted in as good or better suppression of phytophagous mites than releases of either predator singly. When only single species releases were made, the presence of *Zetzellia* generally contributed to biological control, but in one instance (control of the European red mite *Panonychus ulmi* (Koch) in *Metaseiulus* release plots) *Zetzellia* caused poorer control, apparently reflecting consumption of *Metaseiulus* eggs by *Zetzellia*.

Rosenheim *et al.* (1993) conducted field experiments evaluating the separate and joint effects of lacewings and a complex of hemipteran predators (*Geocoris* spp., *Nabis* spp., and *Zelus renardii* [Kolenati]) on cotton aphid populations. Each of the hemipteran predators preyed on lacewing larvae under natural conditions in the field. Experimental units were small (individual plants or parts of plants enclosed in mesh sleeves), and the experiments were of short duration (3–11 days). Experiments demonstrated that lacewing survival decreased by  $\geq 90\%$  in the presence of either *Nabis* spp. alone, *Z. renardii* alone, or a combination of *Nabis* spp., *Z. renardii*, and *Geocoris* spp. The effects of this strong IGP on the efficacy of aphid biological control were variable, apparently reflecting differences in aphid reproduction associated with aphid polyphenism (Wilhoit

and Rosenheim, 1993; Rosenheim *et al.*, 1994). When smaller, less fecund aphids were present, lacewings alone were capable of effective control, but significant negative interactions occurred when either *Nabis* or *Zelus* predators were present with lacewings, and biological control of aphids was disrupted. Thus, IGP was responsible for increases of aphid populations under some conditions. When larger, more fecund aphids were present, neither lacewings alone nor in combination with hemipteran predators effectively suppressed aphid population growth. These short experiments may have underestimated the negative impact of IGP on lacewings because effects on lacewing reproductive recruitment were not measured.

Because IGP is a hybrid of competition and predation, it may be difficult to quantify the relative contributions of competition and predation to negative interactions observed experimentally in the field. However, when disruption of biological control is observed (i.e., herbivore prey abundance is enhanced when IGP occurs), negative effects of IGP can often be ascribed primarily to the effects of predation, as long as the densities of alternate prey are also quantified (e.g., Rosenheim *et al.*, 1993).

#### *Intraguild Predation among Vertebrate and Arthropod Predators*

Some of the clearest examples of higher-order predators disrupting the efficacy of lower-order predators have come from communities of fish and invertebrates in natural freshwater ecosystems (Power, 1990; Carpenter and Kitchell, 1993). The same is true for freshwater agroecosystems, where studies of fish and invertebrate predators of mosquitoes in flooded rice fields have repeatedly demonstrated the potential for IGP to disrupt biological control (Hoy *et al.*, 1972; Farley and Younce, 1977a,b; Blaustein, 1988, 1992). The interactions underlying these disruptions have been elucidated in a series of observational and manipulative field experiments (Hoy *et al.*, 1972; Farley and Younce, 1977a,b; Bence, 1982, 1988; Blaustein, 1988, 1992).

The trophic web associated with rice field mosquitoes is complex. Mosquitoes are eaten by fish, including two species commonly released by mosquito abatement workers: the mosquitofish *Gambusia affinis* Baird and Girard and the green sunfish, *Lepomis cyanellus* Rafinesque. Mosquitoes also are eaten by many invertebrate predators, especially notonectids, but including dragonflies and damselflies (Odonata), predatory beetle larvae (*Tropisternus*), belostomatids, microturbellarian flatworms, and others. Mosquitoes often are a small component of the total diet for these diverse predators; important alternative prey include cladocerans, copepods, ostracods, and chironomids.

IGP is widespread within the community of mosquito



predators. First, the mosquitofish and the green sunfish engage in mutual IGP, with larger stages of each species consuming smaller stages of the other (Blaustein, 1988). Second, predatory fishes often suppress populations of invertebrate predators (Farley and Younce, 1977a; Bence, 1982, 1988; Blaustein, 1988, 1992). Whether direct predation by fish on mosquitoes can compensate for the decreased predation by invertebrates depends on several factors. The first of these is the density of the fish; mosquito outbreaks may occur transiently in response to decreased predation by invertebrates until *Gambusia* or *Lepomis* populations increase to densities where they suppress mosquito populations (Hoy *et al.*, 1972; Farley and Younce, 1977a; Blaustein, 1988). The second factor is the availability of alternate prey; when blooms of microcrustaceans occur, predatory fish may decrease their consumption of less-preferred mosquito prey (Farley and Younce, 1977a; Bence, 1988; Blaustein, 1988, 1992). Third, the microhabitats used by prey and predators may be important; while some mosquito larvae rest at the water surface but feed at the bottom, others, such as *Anopheles freeborni* Aitken, both rest and feed at the water surface, where green sunfish do not forage (Blaustein, 1988, 1992). Thus, outbreaks of top-feeding mosquitoes may be more likely following releases of bottom-feeding predatory fish. Finally, the impact of fish may vary as the fish grow; immature green sunfish appear to suppress mosquitoes more than mature fish, and may therefore be less likely to disrupt biological control exerted by invertebrates or *Gambusia* (Blaustein, 1988).

We have thus far discussed the possibility that releases of predatory fish may disrupt biological control at a local scale, i.e., within the body of water to which the fish are introduced. A more insidious negative effect acting at a regional scale has been suggested by Bence (1982): fish predation may decrease the abundance of predatory insects and thereby decrease the pool of insect migrants available to colonize new temporary bodies of water. No experimentation has yet evaluated this hypothesis.

Although interactions of mosquito predators have provided perhaps the best documented cases of IGP leading to the disruption of biological control, addition of IG predators can also lead to improved mosquito suppression. For example, in one of the experiments reported by Blaustein (1988), the addition of either *Gambusia* or *Lepomis* alone led to a transient increase in mosquitoes before control was exerted, but the combination of these two IG predators produced consistently excellent control. Enhanced mosquito control was obtained even though (i) each fish suppressed the population of the other, (ii) the total density of fishes was not greater than when either fish was present alone, and (iii) the densities of several insect predators were driven to low levels.

### *Pathogen-Natural Enemy Interactions*

Interactions between microorganisms (i.e., pathogens) and arthropod natural enemies have been categorized in several ways (Tamashiro, 1968; Vinson, 1990). Ulyett and Schonken (1940) and Steinhaus (1954) described two principal ways in which pathogens adversely affect natural enemies: (1) they may affect the natural enemy complex indirectly by reducing the host population to a point where predators or parasitoids are not able to find sufficient hosts on which to breed or feed and (2) they may affect the natural enemy complex directly by infecting both the host and natural enemy, or less directly by depleting the host nutritionally so that the natural enemy dies from starvation. In a recent publication, Brooks (1993) used two major categories for interactions between pathogens and arthropod natural enemies. The first category included deleterious aspects of host-parasitoid-pathogen interactions, with six subheadings: (1) premature death of the host, (2) parasitoid death due to pathogen-produced toxins, (3) host ovipositionally unattractive, (4) hosts altered nutritionally or physiologically, (5) direct infection of parasitoids, and (6) preclusion of parasitoid persistence. The second category included beneficial aspects of host-parasitoid-pathogen interactions with two subheadings: (1) the influence of parasitism on host susceptibility and (2) the role of parasitoids as mechanical or biological vectors of pathogens.

No matter which classification scheme is used, clearly some pathogens infect arthropod natural enemies. Our interest is focused on IGP, where pathogens infect both an arthropod that is the target of biological control (usually an herbivore) and its associated predators or parasitoids. There have been several general reviews on the host-arthropod natural enemy-pathogen interactions, including infection of the natural enemies by pathogens (Flexner *et al.*, 1986; Vinson, 1990; Brooks, 1993). More specific reviews of pathogen-arthropod natural enemy interactions have been by Harper (1986) and Gröner (1990) on viruses, Akhurst (1990) on nematodes, Goettel *et al.* (1990) on fungi, and Melin and Cozzi (1990) on bacteria.

When a pathogen infects an arthropod natural enemy, there may be a negative effect on the natural enemy. However, not all interactions among microorganisms, the arthropod hosts, or the arthropod natural enemies of the hosts result in a negative effect. For example, polydnviruses are mutualists associated with many species of braconid or ichneumonid parasitoids (see Stoltz, 1993). Polydnviruses replicate in the epithelial cells of a parasitoid's ovaries. Although polydnviruses do not replicate in the hosts attacked by parasitoids, limited transcription may occur from certain viral circular DNAs. Polydnviruses serve as im-

munosuppressants of the host, such that the host's hemocytes do not encapsulate parasitoid eggs.

IGP has been demonstrated with all pathogen groups. Many studies have involved the safety and compatibility of a specific insect pathogen of a target pest species with the pest's natural enemies (see Laird *et al.*, 1990). Although a few studies have involved naturally occurring host–arthropod natural enemy–pathogen systems, most have been performed primarily under laboratory conditions (Table 2). For more detailed accounts of these interactions, the reader is referred to the general and specific reviews cited earlier.

*Protozoa, fungi, and nematodes.* Reports of IGP are most common with protozoans (especially microsporidia), fungi, and nematodes. Three general scenarios of infection of arthropod natural enemies by these pathogens can be recognized. In the first scenario, IGP occurs in parasitoids where the pathogens cause chronic infections in their hosts. A few microsporidia seem to have evolved an intimate association with both hymenopteran parasitoids and their hosts, where they cause chronic infections. Immature parasitoids are exposed to the protozoans and are utilized as an additional resource. *Nosema pyrausta* (Paillot), *Nosema mesnili* (Paillot), *Nosema heliothidis* Lutz and Splendore, and *Nosema bordati* Goudegnon infect their lepidopteran hosts as well as the associated hymenopteran parasitoids (Table 2). In other cases, microsporidia are specific to lepidopteran hosts and do not infect parasitoids, but sublethal and lethal effects of the protozoans on their hosts or on the associated parasitoids have been observed (Grosch, 1949; Thomson, 1958; Brooks, 1993).

In the second scenario, pathogens may infect arthropods that are usually considered “nonhosts.” Thus, *Nosema algerae* Vavra and Undeen infects a number of mosquito species, which are considered the typical hosts, as well as an atypical host, the hemipteran mosquito predator, *Notonecta undulata* Say. Eight other predatory species, including a dragonfly, two coleopterans, two hemipterans, a megalopteran, a crayfish, and a mosquito fish are not infected (Van Essen and Anthony, 1976). *N. algerae* also infects lepidopteran larvae and crayfish, but only when the hosts' defenses are breached by injecting spores directly into their hemocoel (Undeen and Maddox, 1973).

In the third scenario, IGP occurs because the pathogens have broad host ranges. Entomopathogenic nematodes in the families Heterorhabditidae and Steinernematidae and fungi such as *Beauveria bassiana* (Bals.) Vuill. and *Metarhizium anisopliae* (Metsch.) Sorokin are generalists and will infect a wide array of insects, including predators and parasitoids. Müller-Kögler (1965) and Goettel *et al.* (1990) reviewed the host range and specificity of fungal biological-control agents. Laumond *et al.* (1979), Akhurst (1990), and

Brooks (1993) summarized much of the information on IGP by entomopathogenic and entomogenous nematodes (see also Table 2).

Most of the studies in scenarios 2 and 3 have been done in the laboratory, where ecological and behavioral barriers were removed to assure contact between the pathogen and natural enemy; thus, additional work is needed to assess the importance of IGP in the field. For example, Georgis *et al.* (1991) demonstrated that the application of the entomopathogenic nematode *Steinernema carpocapsae* (Weiser) against several soil and aquatic pests failed to have an impact on the natural enemy complex. Similarly, Baltensweiler and Cerutti (1986) showed that the aerial application of fungal blastospores of *Beauveria brongniartii* (Sacc.) Petch against *Melolontha melolontha* L. along the edge of the forest resulted in only 1.1% infection of 10,165 insect and spider individuals sampled, and they concluded that *B. brongniartii* does not endanger the arthropod fauna.

*Bacteria.* IGP by bacteria appears to be limited even though some bacteria are considered generalists. All reports of infection of natural enemies and hosts with bacteria have been from laboratory studies, where insects tend to be stressed (Bell *et al.*, 1974). We are unable to infer definitively the presence of IGP under field conditions. Even though several subspecies of *Bacillus thuringiensis* Berliner are widely applied against lepidopteran, coleopteran, and dipteran pests, no direct infection of natural enemies has been reported under field conditions (Krieg and Langenbruch, 1981). In one instance, Thompson *et al.* (1977) reported that larval parasitoids in a host can be infected with *B. thuringiensis*, but Niwa *et al.* (1987) could not ascertain whether the death of the parasitoids was due to early death of the host or direct infection by the bacterium. In the laboratory, *B. thuringiensis* fed to adult parasitoids can cause mortality (Dunbar and Johnson, 1975; Hamed, 1979; Mück *et al.*, 1981; Thoms and Watson, 1986; Salama *et al.*, 1991). Among the many new isolates of *B. thuringiensis* that are being discovered, some may have activity against natural enemies. If such a situation arises, the impact on natural enemies, especially under field conditions, will need to be examined.

*Viruses.* Several studies on the effect of viral pathogens on natural enemies have indicated that IGP is not common (Vinson, 1990; Brooks, 1993). IGP between an iridescent virus and a mermithid parasite of isopods has been demonstrated (Poinar *et al.*, 1980; Hess and Poinar, 1985). One recent study suggested that IGP may occur among viruses, parasitoids, and their hosts. Hamm *et al.* (1993) found that the hymenopteran parasitoid *Microplitis croceipes* (Cresson) is infected and can be killed by a nonoccluded baculovirus and a picorna-like virus. IGP does not occur with the nonoc-

TABLE 2

Laboratory, Greenhouse, and Field Studies on Intraguild Infection Involving Natural Enemies and Their Hosts: A Selective Review<sup>a</sup>

Study Type	Crop <sup>b</sup>	Natural Enemy		Arthropod Host	Effect on Arthropod Natural Enemy and/or Biological Control	References
		Arthropod <sup>c</sup>	Pathogen			
VIRUSES						
Laboratory	NA	<i>Thaumamermis cosgrovei</i> <sup>d</sup>	iridovirus	<i>Armadillidium vulgare</i> <i>Porcellio scaber</i>	Not reported	Poinar <i>et al.</i> 1980 Hess and Poinar 1985
BACTERIA						
Laboratory	NA	<i>Exeristes comstockii</i> (P)	<i>Serratia marcescens</i>	<i>Galleria mellonella</i>	Maximum 25% mortality	Bracken and Bucher 1967
Laboratory	NA	<i>Microplitis croceipes</i> (P)	<i>S. marcescens</i>	<i>Helicoverpa zea</i>	Adult mortality 79% in 7 days	Bell <i>et al.</i> 1974
FUNGI						
Laboratory	NA	<i>Encarsia formosa</i> (P)	<i>Verticillium lecanii</i>	<i>Trialeurodes vaporariorum</i>	Adult mortality in 6-8 days	Ekbohm 1979
Laboratory	NA	<i>Nabis alternatus</i> (Pr)	<i>V. lecanii</i>	Aphids	82% mortality	Harper and Huang 1986
Laboratory	NA	<i>Coleomegilla maculata</i> (Pr) <i>Eriopsis connexa</i> (Pr)	<i>Beauveria bassiana</i> <i>B. bassiana</i>	<i>Brevicornye brassicae</i> <i>B. brassicae</i>	10-70% mortality 20-100% mortality	Magalhaes <i>et al.</i> 1988
Laboratory	Aquatic	<i>Toxorhynchites rutilus</i> (Pr)	<i>Coelomomyces macleayae</i> <sup>e</sup>	Mosquito larvae	One larval specimen infected	Nolan <i>et al.</i> 1973
Laboratory	Aquatic	<i>Toxorhynchites amboinensis</i> (Pr)	<i>Metarhizium anisopliae</i>	<i>Aedes albopictus</i>	50-100% mortality	Ravallec <i>et al.</i> 1986
Laboratory	NA	<i>Hippodamia convergens</i> (Pr)	<i>B. bassiana</i> <i>M. anisopliae</i> <i>Paecilomyces fumosoroseus</i>	Aphids Generalist Whitefly, mealybugs, thrips	>95% mortality >95% mortality <56% mortality	James and Lighthart 1994
PROTOZOA						
Laboratory	NA	<i>Trichogramma nubilalis</i> (P)	<i>Nosema pyrausta</i>	<i>Ostrinia nubilalis</i>	Reduced adult emergence and fecundity	Sajap and Lewis 1988

<sup>a</sup> More detailed listings and/or examples can be found in Flexner *et al.* (1986), Vinson (1990), and Brooks (1993). In addition, more examples are found for bacteria in Melin and Cozzi (1990), for fungi in Müller-Kügler (1965) and Goettel *et al.* (1990) and for nematodes in Laumond *et al.* (1979) and Akhurst (1990).

<sup>b</sup> NA, not applicable for most laboratory studies.

<sup>c</sup> Abbreviations in parentheses after the scientific names of arthropod natural enemies refer to (P) for parasitoids and (Pr) for predators.

<sup>d</sup> A mermithid nematode.

<sup>e</sup> *Coelomomyces* requires an obligate alternate copepod host (see Whisler *et al.*, 1975).

<sup>f</sup> A hyperparasitoid with microsporidium that infects both the primary parasitoid and the hyperparasitoid.

cluded baculovirus because the virus does not infect the noctuid host, but the status of the picorna-like virus as a pathogen of the noctuid host needs to be clarified.

#### Field Studies of IGP by Pathogens

Field studies of IGP by pathogens have focused primarily on microsporidia. Tanada (1955) showed that *Nosema mesnili* infected 59% of the imported cabbage-worm *A. rapae* L. with 22% of all cabbageworm larvae containing both the microsporidium and the gregarious

braconid *Cotesia glomerata* (Cresson). The degree of *Nosema* infection in *A. rapae* larvae was categorized as light, moderate, or heavy, and the fate of the parasitoids was monitored. In heavily infected larvae ( $n = 2$ ), only 14% of the parasitoids that successfully formed cocoons ( $n = 42$ ) emerged as adults, and all pupae and adults were infected with the microsporidium. In moderately ( $n = 1$ ) and lightly infected larvae ( $n = 1$ ), 100% of the parasitoids ( $n = 19$ ) emerged as adults; 33% ( $n = 9$ ) of parasitoid adults emerging from the moderately infected cabbageworm larva and 0% of parasitoid

TABLE 2—Continued

Study Type	Crop <sup>b</sup>	Natural Enemy		Arthropod Host	Effect on Arthropod Natural Enemy and/or Biological Control	References
		Arthropod <sup>c</sup>	Pathogen			
Laboratory	NA	<i>Trichogramma evanescens</i> (P)	<i>N. pyrausta</i>	<i>O. nubilalis</i>	Reduced fecundity by half compared with uninfected females.	Huger 1984
Laboratory	Com	<i>Chelonus annulipes</i> (P)	<i>N. pyrausta</i>	<i>O. nubilalis</i>	High parasitoid mortality Affected parasitoid release program	York 1961
		<i>Macrocentrus gifuensis</i> (= <i>grandii</i> ) (P)	<i>N. pyrausta</i>	<i>O. nubilalis</i>	Not reported	York 1961
Laboratory and field	Com	<i>M. grandii</i> (P)	<i>N. pyrausta</i>	<i>O. nubilalis</i>	Affected pupal development. 54% infection in field populations and reduced adult longevity	Andreadis 1980
Laboratory and field	Corn	<i>M. grandii</i> (P)	<i>N. pyrausta</i>	<i>O. nubilalis</i>	Inverse relationship between infection and prevalence of parasitism of <i>Ostrinia</i> by <i>M. grandii</i>	Andreadis 1982
Laboratory and field	Com	<i>M. grandii</i> (P)	<i>N. pyrausta</i>	<i>O. nubilalis</i>	Reduced fecundity and longevity. Inverse relationship between infection and prevalence of parasitism of <i>Ostrinia</i> by <i>M. grandii</i>	Siegel <i>et al.</i> 1986
Laboratory	NA	<i>M. grandii</i> (P)	<i>N. pyrausta</i> <i>Nosema</i> sp. <i>Vairimorpha necatrix</i>	<i>O. nubilalis</i> <i>O. nubilalis</i> <i>O. nubilalis</i>	Decreased adult eclosion Decreased adult eclosion Decreased adult eclosion. Infection limited to alimentary canal	Cossentine and Lewis 1987
Laboratory	NA	<i>Apanteles flavipes</i>	<i>N. bordati</i>	<i>Chilo partellus</i>	Larval mortality. Reduced fecundity and longevity. Transovarially transmitted to progeny.	Bordat <i>et al.</i> 1994
Laboratory	NA	<i>Camptoplex sonorensis</i> (P)	<i>Nosema heliothidis</i>	<i>H. zea</i>	Some mortality of prepupae, pupae, and adults	Brooks and Cranford 1972
Field	Com	<i>C. sonorensis</i> (P)	<i>N. heliothidis</i>	<i>Helicoverpa</i> spp. <i>Heliothis</i> spp.	Low prevalence of disease	Brooks and Cranford 1978
Laboratory	NA	<i>Dahlbominus fuscipennis</i> (P)	<i>Thelophora pristiphora</i>	<i>Neodiprion swainei</i> <i>N. lecontei</i> <i>N. pratti banksianae</i> <i>Pristiphora erichsonii</i>	Infected parasitoids emerged as adults earlier than noninfected ones	Smirnoff 1971

adults from lightly infected larvae were infected. Tanada (1955) concluded that although some parasitoids are killed by the microsporidium, their deaths may not significantly reduce parasitoid populations. The detrimental effects of parasitoid population reduction may not offset the beneficial effects of pest population reduction by the microsporidium.

The European corn borer (ECB) *Ostrinia nubilalis* (Hübner), first discovered in the United States in Massachusetts in 1917, is a major pest of corn. It has two generations per year. The microsporidium *Nosema pyrausta*, which can be transmitted vertically and horizontally, is the major biological mortality factor in ECB populations. Survival of infected larvae is reduced, and surviving infected adults have reduced fecundity and longevity (Zimmack and Brindley, 1957; Kramer, 1959;

Windels *et al.*, 1976). *N. pyrausta* acts in a delayed density-dependent manner, where high infection levels severely reduce ECB populations the following year (Hill and Gary, 1979; Andreadis, 1984; Siegel *et al.*, 1986).

A number of parasitoids have been introduced for biological control of ECB, but only the interaction between the polyembryonic braconid parasitoid *Macrocentrus grandii* Goidanich and *N. pyrausta* has been studied in depth (Andreadis, 1982; Siegel *et al.*, 1986). *M. grandii* will oviposit in all five ECB instars, although wasps tend to parasitize earlier instars. On the average, 6 to 10 larvae develop from each egg, and 25–26 parasitoids will emerge from a single host (Siegel *et al.*, 1986).

Andreadis (1982) collected overwintering larvae from

TABLE 2—Continued

Study Type	Crop <sup>b</sup>	Natural Enemy		Arthropod Host	Effect on Arthropod Natural Enemy and/or Biological Control	References
		Arthropod <sup>c</sup>	Pathogen			
Laboratory	NA	<i>Cotesia glomerata</i> (P)	<i>Nosema polyvora</i>	<i>Pieris brassicae</i>	All tissues infected	Blunck 1958
		<i>C. glomerata</i>	<i>N. cf legeri</i>	<i>P. brassicae</i>	Fat tissues and hemocytes infected	
		<i>C. glomerata</i>	<i>N. mesnili</i>	<i>P. brassicae</i>	All tissues infected	
Laboratory	Field collected herbi-vores	<i>C. glomerata</i>	<i>N. mesnili</i>	<i>P. brassicae</i>	Larval and adult mortality	Hostounsky 1970
		<i>Hyposoter ebeninus</i> (P)		<i>P. brassicae</i>	Salivary glands infected	
		<i>Pimpla instigator</i> (P)		<i>P. brassicae</i>	Poor adult emergence and death	
Laboratory	NA	<i>C. glomerata</i>	<i>N. mesnili</i>	<i>P. brassicae</i>	Tissues infected	Larsson 1979
Field	Cabbage	<i>C. glomerata</i> (P)	<i>N. mesnili</i>	<i>P. rapae</i>	Parasitoids may or may not be infected from infected hosts. Parasitoid and <i>Nosema</i> may be compatible with each other	Tanada 1955
Laboratory	Cotton	<i>Bracon mellitor</i> (P)	<i>Glugea gasti</i>	<i>Anthonomus grandis</i>	Larval mortality Infection uncertain	Bell and McGovern 1975
Laboratory	Hyper-parasitoid	<i>Catolaccus aeneoviridis</i> (P) <sup>f</sup>	<i>Nosema campoletidis</i>	<i>Campoletis sonorensis</i>	No deleterious effects	McNeil and Brooks 1974
Laboratory	NA	<i>Macrocentrus ancylovorus</i> (P)	<i>Nosema destructor</i>	<i>Gnorimoscema operculella</i>	Affected mass production of parasitoid	Allen and Brunson 1945; Allen 1954
Laboratory	Aquatic	<i>Notonecta undulata</i> (Pr)	<i>Nosema algerae</i>	Mosquito larvae	48% infected	Van Essen and Anthony 1976
Laboratory	Beans	<i>Pediobius foveolatus</i> (P)	<i>Nosema epilachnae</i>	<i>Epilachna varivestita</i>	High mortality from heavily infected hosts. Prevalence of infection and mortality of parasitoid related to host infection. Adult longevity affected.	Own and Brooks 1986
		<i>P. foveolatus</i> (P)	<i>N. varivestis</i>	<i>E. varivestita</i>	Same as above. <i>Nosema</i> was transovarially transmitted by parasitoid.	
Laboratory	NA	<i>Microplitis croceipes</i> (P) <i>Cotesia marginiventris</i> (P)	<i>Vairimorpha</i> sp.	<i>Helicoverpa zea</i>	Low level of infection from infected host larvae with both parasitoids	Hamm <i>et al.</i> 1983

several sites over a 3-year period and assessed the prevalence of parasitism by *M. grandii* by holding ECB larvae individually. Larvae that did not produce parasitoids were held until their death and then examined for larval parasitoids or held until adult moths emerged. Unparasitized ECB larvae were examined microscopically for *N. pyrausta* by examining their Malpighian tubules, which are primary sites of infection. Because *M. grandii* consumes the entire ECB larva, *N. pyrausta* infection was determined by microscopic examination of parasitoid tissues. Andreadis (1980) previously had demonstrated that if *M. grandii* developed in a microsporidian infected host, all parasitoids from that host were infected. The data showed a significant inverse correlation between European corn borer larval infection with *N. pyrausta* and parasitism by *M. grandii* in field populations where infections by the microsporidium were relatively high (45%). This

relationship occurred both spatially and temporally (across years), suggesting that the microsporidium adversely affected *M. grandii*.

Siegel *et al.* (1986) collected first and second generation ECB larvae over a 2-year period and reared them on an artificial diet until larvae died or developed to adults, or until parasitoids emerged. All ECB larvae and a sample of parasitoid larvae from each host were examined microscopically for microsporidian infection. Adult parasitoids were allowed to emerge, provided with food, and periodically provided with hosts to parasitize. After the adult parasitoids died, they were checked for *N. pyrausta* infection.

Data from the first and second generation ECB larvae showed an inverse relationship between infection with *N. pyrausta* and parasitism by *M. grandii* (Siegel *et al.*, 1986). Microsporidian infection was 14 and 19% in the first ECB larval generation and 51 and 73%

TABLE 2—Continued

Study Type	Crop <sup>b</sup>	Natural Enemy		Arthropod Host	Effect on Arthropod Natural Enemy and/or Biological Control	References
		Arthropod <sup>c</sup>	Pathogen			
Laboratory	NA	<i>Bracon mellitor</i> (P)	<i>Mattesia grandis</i>	<i>A. grandis</i>	Reduced fecundity	McLaughlin and Adams 1966
Laboratory	Pinus	<i>Rhyssa himalayensis</i> (P) <i>R. persuasoria</i> (P) <i>R. amoena</i> (P)	<i>Deladenus</i> sp.	<i>Sirex</i> spp	NEMATODE <sup>c</sup> Reduced fecundity and longevity	Hocking 1967
Laboratory	NA	<i>Coeloides dendroctoni</i> (P)	<i>Sphaerularia hastata</i>	<i>Dendroctonus monticolae</i> <i>D. pseudotsugae</i>	Pupae in cocoons infected	Khan 1957
Laboratory	NA	<i>Glyptapanteles militaris</i> (P)	<i>Steinernema carpocapsae</i>	<i>Pseudaletia unipuncta</i>	Prepupae and adults infected and killed Adults infected	Kaya 1978a
Laboratory	NA	<i>G. militaris</i> (P)	<i>S. carpocapsae</i> <i>Heterorhabditis bacteriophora</i>	<i>P. unipuncta</i>	Prepupae infected and killed	Kaya 1978b
Laboratory	Alfalfa	<i>Hyposoter exiguae</i> (P)	<i>S. carpocapsae</i>	<i>P. unipuncta</i>	Prepupae infected and killed	Kaya and Hotchkin 1981
Laboratory	NA	<i>Thereva handlirschi</i> (Pr) <i>Rhagio</i> spp.(Pr)	<i>S. kraussei</i>	<i>Cephalcia abietis</i>	Larval predators infected and killed	Mráček and Spitzer 1983
Laboratory	NA	<i>Coccinella septempunctata</i> (Pr)	<i>Steinernema</i> sp.	Aphids	Adult predator infected and killed	Mráček and Ruzicka 1990
Laboratory	NA	<i>Garypus californicus</i> (Pr)	<i>S. carpocapsae</i> <i>H. bacteriophora</i>	Many arthropods	Predator infected and killed	Poinar and Thomas 1985
Laboratory	NA	<i>Pholcus phalangiodes</i> (Pr) <i>Latrodectus mactans</i> (Pr) <i>Pirata</i> sp. (Pr) <i>Phalangium</i> sp. (Pr)	<i>S. carpocapsae</i> <i>H. bacteriophora</i>	Many arthropods	Predators infected and killed	Poinar and Thomas 1985

in the second generation in the first and second year, respectively. In contrast, parasitism by *M. grandis* was 16 and 23% in the first ECB generation and 6 and 4% in the second generation in the first and second year, respectively. Microsporidian infection of the larval parasitoids was 14 and 41% in the first generation and 46 and 75% in the second generation in the first and second year, respectively. Microsporidian-infected parasitoid females lived for an average of 10 days compared with an average of 17 days for uninfected females.

Hill *et al.* (1978) speculated that the tachinid *Lydella thompsoni* Herting, another parasitoid of ECB larvae, disappeared from the field sites in Nebraska in part because of *N. pyrausta*. Although York (1961) suggested that the tachinid was susceptible to the microsporidium, Cossentine and Lewis (1988) showed that this was not the case and concluded that the microsporidium was not instrumental in the disappearance of the parasitoid.

In summary, observational field studies suggest that

pathogens may adversely affect some parasitoid populations. Controlled, manipulative studies are needed to assess the influence of interactions between pathogens and parasitoids on the efficacy of pest suppression.

#### INFLUENCE OF INTRAGUILD PREDATION ON THE EFFICACY OF BIOLOGICAL CONTROL: EMPIRICALLY BASED MODELS

Analysis of the dynamic significance of IGP using empirically based models has been conducted for four communities of arthropods: mites in Ontario apple orchards (Woolhouse and Harmsen, 1987a,b; Clements *et al.*, 1991; Clements and Harmsen, 1992), insects in California alfalfa fields (Gutierrez *et al.*, 1984, 1990; Gutierrez, 1992) and African cassava fields (Gutierrez *et al.*, 1988a,b), and parasitoids attacking the silverleaf whitefly in cotton (Mills and Gutierrez, in press).

*A community of mites in apple orchards.* The mite community in Ontario apples involves unidirectional

IGP: *Z. mali* preys on eggs of phytoseiid predators, and both *Z. mali* and the phytoseiids prey on phytophagous tetranychid and eriophyid mites (see also Croft and MacRae, 1992a,b). Woolhouse and Harmsen (1987a) first constructed a model that represents transitions among eight states, defined by the presence or absence of (i) tetranychids, (ii) *Z. mali*, and (iii) phytoseiids (at the individual leaf level). Their model is empirical in that transition probabilities were derived from field data and phenomenological in that it does not explicitly represent trophic interactions. Simulations suggested that *Z. mali* could either increase or decrease seasonal peaks in tetranychid abundance (Woolhouse and Harmsen, 1987a). Woolhouse and Harmsen (1987a) concluded: "This counterintuitive result may reflect antagonistic interactions between predator populations, through competition and mutual predation." The authors note, however, that the model's conclusions are suspect because it did not successfully predict one year's observed mite dynamics and did not incorporate the influence of eriophyid mites, a potentially important alternate prey.

These problems were addressed in a second modeling effort by Woolhouse and Harmsen (1987b). Their original model was extended to include eriophyid mites, and the resulting transition matrix model accurately predicted mite population dynamics in the field over 2 years. Simulations with the enhanced model suggested that *Zetzellia* has a consistently negative effect on biological control: peak tetranychid mite densities increased as initial *Z. mali* densities increased (Woolhouse and Harmsen, 1987b). The authors again ascribed the negative effect of *Z. mali* to an unresolved combination of predation and competition between *Zetzellia* and phytoseiids, and recommended that phytoseiids be used for pest management without *Zetzellia*.

Clements *et al.* (1991) and Clements and Harmsen (1992) developed more mechanistic simulation models to complement the statistical models of Woolhouse and Harmsen (1987a,b). Their models were based on detailed laboratory studies of prey preferences and functional and numerical responses of *Z. mali* and *Typhlodromus caudiglans* Schuster feeding on the tetranychid *P. ulmi* (Clements and Harmsen, 1990). Alternate prey were not included, and the models were not validated with field data. Contrary to the results of Woolhouse and Harmsen (1987a,b), simulations suggested that combinations of one *Z. mali* and one *T. caudiglans* produce superior biological control of *P. ulmi* than either two *Z. mali* or two *T. caudiglans* predators, although some exceptions were noted. A particularly interesting result was obtained by reducing the preference of *Z. mali* for *T. caudiglans* eggs by 50% (Clements *et al.*, 1991) or eliminating this IGP completely (Clements and Harmsen, 1992); in both cases, the influence on *P. ulmi* densities was minimal. Thus,

Clements *et al.* (1991) concluded that the disruption of biological control of *P. ulmi* by *Z. mali* in the Woolhouse and Harmsen (1987a,b) models was a result of exploitative competition rather than predation on *T. caudiglans* eggs.

Although it is somewhat difficult to summarize definitively these models, we draw two major conclusions: (1) the most complete and the only successfully validated model (Woolhouse and Harmsen, 1987b) suggests that IGP disrupts biological control of tetranychid mites and (2) this disruption may stem primarily from the competition rather than the predation component of IGP.

*A community of insects in California alfalfa.* Gutierrez and colleagues (Gutierrez *et al.*, 1984, 1990; Gutierrez, 1992) developed a series of multitrophic level models describing the growth of alfalfa and population dynamics of up to three species of aphids (the blue alfalfa aphid *Acyrtosiphon kondoi* Shinji, the pea aphid *A. pisum*, and the spotted alfalfa aphid *Therioaphis trifolii f. maculata* Buckton) and several aphid natural enemies. IGP occurs between several of the natural enemies. First, the predatory larvae of the lacewing *Chrysoperla carnea* (Stephens) consume the larval stages of another predator, the coccinellid beetle *H. convergens*, and the immature stages of the parasitoid *Aphidius smithi* Sharma and Subba Rao developing in pea aphids. Second, *H. convergens* also consumes developing parasitoids. Third, the fungal pathogen *Pandora neoaphidis* Humber also attacks parasitized aphids (although whether it actually infects developing parasitoids or simply outcompetes them is not stated).

The Gutierrez *et al.* models are based on energy flow through the community and incorporate functions for the acquisition of resources (functional responses) and the assimilation of resources (based on a metabolic pool model). The models incorporate data from extensive laboratory and field studies used to estimate a series of parameters for each of the component species. The models are modular; thus the influences of IG predators can be assessed by adding and subtracting constituent members of the natural enemy community.

Although Gutierrez and co-workers do not explicitly use the models to address IGP, three of their modeling exercises test the effect of adding an IG predator. First, Gutierrez *et al.* (1984) showed that adding *H. convergens* to a system comprising aphids and a parasitoid results in a slight improvement in aphid control, as assessed by average aphid densities. Aphid densities are, however, destabilized, leading to greater fluctuations and larger peak aphid densities. Second, adding *C. carnea* to a system comprising aphids, the parasitoid, and the coccinellid resulted in dramatically improved control of aphids and the eventual displacement of both the parasitoid and the coccinellid. (The authors



note emphatically, however, that this is not observed in the field.) Finally, Gutierrez (1992) showed that the addition of the fungal pathogen to a system comprising aphids, the parasitoid, and the coccinellid caused little change in the blue alfalfa aphid's dynamics and a slightly greater suppression of the pea aphid. Thus, these models suggest that the addition of IG predators generally enhances biological control. Although not all of the predictions of the models are supported by field observations, aphid population trajectories predicted by the full model are impressively close to the population dynamics observed under unmanipulated field conditions.

While we feel that these multitrophic level models can teach us much about IGP, some aspects of the models that may be pivotal to the predicted effects of IGP were based on as yet unsupported assumptions. Most importantly, the models assumed that predator preferences are directly proportional to the biomass of each population of prey species. Thus, species with the largest standing biomasses (in most cases, the herbivores!) were overrepresented in the diets of the predators. Clearly, and as noted by Gutierrez *et al.* (1984), this will tend to emphasize the role of predators as consumers of herbivores rather than as cannibals or, we feel, IG predators. Indeed, given that the communities of natural enemies on California alfalfa and cotton are very similar, we hypothesize that the striking disparity between the predicted and observed roles of lacewing predators reflects impacts of IGP similar to those observed in cotton (Rosenheim *et al.*, 1993). Multitrophic level models of the sort developed by Gutierrez *et al.*, enhanced with preference indices derived from field observations could, we feel, provide critical insights into IGP.

*A community of insects in African cassava.* Gutierrez *et al.* (1988a,b) developed models similar to those described above for alfalfa to investigate the population dynamics of the cassava mealybug, *Phenacoccus manihoti* Mat.-Ferr. in Africa. Natural enemies of the mealybug include the parasitoid *Epidinocarsis lopezi* (De Santis), which is an exotic species imported for biological control of *P. manihoti*, and a complex of native coccinellid beetles (*Hyperaspis* and *Exochomus* spp.); IGP occurs when the predators consume mealybugs harboring developing parasitoid larvae. Field data demonstrated that the native coccinellid beetles alone are ineffective control agents, whereas the introduced parasitoid gives excellent suppression. Although the simulation model incorporated abundant field and laboratory data for several of the insect community species, information for the predators was not available and was inferred from studies on a closely related species of *Hyperaspis*. Predators were assumed not to distinguish between parasitized and unparasitized mealybugs. The

modeling results were mixed: adding the predators to a system comprised of the mealybug and its parasitoid improved biological control modestly in one simulation and may have caused a slight disruption of biological control in a second simulation. The authors note, however, that the simulation results for the predators must be considered tentative until more is known about their biology.

*Parasitoids attacking the silverleaf whitefly.* Mills and Gutierrez (in press) extended the multitrophic level models developed by Gutierrez and colleagues to assess the biological control potential of parasitoids attacking the silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring, on cotton. Three types of parasitoids are represented in the model: a typical primary parasitoid ("P<sub>1</sub>"), an obligate autoparasitoid ("P<sub>2</sub>," which produces female offspring as primary parasitoids of whitefly, but produces male offspring only via hyperparasitism of conspecific parasitoids developing in whitefly), and a facultative autoparasitoid ("P<sub>3</sub>," which produces female offspring as primary parasitoids of whitefly and produces male offspring via hyperparasitism of either conspecific or heterospecific parasitoids of whitefly). Thus IGP occurs when the facultative autoparasitoid deposits male eggs that develop hyperparasitically on the other parasitoids. The three parasitoids differed only in the mode of development of male offspring and in their sex ratios: P<sub>1</sub> always produces 80% female offspring, whereas P<sub>2</sub> and P<sub>3</sub> produce offspring in direct proportion to the availability of unparasitized whitefly (which are used for daughters) and parasitized whitefly (which are used for sons). We point out that this type of sex allocation is evolutionarily optimal only for parasitoids that are strictly time-limited (i.e., parasitoids that have excess eggs available at all times; Godfray and Waage, 1990; Godfray and Hunter, 1992; Hunter and Godfray, 1995).

Simulations demonstrated that addition of the IG predator (the facultative autoparasitoid) could produce major disruptions of otherwise effective biological control. The most effective combinations of parasitoids (P<sub>1</sub> alone or P<sub>1</sub> + P<sub>2</sub>) were both rendered ineffective by the addition of P<sub>3</sub>. (P<sub>2</sub> alone was not very effective at suppressing whitefly populations, and in this case overall suppression was only marginally improved by adding P<sub>3</sub>.) The facultative autoparasitoid interfered with biological control by laying male eggs in a high proportion of parasitized whitefly when overall exploitation of whitefly hosts was moderately high. Mills and Gutierrez (in press) conclude by cautioning against the indiscriminate introduction of facultative autoparasitoids in classical biological-control programs.

Facultative autoparasitoids may be viewed as functionally intermediate between facultative and obligate hyperparasitoids. Like facultative hyperparasitoids,

they can produce daughters as primary parasitoids. Like obligate hyperparasitoids, none of their progeny that develop hyperparasitically will ever contribute to the suppression of herbivore populations (in the case of facultative autoparasitoids, because these hyperparasitic offspring are all males). It is possible, however, that facultative autoparasitoids may alter their host acceptance patterns to maintain a more nearly optimal sex ratio, increasing their attacks on unparasitized whitefly at times of high host exploitation (Godfray and Waage, 1990; Donaldson and Walter, 1991; Hunter and Godfray, 1995; and references therein) and potentially reducing their disruptive impact on biological control.

To conclude this section, empirically based simulation models suggest that adding IG predators to a complex of biological-control agents can either enhance or disrupt biological control. Of the two clearest examples of disruption, the first involved a group of parasitoids with a highly specialized biology (facultative autoparasitoids), and the second involved the mite *Z. mali*, in which the increased herbivore densities appeared to reflect competition rather than predation between predatory mites.

#### INFLUENCE OF INTRAGUILD PREDATION ON THE EFFICACY OF BIOLOGICAL CONTROL: GENERAL ANALYTICAL MODELS

Our review has uncovered few manipulative experiments that address the influence of IGP on the suppression of pest populations. Empirically based models have likewise been explored for only a few arthropod communities, and in this review we often have been forced to "glean" results on IGP from modeling studies conducted with different objectives. A final potential source of useful insights is a group of general analytical models of IGP. Several of these models were, once again, developed not specifically to assess IGP, but as part of the debate over the relative wisdom of single versus multiple releases in classical biological control programs.

Analytical models have been developed for three forms of IGP that we have discussed here: (i) pathogen-parasitoid-host interactions, (ii) facultative hyperparasitoid-primary parasitoid-host interactions, and (iii) predator-predator-prey interactions.

Hochberg and Lawton (1990) and Hochberg *et al.* (1990) developed a model for competition between a pathogen and a parasitoid sharing a common insect host. Although the model did not explicitly treat the interaction as IGP (that is, whether the pathogen infected the parasitoid or simply competed with the parasitoid in co-infected hosts was not specified), the results seem to be independent of this detail. The model's predictions were highly variable: adding the pathogen (the IG predator) could generate either increases or de-

creases in the equilibrium density of its host. The authors concluded with a general recommendation for multiple introductions, but did not formally support this with modeling results.

A number of models have been developed for competing parasitoids. Only Hassell (1978) and May and Hassell (1981) explicitly treated facultative hyperparasitoids, arguing that facultative hyperparasitoids are dynamically equivalent to "intrinsically superior" primary parasitoids. (Parasitoids are "intrinsically superior" if they are able to eliminate larvae of heterospecific parasitoids developing in or on a single host individual [Smith, 1929].) Thus, here we will discuss models of intrinsically superior parasitoids to infer the dynamics of facultative hyperparasitoids (see caveat below).

May and Hassell (1981) and Hogarth and Diamond (1984) constructed models showing that releases of intrinsically superior parasitoids can cause either increases or decreases in the equilibrium density of the host. Nevertheless, both studies concluded with recommendations for multiple species introductions. Kakehashi *et al.* (1984) developed a more general model, incorporating a broader range of assumptions concerning the degree to which niches of the two parasitoids are differentiated. (Parasitoids with highly differentiated niches attack different subsets of the total host population.) They showed that the result of releasing an intrinsically superior parasitoid was highly dependent on the degree of niche overlap: biological control was more likely to be improved if there was strong niche differentiation. Kakehashi *et al.* (1984) also suggested that the model of May and Hassell produced recommendations for multiple species releases primarily because it implicitly incorporated an assumption of strong niche differentiation. Kakehashi *et al.* (1984) concluded their study with a caution against uncritical multiple species releases. Briggs (1993) created the first general model of parasitoid competition using a continuous time, age-structured framework. Briggs' model again predicted that the release of an intrinsically superior parasitoid could either enhance or disrupt biological control, and Briggs emphasized the risk of multiple species releases. Thus, models of competing parasitoids are universal in predicting that an intrinsically superior parasitoid can either enhance or disrupt biological control; the relative likelihood of these effects depends on a large number of assumptions regarding the biology of competing parasitoids, including their relative searching abilities and degree of niche differentiation.

One caveat is perhaps appropriate in using models of competing parasitoids to infer the role of facultative hyperparasitoids. The argument that facultative hyperparasitoids are dynamically equivalent to intrinsically superior primary parasitoids rests upon the assumption that the facultative parasitoid does not prefer, or have a disproportionate impact on, parasitized

hosts. Models are nearly unanimous in predicting that *obligate* hyperparasitoids disrupt biological control (Hassell, 1978; May and Hassell, 1981; Kakehashi *et al.*, 1984; Briggs, 1993). The one exception was reported by Luck *et al.* (1981), who found that under some conditions hyperparasitoids can decrease the amplitude of pest density fluctuations, potentially enhancing biological control. It seems likely that facultative hyperparasitoids with some preference for attacking already parasitized hosts (see Bennett, 1981) will exhibit dynamics intermediate between those for intrinsically superior primary parasitoids and obligate hyperparasitoids. Additional modeling studies are needed to investigate this hypothesis.

These highly variable and sometimes conflicting results for the effects of IGP by pathogens and facultative hyperparasitoids contrast strikingly with models developed for predator–predator interactions (Rosenzweig, 1966; Levins, 1979; Polis *et al.*, 1989; Polis and Holt, 1992). Using a diversity of modeling approaches, these analyses consistently produced the following conclusions: (1) for predators to coexist, an IG predator must be inferior at exploiting a common herbivore and thus (2) removal of an IG predator will lead to a decrease in herbivore density. Thus, these models predict that IGP consistently disrupts biological control. All of these models, however, assume that the two predators compete for a *single resource* (i.e., a single shared prey species). If, as we have argued earlier, predators engaging in IGP are likely to be generalists, we feel that the assumption of a single shared prey species is likely to be inappropriate. If instead there are multiple prey species and the predators engaged in IGP have only partially overlapping diets, we suspect that a broader range of dynamic results will be obtainable.

## DISCUSSION

Our review suggests that IGP is a widespread interaction within many, but not all, communities of biological-control agents. When the target pest is a plant pathogen, IGP appears to be less common because trophic interactions are less pervasive than competition. Likewise, IGP appears to be relatively uncommon in programs of biological control for weeds, where most biological-control agents restrict their host range (as herbivores or pathogens) to plant hosts and thus, again, interact primarily through competition.

In contrast, communities of biological-control agents associated with nematode or arthropod pests appear to be replete with IGP. Soil ecosystems, although poorly studied, harbor speciose assemblages of pathogens and predators with very broad host/prey ranges, leading to complex webs of trophic links and rampant omnivory (Moore *et al.*, 1988). Although understanding the dynamics of even the simplest two-species interaction is

a formidable task in soil ecosystems, we suspect that critical dynamics may eventually be found to reside in multispecies interactions, including interactions among biological-control agents. IGP has been most extensively documented among communities of natural enemies associated with arthropods. A long-standing interest in the host range of insect pathogens, and in particular the possibility that microbial biological-control agents might infect beneficial insects, has produced an extensive literature on IGP involving pathogens. (The only literature reviews of IGP between biological-control agents conducted prior to this one have focused on insect pathogens.) Despite scant attention paid to multispecies interactions among biological-control agents, IGP among arthropod parasitoids and predators appears to be common.

The literature provides little rigorous evidence concerning the influence of IGP on biological control. Manipulative field experiments involving more than a single biological-control agent are rare. On the one hand, it could be argued that our extensive experience with augmentative biological control has rarely produced evidence of pest outbreaks associated with releases, suggesting that IGP is rarely a cause of disruption. On the other hand, candidates for augmentative biological control are not randomly selected; they are often species with preferences for the target pest, and thus may be unlikely to reveal deleterious effects of IGP. Natural communities of biological-control agents harbor many species that have never been used augmentatively and whose role is therefore poorly understood. We feel, therefore, that it is premature to draw generalizations concerning the effect of IGP on the level of pest suppression achieved by biological control.

Our review has, however, revealed one pattern that may be significant. All the field-documented cases of IGP-based disruption of biological control stem from studies of predators, including mites (Croft and MacRae, 1992b), insects (Rosenheim *et al.*, 1993), and fish (Hoy *et al.*, 1972; Farley and Younce, 1977a,b; Blaustein, 1992). General analytical models have also identified communities of predators as settings in which IGP may release populations of primary consumers (e.g., herbivores) from regulation (Rosenzweig, 1966; Levins, 1979; Polis *et al.*, 1989; Polis and Holt, 1992). Why might predators be particularly likely to be involved in disruption of biological control through IGP?

Ehler (1995) noted a fundamental difference between IGP involving insect parasitoids and predators. When two parasitoids engage in IGP, the interactions occur within or on a *shared host*, and the host does not survive. High levels of IGP will generally be synonymous with high levels of host exploitation. The same is true for interactions between (i) pathogens and parasitoids, and (ii) predators and immature parasitoids, which also occur primarily within a shared host. Thus, green-

house and field tests of IGP mediated by a shared host/prey have shown that the addition of an IG predator either results in no change in pest densities (Ferguson, 1994) or a decrease in pest densities (Colfer and Rosenheim, 1995; Heinz and Nelson, in press). In contrast, IGP between two predators (or between a predator and an adult parasitoid; e.g., Rees and Onsager [1982]) are generally *not mediated by a shared prey*. Predators may encounter each other while foraging freely in the environment. Thus, IGP among predators does not require mortality of the shared prey. IGP among predators can be intense, resulting in high mortality of the IG prey, while the total mortality imposed upon the shared prey population (i.e., the target pest) is minimal. These are conditions under which IGP can lead to the breakdown of biological control (Table 1).

### RECOMMENDATIONS

Our ability to develop successful programs of biological control will be greatly enhanced by field studies that address the complexity of trophic interactions in agroecosystems. Perhaps most critical is our need for additional manipulative experiments conducted in the field under conditions as close to natural as possible. A critical platform for such experimentation is an understanding of trophic webs in agroecosystems (see Cohen *et al.*, 1993, for a recent consensus analysis of optimal protocols for constructing maximally informative trophic webs). Trophic webs are important in defining the existence of interactions between species; experimentation can then be used to assess the dynamical importance of identified interactions.

The very first published trophic web described the community of arthropods inhabiting a cotton agroecosystem (Pierce *et al.*, 1912). Since that time, workers in biological control have largely moved away from community-level studies. Researchers working outside the biological control community have emphasized the relevance to pest management of recent theoretical and empirical advances in our understanding of food web theory and IGP (Pimm *et al.*, 1991; Polis and Holt, 1992; Cohen *et al.*, 1993). We concur with these authors. We feel that those subdisciplines of biological control that have been dominated by theory for simple two-species interactions will benefit from a more eclectic approach that adopts insights from both population and community ecology.

### ACKNOWLEDGMENTS

We thank G. E. Heimpel, K. M. Kester, N. J. Mills, and J. M. Nelson for critical review of the manuscript, and G. English-Loeb, A. P. Gutierrez, R. Hanna, K. M. Heinz, J. Hough-Goldstein, K. M. Kester, M. Kinsey, N. J. Mills, and J. M. Nelson for sharing unpublished data or manuscripts. This work was supported by grants from USDA CSRS NRICGO (91-37302-6226 to B.A.J.; 9202357 and 94-

37302-0504 to J.A.R.), grants from the University of California Statewide IPM Project (J.A.R., H.K.K.), a Western Regional IPM Grant (93-39 to H.K.K.), and a grant from the Elvinia J. Slosson Endowment Fund (H.K.K.).

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