



Intraguild interactions in aphid parasitoids

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Abstract

We reviewed the literature on aphid parasitoids to determine the occurrence, nature and outcome of intraguild interactions. Intraguild interactions were described for larval, pupal and adult aphid parasitoids and by the type of natural enemy (fungus, predator, or parasitoid). They appear to be prevalent in most aphid parasitoid systems and, except for parasitoid-parasitoid interactions, they are mostly asymmetric, with aphidophagous predators and pathogens killing parasitoids. The limited experimental evidence from field studies is insufficient to provide a comprehensive pattern of the consequences of intraguild interactions for aphid parasitoid populations in general and, more specifically, for the efficacy of biological control. However, because intraguild interactions are widespread in aphid-natural enemy communities and mostly detrimental to aphid parasitoids, we conclude that intraguild interactions have a primary effect in driving fluctuations in aphid parasitoid populations. Drawing on case studies, we further argue that intraguild interactions can substantially alter the effectiveness of aphid parasitoids as biological-control agents.

Introduction

As with other biological systems, much recent research on the ecology of aphid parasitoids is conducted within a food-web framework. This includes studies on regulation of aphid populations (Höller et al., 1993; Mackauer & Völkl, 1993; Rosenheim et al., 1998, 1999; Müller et al., 1999; Rosenheim, 2000); foraging behaviour in a multitrophic context (Weisser et al., 1994; Powell et al., 1998; Storeck et al., 2000); apparent competition (Müller & Godfray, 1997, 1999a, b; Müller et al., 1999); indirect mutualism (Völkl, 1992; Müller & Godfray, 1999a); and intraguild predation (Ferguson & Stiling, 1996; Müller & Godfray, 1997, 1999a; Snyder & Ives, 2000; Colfer & Rosenheim, 2000). As stated by Winemiller and Polis (1996), the adoption of a food web paradigm in ecology is consequential, as several population interactions are influenced by other elements of the community.

Predatory interactions between protagonists that occupy the same trophic level and thus compete for similar prey/hosts, are termed intraguild predation (IGP). The killing and eating of a guild member provides energy to the intraguild predator, but may also reduce potential competition for food and the risk of predation in cases of mutual IGP (Polis et al., 1989; Polis & Holt, 1992). Intraguild interactions occur widely in most ecological systems and are now recognized to be functionally important. Theoretical models and empirical evidence suggest that IGP can lead to spatial and temporal exclusion of intraguild predators, competitive coexistence, or alternative stable states (Polis & Holt, 1992; Moran et al., 1996; Holt & Polis, 1997). IGP may also have indirect effects at other trophic levels. For example, in terrestrial arthropod communities, the effects of one predator on another may release extraguild herbivores from intense predation, thereby reducing plant productivity through cascading events (Spiller & Schoener, 1990; Diehl, 1993). Several recent surveys and manipula-

tive experiments conducted in agroecosystems clearly indicate that interactions between natural enemies of herbivorous pests occur widely, and that IGP may either enhance or impede biological control (reviewed by Rosenheim et al., 1995; Sunderland et al., 1997; Rosenheim, 1998).

Intraguild interactions involving aphid parasitoids are necessarily played out within aphid communities. The aphid host is the template that influences ecological interactions at the upper trophic levels, and IGP between natural enemies of aphids cannot be fully evaluated without referring to aspects of the behaviour, reproductive biology and population dynamics of aphids. Aphids are ubiquitous in terrestrial ecosystems and abundant in both natural and managed habitats. Typically, aphids have complex life cycles, that comprise one sexual generation on a primary host plant alternating with several parthenogenetic generations on one or a few secondary host plants (Moran, 1992). Asexual females have a high reproductive rate under favourable conditions and may produce different phenotypes: winged or wingless, aestivating or hibernating, and soldier morphs. Natural populations are patchily distributed in the habitat and characterized by frequent and rapid fluctuations in abundance (Dixon, 1998).

Aphids are attacked by a wide array of pathogens, parasitoids and predators whose densities vary in space and time and which may significantly reduce aphid population growth (Frazer et al., 1981; Turchin & Kareiva, 1989; Dennis & Wratten, 1991; Hopper et al., 1995; Obrycki & Kring, 1998; Müller & Godfray, 1999b). Laboratory and field studies suggest that the spatial population dynamics, foraging behaviour, and oviposition decisions of aphid parasitoids and predators are determined by the density, distribution and quality of aphid resources (Cappuccino, 1988; Morris, 1992; Mackauer & Völkl, 1993; Lucas & Brodeur, 1999; Müller et al., 1999). Of major significance in the context of IGP, most species of predators and parasitoids have a significant functional response to aphid density and tend to aggregate in aphid patches (reviewed by Frazer, 1988; Mackauer & Völkl, 1993), thereby creating favourable situations for intra- and interspecific encounters. Despite their ubiquity and often spectacular impact, the response of entomopathogens to the population dynamics of their host remains poorly understood (Thomas, 1999), but the enhanced opportunities for horizontal transmission in areas of high aphid density is likely to promote IGP.

Aphid systems are thus excellent models to explore food-web interactions.

The main objective of this review is to assess the prevalence, nature and consequences of IGP in aphid parasitoid systems. We first briefly describe the relevant biological attributes of aphid parasitoids and their natural enemies. Then, we report evidence of IGP by parasitoids, predators and fungal pathogens for each developmental stage of aphid parasitoids. Finally, we explore the impact IGP may have on aphid parasitoid populations and biological control. The primary theme of our discussion is the use of an ecological framework to better interpret emerging patterns and to improve predictions.

Aphid parasitoids and their natural enemies

Aphid parasitoids are valuable model insects for evolutionary biologists and ecologists. The approximately 400 described species of aphid primary parasitoids belong to the families Braconidae (Aphidiinae), the most important group, and Aphelinidae (Mackauer & Stary, 1967; Stary, 1988). Aphidiine parasitoids are widely distributed and important as natural enemies of aphids. They are mainly found in northern temperate and subtropical areas, both in natural and managed ecosystems, where they attack most aphid species (Stary, 1988). Aphidiine wasps develop as solitary koinobiont parasitoids. The egg is laid internally in the host, together with ovarian fluid and venom that contribute to the regulation of host development (Digilio et al., 1998; Falabella et al., 2000). At the end of the parasitoid's larval development, the soft portions of the aphid's body are completely devoured by the mature mandibulate larva, with only the cuticle remaining. The cuticle of the aphid (the 'mummy') serves as a shelter, within or under which the parasitoid spins a cocoon and pupates. Adults are small, dark coloured wasps that emerge from the mummy through an emergence hole. Because the aphid mummy is usually attached to the plant substrate, they may persist in the environment even after the parasitoid emerges or after the mummy is attacked by other natural enemies, including fungi and predators. For this reason, mummies provide ecologists with a relatively lasting record of IGP, making aphid systems ideal models for exploring this complex interaction. However, it should be emphasized that, because predator attack may also dislodge some mummies from the plant (e.g., Colfer & Rosenheim, 2000), simple field counts of mummies

with holes left by predator attack may underestimate the actual incidence of IGP.

Most aphid parasitoids are arrhenotokous and synovigenic females produce high numbers of small eggs throughout their lives (Tremblay, 1964; Stary, 1970). Because of their short developmental time, reduced longevity and high fecundity, aphid parasitoids are viewed as typical r-selected organisms (Mackauer & Völkl, 1993). Several species have been used in biological control programs, both in greenhouse and field crops (see Hagvar & Hofsvang, 1991). Although they appear to possess several favourable attributes as biological control agents, aphid parasitoids often fail to regulate pest populations. Hyperparasitism and female foraging patterns that limit the exploitation of high-density patches of aphids have been suggested to explain the low overall rates of parasitism that are often observed (see Mackauer & Völkl, 1993).

A variety of taxonomically and ecologically diverse natural enemies attack aphid parasitoids. They can be infected by viruses, bacteria or fungi; parasitized by hyperparasitoids; or, consumed by predators or competing aphid parasitoid larvae. These natural enemies constitute an ubiquitous source of parasitoid mortality that, in places, may severely reduce parasitoid populations (see below). They may interfere with aphid parasitoids directly by imposing sub-lethal or lethal effects, and indirectly by reducing host aphid populations; in some cases, these negative impacts may act to exclude aphid parasitoids from otherwise suitable habitats.

Unless quantitative data are carefully collected to build life tables or detailed food webs, mortality rates due to each group of agents can not be precisely assessed for each parasitoid developmental stage. For example, some types of natural enemies tend to be overlooked in simple field samples (Müller et al., 1999). Microorganisms that cause subtle host infection or large predators that entirely devour their prey are less likely to be identified as mortality factors than hyperparasitoids or small invertebrate predators that leave distinctive traces following attack. Nevertheless, keeping these caveats in mind, the available literature is adequate to report on the nature of interactions between aphid parasitoids and entomopathogenic fungi, predators or other aphid parasitoids and, in places, suggest general patterns that could be further tested. On the other hand, studies on viruses, bacteria, and vertebrate predators are too few to be meaningfully analyzed. Moreover, because facultative hyperparasitism has not been reported in aphid parasitoids, indicating

that primary parasitoids never share the same guild as hyperparasitoids, we do not include the latter in our discussion. Finally, although ant-parasitoid interactions can significantly limit parasitoid fitness by preventing parasitoid access to the aphid colony and by killing the intruder (reviewed by Völkl, 1997), ants should not be considered as intraguild predators of aphid parasitoids, because they are mostly engaged in mutualistic rather than predatory interactions with aphids.

Intraguild interactions

Parasitoid-parasitoid interactions

In nature, the patchiness of aphid hosts (Dixon, 1998) and the prevalent foraging patterns of parasitoid females, which display chemically-mediated long-range attraction to infested plants (Powell et al., 1998; Storeck et al., 2000), are likely to favour parasitoid aggregation to aphid host patches, thereby promoting intra- and interspecific competition for the same limited oviposition resource. Although exploitation competition for hosts between aphid parasitoids has never been directly quantified in the field (Müller & Godfray, 1999a), it certainly occurs within aphid-parasitoid communities. In a prominent study describing the trophic links within a community of aphids, parasitoids and hyperparasitoids from a natural habitat, Müller et al. (1999) sampled 14 aphid species from which primary parasitoids had been reared. Our analysis of data presented in Müller et al. (1999) indicates that on average 2.7 parasitoid species share each aphid host, with the aphids *Acyrtosiphon pisum* and *Sitobion* spp. being parasitized by 6 and 8 parasitoid species, respectively. Broader surveys of Aphidiine parasitoid communities support the generality of this result (Stary & Rejmanek, 1981; Völkl, 1989; Porter & Hawkins, 1998). Such food-webs, in which hosts are attacked by more than one parasitoid species, coupled with an ecological condition of low host density would likely promote intraguild interactions among primary parasitoids.

Self- and conspecific host discrimination have been reported in a number of aphidiine species (reviewed by Mackauer, 1990) and should reduce interference competition among parasitoid larvae by decreasing the incidence of superparasitism. However, in the laboratory and, to a lesser extent, in the field, superparasitism has been observed (Cloutier, 1984; Liu

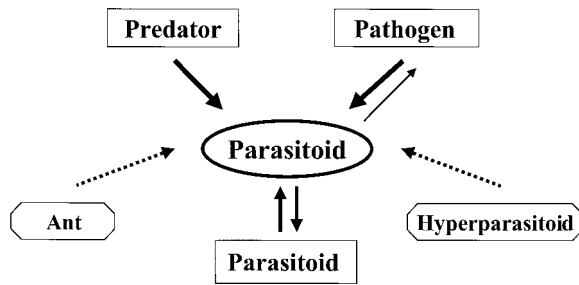


Figure 1. Interactions between natural enemies associated with aphid parasitoids. Thicknesses of solid arrows indicate the strength of the interactions between intraguild protagonists; arrows point from intraguild predator to intraguild prey. Dotted lines indicate links between aphid parasitoids and higher-order arthropod predators belonging to a different trophic level; i.e., obligate hyperparasitoids and ants involved in mutualistic relationships with aphids.

& Morton, 1986; Völkl & Stadler, 1991). As with other solitary parasitoids, the benefits of superparasitism in aphidiines are shaped by the probability of offspring survival in an already parasitized host. These benefits may be greater than the costs of oviposition, and superparasitism may therefore be favoured, when there is strong intraspecific competition, hosts of high quality are rare, and females have high supplies of mature eggs (Hubbard et al., 1987; van Alphen & Visser, 1990; Mangel, 1992).

In aphid parasitoids, supernumerary eggs and larvae are destroyed early in their development through physical combat or chemical and physiological suppression (reviewed by Mackauer, 1990). For larval competitors of similar age, one species is often intrinsically superior to the other (Force & Messenger, 1965; Chow & Mackauer, 1984; McBrien & Mackauer, 1990) although, in some cases, the competitive abilities of two competing species may be similar (Völkl & Stadler, 1991). In nature, however, where a broad range of oviposition intervals occurs, the stage of development of the parasitoids usually determines the outcome of the interaction, with older larvae generally killing their younger competitors (Mackauer, 1990). However, other more complex, competitive patterns have also been reported in interspecific interactions. For example, mandibulate first-instar larva of *Praon pequodorum* have the ability to eliminate amandibulate second-instar larva of *Aphidius smithi* (Chow & Mackauer, 1984).

In summary, within the Aphidiinae, intraguild interactions are often mutual between parasitoids (Figure 1). The most significant factors influencing the

vulnerability of developing parasitoids to intraguild competitors, and thereby the symmetry of the interaction, are the parasitoid species involved and the parasitoid age. Within an aphid-parasitoid community, the intensity of the interactions between parasitoid species is likely to be modulated by the relative number of parasitoid species that share a host and the extent to which aphid hosts are available for oviposition.

Parasitoid-predator interactions

Aphid communities are rich in species of specialist and generalist arthropod predators that vary according to host plant species and phenology, season and weather conditions. Spiders, coccinellids, lacewings, anthocorids, nabids, predatory midges, syrphid flies, and ants are major components of the predatory guild associated with aphid colonies on host plants, while spiders, carabids, staphylinids, and ants are the most common taxa that exploit aphids on the ground (Frazer, 1988; Sunderland 1988). Most of these predators do not restrict their diets to aphids. They may also exploit plant-derived food (Alomar & Wiedenmann, 1996; Rosenheim et al., 1999) or prey on other herbivorous arthropods (Frazer, 1988; Rosenheim et al., 1999), predators, including conspecifics (Rosenheim et al., 1993; Sunderland et al., 1997; Lucas et al., 1998), and parasitic wasps (see below). All developmental stages of aphid parasitoids are vulnerable to predation. Eggs, larvae and pupae can be devoured once the aphid host has been captured, whereas foraging adults can be killed by generalist predators.

Egg and larva. Developing aphid parasitoids are exposed to indirect IGP, i.e., they can be killed by a predator feeding on an aphid host that has also been parasitized.

Parasitized aphids usually remain within the aphid colony throughout parasitoid embryonic and larval development (i.e., prior to the formation of the aphid mummy), where they pursue their feeding and, to a lesser extent, reproductive activities. During this period, parasitized aphids face a risk of attack by foraging aphid predators. Although not primarily designed to examine the susceptibility of parasitized and unparasitized aphids to predation, studies by Hagen & van den Bosch (1968) and Stary (1970) suggested that foraging predators do not distinguish between parasitized and healthy aphids. But, are parasitized aphids more vulnerable to predation than healthy conspecifics?

This question was specifically examined by Brodeur (unpubl.), who compared the susceptibility of parasitized and unparasitized aphids to three species of aphid predators that have different diet breadths and foraging behaviour. In the laboratory, mixed colonies of potato aphids parasitized by *Aphidius nigripes* and unparasitized aphids were exposed to coccinellid, syrphid and predatory midge larvae at different times of parasitoid development. The incidence of predation by the three aphidophagous species was similar for parasitized and unparasitized aphids, regardless of the stage of parasitoid maturation. This suggests that, although aphid parasitoid larvae may suffer from IGP, parasitism does not significantly modify the susceptibility of parasitized aphids to predation. A study by Colfer & Rosenheim (2000) also suggests that there is no strong preference for either parasitized or unparasitized aphids in an aphidophagous predator. Using field cages, they described interactions between the cotton aphid *Aphis gossypii*, the parasitoid *Lysiphlebus testaceipes*, and the convergent lady beetle *Hippodamia convergens*. Levels of parasitism by *L. testaceipes*, estimated by the abundance of mummified aphids, were similar when parasitoids were caged alone with the aphids or in combination with the coccinellids. Thus, the predatory beetles did not appear to capture parasitized aphids more frequently than unparasitized aphids.

There are, however, two ways in which parasitism may increase the susceptibility of parasitized aphids to predation. First, parasitism may alter the host's behavioural responses to predators and thereby the likelihood of being captured. When colonies of pea aphids are disturbed by coccinellid predators, aphids parasitized by *Aphidius smithi* are more likely to drop from the plant than unparasitized individuals (McAllister & Roitberg, 1987). Once on the ground, parasitized aphids have been hypothesized to be subject to high risks of desiccation (Roitberg & Myers, 1978) and have been demonstrated to face significant risks of predation (Losey & Denno, 1998a). However, because the risks of dropping from the plant have still not been quantified relative to the risks of remaining on a plant in the face of a predator attack, it is not yet possible to determine whether dropping from the plant might be an example of 'adaptive suicide'. Because aphids that are parasitized as young nymphs may have essentially zero opportunities to live to a reproductive age, this behavioural alteration affects only the fitness of the parasitoid, which is killed along with its host. Other, non-described, alterations of aphid defenses

following parasitism may also influence parasitized aphid vulnerability to predation. Second, it has been shown that pea aphids parasitized by *A. smithi* ingest more food than unparasitized conspecifics because (i) the parasitoid larva depletes the host tissues of nutrients, and (ii) the host-parasitoid complex is less efficient in assimilating amino acids (Cloutier, 1986). Consequently, parasitized aphids produce more honeydew, a carbohydrate-rich excretion, and are more likely to attract aphid predators, parasitoids and hyperparasitoids that used honeydew as a kairomone (Bouchard & Cloutier, 1984; Carter & Dixon, 1984; Budenberg, 1990; Evans & Swallow, 1993). The area-restricted search and resultant aggregative response of aphid natural enemies to increased honeydew production (Kareiva & Odell, 1987; Ferran & Dixon, 1993; Shaltiel & Ayal, 1998; Monsrud & Toft, 1999) could therefore render parasitized aphids more vulnerable to predation. This prediction needs to be investigated further to better understand the potential relationship between parasitism and predation.

Pupa. During their prepupal and pupal development, non-diapausing aphidiines remain within the mummified aphid for periods ranging from 4 to 8 days (Hagvar & Hofsvang, 1991). The mummy provides physical protection against adverse weather conditions, desiccation, pesticides, and natural enemies (Stary, 1970; Brodeur & McNeil, 1989; Krespi et al., 1994; Couture, 1997; Chow & Mackauer, 1999; Longley, 1999). This protection is, however, imperfect as the mummy can easily be torn by the mandibles of invertebrate predators and pierced by the stylets of predatory bugs or the ovipositors of hyperparasitoids.

The number of species of aphidophagous predators that have been reported preying on aphid mummies is rather large. The literature contains records of attacks by Forficulidae, Carabidae, Coccinellidae, Chrysopidae, Formicidae, and various species of hemipteran predatory bugs such as Miridae, Nabidae and Anthoridae (Stary, 1966; Wheeler et al., 1968; Al-Rawy et al., 1969; Dixon & Russel, 1972; Frazer & van den Bosch, 1973; Frazer & Gilbert, 1976; Wheeler, 1977; Brodeur & McNeil, 1991, 1992; Nakata, 1994; Ferguson & Stiling, 1997; Vinson & Scarborough, 1997; Colfer & Rosenheim, 2000; Snyder & Ives, 2000; Meyhöfer & Hindayana, 2000). Attacked mummies often remain on leaves and can be identified by large, irregular holes made by mandibulate predators or by the dark stained punctures left by piercing-sucking insects. Of interest, predatory midge and syrphid

larvae, which are specific to aphids, may feed on recently parasitized aphids but ignore mummified aphids (Harizanova & Ekblom, 1997; Kindlmann & Ruzicka, 1992; Brodeur, unpubl.).

Members of the guild of mummy predators presumably do not rely solely on mummified aphids for their survival. None of these predators specialize on aphid mummies, but will consume them if encountered. Laboratory choice-tests showed that coccinellids prefer to feed on live *Aphis gossypii* rather than mummies (Colfer & Rosenheim, 2000); however, *A. gossypii* exhibits few defensive responses to coccinellid attack (J.A. Rosenheim, pers. obs.). In other systems where live aphids can adopt effective active defenses against predators, aphid parasitoids that are confined within the mummified aphid may be especially vulnerable to IGP. Carabid beetles foraging on alfalfa plants are more likely to capture sessile pea aphid mummies harboring *A. smithi* than unparasitized or parasitized aphids that actively defend themselves (Snyder & Ives, 2000).

Several reports indicate that predation on aphid mummies can be very intense in agroecosystems. In walnut orchards, predation of walnut aphid mummies may reduce survivorship of *Trioxys pallidus* by 80% (Nowierski, 1979). In potato fields, Couture (1997) observed a gradual increase throughout the season in the incidence of predation on mummies of the potato aphid, with 72.5% and 95.0% of the mummies harboring *Praon simulans* and *A. nigripes*, respectively, being killed by generalist predators prior to harvest. In cotton, Colfer & Rosenheim (2000) observed in field cage experiments that the convergent lady beetle destroyed 73–100% of the mummies containing *L. testaceipes*. Similarly, in sugar-beet plots, mummies of the bean aphid containing *Lysiphlebus fabarum* were highly vulnerable to natural enemies, with an overall level of predation of 57.4% (Meyhöfer & Hindayana, 2000). Using an original video technique to monitor arthropod activities under field conditions, Meyhöfer (unpubl.) further observed that chrysopid larvae (36%), coccinellid larvae (27%), anthorid bugs (27%), and carabid beetles (9%) were the most important predators of aphid mummies. Finally, in a forest ecosystem, Völkl (pers. comm.) observed on pine trees that predatory bugs killed 38–54% of *Cinara pini* and *C. pinea* mummies containing *Pauesia* spp.

The vulnerability of mummified aphids to IGP may be influenced by the spatial distribution of the mummy within the plant canopy. Mummification sites have been shown to vary according to parasitoid species

(Höller, 1991; Müller et al., 1997), parasitoid physiological state (Brodeur & McNeil, 1989), plant architecture (Brodeur & McNeil, 1991), and position of the aphid colony (Brodeur & McNeil, 1991, 1992; Höller, 1991; Müller et al., 1997). The available, and limited, experimental evidence suggests variable relationships between aphid mummy distribution and both hyperparasitism (Brodeur & McNeil, 1991, 1992; Müller et al., 1997; Chow, 2000) and predation (Brodeur & McNeil, 1992; Snyder & Ives, 2000). With regards to IGP, Brodeur & McNeil (1992) reported that the vertical distribution of aphid mummies on potato plants did not influence the overall susceptibility of *A. nigripes* to aphidophagous predators. In contrast, Snyder & Ives (2000) observed that pea aphid mummies harboring *A. smithi* located on lower alfalfa leaves were more likely to be attacked by carabid beetles than those positioned higher on plants.

Besides mummification site, we might expect other biotic and abiotic factors such as parasitoid pupal developmental time, morphology of the mummy, aphid density, predator species and abundance, and ant-attendance to influence the incidence of predation on pupating aphid parasitoids. Furthermore, because none of the generalist predatory species that occasionally attack aphid mummies have been shown to hunt specifically for mummies, common and predictable patterns are unlikely to arise. For example, density-dependent predator aggregation to patches of mummies, as observed under certain ecological conditions for hyperparasitoid species (Schooler et al., 1996; Muller & Godfray, 1998) is unlikely to be a typical response of aphidophagous predators. However, additional work is needed to determine if predators do, in some cases, switch to forage specifically for mummies when unparasitized aphids or alternative prey have been driven to very low densities.

Adult. For various reasons, most of our knowledge of the ecology of adult parasitoids relates to the behaviour of foraging females. Interactions between adult wasps and intraguild competitors remain poorly understood, in part because of the inherent difficulties of tracking small insects in nature. Potential sources of mortality include adverse weather conditions, starvation, microbial infection, parasitism, and predation (see Heimpel et al., 1997; Rosenheim, 1998). Although the occurrence and consequences of predation on adult parasitoids remain largely unexplored, the evolution of morphological and behavioural anti-predator defenses attests of the consequential pressure

exerted by predators (Gauld, 1987; Godfray, 1994; Quicke, 1997). A quantitative field study of the impact of predators on foraging parasitoid females was conducted by Heimpel et al., (1997), who observed that spiders, predatory bugs, and ants have the capacity to capture two different species of *Aphytis* scale parasitoids. Using a simple simulation model, they further inferred that IGP significantly reduced parasitoid fitness during specific seasonal periods of high predation risk.

Until recently, there were no published studies reporting quantitative estimates of predation rates on adult aphid parasitoids in the field. Casual observations in alfalfa fields by Wheeler (1977) indicated that predatory bugs from the genus *Nabis* prey on adult of *Aphidius* spp. Recently, however, W. Völkl has conducted a series of studies of Aphidiine parasitoids foraging in nature, and has quantified the rates at which they fall prey to a range of generalist predators, including particularly spiders and ants (reviewed in Rosenheim, 1998). For example, Völkl and Kraus (1996) measured foraging success and mortality risks of *Pauesia unilachni*, a specialist parasitoid of the grey pine aphid. They showed that females may suffer high levels of predation by linyphiid and araneid spiders when foraging on pine trees. By tracking individual parasitoids, they observed that 11% of the females eventually flew into a spider web and were killed by spiders. In contrast, none of the females died when searching for aphid hosts by walking on pine needles. They further found that the number of parasitoid females that were caught per spider web increased significantly during the season, along with an increase of spider web density per tree. The predation risk faced by *P. unilachni* and four of the other five species studied by Völkl was startlingly large: more than 50% of the adults were expected to be dead during their first 24-h foraging period.

Aphid parasitoid-predator interactions are always asymmetric, in favor of the predators (Figure 1). Implicitly, a specialist parasitoid is not adapted to attack non-host insects, and is thus disadvantaged during confrontations with generalist predators.

Parasitoid-fungus interactions

Host-parasitoid-pathogen interactions are ubiquitous in many terrestrial ecosystems and play an important role in population and community ecology (Hochberg & Lawton, 1990). Pathogens interfere with parasitoids in a variety of ways (see Brooks, 1993, for an exten-

sive review), which may lead to interactions that could be more complex than those observed for parasitoid-parasitoid or parasitoid-predator associations. For one thing, a reliable evaluation of the impact of a pathogen on a parasitoid must integrate sublethal and lethal effects. Also, for immature parasitoids, such an evaluation has to consider whether the death of the parasitoid within the infected host results from direct infection of the parasitoid, unsuitability of the infected host, or early host death (Brooks, 1993).

Entomopathogenic fungi, especially the Deuteromycotina and the Zygomycotina, are the most important aphid pathogens. Fungal epizootics occur naturally in aphid populations and are governed by several biotic and abiotic factors (Carruthers & Hural, 1990; Hajek & St-Leger, 1994). The mode of action is characterized by a sequence of pathological events leading to complete aphid invasion by the fungus (St-Leger, 1993; Askary et al., 1999, and references therein). Fungal pathogens vary notably in their degree of host specificity (Clarkson & Charnley, 1996; Federici & Maddox, 1996). Some are restricted to a genus or host family, whereas others exploit hosts from several orders. Because horizontal transmission of most insect fungal pathogens occurs by simple random contact with fungal spores dispersed from an insect host cadaver, IGP by fungi on aphidiine wasps is likely to occur whenever the fungus has a broad enough host range to infect both aphids and parasitoid wasps and when the fungus and parasitoid are simultaneously active in an aphid population.

Although there is a paucity of information on aphid parasitoid-fungus relationships, some patterns have already been identified, and others can be inferred from diverse parasitoid-pathogen associations. We will describe aspects of the susceptibility of immature and adult aphid parasitoids to fungal infection and examine the consequences on parasitoid fitness.

Larva. In most cases, the death of an aphid parasitoid larva, developing in a fungus-infected host, results from aphid mortality, rather than direct fungal infection. A few reports indicate that larval stages of aphid parasitoids are to some extent immune towards infection by Entomophthorales and Hyphomycetes fungi. Keller (1975) observed that although larvae of *Aphidius* sp. developing in pea aphids infected by *Entomophthora* spp. died prematurely, parasitoid tissues were free of the fungus. Powell et al. (1986) found no direct evidence of infection of *Aphidius rhopalosiphii* larvae when developing in the rose-grain aphid in-

infected by *Erynia neoaphidis*. Histopathological observations of potato aphids parasitized by *A. nigripes* and simultaneously infected by *Verticillium lecanii* showed that fungal blastospores, which develop in the aphid haemocoel, do not penetrate parasitoid tissues (Askary & Brodeur, 1999). However, when aphids were heavily infected, localized penetration of the parasitoid larval cuticle by *V. lecanii* was observed. Although large numbers of blastospores were found in the gut of the parasitoid following feeding on host hemolymph, no evidence of internal fungal invasion of *A. nigripes* tissues was found.

In most cases, the survival of a parasitoid developing in a host infected by a virus, bacterium, protozoan or fungus depends upon the interval between parasitoid oviposition and infection by the pathogen (see Brooks, 1993). Similar patterns apply to aphid parasitoid-fungus interactions (Powell et al. 1986; Fuentes-Contreras et al., 1998; Askary & Brodeur, 1999). For example, 31% and 89% of *A. nigripes* larvae survived to mummification when potato aphids were exposed to *V. lecanii* 2 and 4 days following oviposition, respectively (Askary & Brodeur, 1999).

Powell et al. (1986) reported that parasitism may predispose the aphid host to subsequent fungal infection, thereby jeopardizing the developing parasitoid. The susceptibility of cereal aphids to *E. neoaphidis* increased with the interval between parasitism by *A. rhopalosiphi* and infection. Such a pattern has also been observed in other host-parasitoid-fungus systems (Brooks, 1993). In contrast, several lines of evidence indicate that parasitism may prevent fungal infection (Franzen & van Lenteren, 1994). Parasitoid larvae may produce antimicrobial compounds or induce changes in the host haemolymph or integument that increase resistance to fungal penetration and development (El-Sufty & Führer, 1981; Willers et al., 1982).

Pupa. As described above, the aphid mummy provides physical protection to prepupal, pupal and pre-emerging adult parasitoids. To our knowledge, only one study has examined the susceptibility to fungal infection of aphid parasitoids whilst within the mummy. Askary & Brodeur (unpubl.) showed that once potato aphids parasitized by *A. nigripes* had mummified, *V. lecanii* is not capable of penetrating the mummy and infecting the parasitoid. However, conidia of *V. lecanii* may adhere to the mummified aphid's cuticle and produce a mycelium that grows saprophytically on the surface of the mummy. This may have detrimental

consequences for adult *A. nigripes*, as they can be contaminated by spores during the process of emergence and ultimately become infected if environmental conditions favour germination of the conidia (Askary & Brodeur, unpubl.).

Adult. Foraging adult aphid parasitoids can also be infected by fungal spores. Although more sclerotized than soft-bodied arthropods, and thereby potentially more resistant to penetration structures of invasive pathogens, adult parasitoids are exposed in a number of ways to fungal infection. In the laboratory, Askary & Brodeur (unpubl.) observed that females of *A. nigripes* could be infected by spores of *V. lecanii* through direct cuticular contact with aerial propagules and, as described above, during emergence from a mummy contaminated on its surface. No infection was observed following oviposition in infected potato aphids, mating with infected conspecifics, or through tarsal and antennal contacts when foraging on potato leaves contaminated with spores of *V. lecanii*. Similarly, Poprawski et al. (1992; in Lacey et al., 1997) and Lacey et al. (1997) reported a direct effect of dosage of *Zoophthora radicans* and *Paecilomyces fumosoroseus*, respectively, on mortality of *Aphelinus asychis*, an aphelinid parasitoid of the Russian wheat aphid.

Latent and sublethal effects of entomopathogenic fungi on the biology of insects in general, and parasitoids in particular, are complex, and more detailed experimental studies are needed to better understand their impact. Nonlethal infections have been shown to limit female parasitoid fitness through a decrease in longevity, reproductive period and fecundity (see Brooks, 1993). To our knowledge, only two studies have quantified impacts of sublethal fungal infections on aphid parasitoids. Fuentes-Contreras et al. (1998) showed that the larval developmental time of *Aphidius rhopalosiphi* was not affected by *Pandora neoaphidis* infection for parasitoids that survived to pupation. Lacey et al. (1997) specifically examined sublethal infection of *P. fumosoroseus* on adult females of *A. asychis*. They observed a reduction of longevity of infected females (5.7 d) relative to healthy females (9 d). Infected females also foraged less actively than noninfected females. Their searching capacities were impaired as measured by a decrease in percentage of time walking, walking speed and distance covered. Unexpectedly, infected females continued to oviposit until the day prior to death and had the same daily fecundity as untreated females. However, early death

of infected *A. asychis* females resulted in lower total numbers of Russian wheat aphid attacked per female.

In most cases, aphid parasitoid-fungus interactions are asymmetric, favouring the pathogen (Figure 1). Besides ecological and environmental conditions that influence the infection process, two main factors determine the extent to which the interaction is detrimental to the parasitoid. First, as with most host-pathogen interactions, the consequences of an infection are dose-related for the immature larva developing in infected aphids and the adult parasitoid. Fitness costs remain largely to be quantified, but appear to vary along a continuum from minor sublethal effects to parasitoid death. Second, for immature parasitoids, and to a lesser extent adults, the competitive outcome depends on the timing of the infection. The fungus outcompetes and kills the parasitoid, except when parasitoid larval development is initiated sufficiently in advance of the infection. At the end of its larval development, the parasitoid larva entirely depletes the host, thereby preventing further fungus development and sporulation. Furthermore, parasitoid larvae could potentially reduce fungal populations by feeding on infected aphids. Askary & Brodeur (1999) observed that larvae of *A. nigripes* feeding on host hemolymph and other tissues of infected aphids also ingest fungal spores. The spores accumulate in the gut of the parasitoid, where their viability is possibly reduced by fungistatic factors (Dillon & Charnley, 1991). Parasitoid larvae may therefore indirectly reduce competition for hosts through inactivation of ingested fungal bodies (Askary & Brodeur, 1999). Under this specific circumstance, IGP between aphid parasitoids and entomopathogenic fungi could be considered to be mutual, because the parasitoid may survive the interaction, consume the fungus, and continue to depress aphid population densities, therefore both directly and indirectly interfering with the exploitation of the aphid population by the fungus (Figure 1).

Population biology and biological control

The theory of IGP and its consequences for population ecology and community structure are rapidly evolving fields of ecology. Historically, most of the theories concerning regulation of herbivorous animals have stressed the trophic role of natural enemies. Predators, parasitoids and pathogens were considered to have parallel and largely independent effects on herbivore populations, and potentially significant interactions

between these natural enemies were thereby neglected. Recent attempts to extend current population models by adding interactions between natural enemies have contributed to the emergence of a more dynamic and reliable understanding of the factors that regulate the density of animal populations (see Polis et al., 1989; Polis, 1991; Strong, 1992; Kareiva, 1994; Polis & Strong, 1996; Losey & Denno, 1998b; Rosenheim, 1998).

Empirical research and models repeatedly question the relative importance of host plant resources (bottom-up effects) and natural enemies (top-down effects) in regulating herbivore populations. Several recent field studies in invertebrate communities have shown that although most herbivores are attacked by large guilds of natural enemies, complex and unexpected interactions between predators, parasitoids and pathogens may significantly reduce their impact on herbivore populations. Rosenheim (1998) has recently argued for a 'fundamental change in our view of natural enemy ecology', as we may have underestimated the role of IGP and higher-order predators in shaping arthropod communities. In many terrestrial systems, the ability of natural enemies to suppress herbivore population growth rates may depend critically on intraguild interactions.

A traditional view of biological control, basically classic biological control, considers that herbivore populations can be reduced by adding natural enemies to the ecological system (DeBach & Rosen, 1991; van Driesche & Bellows, 1996; Vinson, 1999). In nature, however, different outcomes have been observed when one or a combination of natural enemies are released in the field. The overall impacts on pest populations vary along a continuum from synergistic effects, the most desirable scenario for biological control, to interference effects, the least desirable scenario (see Ferguson & Stiling, 1996). Interference among biological control agents can significantly reduce the impact of biological control agents on pest populations through direct mortality or competitive displacement, and may even favour the development of pest populations (Rosenheim et al., 1993, 1995; Rosenheim, 1998, and references therein).

The nature and outcome of interactions between biological control agents depend on the specific relationship between antagonists, which is basically determined by their biological attributes and modes of action, and by several extrinsic factors relating to the host plant, the diversity and abundance of extraguild herbivorous prey and hosts, and the envi-

ronmental conditions. For practitioners, these interactions modulate the actions of natural enemies and are important in designing effective biological control programmes. This means in practice that compatibility between biological control agents needs to be identified to better predict how and under which ecological conditions IGP would promote or impair biological control. Presently, most information on the relationships among biological control agents, as well as their consequences for population dynamics, is theoretical and based on limited observation.

Our review indicates that parasitized hosts, mummies and adult parasitoids are attacked by a large guild of natural enemies. Predictably, IGP plays an important role in regulating aphid parasitoid densities and thereby their potential to exert biological control. A few recent experimental field studies have quantified interactions among different types of aphid natural enemies and determined whether combinations of species affect their joint capacity to control aphid populations.

Case studies

Recent evidence for the combined influence of aphid parasitoids and generalist predators on pest population growth rates comes from field experiments in which natural enemy numbers were initially manipulated and the resultant aphid populations compared to controls. These examples demonstrate the range of potential outcomes in parasitoid-predator interactions.

Ferguson & Stiling (1996) used field cages to explore in a natural ecosystem the effect of combining the aphid parasitoid *Aphidius floridaensis* and the coccinellid *Cycloneda sanguinea* on population densities of the saltmarsh aphid *Dactynotus* sp. Aphids were controlled less effectively by a combination of parasitoids and predators than when the parasitoid was released alone at equivalent aphid densities. Such a nonadditive effect of the natural enemies was caused by coccinellids feeding on aphid mummies and, presumably, disturbing foraging parasitoid females.

Analogous experiments were performed by Snyder & Ives (2000) who described in alfalfa fields how generalist carabid beetles curtail the long-term biological control of the pea aphid *A. pisum* through IGP on mummies harboring *A. ervi*. Carabid beetles, which usually forage on the ground, have the capacity to reduce aphid and parasitoid populations substantially during re-growth of alfalfa plants following harvest. During this period, carabid beetles were able to for-

age on short plants and caused high levels of mortality on aphids and aphid mummies. However, later in the season, when plants were tall, carabid beetles had no impact on aphid populations but continued to destroy a large proportion of aphid parasitoid mummies. The increase in plant structural complexity, and in particular the creation of a partial refuge from carabids in the top of the plants, strongly relaxed predation pressure on mobile aphids, which could escape from attacking beetles, but had a smaller effect on reducing predation on the immobile, defenseless aphid mummies. Snyder & Ives (2000) also observed that disruption of aphid biological control by carabid beetles was higher at low initial aphid densities, suggesting that IGP is to some extent density-dependent.

Finally, Colfer & Rosenheim (2000) examined how interactions between the convergent lady beetle *H. convergens* and the aphid parasitoid *L. testaceipes* affected the population dynamics of the cotton aphid *A. gossypii* on caged cotton plants. Although coccinellids destroyed a large proportion of mummified aphids, the study revealed that the addition of lady beetles to the aphid-parasitoid system produced a significant depression of aphid densities. This effect cascaded to plants as measured by increased plant biomass (Colfer & Rosenheim, 2000).

To our knowledge, only one study has explored at the population level the interactions between aphidophagous parasitoids and fungi. Mesquita et al. (1997) examined the interaction between the adult stage of the aphelinid parasitoid *A. asychis* and the entomopathogenic fungus *Paecilomyces fumosoroseus* exploiting the Russian wheat aphid in barley fields. Although laboratory tests showed that adult parasitoids are susceptible to fungal infection (Lacey et al., 1997), field results indicated that parasitoids and fungi can be compatible, working additively to enhance aphid control. At the end of the 13 days experiment period, the mean number of aphids per plant was lower in the treatments Parasitoid and Parasitoid + Fungus than in the treatment Fungus and the control. Only the treatment Parasitoid + Fungus showed a significant difference relative to that of the control in terms of plant dry weight, suggesting an additive effect of the two biological control agents. Furthermore, there were no significant differences in the number of mummies recovered per plant at the end of the experiment and the percentage of *A. asychis* emergence for the treatments Parasitoid versus Parasitoid + Fungus, suggesting that the fungus did not interfere with the action of the parasitoid.

On the capacity of aphid parasitoids to control aphid populations

It remains unclear whether and under which ecological circumstances aphid parasitoids play a determining role in regulating aphid populations. In natural and managed ecosystems, aphid parasitoids usually have limited impact on aphid populations, with an incidence of parasitism of less than 10% (reviewed by Mackauer & Völkl, 1993). Basically, two elements have sustained the debate in the last 40 years. A first argument is that, in many cases, hyperparasitism strongly impedes the actions of primary parasitoids (see Rosenheim, 1998; Sullivan & Völkl, 1999; Brodeur, 2000, and references therein). From their exhaustive study of direct and indirect interactions in a natural aphid-parasitoid community where they estimated rates of primary and secondary parasitism, Müller et al. (1999) also suggested that 'secondary parasitoids regulate primary parasitoids but that primary parasitoids do not regulate aphids'. The second argument comes from the analysis of Mackauer & Völkl (1993) who have interpreted the consistent failure to observe density-dependent parasitism in the field as a consequence of the foraging behaviour of aphid parasitoid females.

We further propose that, in addition to parasitoid foraging behaviour and hyperparasitism, IGP may significantly limit the potential of aphid parasitoids as biological control agents. The quantitative impact and long-term effect of IGP on aphid parasitoids remains indeterminate in most systems. Nevertheless, as described above, evidence is growing for its widespread occurrence and potentially detrimental impact on populations of primary parasitoids. If confirmed by further ecological field studies, this view could have a major impact on our understanding of factors that structure aphid communities and determine the effectiveness of aphid parasitoids in biological control.

The limited number of case studies is insufficient to provide a comprehensive pattern for the compatibility of parasitism and predation or fungal infection in aphid biological control. Obviously, the above case studies do not illustrate the full range of potential scenarios that might be observed in nature. Several ecological factors may have critical impacts on IGP, and the outcome of interactions between natural enemies may change over short or long time scales, resulting from variation in the (i) identity, age-structure and abundance of intraguild competitors, (ii) natural history, spatio-temporal distribution and density of the extraguild aphid prey/host, (iii) host plant phenol-

ogy, architecture and refuges, and (iv) environmental conditions. Assessing whether aphid parasitoids can be used in combination with generalist predators and entomopathogenic fungi is therefore extremely challenging for population ecologists and practitioners of biological control.

Nevertheless, experimental evidence suggests that opportunities exist for enhancing biological control of aphids through judicious combinations of natural enemies. Information on the occurrence and symmetry of IGP involving aphid parasitoids is useful in determining which combinations of natural enemies should be considered for release to maximize aphid mortality. For instance, a 'cocktail' of aphid parasitoids and specialist aphidophagous predators, such as predatory midges or syrphid flies, might be more effective than a combination of aphid parasitoids and generalist predators that may extensively feed on mummified aphids. When a combination of parasitoids and entomopathogenic fungi is considered, special attention should be paid to environmental conditions, namely relative humidity, and the timing of releases and fungal doses to reduce interference between biological control agents. For example, Brodeur & Fournier (unpubl.) showed that *A. nigripes* is less susceptible to infection by *V. lecanii* than the potato aphid, its common host. In this context, sublethal doses could be judiciously applied so as to minimize mortality of the parasitoid, while retaining infectiousness to the aphid pest.

On the 'special status' of insect parasitoids as models for studies in behavioural and evolutionary ecology

Insect parasitoids have been favoured by researchers as model organisms for developing and testing theories in behavioural and evolutionary ecology. Much of this work has been conducted in the laboratory, where many parasitoids are easy to observe and manipulate. The argument has been made (e.g., Godfray, 1994; Rosenheim, 1994) that parasitoids are valuable as model organisms because parasitoid reproductive behaviour (e.g., foraging, oviposition, sex allocation) is particularly intimately connected to fitness returns, facilitating the measurement of the costs and benefits of different behaviours. The implicit assumption underlying this line of reasoning is that fitness returns associated with oviposition can be assessed immediately – an egg laid is assumed to be equivalent to an offspring produced, or at least some readily measurable expecta-

tion of successful reproduction. Traditional models of host-parasitoid population dynamics have reinforced this view: an egg laid by an herbivore only results in recruitment to the adult stage if the juvenile stages survive exposure to parasitoids, whereas an egg laid by a parasitoid always produces new parasitoid adults (e.g. Hassell, 1978; but see Taylor, 1997).

Given the emerging understanding of the biology of aphid parasitoids reviewed above, can this view of parasitoids as 'special' model organisms be sustained? We think not. Parasitoids, like the other insects that they exploit as hosts, face a diverse array of threats during the development of their offspring, and it may be the rare individual that survives from the egg to the adult stage. Most of the mortality factors that impact unparasitized host insects will also impact parasitized hosts. Whereas in some cases parasitoids can manipulate host behaviour to shield themselves from mortality risks, in other cases parasitized hosts suffer from dramatically increased risks of falling prey to other natural enemies (Brodeur, 1994) or, as recently demonstrated by Ives & Settle (1996), dying as a result of exploitative competition.

The view of parasitoid ecology that emerges from our review of aphid parasitoids is, instead, more consistent with the view first proposed by Price (1973), but little considered over the past quarter century. Price emphasized that parasitoid life histories are shaped by a strong expectation of heavy mortality occurring between oviposition and emergence of an adult progeny. This is especially likely to be true for parasitoids, like the Aphidiinae, that develop as koinobionts in exposed, aggregated, conspicuous, and poorly-defended insect hosts. Many aphidiine parasitoids have high fecundities and high realized rates of oviposition in the field (Rosenheim, 1999), and yet their populations often do not explode; we suggest that this is in large part a reflection of IGP. Thus, IGP is relevant not only for biological control workers and agricultural ecologists, but also for behavioural and evolutionary ecologists attempting to understand the evolution of parasitoid life histories.

Conclusion

Detailed analyses of individual systems are producing a deeper understanding of the complex interactions occurring within arthropod communities. The ubiquity, rapid population growth, and economic significance of aphids make them exceptionally well suited as models

for quantitative and manipulative experimentation in the field. They have become a favourite and fruitful model in terrestrial ecology for evaluations of factors that shape direct and indirect food-web interactions.

In this review, we have described how parasitized aphids, mummified aphids, and adult aphid parasitoids may interact with a large guild of natural enemies. Field survey and manipulative experiments reveal that IGP on aphid parasitoids occurs widely and appears to be ecologically significant in aphid communities. When aphid parasitoids and predators or fungi compete for aphid hosts there are usually severe costs to the parasitoid. We believe that the symmetry of patterns, illustrated for aphid parasitoids in Figure 1, also pertains to many other groups of insect parasitoids. Because of their life-history characteristics and specialized mode of development, parasitoids are disadvantaged during direct interactions with intraguild generalist predators and, to a lesser extent, entomopathogens.

The compatibility of aphid parasitoids with other biological control agents of aphid pests remains poorly understood. Entomopathogenic fungi, predators, and parasitoids have the potential to complement or interfere with one another, and different scenarios have emerged from the few quantitative field studies reported to date. Whether natural enemies with different modes of action and host/prey specificity can be integrated in biological control programmes, depends on a variety of abiotic and ecological factors. Understanding the complex relationships between intraguild natural enemies of aphids is a crucial step towards implementing biological control strategies.

Results from field studies raise questions about the long-term consequences of IGP for aphid-parasitoid communities. Efforts should therefore be directed toward multigenerational studies. Potential outcomes presumably include (i) competitive coexistence with intraguild competitors, (ii) persistent exclusion, or (iii) recurrent invasions and extinctions. The integration of intraguild interactions in modern population models would contribute to better comprehension of the determinants of food web structure and to the formulation of pest management solutions.

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