Review

Natural enemies of the Coccinellidae: Parasites, pathogens, and parasitoids

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A B S T R A C T

We review aspects of the life histories of representative enemies of coccinellids (both entomophagous and phytophagous species) and expose both potential and real effects that they have on life parameters of their hosts. Lady beetles are attacked by a variety of natural enemies (bacteria, fungi, mites, nematodes, protozoa, wasps, flies). Few of these enemies have the ability to alter significantly the population dynamics of their hosts. This review should encourage further research to help define the role of natural enemies in the population dynamics of coccinellids. Ultimately, the conservation of beneficial lady beetles and the management of nuisance and pestiferous ones should be major emphases of research on coccinellid–natural enemy interactions.

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1. Introduction

Although knowledge of naturally occurring parasites, pathogens, and parasitoids of coccinellids has increased in recent years, a limited number of studies have investigated the biology and ecology of those species that attack beneficial lady beetles, which often contribute to the reduction of herbivore populations in managed and unmanaged ecosystems. Recent advances have been made in the biology of dipteran and hymenopteran parasitoids of coccinellids (Nalepa et al., 1996; Disney, 1997; Hoogendoorn and Heimpel, 2002; Nalepa and Kidd, 2002; Firlej et al., 2005; Koyama and Majerus, 2008), as well as pathogenic bacteria (Majerus et al., 1998), pathogenic fungi (Cottrell and Shapiro-Ilan, 2003, 2008; Roy et al., 2008), and nematodes (Shapiro-Ilan and Cottrell, 2005). However, the biology and ecology of viruses, nematodes, mites, and fungi that attack coccinellids are largely unknown. Here we emphasize the primary literature published since the excellent review of coccinellid natural enemies by Ceryngier and Hodek (1996), and some pre-1996 literature that was omitted from this earlier review. In addition, the literature was searched to determine whether any enemy demonstrated the potential of regulating the population dynamics of any coccinellid species.

2. Parasites

Parasites of lady beetles can be loosely grouped as endo- and ectoparasites. Ceryngier and Hodek (1996) reviewed roundworms (Nematoda: families Allantonematidae and Mermithidae) as endoparasites of the adult stage of entomophagous lady beetles in Europe. Raju and Uma Maheswari (2005) reported a Mermis sp. (Mermithidae) from fourth instars of a phytophagous lady beetle, Henosepilachna vigintioctopunctata F., in India. Ectoparasitic fungi (order Laboulbeniales, family Laboulbeniaceae) and ectoparasitic mites (order Acarina, family Podapolipidae) have been found on coccinellids throughout the world. The parasitic fungi and mites will be reviewed in the following paragraphs.

2.1. Parasitic fungi

The order Laboulbeniales contains ascomycetous fungi that parasitize arthropods. Approximately 80% of the 2000 described laboulbeniaceous species include beetles as their hosts (Santamaria, 2001; Weir and Blackwell, 2004). As far as is known, all Laboulbeniales are biotrophic; that is, they require a living host for continued survival and propagation. Horizontal transmission of Laboulbeniales, likely through direct contact between adult hosts, is the common mode of perpetuation. This process is greatly facilitated when coccinellid hosts aggregate at feeding or overwintering sites (Welch et al., 2001; Riddick and Schaefer, 2005; Riddick, 2006; Nalepa and Weir, 2007). The propensity of entomophagous males to repeatedly attempt to copulate with conspecific males and females under field conditions may facilitate the
spread of laboulbenialean fungi through populations of susceptible species. Four Laboulbeniales species within the genus Hesperomyces Thaxter attack entomophagous lady beetles (Table 1). Hesperomyces virescens Thaxter has multiple hosts including Harmonia axyridis (Pallas). Whether H. virescens can develop and thrive on phytophagous coccinellids is unknown.

Tavares (1979) and Weir and Beakes (1995) claim that most Laboulbeniales species are avirulent and cause little harm to their hosts. However, Kamburov et al. (1967) reported that Laboulbeniales species are avirulent and cause little harm to their phytophagous coccinellids is unknown. (Pallas). Whether Coccipolipus found in host reproductive organs or tracheal systems ( Hajiqanbar cally underneath the elytra of their hosts, some are endoparasites commonly attack beetles. Although most species live ectoparasitically, some appear to attack within Coccinellinae, Epilachninae, and Chilocorinae. No species in Coccidulinae, Sticholotidinae, or Scymninae are known hosts of Coccipolipus. Several additional parasite–host associations have been reported recently for two widely distributed mites, Coccipolipus macfarlanei Husbands and Coccipolipus hippodamiae McDaniel and Morrill. Coccipolipus macfarlanei was found on Coccinella septempunctata L and on Coccinella undecimpunctata L in Iran (Hajiqanbar et al., 2007). Coccipolipus (Tetrailus) hippocamiae was recently found attacking several coccinellids in Europe, including Adalia decempunctata (L.), Synharmonia conglobata (L.), and Calvia quatuordecimguttata (L.) (Webberley et al., 2004). Most species are considered avirulent, having little or no impact on the population dynamics of their hosts (Knell and Webberley, 2004). Coccipolipus epilachnae Smiley parasitizes phytophagous coccinellids such as the Mexican bean beetle Epilachna varivestis Multisan (Epilachninae) (Schröder, 1979, 1982). However, the ability of C. epilachnae to suppress E. varivestis populations is doubtful (Cantwell et al., 1985; Hochmuth et al., 1987). The effects of C. hippocamiae on entomophagous coccinellids in Europe have been recently described. The fecundity and egg viability of three coccinellids, Adalia bipunctata, A. decempunctata, and S. conglobata, were significantly reduced by C. hippocamiae (Hurst et al., 1995; Webberley et al., 2004). This mite also increased overwintering mortality of A. bipunctata males (Webberley and Hurst, 2002; Webberley et al., 2006). Recently, Kenis et al. (2008) proposed the use of C. hippocamiae as a biocontrol agent within an integrated pest management program against the nuisance coccinellid, H. axyridis. Before this occurs, a risk assessment on the non-target implications of releasing this polyphagous mite seems warranted. As part of this risk assessment, the potential efficacy of the mite on H. axyridis fitness should be considered.

3. Pathogens

Ceryngier and Hodek (1996) commented that microorganisms attacking Coccinellidae are not well known, and this is still true today (Roy and Cottrell, 2008). As a whole, research on the natural interaction of coccinellids and their pathogens (as with the pathogens of most natural enemies) has received less attention than the pathogens of herbivorous pests, and most research concerns non-target effects of biorational insecticides on coccinellids. This notwithstanding, attention to recent advances in male-killing bacteria, fungi, and microsporidia merit discussion.

| Table 1 Parasitic Laboulbeniales of the genus Hesperomyces and their lady beetle hosts. |

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<td>Hippodamia convergens (USA)</td>
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<td>Eriopis connexa (Argentina)</td>
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<td>Cycloneda sanguinea (England)</td>
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<td>Psyllobora (+) sp. (France)</td>
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<td>Adalia bipunctata (southern Europe)</td>
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<td>Psyllobora vigintimaculata (USA)</td>
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suspected virus is thought to be transmitted vertically. Viruses infecting coccinellids are likely chronic and asymptomatic.

3.2. Protozoa: microsporidia and eugregarines

Brooks et al. (1980) reported gradual declination of an E. varivestis colony that had nearly 100% microsporidiosis caused by Nosema epilachnae Brooks, Hazard and Becnel and N. varivistis Brooks, Hazard and Becnel (Brooks et al., 1985). Mechanical transmission of N. epilachnae and N. varivistis between diseased and healthy E. varivestis is possible through oviposition by the parasite Pedidiobius foveolatus (Crawford) (Hymenoptera: Eulophidae); P. foveolatus is highly susceptible to N. epilachnae and N. varivistis (Owen and Brooks, 1986). Parasitoid females infected with N. varivistis were capable of transmitting this pathogen transovarially to F6 progeny at rates ranging from 6% to 70% (Owen and Brooks, 1986). The ability of P. foveolatus to facilitate transmission of the pathogen to a shared host may or may not further suppress E. varivestis populations.

Bjornson (2008) reported that 0.9% of winter-collected Hippodamia convergens adults (purchased from commercial suppliers) were infected with microsporidia, most likely Nosema hippocaudae Lipa & Steinhaus, N. tracheophila Cali & Briggs, and N. coccinellae Lipa. Joudrey and Bjornson (2007) found that infection reduced longevity and increased development rates of H. convergens. Both vertical and horizontal transmission of spores can be highly efficient. Saito and Bjornson (2006) reported 100% horizontal transmission of an unidentified microsporidium from H. convergens to larval C. septempunctata, Coccinella trifasciata perplexa Mulsant, and H. axyridis when these larvae consumed infected H. convergens eggs. Thus, human redistribution of H. convergens for aphid control outside of its native range may introduce new microsporidia to previously unexposed coccinellid species. Interestingly, of the coccinellids tested for horizontal transmission, invasive species may be less affected by microsporidian infection than native ones (Saito and Bjornson, 2006, 2008).

Eugregarine protozoans (Apicomplexa: Gregariniia: Eugregarinida) are mostly pathogenic of annelids and arthropods, but some are commensals or even mutualists. They are extracellular and suspected to be transmitted vertically. Viruses infecting coccinellids are likely chronic and asymptomatic.

3.3. Fungi

Field data on the impact of natural fungal pathogens attacking coccinellids is limited but suggests that natural infection levels are less than 20% (Ceryngier, 2000; Beyene et al., 2007). Beauveria bassiana (Balsamo) (Ascomycota: Hypocreales: Clavicipitaceae) is a generalist pathogen most often reported infecting phytophagous (Uma Devi et al., 2008) and entomophagous (Roy and Cottrell, 2008) coccinellids. Larvae of the phytophagous Epilachna vigintioctomaculata F. and Henosepilachna vigintioctomaculata (Motschulsky) are susceptible to B. bassiana (Kuznetsov, 1997; Uma Devi et al., 2008). Even though H. vigintioctomaculata field populations were decimated by fungal pathogens during the 1960s, only about 6% of H. vigintioctomaculata were found infected in the field at two subsequent points in time (Kuznetsov, 1997).

Field observations by Cottrell and Shapiro-Ilan (2003) led to a series of experiments testing an apparent endemic B. bassiana against native and exotic entomophagous coccinellids. This B. bassiana was collected from small aggregations of overwintering Olla v-nigrum Mulsant under tree bark where some dead individuals exhibited B. bassiana mycosis. However, B. bassiana infection also was detectable on non-overwintering O. v-nigrum during the spring and fall with 4% and 38% mycosis, respectively. Harmonia axyridis collected from the same habitats and at the same time as O. v-nigrum had low mortality and none were infected with B. bassiana indicating possible differential susceptibility between this introduced species and the native O. v-nigrum. Summer collections of both species from the same vicinity five years later revealed the same trend with 9% of O. v-nigrum having B. bassiana mycosis but none for H. axyridis (TEC, unpublished data). Thus, specific strains of B. bassiana may be better-adapted to infecting certain native species as shown by Cottrell and Shapiro-Ilan (2003, 2008). They documented that isolates of B. bassiana, from naturally infected O. v-nigrum, were pathogenic to the native species O. v-nigrum, C. munda, and H. convergens but not to the native C. maculata or the exotic H. axyridis. Their studies used much lower conidia rates (i.e., the predetermined LD50 of 2.5 x 10^5 conidia/ml against O. v-nigrum) in their assays compared with studies that assay non-target impacts of fungal products using from 10^7 to 10^8 conidia/ml (Haseeb and Murad, 1997; James et al., 1998; Poprawski et al., 1998; Cagàñ and Uhlik, 1999; Todorova et al., 2000). When non-coccinellid sources of B. bassiana (i.e., strain GHA and BbAR1) were tested at 2.5 x 10^8 conidia/ml, there was little activity against C. maculata. C. munda, H. convergens, or O. v-nigrum (Cottrell and Shapiro-Ilan, 2008). In another example of differential susceptibility among species, Todorova et al. (2000) found that C. maculata was differentially susceptible to B. bassiana isolates. Susceptibility depends on rates of inoculum; for example, Roy et al. (2008) used high rates of B. bassiana (strain GHA) conidia (>10^8 per ml) to achieve an LD50 against H. axyridis in contrast to rates used by Cottrell and Shapiro-Ilan (2003). It is probable that H. axyridis is resistant to endemic B. bassiana within introduced regions, as demonstrated by Cottrell and Shapiro-Ilan (2003, 2008); but within its native range, Kuznetsov (1997) reports that H. axyridis was found naturally infected by Beauveria spp. Coccinellid mortality resulting from B. bassiana infection does occur naturally but has not clearly been shown to regulate populations.

Fungi other than B. bassiana are also reported from Coccinellidae (Bjornson, 2008). Ceryngier (2000) found overwintering populations of C. septempunctata in Poland also infected by Paecilomyces farinosus (Holm & Gray), Verticillium lecanii (Zimmerman), and Cephalosporium sp. Bot V. lecanii and Cephalosporium sp. were found to be weak pathogens, whereas P. farinosus was intermediate and B. bassiana was highly virulent against C. septempunctata. Although two species of Metarhizium are used widely, there is surprisingly little information on their impact on coccinellid populations (but see Peveling and Demba, 1997; Ginsberg et al., 2002).

3.4. Bacteria

Most studies on bacterial infections of Coccinellidae concern male-killing bacteria (Hurst et al., 1994, 1996, 1997, 1999a,b,c; Majerus et al., 1998, 2000b; Majerus and Majerus, 2000; Schultenburg et al., 2001; Sokolova et al., 2002; Dyson and Hurst, 2004; Nakamura et al., 2005). Male-killing agents include Rickettsia, Spiroplasma, Wolbachia, flavobacteria, γ-proteobacteria, and some yet to be identified agents (Majerus, 2006). Maternally inherited bacteria kill males during early embryogenesis, and infection provides an adaptive advantage for female offspring that feed on unhatched male eggs. Entomophagous species infected by one or more of these agents are in the genus Adalia, Adonia, Anisosticta, Calvia, Chelomenes, Coccinella, Coccinula, Coleomegilla, Harmonia, Hippodamia, and Propylea from Africa, Asia, Europe, and North
America (Majerus, 2006). Coccinellids are not only affected by male-killing bacteria. Hall and Badgley (1957) implicate an infection of Rickettsiella stethorae as killing the larvae of five cultured Stethorus spp.

A few reports indicate that phytophagous coccinellids are attacked by bacteria. Ping et al. (2008) reported that a WZ-9 strain of Bacillus thuringiensis Berliner was harmful to H. vi­gintioctopunctata larvae but not adults. The LC50 to second instars was 2.95 × 10³ cells/ml after 72 h. Otzu et al. (2003) reported that the chitinase secreting strain (KPM-012A) of the bacteria Alcaligenes paradoxus Davis had a suppressive effect on E. vigintioctopunctata adults. A suspension of A. paradoxus (entrapped in alginate beads) inhibited feeding and oviposition but had no effect on longevity of E. vigintioctopunctata.

3.5. Nematodes

Unlike endoparasitic nematodes, the entomopathogenic Steiner­nema and Heterorhabditis nematode spp. can be highly virulent to susceptible hosts causing death within 24–48 h after infection. Shapiro-Ilan and Cottrell (2005) reported lower susceptibility for both the exotic H. axyridis and C. septempunctata than for the native C. maculata and O. n-v-nigrum to the nematodes Steinernema carpocapsae (Weiser) and Heterorhabditis bacteriophora Poinar. Given their foraging ecology, it seems unlikely that entomopathogenic coccinellids will be frequent hosts of soil-borne entomopathogenic nematodes. Abdel-Moniem and Gesraha (2001) reported that fourth instar larvae of the phytophagous Epilachna chrysonemelina F. experienced 65%, 44%, and 84% mortality when exposed to squash seedlings treated with formulations of Heterorhabditis tay­sareae Shamseldain, H. bacteriophora (strain Hp88), and S. carpo­capsae (strain S2), respectively.

4. Parasitoids

Coccinellids are attacked in all life stages by nearly 100 species of parasitoids, which primarily belong to the orders Hymenoptera and Diptera (Ceryngier and Hodek, 1996). Most reports are host records with scant data on population dynamics or ecological impact.

4.1. Hymenopterous parasitoids of phytophagous coccinellids

The effects of parasitoids on populations of phytophagous Epi­lachninae have been documented more often than on entomophagous species. In the eastern USA, augmentative releases of P. foveolatus have been used to provide control of E. varivestis on soy­beans and other legume plantings (Fess, 2008). Pedioius foveolatus provides control of the introduced Epilachna vigintioctopunctata (Boisdulau) feeding on solanaceous crops in Guam. Although the beetle remains present, P. foveolatus also persists, reducing the need for additional control measures (Vargo and Schreiner, 2000). Parasitoids commonly attack immature life stages of Hen­osehipacha vigintioctopunctata F. on Solanum melongena (brinjal) and eggplant in India where parasitism rates vary over the year, but can approach substantial reductions (as high as 38% of eggs and 68% of larvae) (Raju and Uma Maheswari, 2005; Hussain et al., 2006).

Parasitoids may not provide economic control, in spite of high parasitism rates of phytophagous coccinellids. In Ethiopia, although the egg parasitoid Oenocyrus epulus Annecke (Hymen­optera: Encyrtidae) and the pupal parasitoids P. foveolatus and Mesopo­lopus sp. (Hymenoptera: Pteromalidae) were key mortality factors of Cha­nootriba similis, the parasitoids did not reduce pest populations below economically damaging levels (Beyene et al., 2007). Similarly, in Indonesia, 36% egg parasitism by Tetrastichus sp. against Epilachna sp. nr. sparsa (Herbst) was not sufficient to prevent lethal defoliation of Momordica charantia (bitter cucumber) (Abbas and Nakamura, 1985).

4.2. Hymenopterous parasitoids of entomophagous coccinellids

Few parasitoids of entomophagous coccinellids are specialists, some are widely distributed and attack within a subfamily or tribe. One of the best understood parasitoids is Dinocampus (Perilus) coccinellae Schrank (Hymenoptera: Braconidae), whose host preference, life history, ecology, and behavior have been thoroughly investigated (Ceryngier and Hodek, 1996; Majerus, 1997; Majerus et al., 2000a; Okuda and Ceryngier, 2001; Al Abassi et al., 2001; Davis et al., 2006; Firlej et al., 2006; Koyama and Majorus, 2008). Adult coccinellids are preferred, especially older females (Majerus et al., 2000a; Davis et al., 2006), but immature parasitoids have been found in host larvae and pupae (Geoghegan et al., 1998). As a solitary endoparasitoid of adults, D. coccinellae prefers larger species of Coccinellinae (Ceryngier and Hodek, 1996). Coccinellids vary in their suitability as hosts for D. coccinellae (Orr et al., 1992; Firlej et al., 2006; Koyama and Majorus, 2008), but the mechanisms that influence realized rates of parasitism of various coccinellid species are unknown for many species. Comparing primary and secondary parasitism rates suggests that at least some coccinellids are able to overcome parasitoid larvae (Hoogendoorn and Heimpel, 2002; Koyama and Majorus, 2008). Although much of the biology of D. coccinellae has been determined in the laboratory, further field studies on its impact on population dynamics and ecology of coccinellid communities are warranted. This is especially true when exotic species invade new biotas where they alter coccinellid communities.

A number of other Hymenoptera are larval or larval/pupal parasitoids of entomophagous coccinellids. Oomyzus scaposus (Thom­son) (Hymenoptera: Eulophidae) is a widely distributed gregarious parasitoid of coccinellids. It has a wide host range that includes Coccinellinae, Chilocorinae, and Scymninae (Ceryngier and Hodek, 1996), including H. axyridis (Kuznetsov, 1997). Females lay eggs in third and fourth instars, and adult wasps emerge from pupal mummies. Forty-four percent of 48 H. axyridis pupae collected in North Carolina, USA, were parasitized by O. scaposus (KAK, unpublished data). Other parasitoids present were Homalotylus terminalis (Say) (Hymenoptera: Encyrtidae), Aprostocetus neglectus (Domenichini) (Hymenoptera: Eulophidae), and Pachyneuron altiscutum Cook (Hymenoptera: Pteromalidae). Several species of the genus Homalotylus have been recorded as parasitoids of coccinellid larvae in the subfamilies Coccinellinae, Chilocorinae, and Scymninae (Ceryngier and Hodek, 1996). Many have wide host ranges and the rate of parasitism can reach 90–95% within a population (Ceryngier and Hodek, 1996; Kenis et al., 2008). Aprostocetus neglectus specializes on hosts in the subfamily Chilocorinae in Eurasia, North Africa and North America (Ceryngier and Hodek, 1996). In eastern North America A. neglectus attacks Chilocorus kuwanneae (Silvestri), which was imported for biological control of euonymus scale Unaspis euonymi (Comstock) (Nalepa et al., 1993; Matadha et al., 2003), although the implications of this parasitoid for North American chilocorines are largely unknown.

4.3. Dipteran parasitoids of phytophagous and entomophagous coccinellids

Strongygaster triangulifer (Loew) (Diptera: Tachinidae) is common in North America and has been found in coccinellids and a variety of other adult Coleoptera and numerous other insect orders. This tachinid exploits novel hosts, but because it attacts low numbers within a population (usually less than 10%) it is not likely a key mortality factor for any of its coccinellid hosts. Smith
and Kok (1983) noted that of 20 reported hosts of *S. triangulifera* in North America, nine were introduced species.

*Strongygastrer triangulifer* parasitizes the phytophagous *Epi-
lachna* spp., including *E. varivestis*, as well as several species of
tautomorphic Coccinellinae (Katsyannos and Alinizee, 1998; 
Nalepa and Kidd, 2002). In North Carolina, aggregating *H. axyridis*
were sampled for parasitoids over seven years (Nalepa and Kidd,
2002). In 1992, parasitism in aggregating beetles averaged 14.2%
(range, 3–31%) but dropped below 5% for each of the next six years
(Nalepa and Kidd, 2002) and does not regulate the populations
(Koch and Galvan, 2008; KAK, unpublished data). Similarly, 15.4% 
and 11.4% of overwintering *H. axyridis* were parasitized by *S. trian-
gulifer* in Oregon, USA during 1997 (Katsyannos and Alinizee,
1998).

Dipteran pupal parasitoids in the family Phoridae attack ento-
morphic coccinellids in Europe and Asia (Ceryngier and Hodek,
1996). Two common species, *Phalacrotophora berolinensis* Schmitz
and *P. fasciata* Fallen, parasitize up to 80% of individuals of some
species of Coccinellinae and Chlorocorinae (Ceryngier and Hodek,
sp. from 17.7% of 249 *H. axyridis* pupae collected in Japan. In
another year, about 10% of pupae were parasitized (Osawa, 1992).
*Phalacrotophora beuki* Disney appears to be a specialist of *Anatis
cellata* (L.) in Scots pine forests in central Poland (Durska et al.,
2003). From 35% to 40% of *A. ocellata* pupae were parasitized by
*P. beuki* in samples collected from 1998 to 2000 (Durska et al.,
2003). *Phalacrotophora philosyridis* Disney parasitized *H. axyridis*
in Japan, but additional work on host range is necessary before this
can be a viable candidate for biological control of *H. axyridis* (Kenis
et al., 2008).

5. Concluding remarks

Differences in the behavior, biology, and ecology of phytopha-
gous versus entomophagous coccinellids may affect attack by nat-
ural enemies. Typically sedentary and found on fewer plant
species, phytophagous species contrast with highly mobile ento-
morphic species found on many plant species. Thus, increased
mobility and dispersal of entomophagous species could decrease
efficiency of host finding by parasitoids and increase the need for
parasitoids to attack several host species. Field epizootics within
the Coccinellidae are not known, but clumped field populations
of phytophagous coccinellids may be subject to conditions favor-
able for the development of epizootics. Some entomophagous spe-
cies congregate to overwinter, thereby increasing transmission of
pathogens and parasites. The propensity of entomophagous males
to repeatedly attempt to copulate with con- and heterospecific
males and females under field conditions may facilitate the spread
of parasitic fungi and mites through populations of susceptible
species.

The role that natural enemies play in the population dynamics
of the Coccinellidae needs to be better defined for both entomoph-
agous and phytophagous species. The inability of natural enemies
to regulate coccinellid populations was reported by Hodek (1973)
and reiterated by Majerus (1994) and Ceryngier and Hodek
(1996). Overall, current research has not demonstrated otherwise
except that one parasitoid wasp (*P. foveolatus*) apparently has the
potential to alter the population dynamics of a phytophagous cocc-
ineid (Vargo and Schreiner, 2000). The ability of *P. foveolatus* to
facilitate transmission of a microsporidian (*N. varivestis*) to a
shared host (Own and Brooks, 1986) may or may not further sup-
press host populations. One parasitoid *B. foveolatus* may have the
potential to limit populations of an entomophagous coccinellid in
pine forests (Durska et al., 2003), but further host specificity test-
ing is necessary. Ectoparasitic fungi or ectoparasitic mites are not
likely to alter the population dynamics of their coccinellid hosts.
Nevertheless, an ectoparasitic mite (*C. epilachnae*) has been consid-
ered as a potential biological control agent of a phytophagous cocc-
ineid (Schroder, 1982). Recently, an ectoparasitic mite (*C. hippocam-
dis*) within an IPM framework (Kenis et al., 2008). A research pro-
gram to address this proposition is needed but is complicated
given the value of *H. axyridis* as an important predator of stern-
orrhyxious pests in agricultural landscapes and the low host spe-
cialization of the mite.

More research is necessary to determine the capacity of coccin-
ellids to defend themselves against attack from their natural ene-
 mies. Coccinellides rely heavily on chemical defense (commonly
accompanied by warning coloration) to thwart attacks from verte-
brate and invertebrate predators (Majerus et al., 2007; Pasteels,
2007). The role of defensive compounds in protection of coccinell-
ids against parasites, pathogens, and parasitoids remains largely
unknown. A variety of parasitoids are found attacking different life
stages of coccinellids in spite of their many defense mechanisms.
In fact, one species (*D. coccinella*) uses the defensive compounds of
its host as a kairomone (Al Abassi et al., 2001). The ability to mount
a humoral or cellular immune response against their enemies has
not been demonstrated for most species.

Most reports of parasitoids present only a host record with little
data about the impact on populations of entomophagous species
and, by extension, their impact on the benefit provided by these
coccinellids as biological control agents. Many of the parasitoids
have broad host ranges or in some cases are restricted to attacking
many members of a single tribe or subfamily. This is advantageous
for parasitoids of Epilachninae because all of these species are phy-
tophagous and many are economically important crop pests. Fur-
ther research is needed to understand the impact of native
parasitoids on introduced entomophagous coccinellids, such as *H.
axyridis* and *C. septempunctata*.

Protocols for pre-release tests of field-collected lady beetles are
needed. Each year countless *H. convergens* adults are harvested
from overwintering sites in California destined for use in augmenta-
tive biological control of aphids in agriculture and home gardens
in the USA and Canada (Bjornson, 2008). This practice may result in
unintended dispersal of coccinellid natural enemies outside of na-
tive ranges with unknown impacts on previously unexposed cocc-
ineid species. Human involvement in the spread of coccinellid
pathogens can undermine the success of biological control pro-
grams and the integrity of native coccinellid communities.

This review has shown that parasites, pathogens, and parasit-
oids have limited potential of regulating the population dynamics
of coccinellids when acting alone. Perhaps, the action of multiple
natural enemies acting together on the same host population could
provide a greater impact on host dynamics than any one species
acting alone. Finally, the benefits and limitations of incorporating
effective natural enemies into an IPM framework to manage pestif-
erous and nuisance coccinellids need to be assessed.

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Wolbachia
Wolbachia
Xeniosporidium