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PII: S1049-9644(09)00147-9
DOI: 10.1016/j.biocontrol.2009.05.008
Reference: YBCON 2293

To appear in: *Biological Control*

Received Date: 6 January 2009
Revised Date: 18 May 2009
Accepted Date: 26 May 2009

Please cite this article as: Riddick, E.W., Cottrell, T.E., Kidd, K.A., Natural Enemies of the Coccinellidae: Parasites, Pathogens, and Parasitoids, *Biological Control* (2009), doi: 10.1016/j.biocontrol.2009.05.008

Natural Enemies of the Coccinellidae: Parasites, Pathogens, and Parasitoids

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Abstract

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.

Keywords: *Beauveria bassiana*, *Coccipolipus hippodamiae*, *Dinocampus coccinellae*, *Hesperomyces virescens*, *Pediobius foveolatus*, *population dynamics*

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 & 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 parasitic 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.

1. Parasites

Parasites of lady beetles can be loosely grouped as endo- and ecto-parasites. 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.

1.1. Parasitic fungi. The order Laboulbeniales contains ascomycetous fungi that parasitize arthropods. Approximately 80% of the 2,000 described laboulbenialean 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 con- and heterospecific 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 *H. virescens* caused premature mortality when it infected up to 95% of the adults of the coccinellid *Chilocorus bipustulatus* in Israel (but see Applebaum et al., 1971). Numerous *H. virescens* thalli concentrated around the host's (*H. axyridis*) mouthparts, head or antennae, can hamper the detection of food, mates or predators (Nalepa and Weir, 2007). Additionally, infected females mate less frequently (Nalepa and Weir, 2007). Apparently, there is little evidence to suggest that laboulbenialean parasites have significant effects on coccinellid populations.

1.2. Parasitic mites. Acarine parasites in the family Podapolipidae are biotrophic and commonly attack beetles. Although most species live ectoparasitically underneath the elytra of their hosts, some are endoparasites found in host reproductive organs or tracheal systems (Hajiqanbar et al., 2007). Their horizontal transmission is greatly facilitated via social contact between mating (Knell and Webberley, 2004) or overwintering coccinellid hosts (Webberley and Hurst, 2002).

The 14 species that attack lady beetles are confined to the genus *Coccipolipus* (Husband, 1984; Ceryngier and Hodek, 1996). Husband (1984) stated that some mite species may be quite specific within a host clade. For example, *Coccipolipus chilocori* Husband has been discovered attacking five central African *Chilocorus* species, but not other sympatric coccinellids. Most *Coccipolipus* species 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* Husband 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* (*Tetrapolipus*) *hippodamiae* 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* Mulsant (Epilachninae) (Schroder, 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 *Coccipolipus hippodamiae* on entomophagous coccinellids in Europe have been recently described. The fecundity and egg viability of three coccinellids, *A. bipunctata*, *A. decempunctata*, and *S. conglobata*, were significantly reduced by *C. hippodamiae* (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. hippodamiae* 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.

2. 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.

2.1. Viruses. No reports of viral infection in entomophagous Coccinellidae could be found. Kitajima et al. (1985) reported the presence of Reovirus-like particles from the phytophagous *E. varivestis*. These apparently latent, virus-like particles were found in nurse cells of the ovariole, oocytes, egg cytoplasm, and sperm nuclei. This suspected virus is thought to be transmitted vertically. Viruses infecting coccinellids are likely chronic and asymptomatic.

2.2. Protozoa: Microsporidia and Eugregarines. Brooks et al. (1980) reported gradual decimation of an *E. varivestis* colony that had nearly 100% microsporidiosis caused by *Nosema epilachnae* Brooks, Hazard and Becnel and *N. varivestis* Brooks, Hazard and Becnel (Brooks et al., 1985). Mechanical transmission of *N. epilachnae* and *N. varivestis* between diseased and healthy *E. varivestis* is possible through oviposition by the parasitoid *Pediobius foveolatus* (Crawford) (Hymenoptera: Eulophidae); *P. foveolatus* is highly susceptible to *N. epilachnae* and *N. varivestis* (Own and Brooks, 1986). Parasitoid females infected with *N. varivestis* were capable of transmitting this pathogen transovarially to F_6 progeny at rates ranging from 6 to 70% (Own 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.

Bjørnson (2008) reported that 0.9% of winter-collected *H. convergens* adults (purchased from commercial suppliers) were infected with Microsporidia, most likely *Nosema hippodamiae* Lipa & Steinhaus, *N. tracheophila* Cali & Briggs and *N. coccinellae* Lipa. Joudrey and Bjørnson (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 Bjørnson (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 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 Bjørnson, 2006, 2008).

Eugregarine protozoans (Apicomplexa: Gregarinia: Eugregarinida) are mostly pathogens of annelids and arthropods, but some are commensals or even mutualists. They are extracellular and are found in the digestive tracts and body cavities of hosts (Tanada and Kaya, 1993). Bjørnson (2008) reported that 0.2% of winter-collected *H. convergens* purchased from commercial suppliers were infected with eugregarines. Three different-sized eugregarines were collected, but none were identified. Saito and Bjørnson (2008) found three unidentified eugregarines in two *A. bipunctata* adults. These protozoans probably have little impact on populations of entomophagous coccinellids. Eugregarine protozoans of phytophagous species are not reported.

2.3. 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, 2007) coccinellids. Larvae of the phytophagous *Epilachna vigintioctopunctata* 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 1960's, 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 LC_{50} of 2.5×10^5 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 10^9 conidia/ml (Haseeb and Murad, 1997; James et al., 1998; Poprawski et al., 1998; Cagáň and Uhlík, 1999; Todorova et al., 2000). When non-coccinellid sources of *B. bassiana* (i.e., strain GHA and BbAR1) were tested at 2.5×10^5 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 LD_{50} 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 (Bjørnson, 2008). Ceryngier (2000) found overwintering populations of *C. septempunctata* in Poland also infected by *Paecilomyces farinosus* (Holm & Gray), *Verticillium lecanii* (Zimmerman) and *Cephalosporium* sp. Both *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).

2.4. Bacteria. Most studies on bacterial infections of Coccinellidae concern male-killing bacteria (Hurst et al., 1994; Hurst et al., 1996; Hurst et al., 1997; Hurst et al., 1999a; 1999b; 1999c; Majerus et al., 1998; Majerus and Majerus, 2000; Majerus et al., 2000b; Schulenburg et al., 2001; Sokolova et al., 2002; Dyson and Hurst, 2004; Nakamura et al., 2005). Male-killing agents include *Rickettsia*, *Spiroplasma*, *Wolbachia*, Flavobacteria, γ-proteobacterium, 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, Cheilomenes, 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. vigintioctomaculata* larvae but not adults. The LC_{50} to second-instar larvae was 2.95 x 10^7 cells/ml after 72 h. Otsu 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*.

2.5. Nematodes. Unlike endoparasitic nematodes, the entomopathogenic *Steinernema* and *Heterorhabditis* nematode spp. can be highly virulent to susceptible hosts causing death within 24-48 hr after initial 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. v-nigrum* to the nematodes *Steinernema carpocapsae* (Weiser) and *Heterorhabditis bacteriophora* Poinar. Given their foraging ecology, it seems unlikely that entomophagous coccinellids will be frequent hosts of soil-borne entomopathogenic nematodes. Abdel-Moniem and Gesraha (2001) reported that fourth instar larvae of the phytophagous *Epilachna chrysomelina* F. experienced 65, 44, and 84% mortality when exposed to squash seedlings treated with formulations of *Heterorhabditis taysearae* Shamseldean, *H. bacteriophora* (strain Hp88) and *S. carpocapsae* (strain S2), respectively.

3. 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.

3.1. 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 *Pediobius foveolatus* have been used to provide control of *E. varivestis* on soybeans and other legume plantings (Fess, 2008). *P. foveolatus* provides control of the introduced *Epilachna viginsexpunctata* (Boisduval) 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 *Henosepilachna viginitioctopunctata* F. on *Solanum melongena* (brinjal/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 *Ooencyrtus epulus* Annecke (Hymenoptera: Encyrtidae) and the pupal parasitoids *P. foveolatus* and *Mesopolobus* sp. (Hymenoptera: Pteromalidae) were key mortality factors of *Chnootriba 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 charntia* (bitter cucumber) (Abbas and Nakamura, 1985).

3.2. 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 (Perilitus) coccinellae* Schrank (Hymenoptera: Braconidae), whose host preference, life history, ecology and behavior of have been thoroughly investigated (Ceryngier and Hodek, 1996; Majerus, 1997; Majerus et al., 2000a; Okuda and Ceryngier, 2000; Al Abassi et al., 2001; Davis et al., 2006; Firlej et al., 2006; Koyama and Majerus, 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 Majerus, 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 Majerus, 2008). Although much of the biology of *D. coccinellae* has been determined in the lab, 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 3rd and 4th 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, unpubl. 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 kuwanae* (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.

3.3. 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 attacks 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. triangulifer* in North America, nine were introduced species.

Strongygaster triangulifer parasitizes the phytophagous *Epilachna* spp., including *E. varivestis*, as well as several species of entomophagous Coccinellinae (Katsoyannos and Aliniazee, 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, unpubl. data). Similarly, 15.4% and 11.4% of overwintering *H. axyridis* were parasitized by *S. triangulifer* in Oregon, USA during 1997 (Katsoyannos and Aliniazee, 1998).

Dipteran pupal parasitoids in the family Phoridae attack entomophagous 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 Chilocorinae (Ceryngier and Hodek, 1996; Hurst et al., 1998). Osawa (1992) reared *Phalacrotophora* 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 ocellata* (L.) in Scots pine forests in central Poland (Durska et al., 2003). From 35-40% of *A. ocellata* pupae were parasitized by *P. beuki* in samples collected from 1998-2000 (Durska et al., 2003). *Phalacrotophora philaxyridis* 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).

4. Concluding remarks.

Differences in the behavior, biology and ecology of phytophagous versus entomophagous coccinellids may affect attack by natural enemies. Typically sedentary and found on fewer plant species, phytophagous species contrast with highly mobile entomophagous 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 favorable for the development of epizootics. Some entomophagous species 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 entomophagous 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 coccinellid (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 suppress host populations. One parasitoid fly (*P. beuki*) may have the potential to limit populations of an entomophagous coccinellid in pine forests (Durska et al., 2003), but further host specificity testing 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 considered as a potential biological control agent of a phytophagous coccinellid (Schroder, 1982). Recently, an ectoparasitic mite (*C. hippodamiae*) has been identified that might aid in the suppression of populations of an invasive entomophagous coccinellid (*H. axyridis*) within an IPM framework (Kenis et al., 2008). A research program to address this proposition is needed but is complicated given the value of *H. axyridis* as an important predator of sternorrhynchan pests in agricultural landscapes and the low host specialization of the mite.

More research is necessary to determine the capacity of coccinellids to defend themselves against attack from their natural enemies. Coccinellids rely heavily on chemical defense (commonly accompanied by warning coloration) to thwart attacks from vertebrate and invertebrate predators (Majerus et al., 2007; Pasteels, 2007). The role of defensive compounds in protection of coccinellids 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. coccinellae*) 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 phytophagous and many are economically important crop pests. Further 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 augmentative biological control of aphids in agriculture and home gardens in the USA and Canada (Bjørnson, 2008). This practice may result in unintended dispersal of coccinellid natural enemies outside of native ranges with unknown impacts on previously unexposed coccinellid species. Human involvement in the spread of coccinellid pathogens can undermine the success of biological control programs and the integrity of native coccinellid communities.

This review has shown that parasites, pathogens, and parasitoids 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 pestiferous and nuisance coccinellids needs to be assessed.

Acknowledgments

Don Weber and Jonathan Lundgren reviewed and commented on an earlier version of this manuscript. We thank J. Lundgren and D. Weber for inviting us to write this manuscript. Two anonymous reviewers provided useful comments that improved the text. The United States Government has the right to retain a non-exclusive, royalty-free license in and to any copyright of this article. This article reports the results of research only. Mention of a commercial or proprietary product does not constitute an endorsement of the product by the United States Department of Agriculture.

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

Hesperomyces species	Hosts and distribution	References
H. chilomenis (Thaxter)	*Cheilomenes lunata* (East Africa)	Thaxter, 1931
H. coccinelloides (Thaxter)	*Scymnus* sp. (West Indies)	Thaxter, 1931
	Scymnus tardus (West Indies)	Thaxter, 1931
	Scymnus sp. (Spain)	Santamaria, 1995
	Diomus sp. (Ecuador)	Castro and Rossi, 2008
H. hyperaspidis Thaxter	*Hyperaspis* sp. (West Indies)	Thaxter, 1931
H. virescens Thaxter	*Chilocorus stigma* (USA)	Thaxter, 1931
	Hippodamia convergens (USA)	Thaxter, 1931
	Eriopis connexa (Argentina)	Thaxter, 1931
	Chilocorus bipustulatus (Israel)	Kamburov et al., 1967
	Cycloneda sanguinea (England)	Tavares, 1979
	Psyllobora (= *Thea*) sp. (France)	Tavares, 1985
	Adalia bipunctata (southern Europe)	Weir, 1996
	Olla v-nigrum (Fiji)	Weir and Beakes, 1996
	Harmonia axyridis (USA)	Garcés and Williams, 2004
	Coccinella septempunctata (USA)	Harwood et al., 2006a
	Cycloneda munda (USA)	Harwood et al., 2006b
	Brachiacantha quadripunctata (USA)	Harwood et al., 2006b
	Psyllobora vigintimaculata (USA)	Harwood et al., 2006b