



## Lady beetles as predators of insects other than Hemiptera

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### ABSTRACT

Entomophagous lady beetles often prey on a variety of insects in addition to the Hemiptera (Sternorrhyncha) for which they are well-known natural enemies. Many species (particularly those well-adapted for consuming aphids) appear opportunistic in their use of non-hemipteran prey. Others may have evolved especially from aphidophagous habits to use non-hemipteran prey (particularly eggs and larvae of Coleoptera) as primary prey. Numerous field studies of lady beetles as both opportunistic and more specialized predators of non-hemipteran prey (e.g., immature stages of Lepidoptera and Coleoptera) collectively reveal wide variation from little to large impact both among prey species, and within single prey species in differing settings. Opportunistic species of lady beetles in particular are quite variable in their abilities to grow, develop, and reproduce on diets of non-hemipteran prey. They are also quite variable in prey preferences and in their apparent predilections to attack non-hemipteran prey. Additional studies of behavioral and numerical responses of different groups of lady beetles to different kinds of insect prey, and of the relative abilities of lady beetles to thrive on diets of non-hemipteran as well as hemipteran prey, are needed for further insights into the evolutionary basis and ecological significance of diet among entomophagous lady beetles. Such insights in turn will strengthen our ability to assess the impact of lady beetle predation in the population dynamics of non-hemipteran prey, and to capitalize on the potential of such impact by promoting lady beetle predation in the management of non-hemipteran insect pests.

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### 1. Introduction

Entomophagous lady beetles are well-known predators of Hemiptera Sternorrhyncha, including aphids, scale insects, whiteflies, psyllids, and allies. In addition, they attack a variety of other insects. Prominent prey are Thysanoptera, and eggs and larvae of Lepidoptera, Coleoptera, Hymenoptera and Diptera (Hoddek 1973, 1996; Gordon, 1985; Hagen, 1987; Majerus, 1994). In this review, I first survey the range of insect prey other than Sternorrhyncha attacked by lady beetles. I next review studies of the impact of lady beetle predation on these prey, and of the suitability of these prey for lady beetle growth, development and reproduction. This leads naturally to studies of prey selection, consumption rates, and functional and numerical responses of lady beetles attacking insects other than Hemiptera. I follow with a brief review of published efforts to incorporate and enhance biological control by lady beetles in IPM programs for pest insects in addition to Sternorrhyncha, and I conclude with summary observations on lady beetle diets as they include non-hemipteran prey.

### 2. Range of prey consumed

#### 2.1. Field observations

Most reported instances of predation on non-hemipteran insect prey involve members of the primarily aphidophagous tribe Coccinellini. Field observations, arising particularly in studies of pest insects, provide many examples. Warren and Tadic (1967), for example, reviewed early records and added observations of the highly polyphagous *Coleomegilla maculata* (De Geer) preying on eggs and larvae of natural populations of pest Lepidoptera, including the European corn borer (*Ostrinia nubilalis* (Hübner)), corn earworm (*Helicoverpa [Heliothis] zea* [Boddie]), fall armyworm *Spodoptera frugiperda* (J.E. Smith), and fall webworm *Hyphantria cunea* (Drury). Allen et al. (1970) reported larvae and adults of *Anatis ocellata* (L.) as frequent predators of larvae of the Jack-pine budworm, *Choristoneura pinus* Freeman (Tortricidae), noting (p. 61) that adults “stopped [1–2 cm] from the prey momentarily before moving forward and quickly snatching it in their mandibles.” Cook and Webb (1995) observed larvae of *Anatis labiculata* (Say) feeding on early instars of another lepidopteran forest pest, the gypsy moth (*Lymantria dispar* [L.]).

Coccinellids have also been reported frequently to prey on eggs and young larvae of Coleoptera, especially Chrysomelidae. Example prey include the cereal leaf beetle *Oulema melanopus* (L.) (Shade

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et al., 1970), Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Grodén et al., 1990; Cappaert et al., 1991), alfalfa weevil *Hypera postica* (Gyllenhal) (Essig and Michelbacher, 1933; Yakhontov, 1934), elm leaf beetle *Pyrrhalta luteola* (Mueller) (Weber and Holman, 1976), cottonwood leaf beetle *Chrysomela scripta* (F.) (Head et al., 1977), and the chrysomelid eucalypt defoliators *Paropsis atomaria* Oliver (Tanton and Kahn, 1978) and *Chrysophtharta bimaculata* (Oliver) (Elliott and de Little, 1980). Stuart et al. (2002) suggest coccinellids may be important predators of root weevil (*Diaprepes abbreviatus* [L.]) eggs and neonates in the citrus canopy before the weevil larvae drop to the soil. In yet another well-known use of coleopteran prey, coccinellids also attack each other as cannibals and intraguild predators (e.g., Takahashi, 1989; Yasuda and Shinya, 1997; Cottrell and Yeorgan, 1998a; Schellhorn and Andow, 1999; Snyder, 2009).

## 2.2. Gut and frass analyses

Methods that augment field observations also have revealed frequent coccinellid consumption of insect prey other than Sternorrhyncha (Weber and Lundgren, 2009b). The remarkable nineteenth century ecologist Forbes (1883) documented consumption of chinch bugs (*Blissus leucopterus* (Say); Hemiptera: Lygaeidae) in an Illinois cornfield by dissecting guts of larval and adult *Hippodamia convergens* Guerin and *H. glacialis glacialis* (F.). Putman (1964) examined frass as well as guts, and confirmed that nine species of Coccinellini characterized as aphidophagous indeed consumed primarily aphids (especially *Myzus persicae* [Sulzer]) and less frequently coccoids and mites in Ontario peach orchards. Six of these species also consumed other arthropods (including insects, among which could be recognized thrips, small nematocerosus dipterans, and coccinellid larvae). Triltsch (1997, 1999) found mostly aphid remains in the guts of *Coccinella septempunctata* L. collected from a variety of habitats throughout the growing season in Germany. However, he frequently found remains of other insects as well (Thysanoptera, Hymenoptera, Collembola, and larval Diptera and Coleoptera [including Coccinellidae]). Adults emerging in July, when aphid numbers were low, especially consumed non-aphid arthropods (in particular Thysanoptera; Triltsch, 1999). Using frass analysis, Davidson (2008) similarly found adults of *C. septempunctata*, *C. transversoguttata richardsoni* Brown and *H. convergens* to consume Thysanoptera (and also many larvae of the alfalfa weevil) in spring alfalfa fields in Utah.

Rapidly developing molecular methods have provided yet another means to assess lady beetle consumption of non-hemipteran prey. Rodríguez et al. (2005), for example, used ELISA to determine that 2% of *Scymnus suturalis* Thunberg individuals on Spanish olive trees had recently consumed (i.e., tested positive for proteins of) the pyralid *Euzophera pinguis* Haworth. PCR methods also can document coccinellid consumption of non-hemipteran insect prey such as eggs (Hoogendoorn and Heimpel, 2001; Greenstone et al., 2007; Weber and Lundgren, 2009a) that are not well detected by their remains in gut or frass analysis (Triltsch, 1999).

## 2.3. Population responses to prey

As illustrated by examples above, it appears that particularly coccinellid species focused on consuming aphids often expand their diet to include other insect prey upon encounter. This may happen especially when preferred prey are scarce or absent, as likely happens often with the boom-bust population dynamics of aphids (Gordon, 1985; Triltsch, 1999; Dixon, 2000; Sloggett and Majerus, 2000). In addition, however, some species of Coccinellini seemingly exploit eggs and larvae of Coleoptera as primary prey. These tend to be large lady beetle species, reflecting the relatively large size of their prey (Dixon and Hemptinne, 2001). During out-

breaks of the *Galerucella nymphaeae*-complex (Chrysomelidae) on cloudberry (*Rubus chamaemorus* L.) in bogs of northern Finland, *Coccinella hieroglyphica* L. can complete its life cycle by consuming *Galerucella* eggs and larvae (Hippa et al., 1976, 1978). Similarly, *Cleobara mellyi* Mulsant and *Harmonia conformis* (Boisduval) can complete their life cycles by consuming eggs and young larvae of the chrysomelid *C. bimaculata*, which served as the major if not sole food source for these predators during a field study of two eucalyptus plantations in Tasmania (Elliott and de Little, 1980; de Little et al., 1990).

Other lady beetles may be even more intimately associated with chrysomelid prey. Iwata (1932, 1965) found that in captivity, larvae of *Aiolocaria* (formerly *Leis*) *mirabilis* Motschulsky readily fed on immatures of numerous species of Chrysomelidae, Curculionidae, Lepidoptera and Hymenoptera, as well as on many species of aphids. In the field, however, the life cycle and habits of this predator appeared adapted particularly to exploit eggs and larvae of arboreal chrysomelids, including *Melasoma vigintipunctata* Scopoli and *Plagioderia distincta* Baly on willow (Iwata, 1932, 1965) and *Gastrolina depressa* Baly on walnut (Matsura, 1976). Hodek (1996) summarized field observations of *Calvia quindecimguttata* (F.) (and other lady beetles) feeding on *Melasoma aenea* L. and other chrysomelids as made by V. Kanervo in Finland, who concluded that *C. quindecimguttata* is a specialized feeder of chrysomelids and uses aphids only as secondary prey (Kanervo, 1940, 1946; as cited by Hodek, 1996). Another seeming chrysomelid specialist, from the Nearctic Region, is *Neoharmonia venusta* (Melsheimer), which completes its life cycle by attacking (and overcoming the defensive secretions of) larvae and pupae of the willow leaf beetle *Plagioderia versicolora* (Laicharteg) (Whitehead and Duffield, 1982).

It is interesting to consider how such unusual prey associations for coccinellids might evolve. Sloggett and Majerus (2000) suggest that the evolution of such novel diets among lady beetles may be driven primarily by prey (e.g., aphid) shortage early or late in the season, and may in turn lead to restricted habitat preferences. These authors note that initial inclusion of novel prey types can occur rapidly (as in the cited case of *Cheilomenes lunata* F. in Kenya expanding its aphid-dominated diet to include an introduced mealybug). In addition, Rana et al. (2002) have documented rapid improvement in the ability of aphidophagous lady beetles to grow and reproduce on a diet of a particular prey through artificial selection. The evolution of a non-hemipteran, insect diet may require little morphological specialization. Samways et al. (1997), for example, found no structural adaptations of the mandibles of *Aiolocaria mirabilis* or *Calvia quatuordecimguttata* [L.] for feeding on immature Coleoptera.

## 3. Impact of lady beetles on prey populations

### 3.1. Field assessment of predation

A surprisingly large number of field studies in recent decades have assessed the suppressive potential of lady beetles on numbers of insect prey other than aphids and allies, especially for pest species. Collectively, these studies document wide variation from little to heavy predation among prey species, as well as for single species of prey studied in multiple settings. A recurring theme, however, is that lady beetles often inflict high mortality, especially for eggs and young larvae of Lepidoptera and Coleoptera.

#### 3.1.1. *Coleomegilla maculata* and lepidopteran prey

Most attention has focused on *C. maculata* as a predator of pest eggs. Conrad (1959) used the presence of *C. maculata* frass to implicate this lady beetle as preying on 3–36% of European corn borer (ECB) egg masses laid weekly over the growing season in Delaware

cornfields. In Maryland, peak densities of *C. maculata* in corn coincided with peak densities of second generation ECB eggs and larvae (Coll and Botrell, 1991). In Iowa cornfields, however, numbers of *C. maculata* peaked very early in the growing season, and dropped dramatically before egg-laying by first generation ECB commenced (Bruck and Lewis, 1998). From observations of tagged ECB egg masses in field plots of sweet corn in Quebec, Hudon and LeRoux (1986) estimated yearly rates of egg predation (especially by *C. maculata*) between 1.6% and 11.2% over an 8-year period (1957–1964). Using sentinel ECB eggs masses placed into field plots, Andow and Risch (1985) found increasing rates of predation (especially by *C. maculata*) with increasing days after planting (DAP), with proportions of eggs masses preyed upon after 3 days of field exposure reaching 20–75% by 80–100 DAP. Predation was consistently greater in corn monocultures than in corn-bean-squash polycultures, likely reflecting that more *C. maculata* occurred in the former plots (see also Coll and Bottrell, 1995). In a subsequent assessment in Minnesota corn fields variously tilled, Andow (1992) found adults of *C. maculata* to consume only 0.2–11.6% of first generation ECB eggs. Among adults of eight aphidophagous lady beetle species collected from corn fields in Minnesota, only those of *C. maculata* ate large numbers of ECB eggs (Andow, 1990). Most other species failed to consume ECB eggs when provided in the lab, although they readily consumed neonate ECB larvae (Andow, 1990). Interestingly, Putman (1957) similarly found that *C. maculata* as both adults and larvae ate eggs of the oriental fruit moth, *Grapholitha molesta* (Busck), much more readily than did other aphidophagous lady beetles co-occurring with this insect pest in Ontario peach orchards.

Predation by *C. maculata* has also been assessed for another lepidopteran pest of corn, corn earworm. Cottrell and Yeargan (1998a) found greater predation of corn earworm eggs by *C. maculata* in weedy sweet corn plots in Kentucky than in weed-free plots. More *C. maculata* eggs and larvae occurred in the weedy plots, where *Acalypha ostryaefolia* Riddell (Euphorbiaceae) served as a preferred oviposition site and provided a refuge from egg cannibalism. Overall, very high percentages of sentinel corn earworm eggs pinned to corn plants in weedy and weed-free plots were preyed upon (40–60% every 3 h), with *C. maculata* (especially larvae) accounting for over half of this predation (Cottrell and Yeargan 1998a). Similar experiments in weed-free cornfields by Pfannenstiel and Yeargan (2002) yielded similarly high estimates of 53–97% predation of corn earworm eggs over 24-h exposure, with *C. maculata* again accounting for much (44–46%) of the predation. When Cottrell and Yeargan (1998b) experimentally removed pollen from sweet corn plots, significantly greater predation of sentinel corn earworm eggs (primarily by *C. maculata*) occurred during anthesis in one of two years in plots without versus with pollen (45% versus 25% every 3 h). The difference likely reflects that the highly pollinivorous *C. maculata* was diverted from attacking eggs in the presence of pollen (see also Lundgren et al., 2004).

### 3.1.2. *C. maculata* and coleopteran prey

Adults of *C. maculata* also can consume large numbers of Colorado potato beetle (CPB) eggs in potato fields. The appearance and activity of *C. maculata* adults in early season potato fields of eastern North America generally is well synchronized with and appears to be in response to CPB eggs and young larvae, rather than to aphids (Grodén et al., 1990; Hazzard et al., 1991; Hilbeck and Kennedy, 1996). Cage studies confirmed that *C. maculata* adults can significantly reduce populations of CPB eggs and small (but not large) larvae on potato plants at realistic densities (Grodén et al., 1990). Repeated censusing, and marking of newly laid CPB egg masses, enabled Hazzard et al. (1991) to estimate that 40–60% of first and second generation CPB eggs in Massachusetts were eaten by predators, especially adults of *C. maculata*. Hilbeck et al. (1997)

used muslin bags in North Carolina potato fields to exclude predators, and estimated that mean egg survivorship during two years was reduced from 69% to 26% by predators (especially *C. maculata*). There was no clear relation between egg density and intensity of predation. Such high rates of egg predation are very encouraging, but successful integration of native populations of *C. maculata* in CPB management programs will depend on other practices such as crop rotation and careful use of insecticides, as well as on initial CPB densities and landscape context (Grodén et al., 1990; Hazzard et al., 1991; Hilbeck and Kennedy, 1996; Hilbeck et al., 1997; Nault and Kennedy, 2000).

Considerable interest in lady beetle predation of chrysomelid beetles has been stimulated recently in North America by the possibility that these predators might interfere with establishment of *Galerucella calmariensis* L. and *Galerucella pusilla* Duftschmidt as classical biological control agents of purple loosestrife, *Lythrum salicaria* L. In a study prior to North American releases of these agents, Nechols et al. (1996) documented that throughout the summer in wetlands in central New York, about one-third of egg masses of the native *G. nymphaeae* L. in stands of loosestrife were preyed upon, most likely especially by *C. maculata*. Wiebe and Obrycki (2004) similarly found that 26% of sentinel egg masses of *G. pusilla* were preyed upon when placed on loosestrife for 48 h at intervals throughout the summer in Iowa wetlands; again *C. maculata* was likely a major predator (another study of Iowa wetlands, however, found very low levels of predation on eggs of *G. calmariensis*; Matos and Obrycki, 2007). In a Michigan wetland where predator densities were low but *C. maculata* was again the most abundant predator present, 10–27% of sentinel egg masses of *C. calmariensis* were preyed upon (Sebolt and Landis, 2004). Young *Galerucella* larvae are also vulnerable to predation by *C. maculata*. Sebolt and Landis (2002) found, however, that first instars of *G. calmariensis* escape predation by *C. maculata* by feeding in protected sites in shoot tips of loosestrife (but as herbivore density increases, some larvae may be forced into more vulnerable feeding sites). Overall, while *C. maculata* and other predators at times may inflict considerable mortality, it remains unclear whether they cause significant biotic interference for the establishment and spread of *Galerucella* spp. as biological control agents of purple loosestrife in North America (Sebolt and Landis, 2004).

### 3.1.3. Other Coccinellids

Lady beetles other than *C. maculata* have also attracted attention as potentially consuming significant numbers of coleopteran and lepidopteran prey. Shade et al. (1970) identified adults of *H. convergens* as well as of *C. maculata* as the primary biological agents responsible for high egg and larval mortality in field populations of the cereal leaf beetle in northern Indiana. Hippy et al. (1976) judged from field observations that feeding by larvae and adults of *C. hieroglyphica* was largely responsible for the nearly 100% mortality from egg to pupation in an outbreak population of *G. nymphaeae* in northern Finland in 1975; much predation was inflicted on the prey as larvae as well as eggs. Similar results were reported by Matsura (1976) for *Aiolocaria hexaspilota* (=mirabilis) Hope attacking the chrysomelid, *G. depressa*, on walnuts in Japan. De Little et al. (1990) estimated that 66–84% of *C. bimaculata* eggs and young larvae died, primarily from predation by *C. mellyi*, in populations infesting Tasmanian *Eucalyptus* plantations.

Measurements of field densities combined with results of lab feeding trials suggest significant predation on eggs and/or larvae of the following Lepidoptera: beet armyworm (*Spodoptera exigua* [Hübner]) in alfalfa fields of northern California by *H. convergens* (Ehler, 2007); *Spodoptera littoralis* (Boisduval) in Egyptian cotton fields by *Coccinella undecimpunctata* (Hassanein and Hamed, 1984); *Alabama argillacea* (Hübner) (Noctuidae) in Brazilian cotton fields (Gravena and Da Cunha, 1991) by various lady beetles;

*Rivula atimeta* Swinhoe (Noctuidae) in rice fields in the Philippines by *Micraspis nr. crocea* (Mulsant) (Van den Berg et al., 1992); *Pieris rapae* L. (Pieridae) on cabbage in New York by *Hippodamia variegata* (Goeze) as well as *C. maculata* (Schmaedick and Shelton, 2000); and the leafminer *Tuta absoluta* (Meyrick) (Gelechiidae) on Brazilian tomatoes (Miranda et al., 1998) by *Cycloneda sanguinea* (which is likely important as well in attacking *Leptinotarsa undecimlineata* Stål, on *Solanum lanceolatum* Cavanilles in Honduras; Cañas et al., 2002). In addition, the introduced *C. septempunctata* may have an adverse, non-target effect in consuming eggs and young larvae of endangered Lycaenidae in wet prairies of Ohio (Horn, 1991; see also Schellhorn et al., 2005). A similar situation may occur with Monarch butterflies attacked by *Harmonia axyridis* (Pallas) introduced to North America (Koch et al., 2003, 2005).

### 3.2. Field assessments of cannibalism

Field studies also have examined lady beetles as predators of conspecifics (and also as intraguild predators; e.g., Obrycki et al., 1998; Hoogendoorn and Heimpel, 2004; Snyder, 2009; Weber and Lundgren, 2009b). In field settings, non-sibling cannibalism by lady beetles larvae may occur especially when food is limited (e.g., Takahashi, 1989) rather than under less stressful conditions (e.g., Triltsch, 1997). Egg cannibalism by *C. maculata* occurred less frequently during anthesis in control plots (with pollen abundant as an alternate food) than in experimental plots of corn without pollen (the corn was detassled; Cottrell and Yeorgan, 1998a). Similarly, cannibalism (as well as IGP with *C. septempunctata* as prey) of eggs and fourth instars by *H. axyridis* was observed frequently on hibiscus trees in Japan, as *H. axyridis* larvae matured late in the season when aphids were scarce (Yasuda and Shinya, 1997). Larval and pupal cannibalism in field populations of *C. maculata*, *Adalia bipunctata* (L.) and *H. convergens* foraging on corn, occurred only after large aphid populations on the host plants had collapsed (Schellhorn and Andow, 1999).

## 4. Suitability of insect prey other than *Sternorrhyncha* for lady beetles

Field observations of lady beetles attacking prey can be misleading as indications of the suitability of the prey for the predator (Thompson, 1951). Hodek (1962) drew a broad distinction for lady beetles and other insect predators between essential prey that permit full development of the larval predator and full reproductive activity of the adult, versus alternative prey that serve only to sustain the predator over the short term in the absence of essential prey. There is of course much variation among prey species along the continuum of suitability between these endpoints (Hodek, 1996). Also, as further discussed below, suitability of any one prey species may vary as other items are included in a mixed diet, such as may often occur under natural conditions. Nonetheless, this basic conceptual framework remains highly useful when considering the feeding habits of lady beetles. It is intriguing and informative to consider in particular the degree to which different species of insect prey other than Hemiptera are suitable for larval growth and development and adult reproduction of lady beetles.

### 4.1. Larval growth and development

#### 4.1.1. Lepidoptera as prey

Understanding of the suitability of non-hemipteran prey has grown in part from use of moth eggs as an alternative to aphids or artificial diets in mass rearing of lady beetles. Eggs of the Mediterranean flour moth, *Ephestia (Anagasta) kuehniella* Zeller (Pyralidae), can be produced in vast quantities for rearing natural enemies such

as *Trichogramma* spp. and predatory hemipterans. Iperti et al. (1972) found these eggs also to be very suitable for producing multiple generations of *Coccinella decempunctata* L. (aphidophagous) and *Pharoscygnus semiglobosus* Karsch (coccidophagous). In subsequent studies, larval rates of development and survival, and weights of newly eclosed *H. axyridis* (Schanderl et al., 1988), *H. convergens* (Kato et al., 1999) and *Propylea japonica* (Thunberg) (Hamasaki and Matsui, 2006) were similar on diets of these eggs and pea aphids. Adult weights were markedly lower for *Ephestia*-reared *Semiadalia undecimnotata* Schneider (Schanderl et al., 1988), and higher for *A. bipunctata* (De Clercq et al., 2005). Red individuals of *H. axyridis* developed faster than black individuals when fed *Ephestia* eggs but not when fed pea aphids (Berkvens et al., 2008).

Another factitious prey (i.e., a host not naturally attacked by these predators) of potential for mass rearing of lady beetles is the egg of the grain moth *Sitotroga cerealella* Olivier (Gelechiidae). Olszak (1986) succeeded in rearing relatively large adults of *Propylea quatuordecimpunctata* (L.) on a diet of grain moth eggs. First instars appeared to have difficulty breaking the chorion of these eggs, however, and survivorship was increased significantly by feeding the first instars with *Acyrtosiphon pisum* before switching the larvae thereafter to a diet of grain moth eggs. Abdel-Salam and Abdel-Baky (2001) reared *H. axyridis* from egg to adult on *S. cerealella* eggs, with high survivorship and rates of development very similar to those reported for aphid diets. Rates of development of *Brumoides suturalis* (F.) were also normal but survivorship was reduced when larvae were provided with eggs of the potato-tuber moth, *Phthorimaea operculella* (Zeller) (Gautam, 1990).

Other researchers have evaluated the abilities of lady beetles to develop on diets of insect eggs (and in some cases, young larvae) consumed by these predators in nature. Warren and Tadic (1967) found larvae of *C. maculata* to mature readily on a diet of eggs (but not newly hatched first instars or immobilized second instars) of the fall webworm. Andow (1990) reported that larvae of *C. maculata* could complete development by eating only ECB eggs. This polyphagous lady beetle appears distinctive, however, in its ability to use ECB eggs. Larvae of other lady beetles common in Minnesota cornfields ate few ECB eggs under laboratory conditions (Andow, 1990). Similarly, Obrycki and Orr (1990) found that first instars of three lady beetles introduced to North America (*C. septempunctata*, *H. variegata*, and *P. quatuordecimpunctata*) failed to feed on these eggs, and rapidly died when provided the eggs as their sole diet. Musser and Shelton (2003) found that *H. axyridis* also could not develop on a diet of ECB eggs (furthermore, adults of *H. axyridis* ate fewer ECB eggs after several days than they did initially, when placed on a diet solely of these eggs). Reflecting the distinctive ability of *C. maculata*, Phoofolo and Obrycki (1997) reported similar rates of larval development and survivorship for this species on diets of ECB eggs and pea aphids, and greater weight as newly eclosed adults that fed on the eggs.

#### 4.1.2. Coleoptera as prey

Larvae of *C. maculata* were also able to develop on a diet solely of CPB eggs, but they did so with slower development and reduced survival than on diets of green peach aphids or corn pollen (Hazzard and Ferro, 1991). In particular, the chorion of CPB eggs may be difficult for young larvae of *C. maculata* to pierce with their mouthparts. Munyaneza and Obrycki (1998a) found very low survival as well as delayed development of *C. maculata* when transferred immediately upon hatching and placed on a diet of CPB eggs versus pea aphids. Survivorship improved and development was not delayed, however, if the larvae fed as first and second instars on pea aphids before they were transferred to CPB eggs. Intriguingly, larvae from Rhode Island populations of *C. maculata* survived better on CPB eggs than did larvae from Iowan and Honduran populations. This may reflect that *C. maculata* individuals are

better adapted to use CPB as prey in Rhode Island, where CPB is a major pest of potatoes (Munyanenza and Obyrcki, 1998a). Snyder and Clevenger (2004) found that larvae of four species of lady beetles (*C. transversoguttata*, *C. septempunctata*, *H. convergens* and *H. axyridis*) were unable to complete larval development when provided at hatching with a pure diet of Colorado potato beetle eggs.

Lady beetles naturally associated with other chrysomelids in some cases thrive on a larval diet of prey eggs and young larvae. Larvae of *Cleobora mellyi* and *H. conformis* readily completed development in the laboratory on a diet of eggs of the Tasmanian eucalypt defoliator *C. bimaculata* (Elliott and de Little, 1980). Bain et al. (1984) in New Zealand succeeded in rearing *C. mellyi* also on eggs of the eucalyptus tortoise beetle *Paropsis charybdis* Stål (as well as on diets of dried and ground tuberworm or cerambycid larvae mixed with vitamins, yeast, or sugar). Kagata et al. (2005) provided newly hatched larvae of *A. hexaspilota* Hope, a specialist predator of leaf beetles, initially with eggs and subsequently with larvae of the willow leaf beetle *P. versicolora*. Over 70% of the lady beetle larvae survived to pupate, with development time being especially short and weight of newly emerged adults greatest when the larvae were fed from prey taken from foliage of recently cut versus uncut willow trees (the mechanism underlying enhanced predator performance on such prey larvae, however, is not yet clear; Kagata and Ohgushi, 2007).

As with lepidopteran eggs, the chorion of chrysomelid eggs can reduce their suitability for larval lady beetles. Hippa et al. (1984) assessed larval performance of *C. hieroglyphica* in northern Finland when fed eggs and larvae of *Galerucella sagittariae* (Gyllenhal). First instars had difficulty breaking the *G. sagittariae* egg surface. Consequently they died in large numbers on a diet of eggs, but later instars developed at a relatively fast rate. Larvae fed with *G. sagittariae* larvae grew at rates comparable to larvae fed with eggs or either of two aphid species (*M. persicae* and the birch-dwelling *Symydobius oblongus* [von Heyden]), and in so doing had highest survivorship and achieved greatest pupal weights.

Other lady beetles appear to receive much less benefit from preying on immature stages of *Galerucella*. Although *C. maculata* has been identified as a major predator in eastern North America of eggs and larvae of the introduced biological control agents of purple loosestrife, *G. pusilla* and *G. californiensis*, larvae of this lady beetle perform poorly on these prey. Wiebe and Obyrcki (2002) recorded high mortality (especially of second instars), greatly prolonged development, and much smaller newly emerged adults of *C. maculata* when larvae fed on eggs of *G. pusilla* versus a mixed diet of pea aphids and eggs of *E. kuehniella*. Larvae of *C. maculata* failed to survive to the adult stage on diets of *G. californiensis* eggs or larvae (Matos and Obyrcki, 2006). Larvae of *H. axyridis* also failed to survive on a diet of *G. californiensis* eggs, and only 27% survived on a diet of *G. californiensis* larvae, with slow development and reduced size as adults (Matos and Obyrcki, 2006).

Kalaskar and Evans (2001) compared the ability of larvae of *C. septempunctata* and *H. axyridis* to develop in the laboratory on a diet of larvae of the alfalfa weevil, versus their primary prey, pea aphids, in alfalfa fields of Utah. First instars of both species failed to molt to the second stadium when provided only young larvae of the weevil. Fourth instars, especially of *H. axyridis*, were able to molt into pupae (and then adults) when feeding on older weevil larvae, but with markedly less success than when feeding on the aphids. Behavioral observations (coupled with performance comparison when larvae were provided with live versus dead weevils) suggested that the unsuitability of the weevil diet derived largely from the lady beetles' reduced tendency to attack weevils versus aphids, and from the ability of attacked weevils to defend themselves (Kalaskar and Evans, 2001).

Coleoptera as prey include other coccinellids (Snyder, 2009; Weber and Lundgren, 2009b). The implications of cannibalism

among lady beetles for larval growth and development have been studied extensively. Cannibalism of siblings as eggs provides critical energy and nutrients for newly hatched lady beetle larvae, speeding their development and increasing their survival (e.g., Banks, 1956; Osawa, 1992; Michaud and Grant, 2004; Perry and Roitberg, 2005; Roy et al., 2007). Similarly, non-sibling egg cannibalism often provides an excellent diet for larval development (e.g., Agarwala and Dixon, 1992; Gagné et al., 2002). Because of their chemical defenses, however, eggs may be poor food for other lady beetle species, and intraguild predation thereby may be discouraged (e.g., Agarwala and Dixon, 1992; Cottrell, 2004). Cannibalism and intraguild predation of other lady beetle larvae may benefit lady beetle larvae that develop under limited food conditions (e.g., Wagner et al., 1999; Snyder et al., 2000). But even larvae rendered helpless against attack may be relatively unsuitable as prey, as they may be nutritionally poor in quality (e.g., Yasuda and Ohnuma, 1999). Kagata and Katayama (2006) tested the hypothesis that intraguild predation is an adaptive response to nitrogen shortage in the diet, but concluded that such does not appear to account well for the marked tendency of *H. axyridis* in particular to attack and consume larvae of other lady beetles.

#### 4.1.3. Additional insect orders as prey

In contrast to the many studies of Lepidoptera and Coleoptera as prey, there are few studies of other non-hemipteran insects as prey for coccinellids. Thrips are attacked in large numbers by *C. septempunctata* in alfalfa (Triltsch, 1999), with unknown suitability for larval development. Larvae of *H. convergens* were found to develop to adulthood on an exclusive diet of *Thrips tabaci* Lindeman, albeit much more slowly and with much more mortality than on a diet of pea aphids (Schade and Sengonca, 1998). The active nature of thrips may contribute to their reduced suitability as prey. Third instars of *H. axyridis* were found to develop on nymphs of *Hyaliodes vitripennis* (Say) (Miridae), but their ability to do so was weakened by the prey's ability to escape most attacks by fleeing (Provost et al., 2006). Larvae of *C. maculata* were often successful (even as early instars) in attacking both young and old larvae (and also eggs) of *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae), as well as young larvae and eggs of *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae) (Lucas et al., 1998). The suitability of these intraguild prey for larval development of *C. maculata*, however, has yet to be determined.

#### 4.1.4. Overview for non-hemipterans as prey

In summary, a wide range of results emerges from studies of larval lady beetles developing on diets of insects other than Sternorrhyncha. Diverse lady beetle species have been well-documented as able to mature well on diets of a variety of lepidopteran and coleopteran eggs and larvae. In other cases, however, such diets have proved inadequate, and the prey is best characterized as alternative (Hodek, 1962, 1996). Much remains to be learned about reasons for inadequacies. One theme that emerges is that very young lady beetle larvae may often lack ability to penetrate the chorion of eggs, or to overcome the defenses (struggling or fleeing) of larval or nymphal prey. In these cases, a non-sternorrhynchan diet may be highly suitable nutritionally for lady beetle development, but "accessible" only to older larvae. High suitability is reflected, for example, in the much higher efficiency of conversion by fourth instars of *H. axyridis* of eggs of *E. kuehniella* (characterized by high protein and lipid content) than of pea aphids (with especially high carbohydrate content) (Specty et al., 2003). In other cases, nutritional properties (including chemical defenses) of prey may adversely affect lady beetle development. In general, it is difficult to determine from the literature at present how and why some species (e.g., *C. maculata*) are more able than others to be polyphagous as larvae, as reflected particularly in their use of non-sternorrhynchan prey.

#### 4.2. Reproduction

It is instructive to consider reproduction by lady beetles as distinct from larval development, as prey may not be equally suitable for these two life processes (Michaud, 2005). Diets solely of eggs of Lepidoptera and Coleoptera have been found to support egg production for a number of lady beetle species. Iperti et al. (1972) found eggs of *E. kuehniella* very suitable as food in eliciting egg production by *P. semiglobosus* and *C. decempunctata*. Schanderl et al. (1988) found the same for egg production by *H. axyridis*; *S. undecimnotata* also laid eggs when consuming only *E. kuehniella* eggs, although this diet was suboptimal (compared with pea aphids) for larval growth and development. Drawing on stock cultures reared continuously on *E. kuehniella*, Berkvens et al. (2008) recorded a longer pre-oviposition period but more oviposition days when females of *H. axyridis* fed on the moth eggs versus pea aphids. Hamasaki and Matsui (2006) similarly reported considerable reproduction by *P. japonica* on a diet of *E. kuehniella* eggs, although the rate of egg production was lower and the pre-oviposition period was longer than on a diet of pea aphids (regardless of whether the larval diet had been eggs or aphids). Strikingly different results were obtained, however, for *A. bipunctata* (De Clercq et al., 2005): females laid twice as many eggs on a diet of *E. kuehniella* eggs versus pea aphids, although the percentage of eggs hatching was less than half than on the aphid diet (interestingly, supplementing the moth egg diet with moist [but not dry] bee pollen substantially increased the percentage of eggs that hatched). Abdel-Salam and Abdel-Baky (2001) found that *H. axyridis* females, when fed either fresh or frozen eggs of *S. cerealella*, readily produced eggs in numbers comparable to those fed aphids. Gautam (1990) recorded greatly reduced egg production by *B. suturalis*, however, when provided with eggs of the potato-tuber moth.

Eggs attacked naturally by lady beetles also have proved capable of supporting reproduction, although to varying degrees. Phoofolo and Obrycki (1997) found that females of *C. maculata* laid more eggs when fed ECB eggs versus pea aphids (regardless of whether they fed as larvae on ECB eggs or pea aphids). In contrast, females of *C. maculata* on average laid four times as many eggs on a diet of green peach aphids than on a diet of CPB eggs when prey were provided in excess (Hazzard and Ferro, 1991). When reared on pea aphids throughout the larval period, or on pea aphids as first instars and on CPB eggs thereafter, females of *C. maculata* that fed only pea aphids as adults had the shortest pre-oviposition periods, but did not differ clearly in their lifetime fecundities from females fed CPB eggs (Munyaneza and Obrycki, 1997a). Females of *C. hieroglyphica* laid eggs in large numbers when fed eggs of *G. sagittariae* (Hippa et al., 1984). Similarly, females of *H. conformis* and *C. mellyi* laid eggs when fed eggs of *C. bimaculata* (Elliott and de Little, 1980). Bain et al. (1984), however, reported that adults of *C. mellyi* laid few or no eggs when feeding on eggs of *P. charybdis*, but initiated oviposition after being switched to a diet of psyllids for 7–8 days.

Fewer studies have examined lady beetle egg production on diets of larval Lepidoptera and Coleoptera. Riddick and Barbosa (1998) found adults of *C. maculata* to lay eggs when provided with CPB larvae supplemented with bee larvae. When only beetle (alfalfa weevil) larvae were provided, females of *C. transversoguttata* and *C. septempunctata* ate sufficient larvae to gain body weight but did not lay eggs (Richards and Evans, 1998). Evans (2000) similarly failed to obtain eggs from *Coccinella transversalis* when females were fed solely with *Helicoverpa* larvae.

For these species of *Coccinella* as well as of various other genera (e.g., *Hippodamia* spp.), aphid consumption appears required to support high levels of egg production, as revealed by lack of success in efforts to develop artificial diets (Racioppi et al., 1981; Hagen, 1987; Hodek and Honěk, 1988). It is therefore intriguing that *C. septempunctata*, *C. transversoguttata*, and *C. transversalis* F.

will engage in limited egg production when feeding on coleopteran and lepidopteran larvae supplemented with sugar, as might be obtained in nature from plant nectar (Richards and Evans, 1998; Evans et al., 1999; Evans, 2000). One interpretation is that females are investing to a limited degree in egg production even in the absence of preferred aphid prey, to enhance their ability to oviposit quickly upon locating patches of high aphid density (Evans, 2003).

Females of *H. axyridis* also failed to produce eggs when maintained on a diet solely of alfalfa weevil larvae, but laid small numbers of eggs when provided with sugar as well as weevils (Evans and Gunther, 2005). Lower rates of food intake and assimilation, and greater allocation of nutrients and energy to searching, appear to contribute to the reduced egg production of females that eat weevils (with sugar) versus pea aphids. Nonetheless, weevils can serve as important alternative prey that benefit lifetime egg production by *H. axyridis* females: when they were placed on a diet of aphids, females began laying eggs earlier and laid more eggs altogether, when they had fed previously on weevils versus only sugar (Evans and Gunther, 2005).

#### 4.3. Effects of mixed diets

The tendencies of lady beetles to include other insect prey in their diet often may arise from shortages of preferred hemipteran prey (e.g., Gordon, 1985; Sloggett and Majerus, 2000). Such tendencies in some cases may arise also from the benefits of meeting nutritional requirements through a mixed diet, as suggested from studies of a variety of predatory arthropods (e.g., Greenstone, 1979; Soares et al., 2004; Mayntz et al., 2005). In general, dietary preferences by lady beetles will reflect the ability to balance nutritional needs against the nutritional properties of prey. For example, Specty et al. (2003) found that when *H. axyridis* individuals were reared on a diet of *E. kuehniella* eggs or nymphs and pea aphid adults, their body composition had higher protein and lipid content when reared on eggs (also higher than aphids in these respects), but the difference in body composition was less marked between the two groups of adult predators than between the two types of prey.

There are relatively few studies of the effects of mixed diets on lady beetles (see also Lundgren, 2009a). Riddick and Barbosa (1998) found benefits of a mixed larval diet: among individuals of *C. maculata* reared on bee pollen, those that were allowed to feed as well on CPB larvae (intoxicated from feeding on Bt-transgenic potato) had greater survivorship to the adult stage, and tended to achieve greater weights in so doing. But the benefits of mixed larval diets vary with the food combinations tested. When Snyder and Clevenger (2004) provided larvae of four other species of lady beetles (*C. transversoguttata*, *C. septempunctata*, *H. convergens* and *H. axyridis*) with a mixed diet of CPB eggs and green peach aphids, the larvae consumed eggs even when aphids were provided *ad libitum*, and generally suffered lower rates of development and survivorship on the mixed diet than on a pure diet of aphids.

Phoofolo and Obrycki (1997) compared larval development and adult reproduction of *C. maculata* on both mixed and pure diets of ECB eggs and pea aphids. For the mixed diet, larvae and/or adults were fed either eggs or aphids on alternate days. Larvae that fed on mixed diets developed at rates very similar to others that fed on either aphids or eggs, and achieved sizes as newly molted adults that were intermediate between the relatively small individuals that had matured on the aphid diet and the larger individuals that had matured on the egg diet. Benefits of a mixed larval diet were particularly realized in the adult stage: females laid more eggs on either a pea aphid or egg diet when they had been fed a mixed diet as larvae versus a diet of either eggs or aphids. Interestingly, among females that had been reared as larvae on a mixed diet, those that fed as adults on mixed diets laid fewer eggs on average than those that fed on either eggs or aphids alone.

Michaud and Jyoti (2008) recorded reproductive benefits also in switching individuals of *C. maculata* between larval and adult diets of the greenbug (*Schizaphis graminum* Rondani) and *E. kuehniella* eggs. Individuals reared as larvae on aphids more rapidly produced clutches of eggs (which in turn had a high hatch rate) on an adult diet of moth eggs versus aphids. Also showing evidence of dietary complementation across life stages, individuals reared on moth eggs had higher fecundity on an adult diet of aphids versus eggs.

Even among lady beetles that are less polyphagous than *C. maculata*, a mixed adult diet may benefit reproduction. Egg production of *C. septempunctata* and *C. transversoguttata* was found to depend primarily on the rate of aphid consumption but nonetheless was slightly increased by the addition of weevils to the diet (Evans et al., 1999, 2004). Consumption of weevil larvae may have served in self-maintenance, thus enabling females to direct more nutrients and energy from consumed aphids into egg production.

## 5. Prey selection, consumption rates, and functional and numerical responses

Fewer non-hemipteran prey typically are consumed by aphidophagous lady beetles when aphids are also available than when these non-sternorrhynchans are offered alone (Ables et al., 1978; Groden et al., 1990; Hazzard and Ferro, 1991; Horn, 1991; Agarwala and Dixon, 1992; Lucas et al., 1998, 2004a; Kajita et al., 2000; Musser and Shelton, 2003; Koch et al., 2005; Mallampalli et al., 2005). The effects of the presence of non-hemipteran prey on lady beetle consumption rates of aphids and other Hemiptera, on the other hand, are largely unexplored. But in an interesting twist, Lucas et al. (2004a) found that in the presence of larvae of the oblique banded leaf roller (*Choristoneura rosaceana* [Harris], Tortricidae), adults of *H. axyridis* and *C. septempunctata* ate more rather than fewer apple aphids (*Aphis pomi* DeGeer).

### 5.1. Prey choice

#### 5.1.1. Relative consumption of aphids versus non-hemipteran prey

Relative consumption of non-hemipteran versus aphid prey (often simply referred to as prey preference) by lady beetles has been examined in choice assays by presenting the prey together in varying absolute and/or relative densities. Because assay settings are often artificial, and because the degree of predator satiation may vary among experiments, interpretations and comparisons of results require caution. Nonetheless, it is intriguing that results differ widely as to whether lady beetles prefer aphids over non-hemipteran prey. Ables et al. (1978) found that as densities of tobacco budworm (*Heliothis virescens* [F.]) eggs and cotton aphids (*Aphis gossypii* Glover) were increased proportionately, the percentage predation of the non-hemipteran prey over aphids decreased. Similarly, Hazzard and Ferro (1991) found no preference by *C. maculata* females when CPB eggs and *M. persicae* were present in low numbers, but increasing preference for (i.e., proportionately greater consumption of) aphids as densities and consumption of both prey increased. Groden et al. (1990), however, found that the percentage of prey consumed that was represented by CPB first instars (versus either of two species of aphids) remained constant as aphid density increased and CPB density remained constant (i.e., as the relative density of CPB decreased). Koch et al. (2005) found that when *H. axyridis* adults were presented with a set number of *Danaus plexippus* larvae and varying numbers of aphids (*Aphis nerii* Boyer de Fonscolombe), the relative biomass of each prey species consumed was the same as that species' percentage of total prey biomass available; i.e., no prey preference for either aphids or the non-hemipteran prey was detected. Corlay et al. (2007) found that adults of *H. axyridis* ate

similar numbers of larvae of swede midge (*Contarinia nasturtii* Kieffer [Cecidomyiidae]) and green peach aphids when these two prey species were provided simultaneously in equal numbers.

In at least some cases, aphidophagous lady beetles may have innate preference for consuming aphids versus non-hemipteran prey. Although frequent field observations have been made of lady beetles consuming alfalfa weevil larvae, several laboratory studies have found various species of lady beetles to consume more biomass of aphids (*A. pisum*) than weevils (Yadava and Shaw, 1968; Hussain, 1975; Ouayogode and Davis, 1981; Evans and Gunther, 2005). Such results likely reflect in part the greater ability of the weevils to defend themselves when attacked (e.g., Kalaskar and Evans, 2001). But the predator's tendency to initiate attacks of aphids versus weevils may also be important in leading to differences in consumption rates of these two kinds of prey. Thus, Evans et al. (2004) found that females of *C. septempunctata* more readily attacked pea aphids than weevil larvae, regardless of whether the females had fed previously on one or the other prey.

#### 5.1.2. Preferences among non-hemipteran prey

Other studies indicate that lady beetles may be subtly selective in their consumption of non-hemipteran prey. Hippen et al. (1982) found that adults of *C. hieroglyphica* ate conspecific eggs and eggs of *G. nymphaeae* more readily than eggs of two other Chrysomelid beetles. Roger et al. (2001) found that larvae of *C. maculata* preferred the more nutritious young eggs to older eggs of *Trichoplusia ni* (Hübner) (Noctuidae) (the larvae did not discriminate, however, between unparasitized eggs and eggs parasitized by *Trichogramma evanescens* [Westwood]).

Eggs of conspecifics may be preferred prey of newly hatched lady beetle larvae. Gagné et al. (2002) found that *C. maculata* first instars preferred conspecific eggs over aphids, and that the eggs were superior to aphids as food. The first instars also preferred aphids painted with egg extract over eggs painted with aphid extract, suggesting that the first instars were attracted to eggs by chemical cues. Omkar et al. (2006) obtained similar results for an additional three lady beetle species (*C. transversalis*, *Propylea dissecta* [Mulsant], and *Coelophora saucia* [Mulsant]) presented with conspecific eggs and the essential prey, *A. gossypii*.

While conspecific eggs may often be highly preferred, eggs of other coccinellids are often avoided by foraging lady beetles (e.g., Hemptinne et al., 2000; Burgio et al., 2002; Sato and Dixon, 2004; Cottrell, 2007; Rieder et al., 2008). For example, in an early demonstration of interspecific chemical defense of eggs, Agarwala and Dixon (1992) found that larvae and adults of *A. bipunctata* and *C. septempunctata* consumed conspecific eggs, but were reluctant to do so when eggs were painted with a water extract of each others' eggs.

### 5.2. Functional response

Laboratory experiments have been used frequently to estimate consumption rates and the functional responses of lady beetles attacking species of prey other than Hemiptera. For example, linear increases with increasing temperatures have been observed in the attack rates on coleopteran and lepidopteran eggs and larvae by lady beetle larvae and adults (e.g., Groden et al., 1990; Giroux et al., 1995; Parajulee et al., 2006). Functional responses to these prey have generally been described as Type II, with an increasing but decelerating rate of consumption with increasing prey density (e.g., Groden et al., 1990; Hazzard and Ferro, 1991; Arpaia et al., 1997; Koch et al., 2003; Parajulee et al., 2006). In some cases, responses were best characterized as increasing linearly (i.e., Type I) over the range of prey densities examined (e.g., Ables et al., 1978; Koch et al., 2003).

Functional responses recorded in the laboratory must be interpreted with care. Laboratory tests likely overestimate field consumption rates. Consumption rates of CPB eggs by *C. maculata* larvae at a given prey density on excised potato leaves in the laboratory were found by Munyaneza and Obrycki (1997b) to be double those on caged potato plants in the field (in both settings, however, a type II response was observed). Roger et al. (2000) reported that both larvae and adults of *C. maculata* consumed most biomass of three lepidopterans when offered caterpillars of intermediate size (instar). Lu et al. (1996) found that adults of *C. maculata* consumed more CPB larvae from a New York population than from a Maryland population. Individuals from the New York population were less well-adapted to feed on the host plant (tomato). They therefore attained smaller sizes and were more readily overpowered by the predator.

### 5.3. Searching behavior

Encounters with non-hemipteran prey can modify subsequent searching behavior of individual lady beetles in ways that are similar to those well-documented for encounters with hemipteran prey (e.g., Ferran and Dixon, 1993). Munyaneza and Obrycki (1998b), for example, found that fourth instars of *C. maculata* typically engaged in area-restricted (i.e., intensive, versus extensive) search after contacting a CPB egg mass. Fourth instars of *C. maculata* also spent less time foraging in prey patches with less preferred prey (older [and parasitized] eggs of *T. ni*) than in patches with more preferred prey (young [unparasitized] eggs of *T. ni*) (Roger et al., 2001). Interestingly, Ettifouri and Ferran (1993) found that for *H. axyridis* reared on either eggs of *E. kuehniella* or *A. pisum*, larvae engaged in intensive searching only after feeding on the same prey upon which they had been reared. Furthermore, Ferran et al. (1997) found that larvae of *H. axyridis* reared on *A. pisum* switched from extensive to intensive search upon encountering a substrate previously occupied and contaminated by *A. pisum*; this same behavior was not demonstrated for *H. axyridis* reared on *E. kuehniella* eggs. Conditioning is suggested, because the behavior of egg-reared larvae was easily modified by contact with novel aphid prey.

### 5.4. Numerical response

The collective outcome of individuals searching for preferred prey can lead to populations of aphidophagous lady beetles becoming strongly aggregated in response to high aphid density (e.g., Kareiva and Odell, 1987; Evans and Toler, 2007; Křivan, 2008). Some aphidophagous lady beetles at times respond similarly to high densities of non-hemipteran prey as well. For example, adults of *C. maculata* aggregated on plants with highest numbers of CPB first instars in a natural population of horsenettle (*Solanum carolinense* L.) (Mena-Covarrubias et al., 1996). In investigating the impact of predation on the evolution of pest resistance associated with deployment of Bt-transgenic potatoes, Arpaia et al. (1997) reported that *C. maculata* adults aggregated in both greenhouse and field experiments on potato plants with high CPB egg densities; the strength of the aggregative response, however, was not sufficient to result in spatially density-dependent predation. In further field plot studies of the same predator (but with lower predator densities), Mallampalli et al. (2005) found neither aggregation nor spatially density-dependent predation of CPB eggs on potatoes. These results were used to generate a prediction that Bt resistance might evolve faster with predators present, in interesting contrast to an earlier prediction from Arpaia et al. (1997) of delayed evolution of Bt resistance resulting from egg predation by *C. maculata*.

At a larger spatial scale, Evans and Youssef (1992) found strong positive correlations of coccinellid numbers with densities of pea

aphids, but no correlations with densities of alfalfa weevil larvae, among Utah alfalfa fields. In Iowa, however, Giles et al. (1994) found that within alfalfa fields, numbers of *C. maculata* and alfalfa weevil larvae were positively related among pooled samples as taken between mid-April and early June. Also, adults of the recently introduced species *C. septempunctata* aggregated in response to within-field variation in alfalfa weevil larval density when local numbers of weevil and pea aphids were manipulated experimentally (Evans and Toler, 2007). Indeed, the presence of non-hemipteran prey such as the abundant alfalfa weevil may promote relatively high numbers of *C. septempunctata* that also reduce pea aphid numbers early in the growing season in Utah alfalfa fields. As a consequence, formerly abundant (and seemingly more strictly aphidophagous) native lady beetles may no longer linger to forage in these fields in the absence of sufficient numbers of pea aphids to retain them (Evans, 2004).

## 6. Efforts to promote biological control

The responsiveness of lady beetle populations to prey other than Sternorrhyncha has generated considerable interest in promoting these predators as biological control agents. Incorporation of lady beetles into IPM programs against various insect pests has therefore received attention from researchers. Although lady beetles have been released and promoted for biological control primarily of aphids, scale insects and mites (Obrycki and Kring, 1998; Biddinger et al., 2009; Obrycki et al., 2009), releases of these predators against insect pests other than Sternorrhyncha have also been studied. In an early effort, Yakhontov (1938) reported considerable reduction in alfalfa weevil numbers and a sizeable increase in yield of the first crop of lucerne (alfalfa) in Central Asia following release of *S. undecimnotata* (Schneider) and *Brumus octosignatus* Gebler at a rate of 1 adult to 20–50 weevil larvae. In evaluating *C. hieroglyphica* larvae and adults as biological control agents of leaf beetles (*G. nymphaeae*-complex) that attack cloudberries and cultivated strawberry in northern Finland, Hippa and Kaponen (1979) also found high rates of pest reduction in cage studies with similar predator–prey ratios. Based on consumption studies, Rondon et al. (2003) suggested that releases of larvae and adults of *C. maculata* might serve to control first instars of the squash bug (*Anasa tristis* DeGeer) on cucumbers in commercial greenhouses.

### 6.1. Food sprays

Other studies have explored the use of food sprays (e.g., Hagen et al., 1971; Evans and Richards, 1997; Wade et al., 2008; Lundgren, 2009b) to manipulate dispersal and aggregation of lady beetles to promote biological control of insect pests other than Hemiptera in agricultural and silvicultural settings. Aggregating in response to sucrose applications, lady beetles contributed to reductions in numbers of ECB larvae before they entered corn stalks (Carlson and Chiang, 1973), and of alfalfa weevil larvae in sugar-treated alfalfa fields (Evans and England, 1996). Mensah (1997, 2002a,b) and Mensah and Singleton (2003) sprayed sugar–protein mixtures onto Australian cotton fields and succeeded in attracting and concentrating adult lady beetles and other predators of larvae of *Helicoverpa* spp.

Mensah and Madden (1994) used sucrose (both as a spray and as granules at a feeding station) to retain and enhance the efficacy of adults of *C. mellyi* in stands of regeneration eucalypt forests of Tasmania, as larval populations of their chrysomelid prey *C. bimaculata* matured and declined in number. Bashford (1999) proposed combining use of sucrose with mass supplemental releases of *C. mellyi*. Baker et al. (2003) made inundative point releases of this lady beetle against the pest defoliator, and noted large decreases in



leaf beetle numbers on release trees with many lady beetles. Baker and colleagues concluded that such augmentation could be economically viable in small stands of eucalypts where chemical treatment might incur excessive financial or environmental cost.

## 6.2. *Bt* and Colorado potato beetle egg predation

Several recent studies have focused on the effects of foliar applications of *Bt* and planting of *Bt*-transgenic potatoes on CPB egg predation by *C. maculata*. Such studies reflect a widespread, general interest in integration of biological control into IPM, with much current attention on transgenic plants (Lovei and Arpaia 2005; Marvier et al., 2007). From feeding and rearing studies, Giroux et al. (1994a) concluded that there was minimal adverse physiological effect on larvae of *C. maculata* from consuming CPB eggs treated with a formulation of *Bacillus thuringiensis* subsp. *san diego* at the manufacturer's recommended rate. But Giroux et al. (1994b) also found reduced consumption of such CPB eggs in the laboratory. Hilbeck et al. (1998), however, did not detect a significant difference in CPB egg predation rates between field plots of potatoes that were treated or untreated with foliar applications of *B. thuringiensis* var. *tenebrionis*. In addition, Riddick and Barbosa (1998) found no difference in larval consumption rate, development, and survivorship, or in fecundity (when the diet also included bee pollen), between individuals of *C. maculata* that fed on CPB larvae reared on *Bt* (Cry3A)-transgenic or nontransgenic potatoes. Lucas et al. (2004b) found little direct, lethal effect of *B. thuringiensis* var. *tenebrionis* and cyromazine on *C. maculata* adults and larvae, but substantial lethal effect of two other insecticides (cryolite and especially imidacloprid) targeted against CPB. Collectively, these results suggest that biological control of CPB by *C. maculata* will not be jeopardized by *Bt* sprays or transgenic plants in potato cultivation.

## 7. Concluding observations

This review highlights a large literature from throughout the world showing that many predatory lady beetles have clear generalist tendencies to consume many kinds of prey. Two major themes, often intertwined, are explored in this literature: the importance of lady beetles as predators of insects other than sternorrhynchans, and the importance of these insects as prey for lady beetles.

Concerning the second theme, most predatory lady beetles seem first and foremost opportunistic in their use of many insect prey. Such opportunism appears interwoven into life histories and habits that have evolved particularly for exploitation of Sternorrhyncha, especially among lady beetles considered as primarily aphidophagous. The basic aphidophagous nature of many lady beetles is thus reflected not in a strict adherence to aphids alone as prey, but rather in their searching and reproductive behaviors, including their tendencies to accumulate (aggregate) as adults and to lay eggs especially where aphids occur in large numbers; i.e., situations in which larval stages of these predators are especially well-adapted to thrive (e.g., Hodek and Honěk, 1996; Dixon, 2000; Evans, 2003). These predators' consumption of prey other than aphids thus occurs especially when aphids are in short supply, as may happen frequently given the patchy nature of boom-bust aphid populations over both space and time.

There are also intriguing indications in the literature that some species of lady beetles are much less opportunistic in their use of insect prey other than Sternorrhyncha; i.e., some species appear to have evolved with life histories and behaviors especially suited to exploiting non-hemipterans as their primary prey. Although the opposite could be true (Giorgi et al., 2009), it appears most likely that such lady beetles have arisen especially from aphidophagous

ancestry, and this may well be an evolutionary response to frequent shortage of aphids (Sloggett and Majerus, 2000). As might be expected from this general hypothesis, there appears a continuum of life histories among lady beetle species from those species tightly bound to exploitation of Sternorrhyncha to those more strongly linked to exploitation of other insect prey.

A fruitful approach to exploring these ideas more fully is to expand studies on the behavioral responses of different groups of lady beetles to different kinds of insect prey. Consider, for example, the key choices facing female lady beetles of when to produce eggs and where to lay them (e.g., Dixon, 2000; Evans, 2003; Seagraves, 2009). The importance of aphids in the diet for promoting egg production among various groups of lady beetles (e.g., Hagen, 1987) could be interpreted as reflecting an evolved "firm commitment" to aphidophagy. Yet studies to date reveal a fascinating range of reproductive responses among aphidophagous lady beetles to a variety of prey, including eggs of factitious lepidopteran hosts. To understand better both the evolutionary basis and the ecological significance of such a range of responses, more comparative studies are needed of how more and less strongly aphidophagous species of lady beetles respond reproductively to aphid versus other insect prey and mixed diets. Similar remarks apply to the searching and attack behaviors of both adult and larval lady beetles, which studies reviewed here illustrate can vary widely among lady beetles as they interact with different kinds of prey. And of course, much remains to be done in determining to what degree, and why, different prey are suitable for larval growth and development among species of lady beetles.

Further insights into the evolutionary basis and ecological significance of diet among lady beetles will in turn strengthen our ability to assess the importance of lady beetles as predators of insects other than Sternorrhyncha. This will yield many practical benefits as efforts continue to incorporate biological control by lady beetles into IPM programs against insect pests. For example, these insights may help in predicting when the presence of aphids in or near a crop may promote or diminish biological control of other insect pests by lady beetles (e.g., Munyaneza and Obrycki, 1998a; Musser and Shelton, 2003). Similarly, these insights may help in predicting when and how the availability of other insects as alternate prey may affect predation pressure of lady beetles on pest aphids (e.g., Lucas et al., 2004a; Evans and Toler, 2007). The studies reviewed herein collectively reveal that lady beetles often hold much potential to contribute to population suppression and management of insect pests other than the Sternorrhyncha. Realization of such potential, however, is likely to come only with firmer understanding of how these predators have evolved in their use of and dependence on a wide range of potential prey.

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## References

- Abdel-Salam, A.H., Abdel-Baky, N.F., 2001. Life table and biological studies of *Harmonia axyridis* (Col., Coccinellidae) reared on the grain moth eggs of *Sitotroga cerealella* Olivier (Lep., Gelechiidae). *Journal of Applied Entomology* 125, 455–462.
- Ables, J.R., Jones, S.L., McCommas Jr., D.W., 1978. Response of selected predator species to different densities of *Aphis gossypii* and *Heliothis virescens* eggs. *Environmental Entomology* 7, 402–404.
- Agarwala, B.K., Dixon, A.F.G., 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecological Entomology* 17, 303–309.

- Allen, D.C., Knight, F.B., Foltz, J.L., 1970. Invertebrate predators of the jack-pine budworm, *Choristoneura pinus*, in Michigan. *Annals of the Entomological Society of America* 63, 59–64.
- Andow, D.A., 1990. Characterization of predation on egg masses of *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Annals of the Entomological Society of America* 83, 482–486.
- Andow, D.A., 1992. Fate of eggs of first-generation *Ostrinia nubilalis* (Lepidoptera: Pyralidae) in three conservation tillage systems. *Environmental Entomology* 21, 388–393.
- Andow, D.A., Risch, S.J., 1985. Predation in diversified agroecosystems: relations between a coccinellid predator *Coleomegilla maculata* and its food. *Journal of Applied Ecology* 22, 357–372.
- Arpaia, S., Gould, F., Kennedy, G., 1997. Potential impact of *Coleomegilla maculata* predation on adaptation of *Leptinotarsa decemlineata* to Bt-transgenic potatoes. *Entomologia Experimentalis et Applicata* 82, 91–100.
- Bain, J., Singh, P., Ashby, M.D., van Boven, R.J., 1984. Laboratory rearing of the predatory coccinellid *Cleobora mellyi* [Col.: Coccinellidae] for biological control of *Paropsis charybdis* [Col.: Chrysomelidae] in New Zealand. *Entomophaga* 29, 237–244.
- Baker, S.C., Elek, J.A., Bashford, R., Paterson, S.C., Madden, J., Battaglia, M., 2003. Inundative release of coccinellid beetles into eucalypt plantations for biological control of chrysomelid leaf beetles. *Agricultural and Forest Entomology* 5, 97–106.
- Banks, C.J., 1956. Observations on the behaviour and mortality in Coccinellidae before dispersal from the egg shells. *Proceedings of the Royal Entomological Society of London (A)* 31, 56–60.
- Bashford, R., 1999. Predation by ladybird beetles (coccinellids) on immature stages of the *Eucalyptus* leaf beetle *Chrysophtharta bimaculata* (Olivier). *Tasforests* 11, 77–85.
- Berkvens, N., Bonte, J., Berkvens, D., Tirry, L., De Clercq, P., 2008. Influence of diet and photoperiod on development and reproduction of European populations of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *BioControl* 53, 211–221.
- Biddinger, D.J., Weber, D.C., Hull, L.A., 2009. Coccinellidae as predators of mites: Stethorini in biological control. *Biological Control* 51, 268–283.
- Bruck, D.J., Lewis, L.C., 1998. Influence of adjacent cornfield habitat, trap location, and trap height on capture numbers of predators and a parasitoid of the European corn borer (Lepidoptera: Pyralidae) in central Iowa. *Environmental Entomology* 27, 1557–1562.
- Burgio, G., Santi, F., Maini, S., 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biological Control* 24, 110–116.
- Cañas, L.A., O'Neil, R.J., Gibb, T.J., 2002. Population ecology of *Leptinotarsa undecimlineata* Stål (Coleoptera: Chrysomelidae): population dynamics, mortality factors, and potential natural enemies for biological control of the Colorado potato beetle. *Biological Control* 24, 50–64.
- Cappaert, D.L., Drummond, F.A., Logan, P.A., 1991. Population dynamics of the Colorado potato beetle (Coleoptera: Chrysomelidae) on a native host in Mexico. *Environmental Entomology* 20, 1549–1555.
- Carlson, R.E., Chiang, H.C., 1973. Reduction of an *Ostrinia nubilalis* population by predatory insects attracted by sucrose sprays. *Entomophaga* 18, 205–211.
- Coll, M., Bottrell, D., 1991. Microhabitat and resource selection of the European corn borer (Lepidoptera: Pyralidae) and its natural enemies in Maryland corn field. *Environmental Entomology* 20, 526–533.
- Coll, M., Bottrell, D., 1995. Predator–prey association in mono- and di-cultures: effect of maize and bean vegetation. *Agriculture, Ecosystems and Environment* 54, 115–125.
- Conrad, M.S., 1959. The spotted lady beetle, *Coleomegilla maculata* (DeGeer) as a predator of European corn borer eggs. *Journal of Economic Entomology* 52, 843–847.
- Cook, S.P., Webb, R.E., 1995. Predation of early-instar gypsy moth larvae by a generalist predator, *Anatis labiculata* (Say) (Coleoptera: Coccinellidae). *Journal of Entomological Science* 30, 258–261.
- Corlay, F., Boivin, G., Bélair, G., 2007. Efficiency of natural enemies against the swede midge *Contarinia nasturtii* (Diptera: Cecidomyiidae), a new invasive species in North America. *Biological Control* 43, 195–201.
- Cottrell, T.E., 2004. Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biological Control* 31, 362–371.
- Cottrell, T.E., 2007. Predation by adult and larval lady beetles (Coleoptera: Coccinellidae) on initial contact with lady beetle eggs. *Environmental Entomology* 36, 390–401.
- Cottrell, T.E., Yeagan, K.V., 1998a. Influence of a native weed, *Acalypha ostryaefolia* (Euphorbiaceae), on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology* 27, 1375–1385.
- Cottrell, T.E., Yeagan, K.V., 1998b. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation, and cannibalism in sweet corn. *Environmental Entomology* 27, 1402–1410.
- Davidson, L.N., 2008. Diets of ladybird beetles (Coleoptera: Coccinellidae) in Utah alfalfa fields. MS Thesis. Utah State University, Logan, UT.
- De Clercq, P., Bonte, M., van Speybroeck, K., Bolckmans, K., Deforce, K., 2005. Development and reproduction of *Adalia bipunctata* (Coleoptera: Coccinellidae) on eggs of *Ephesthia kuehniella* (Lepidoptera: Phycitidae) and pollen. *Pest Management Science* 61, 1129–1132.
- de Little, D.W., Elliott, H.J., Madden, J.L., Bashford, R., 1990. Stage specific mortality in two field populations of immature *Chrysophtharta bimaculata* (Olivier) (Coleoptera, Chrysomelidae). *Journal of the Australian Entomological Society* 29, 51–55.
- Dixon, A.F.G., 2000. *Insect Predator–Prey Dynamics*. Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge.
- Dixon, A.F.G., Hemptinne, J.-L., 2001. Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology* 82, 1847–1856.
- Ehler, L.E., 2007. Impact of native predators and parasites on *Spodoptera exigua*, an introduced pest of alfalfa hay in northern California. *BioControl* 52, 323–338.
- Elliott, H.J., de Little, D.W., 1980. Laboratory studies on predation of *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae) eggs by the coccinellids *Cleobora mellyi* Mulsant and *Harmonia conformis* (Boisduval). *General and Applied Entomology* 12, 33–36.
- Essig, E.O., Michelbacher, A.E., 1933. The alfalfa weevil. *California Agricultural Experiment Station Bulletin*, 567.
- Ettifouri, M., Ferran, A., 1993. Influence of larval rearing diet on the intensive searching behaviour of *Harmonia axyridis* (Col.: Coccinellidae) larvae. *Entomophaga* 38, 51–59.
- Evans, E.W., 2000. Egg production in response to combined alternative foods by the predator *Coccinella transversalis*. *Entomologia Experimentalis et Applicata* 94, 141–147.
- Evans, E.W., 2003. Searching and reproductive behaviour of female aphidophagous ladybirds: a review. *European Journal of Entomology* 100, 1–10.
- Evans, E.W., 2004. Habitat displacement of North American ladybirds by an introduced species. *Ecology* 85, 637–647.
- Evans, E.W., England, S., 1996. Indirect interactions in biological control of insects: pests and natural enemies in alfalfa. *Ecological Applications* 6, 920–930.
- Evans, E.W., Gunther, D.L., 2005. The link between food and reproduction in aphidophagous predators: a case study with *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology* 102, 423–430.
- Evans, E.W., Richards, D.R., 1997. Managing the dispersal of ladybird beetles (Coleoptera: Coccinellidae): use of artificial honeydew to manipulate spatial distributions. *Entomophaga* 42, 93–102.
- Evans, E.W., Toler, T., 2007. Aggregation of polyphagous predators in response to multiple prey: ladybirds (Coleoptera: Coccinellidae) foraging in alfalfa. *Population Ecology* 49, 29–36.
- Evans, E.W., Youssef, N.N., 1992. Numerical responses of aphid predators to varying prey density among Utah alfalfa fields. *Journal of the Kansas Entomological Society* 65, 30–38.
- Evans, E.W., Stevenson, A.T., Richards, D.R., 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia* 121, 107–112.
- Evans, E.W., Richards, D.R., Kalaskar, A., 2004. Using food for different purposes: female responses to prey in the predator *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Ecological Entomology* 29, 27–34.
- Ferran, A., Dixon, A.F.G., 1993. Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *European Journal of Entomology* 90, 383–402.
- Ferran, A., Gambier, J., Parent, S., Legendre, K., Tournière, R., Giuge, L., 1997. The effect of rearing the ladybird *Harmonia axyridis* on *Ephesthia kuehniella* eggs on the response of its larvae to aphid tracks. *Journal of Insect Behavior* 10, 129–144.
- Forbes, S.A., 1883. The food relations of the Carabidae and Coccinellidae. *Bulletin of the Illinois State Laboratory of Natural History – Urbana* 2, 33–64.
- Gagné, I., Coderre, D., Mauffette, Y., 2002. Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecological Entomology* 27, 285–291.
- Gautam, R.D., 1990. Mass-multiplication technique of coccinellid predator, lady bird beetle (*Brumoides suturalis*). *Indian Journal of Agricultural Sciences* 60, 747–750.
- Giles, K.L., Obrycki, J.J., DeGooyer, T.A., 1994. Prevalence of predators associated with *Acyrtosiphon pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. *Biological Control* 4, 170–177.
- Giorgi, J.A., Vandenberg, N.J., McHugh, J.V., Forrester, J.A., Ślipiński, S.A., Miller, K.B., Shapiro, L.R., Whiting, M.F., 2009. The evolution of food preferences in Coccinellidae. *Biological Control* 51, 215–231.
- Giroux, S., Coderre, D., Vincent, C., Côté, J.-C., 1994a. Effects of *Bacillus thuringiensis* var. *san diego* on predation effectiveness, development and mortality of *Coleomegilla maculata lengi* (Col.: Coccinellidae) larvae. *Entomophaga* 39, 61–69.
- Giroux, S., Côté, J.-C., Vincent, C., Martel, P., Coderre, D., 1994b. Bacteriological insecticide M-One effects on predation efficiency and mortality of adult *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* 87, 39–43.
- Giroux, S., Duchesne, R.-M., Coderre, D., 1995. Predation of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) by *Coleomegilla maculata* (Coleoptera: Coccinellidae): comparative effectiveness of predator developmental stages and effect of temperature. *Environmental Entomology* 24, 748–754.
- Gordon, R.D., 1985. The Coccinellidae (Coleoptera) of America north of Mexico. *Journal of the New York Entomological Society* 93, 1–912.
- Gravena, S., Da Cunha, H.F., 1991. Predation of cotton leafworm first instar larvae, *Alabama argillacea* [Lep.: Noctuidae]. *Entomophaga* 36, 481–491.
- Greenstone, M.H., 1979. Spider feeding behaviour optimizes dietary essential amino acid composition. *Nature* 282, 501–503.
- Greenstone, M.H., Rowley, D.L., Weber, D.C., Payton, M.E., Hawthorne, D.J., 2007. Feeding mode and prey detectability half-lives in molecular gut-content analysis: an example with two predators of the Colorado potato beetle. *Bulletin of Entomological Research* 97, 201–209.
- Groden, E., Drummond, F.A., Casagrande, R.A., Haynes, D.L., 1990. *Coleomegilla maculata* (Coleoptera: Coccinellidae): its predation upon the Colorado potato

- beetle (Coleoptera: Chrysomelidae) and its incidence in potatoes and surrounding crops. *Journal of Economic Entomology* 83, 1306–1315.
- Hagen, K.S., 1987. Nutritional ecology of terrestrial insect predators. In: Slansky, F., Rodriguez, J.G. (Eds.), *Nutritional Ecology of Insects, Mites, Spiders and Related Invertebrates*. John Wiley & Sons, New York, pp. 533–577.
- Hagen, K.S., Sawall Jr., E.F., Tassan, R.L., 1971. The use of food sprays to increase effectiveness of entomophagous insects. *Proceedings of the Tall Timbers Conference on Ecological Animal Control and Habitat Management* 2, 59–81.
- Hamasaki, K., Matsui, M., 2006. Development and reproduction of an aphidophagous coccinellid, *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae), reared on an alternative diet, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. *Applied Entomology and Zoology* 41, 233–237.
- Hassanein, F.A., Hamed, A.R., 1984. Assessment of the role of larvae of *Coccinella undecimpunctata* L. (Col., Coccinellidae) as a biological control agent against *Spodoptera littoralis* Bois. (Lep., Noctuidae) in Egypt. *Zeitschrift für angewandte Entomologie* 97, 506–509.
- Hazzard, R.V., Ferro, D.N., 1991. Feeding responses of adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of the Colorado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphididae). *Environmental Entomology* 20, 644–651.
- Hazzard, R.V., Ferro, D.N., Van Driesche, R.G., Tuttle, A.F., 1991. Mortality of eggs of Colorado potato beetle (Coleoptera: Chrysomelidae) from predation by *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environmental Entomology* 20, 841–848.
- Head, R.B., Neel, W.W., Morris, R.C., 1977. Seasonal occurrence of the cottonwood leaf beetle *Chrysomela scripta* (Fab.) and its principal insect predators in Mississippi and notes on parasites. *Journal of the Georgia Entomological Society* 12, 157–163.
- Hemptinne, J.-L., Lognay, G., Gauthier, C., Dixon, A.F.G., 2000. Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera: Coccinellidae). *Chemoecology* 19, 123–128.
- Hilbeck, A., Kennedy, G.G., 1996. Predators feeding on the Colorado potato beetle in insecticide-free plots and insecticide-treated commercial potato fields in eastern North Carolina. *Biological Control* 6, 273–282.
- Hilbeck, A., Eckel, C., Kennedy, G.G., 1997. Predation on Colorado potato beetle eggs by generalist predators in research and commercial potato plantings. *Biological Control* 8, 191–196.
- Hilbeck, A., Eckel, C., Kennedy, G.G., 1998. Impact of *Bacillus thuringiensis* – insecticides on population dynamics and egg predation of the Colorado potato beetle in North Carolina potato plantings. *BioControl* 43, 65–75.
- Hippa, H., Koponen, S., 1979. Experiments on biological control of leaf beetles (Col., Chrysomelidae) on the cloudberry (*Rubus chamaemorus* L.). *Reports of the Kevo Subarctic Research Station* 15, 8–10.
- Hippa, H., Koponen, S., Laine, T., 1978. On the feeding biology of *Coccinella hieroglyphica* L. (Col., Coccinellidae). *Reports of the Kevo Subarctic Research Station* 14, 18–20.
- Hippa, H., Koponen, S., Neuvonen, S., 1976. Population dynamics of the form of *Galerucella nymphaeae*-complex (Col., Chrysomelidae) living on cloudberry in northern Finland. *Reports of the Kevo Subarctic Research Station* 13, 36–39.
- Hippa, H., Koponen, S., Roine, R., 1982. Feeding preference of *Coccinella hieroglyphica* (Col., Coccinellidae) for eggs of three chrysomelid beetles. *Reports of the Kevo Subarctic Research Station* 18, 1–4.
- Hippa, H., Koponen, S., Roine, R., 1984. Larval growth of *Coccinella hieroglyphica* (Col., Coccinellidae) fed on aphids and preimaginal stages of *Galerucella sagittariae* (Col., Chrysomelidae). *Reports of the Kevo Subarctic Research Station* 19, 67–70.
- Hodek, I., 1962. Essential and alternative foods in insects. In: Strouhal, H., Beier, M. (Eds.), *Transactions of the XIth International Congress of Entomology*, vol. 2. Organisationskomitee des XI Internationalen Kongress für Entomologie, Vienna, pp. 697–698.
- Hodek, I., 1973. *Biology of Coccinellidae*. Czechoslovak Academy of Science, Prague.
- Hodek, I., 1996. Food relationships. In: Hodek, I., Honěk, A. (Eds.), *Ecology of Coccinellidae*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 143–238.
- Hodek, I., Honěk, A., 1988. Sampling, rearing and handling of aphid predators. In: Minks, A.K., Harrewijn, P. (Eds.), *Aphids, Their Biology, Natural Enemies and Control*, vol. 2B. Elsevier, Amsterdam, pp. 311–321.
- Hodek, I., Honěk, A., 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Hoogendoorn, M., Heimpel, G.E., 2001. PCR-based gut content analysis of insect predators: using ribosomal ITS-1 fragments from prey to estimate predation frequency. *Molecular Ecology* 10, 2059–2067.
- Hoogendoorn, M., Heimpel, G.E., 2004. Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomologia Experimentalis et Applicata* 111, 19–28.
- Horn, D.J., 1991. Potential impact of *Coccinella septempunctata* on endangered Lycaenidae (Lepidoptera) in Northwestern Ohio, USA. In: Polgár, L., Chambers, R.J., Dixon, A.F.G., Hodek, I. (Eds.), *Behaviour and Impact of Aphidophaga*. SPB Academic Publishing, The Hague, The Netherlands, pp. 159–162.
- Hudon, M., LeRoux, E.J., 1986. Biology and population dynamics of the European corn borer (*Ostrinia nubilalis*) with special reference to sweet corn in Quebec. III. Population dynamics and spatial distribution. *Phytoprotection* 67, 93–115.
- Hussain, M., 1975. Predators of the alfalfa weevil, *Hypera postica* in western Nevada – a greenhouse study. (Coleoptera: Curculionidae). *Journal of the New York Entomological Society* 83, 226–228.
- Iperti, G., Brun, J., Daumal, J., 1972. Possibilité de multiplication des coccinelles coccidiphages et aphidiphages (Coleopt. Coccinellidae) à l'aide d'oeufs d'*Anagasta kuehniella* Z. (Lepidopt. Pyralidae). *Annales de Zoologie Ecologie Animale* 4, 555–567.
- Iwata, K., 1932. On the biology of two large lady-birds in Japan. *Transactions of the Kansai Entomological Society* 3, 13–27.
- Iwata, K., 1965. Supplement of the biology of two large lady-birds in Japan. *Acta Coleopterologica* 2, 57–68.
- Kagata, H., Katayama, N., 2006. Does nitrogen limitation promote intraguild predation in an aphidophagous ladybird? *Entomologia Experimentalis et Applicata* 119, 239–246.
- Kagata, H., Ohgushi, T., 2007. Carbon–nitrogen stoichiometry in the tritrophic food chain willow, leaf beetle, and predatory ladybird beetle. *Ecological Research* 22, 671–677.
- Kagata, H., Nakamura, M., Ohgushi, T., 2005. Bottom-up cascade in a tri-trophic system: different impacts of host-plant regeneration on performance of a willow leaf beetle and its natural enemy. *Ecological Entomology* 30, 58–62.
- Kajita, Y., Takano, F., Yasuda, H., Agarwala, B.K., 2000. Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Applied Entomology and Zoology* 35, 473–479.
- Kalaskar, A., Evans, E.W., 2001. Larval responses of aphidophagous lady beetles (Coleoptera: Coccinellidae) to weevil larvae versus aphids as prey. *Annals of the Entomological Society of America* 94, 76–81.
- Kanervo, V., 1940. Beobachtungen und versuche sur ermittlung der nahrung einiger Coccinelliden. *Annales Entomologici Fennici* 6, 89–110.
- Kanervo, V., 1946. Studien über die natürlichen feinde des Erlenblattkäfers, *Melasma aenea* L. (Col., Chrysomelidae). *Annales Zoologici Societatis Vanamo* 12, 1–206.
- Kareiva, P., Odell, G., 1987. Swarms of predators exhibit “prey-taxis” if individual predators use area-restricted search. *American Naturalist* 130, 233–270.
- Kato, C.M., Bueno, V.H.P., Moraes, J.C., Auad, A.M., 1999. Rearing of *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae) on eggs of *Anagasta kuehniella* (Zeller) (Lepidoptera: Pyralidae). *Anais da Sociedade Entomologica do Brasil* 28, 455–459.
- Koch, R.L., Hutchison, W.D., Venette, R.C., Heimpel, G.E., 2003. Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Control* 28, 265–270.
- Koch, R.L., Venette, R.C., Hutchison, W.D., 2005. Influence of alternate prey on predation of monarch butterfly (Lepidoptera: Nymphalidae) larvae by the multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environmental Entomology* 34, 410–416.
- Křivan, V., 2008. Dispersal dynamics: distribution of lady beetles (Coleoptera: Coccinellidae). *European Journal of Entomology* 105, 405–410.
- Lovei, G.L., Arpaia, S., 2005. The impact of transgenic plants on natural enemies: a critical review of laboratory studies. *Entomologia Experimentalis et Applicata* 114, 1–14.
- Lu, W., Kennedy, G.G., Gould, F., 1996. Differential predation by *Coleomegilla maculata* on Colorado potato beetle strains that vary in growth on tomato. *Entomologia Experimentalis et Applicata* 81, 7–14.
- Lucas, E., Coderre, D., Brodeur, J., 1998. Intraguild predation among aphid predators: characterization and influence of extraguild prey density. *Ecology* 79, 1084–1092.
- Lucas, E., Demougeot, S., Vincent, C., Coderre, D., 2004a. Predation upon the oblique-banded leafroller, *Choristoneura rosaceana* (Lepidoptera: Tortricidae), by two aphidophagous coccinellids (Coleoptera: Coccinellidae) in the presence and absence of aphids. *European Journal of Entomology* 101, 37–41.
- Lucas, E., Giroux, S., Demougeot, S., Duchesne, R.-M., Coderre, D., 2004b. Compatibility of a natural enemy, *Coleomegilla maculata lengi* (Col., Coccinellidae) and four insecticides used against the Colorado potato beetle (Col., Chrysomelidae). *Journal of Applied Entomology* 128, 233–239.
- Lundgren, J.G., 2009a. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control* 51, 294–305.
- Lundgren, J.G., 2009b. Relationships of Natural Enemies and Non-prey Foods. Springer, Dordrecht, The Netherlands.
- Lundgren, J.G., Razzak, A.A., Wiedenmann, R.N., 2004. Population responses and feeding behaviors of the predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. *Environmental Entomology* 33, 958–963.
- Mallampalli, N., Gould, F., Barbosa, P., 2005. Predation of Colorado potato beetle eggs by a polyphagous ladybeetle in the presence of alternate prey: potential impact on resistance evolution. *Entomologia Experimentalis et Applicata* 114, 47–54.
- Majerus, M.E.N., 1994. *Ladybirds*. HarperCollins, London.
- Marvier, M., McCreedy, C., Regetz, J., Kareiva, P., 2007. A meta-analysis of effects of Bt cotton and maize on nontarget invertebrates. *Science* 316, 1475–1477.
- Matos, B., Obyrcki, J.J., 2006. Prey suitability of *Galerucella californiensis* L. (Coleoptera: Chrysomelidae) and *Myzus lythri* (Schrank) (Homoptera: Aphididae) for development of three predatory species. *Environmental Entomology* 35, 345–350.
- Matos, B., Obyrcki, J.J., 2007. Evaluation of mortality of *Galerucella californiensis* L. (Coleoptera: Chrysomelidae) preimaginal life stages and pupal survival at two wetlands in Iowa. *Journal of the Kansas Entomological Society* 80, 16–26.
- Matsura, T., 1976. Ecological studies of a coccinellid, *Aiolocaria hexaspilota* Hope. I. Interaction between field populations of *A. hexaspilota* and its prey, the walnut leaf beetle (*Gastrolina depressa* Baly). *Japanese Journal of Ecology* 26, 147–156.
- Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S., Simpson, S.J., 2005. Nutrient specific foraging in invertebrate predators. *Science* 307, 111–113.

- Mena-Covarrubias, J., Drummond, F.A., Haynes, D.L., 1996. Population dynamics of the Colorado potato beetle (Coleoptera: Chrysomelidae) on horsenettle in Michigan. *Environmental Entomology* 25, 68–77.
- Mensah, R.K., 1997. Local density responses of predatory insects of *Helicoverpa* spp. to a newly developed food supplement 'Envirofeast' in commercial cotton in Australia. *International Journal of Pest Management* 43, 221–225.
- Mensah, R.K., 2002a. Development of an integrated pest management programme for cotton. Part 1. Establishing and utilizing natural enemies. *International Journal of Pest Management* 48, 87–94.
- Mensah, R.K., 2002b. Development of an integrated pest management programme for cotton. Part 2. Integration of a lucerne/cotton interplant system, food supplement sprays with biological and synthetic insecticides. *International Journal of Pest Management* 48, 95–105.
- Mensah, R.K., Madden, J.L., 1994. Conservation of two predator species for biological control of *Chrysophtharta bimaculata* (Col.: Chrysomelidae) in Tasmanian forests. *Entomophaga* 39, 71–83.
- Mensah, R.K., Singleton, A., 2003. Optimum timing and placement of a supplementary food spray Envirofeast® for the establishment of predatory insects of *Helicoverpa* spp. in cotton systems in Australia. *International Journal of Pest Management* 49, 163–168.
- Michaud, J.P., 2005. On the assessment of prey suitability in aphidophagous Coccinellidae. *European Journal of Entomology* 102, 385–390.
- Michaud, J.P., Grant, A.K., 2004. Adaptive significance of sibling egg cannibalism in Coccinellidae: comparative evidence from three species. *Annals of the Entomological Society of America* 97, 710–719.
- Michaud, J.P., Jyoti, J.L., 2008. Dietary complementation across life stages in the polyphagous lady beetle *Coleomegilla maculata*. *Entomologia Experimentalis et Applicata* 126, 40–45.
- Miranda, M.M.M., Picanço, M., Zanoncio, J.C., Guedes, R.N.C., 1998. Ecological life table of *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae). *Biocontrol Science and Technology* 8, 597–606.
- Munyanza, J., Obyrcki, J.J., 1997a. Reproductive response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle (Coleoptera: Chrysomelidae) eggs. *Environmental Entomology* 26, 1270–1275.
- Munyanza, J., Obyrcki, J.J., 1997b. Functional response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle eggs (Coleoptera: Chrysomelidae). *Biological Control* 8, 215–224.
- Munyanza, J., Obyrcki, J.J., 1998a. Development of three populations of *Coleomegilla maculata* (Coleoptera: Coccinellidae) feeding on eggs of Colorado potato beetle (Coleoptera: Chrysomelidae). *Environmental Entomology* 27, 117–122.
- Munyanza, J., Obyrcki, J.J., 1998b. Searching behavior of *Coleomegilla maculata* larvae feeding on Colorado potato beetle eggs. *Biological Control* 13, 85–90.
- Musser, F.R., Shelton, A.M., 2003. Predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. *Environmental Entomology* 32, 1131–1138.
- Nault, B.A., Kennedy, G.G., 2000. Seasonal changes in habitat preference by *Coleomegilla maculata*: implications for Colorado potato beetle management in potato. *Biological Control* 17, 164–173.
- Nichols, J.R., Obyrcki, J.J., Tauber, C.A., Tauber, M.J., 1996. Potential impact of native natural enemies on *Galerucella* spp. (Coleoptera: Chrysomelidae) imported for biological control of purple loosestrife: a field evaluation. *Biological Control* 7, 60–66.
- Obyrcki, J.J., Orr, C.J., 1990. Suitability of three prey species for nearctic populations of *Coccinella septempunctata*, *Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Journal of Economic Entomology* 83, 1292–1297.
- Obyrcki, J.J., Kring, T.J., 1998. Predaceous Coccinellidae in biological control. *Annual Review of Entomology* 43, 295–321.
- Obyrcki, J.J., Giles, K.L., Ormond, A.M., 1998. Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environmental Entomology* 27, 1280–1288.
- Obyrcki, J.J., Harwood, J.D., Kring, T.J., 2009. Aphidophagy by Coccinellidae: application of biological control in agroecosystems. *Biological Control* 51, 244–254.
- Olszak, R.W., 1986. Suitability of three aphid species as prey for *Propylea quatuordecimpunctata*. In: Hodek, I. (Ed.), *Ecology of Aphidophaga*, vol. 2. Academia, Prague, pp. 51–56.
- Omkar, Pervez, A., Gupta, A.K., 2006. Why do neonates of aphidophagous ladybird beetles preferentially consume conspecific eggs in presence of aphids? *Biocontrol Science and Technology* 16, 233–243.
- Osawa, N., 1992. Sibling cannibalism in the ladybird beetle *Harmonia axyridis*: fitness consequences for mother and offspring. *Researches in Population Ecology* 34, 45–55.
- Ouayogode, B.V., Davis, D.W., 1981. Feeding by selected predators on alfalfa weevil larvae. *Environmental Entomology* 10, 62–64.
- Parajulee, M.N., Shrestha, R.B., Leser, J.F., Wester, D.B., Blanco, C.A., 2006. Evaluation of the functional response of selected arthropod predators on bollworm eggs in the laboratory and effect of temperature on their predation efficiency. *Environmental Entomology* 35, 379–386.
- Perry, J.C., Roitberg, B.D., 2005. Ladybird mothers mitigate offspring starvation risk by laying trophic eggs. *Behavioral Ecology and Sociobiology* 58, 578–586.
- Pfannenstiel, R.S., Yeargan, K.V., 2002. Identification and diel activity patterns of predators attacking *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs in soybean and sweet corn. *Environmental Entomology* 31, 232–241.
- Phoofolo, M.W., Obyrcki, J.J., 1997. Comparative prey suitability of *Ostrinia nubilalis* eggs and *Acyrtosiphon pisum* for *Coleomegilla maculata*. *Biological Control* 9, 167–172.
- Provost, C., Lucas, E., Coderre, D., Chouinard, G., 2006. Prey selection by the lady beetle *Harmonia axyridis*: the influence of prey mobility and prey species. *Journal of Insect Behavior* 19, 265–277.
- Putman, W.L., 1957. Laboratory studies on the food of some coccinellids (Coleoptera) found in Ontario peach orchards. *Canadian Entomologist* 89, 572–579.
- Putman, W.L., 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Canadian Entomologist* 96, 1149–1155.
- Racioppi, J.V., Burton, R.L., Eikenbary, R., 1981. The effects of various oligidic synthetic diets on the growth of *Hippodamia convergens*. *Entomologia Experimentalis et Applicata* 30, 68–72.
- Rana, J.S., Dixon, A.F.G., Jarosik, V., 2002. Costs and benefits of prey specialization in a generalist insect predator. *Journal of Animal Ecology* 71, 15–22.
- Richards, D.R., Evans, E.W., 1998. Reproductive responses of aphidophagous lady beetles (Coleoptera: Coccinellidae) to non-aphid diets: an example from alfalfa. *Annals of the Entomological Society of America* 91, 632–640.
- Riddick, E.W., Barbosa, P., 1998. Impact of Cry3A-intoxicated *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) and pollen on consumption, development, and fecundity of *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Annals of the Entomological Society of America* 91, 303–307.
- Rieder, J.P., Newbold, T.A.S., Sato, S., Yasuda, H., Evans, E.W., 2008. Intra-guild predation and variation in egg defence between sympatric and allopatric populations of two species of ladybird beetles. *Ecological Entomology* 33, 53–58.
- Rodríguez, E., Lozano, C., Campos, M., 2005. Detection of predation on *Euzophera pinguis* (Lepidoptera: Pyralidae) using an enzyme-linked immunosorbent assay. *European Journal of Entomology* 102, 793–796.
- Roger, C., Coderre, D., Boivin, G., 2000. Differential prey utilization by the generalist predator *Coleomegilla maculata* lengi according to prey size and species. *Entomologia Experimentalis et Applicata* 94, 3–13.
- Roger, C., Coderre, D., Vigneault, C., Boivin, G., 2001. Prey discrimination by a generalist coccinellid predator: effect of prey age or parasitism? *Ecological Entomology* 26, 163–172.
- Rondon, S.I., Cantliffe, D.J., Price, J.F., 2003. *Anasa tristis* (Heteroptera: Coreidae) development, survival and egg distribution on beet alpha cucumber and as prey for *Coleomegilla maculata* (Coleoptera: Coccinellidae) and *Geocoris punctipes* (Heteroptera: Lygaeidae). *Florida Entomologist* 86, 488–490.
- Roy, H.E., Rudge, H., Goldrick, L., Hawkins, D., 2007. Eat or be eaten: prevalence and impact of egg cannibalism on two-spot ladybirds, *Adalia bipunctata*. *Entomologia Experimentalis et Applicata* 125, 33–38.
- Samways, M.J., Osborn, R., Saunders, T.L., 1997. Mandible form relative to the main food type in ladybirds (Coleoptera: Coccinellidae). *Biocontrol Science and Technology* 7, 275–286.
- Sato, S., Dixon, A.F.G., 2004. Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agricultural and Forest Entomology* 6, 21–24.
- Schade, V.M., Sengonca, C., 1998. On the development, feeding activity and prey preference of *Hippodamia convergens* Guer.-Men. (Col., Coccinellidae) preying on *Thrips tabaci* Lind. (Thys., Thripidae) and two species of Aphidae. *Anzeiger für Schädlingkunde Pflanzenschutz Umweltschutz* 71, 77–80.
- Schanderl, H., Ferran, A., Garcia, V., 1988. L'élevage de deux coccinelles *Harmonia axyridis* et *Semiadalia undecimnotata* à l'aide d'oeufs d'*Anagasta kuehniella* tués aux rayons ultraviolets. *Entomologia Experimentalis et Applicata* 49, 235–244.
- Schellhorn, N.A., Andow, D.A., 1999. Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. *Environmental Entomology* 28, 1092–1100.
- Schellhorn, N.A., Lane, C.P., Olson, D.M., 2005. The co-occurrence of an introduced biological control agent (Coleoptera: *Coccinella septempunctata*) and an endangered butterfly (Lepidoptera: *Lycaedes melissa samuelis*). *Journal of Insect Conservation* 9, 41–47.
- Schmaedick, M.A., Shelton, A.M., 2000. Arthropod predators in cabbage (Cruciferae) and their potential as naturally occurring biological control agents for *Pieris rapae* (Lepidoptera: Pieridae). *Canadian Entomologist* 132, 655–675.
- Seagraves, M.P., 2009. Lady beetle oviposition behavior in response to the trophic environment. *Biological Control* 51, 313–322.
- Sebolt, D.C., Landis, D.A., 2002. Neonate *Galerucella californiensis* (Coleoptera: Chrysomelidae) behavior on purple loosestrife (*Lythrum salicaria*) contributes to reduced predation. *Environmental Entomology* 31, 880–886.
- Sebolt, D.C., Landis, D.A., 2004. Arthropod predators of *Galerucella californiensis* L. (Coleoptera: Chrysomelidae): an assessment of biotic interference. *Environmental Entomology* 33, 356–361.
- Shade, R.E., Hansen, H.L., Wilson, M.C., 1970. A partial life table of the cereal leaf beetle, *Oulema melanopus*, in northern Indiana. *Annals of the Entomological Society of America* 63, 52–59.
- Sloggett, J.J., Majerus, M.E.N., 2000. Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biological Journal of the Linnean Society* 70, 63–88.
- Snyder, W.E., 2009. Coccinellids in diverse communities: which niche fits. *Biological Control* 51, 323–335.
- Snyder, W.E., Clevenger, G.M., 2004. Negative dietary effects of Colorado potato beetle eggs for the larvae of native and introduced ladybird beetles. *Biological Control* 31, 353–361.

- Snyder, W.E., Joseph, S.B., Preziosi, R.F., Moore, A.J., 2000. Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Environmental Entomology* 29, 1173–1179.
- Soares, A.O., Coderre, D., Schanderl, H., 2004. Dietary self-selection behaviour by the adult of the aphidophagous ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Journal of Animal Ecology* 73, 478–486.
- Specty, O., Febvay, G., Grenier, S., Delobel, B., Piotte, C., Pageaux, J.-F., Ferran, A., Guillaud, J., 2003. Nutritional plasticity of the predatory ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae): comparison between natural and substitution prey. *Archives of Insect Biochemistry and Physiology* 52, 81–91.
- Stuart, R.J., Michaud, J.P., Olsen, L., McCoy, C.W., 2002. Lady beetles as potential predators of the root weevil *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in Florida citrus. *Florida Entomologist* 85, 409–416.
- Takahashi, K., 1989. Intra- and inter-specific predations by lady beetles in spring alfalfa fields. *Japanese Journal of Entomology* 57, 199–203.
- Tanton, M.T., Kahn, S.M., 1978. Aspects of the biology of the Eucalypt-defoliating chrysomelid beetle *Paropsis atomaria* Ol. in the Australian Capital Territory. *Australian Journal of Zoology* 26, 113–120.
- Thompson, W.R., 1951. The specificity of host relationships in predaceous insects. *Canadian Entomologist* 83, 262–269.
- Triltsch, H., 1997. Gut contents in field sampled adults of *Coccinella septempunctata* (Col.: Coccinellidae). *Entomophaga* 42, 125–131.
- Triltsch, H., 1999. Food remains in the guts of *Coccinella septempunctata* (Coleoptera: Coccinellidae) adults and larvae. *European Journal of Entomology* 96, 355–364.
- Van den Berg, H., Litsinger, J.A., Shepard, B.M., Pantua, P.C., 1992. Acceptance of eggs of *Rivula atimeta*, *Naranga aenescens* [Lep.: Noctuidae] and *Hydrellia philippina* [Dipt.: Ephydriidae] by insect predators on rice. *Entomophaga* 37, 21–28.
- Wade, M.R., Zalucki, M.P., Wratten, S.D., Robinson, K.A., 2008. Conservation biological control of arthropods using artificial food sprays: current status and future challenges. *Biological Control* 45, 185–199.
- Wagner, J.D., Glover, M.D., Moseley, J.B., Moore, A.J., 1999. Heritability and fitness consequences of cannibalism in *Harmonia axyridis*. *Evolutionary Ecology Research* 1, 375–388.
- Warren, L.O., Tadic, M., 1967. Biological observations on *Coleomegilla maculata* and its role as a predator of the fall webworm. *Journal of Economic Entomology* 60, 1492–1496.
- Weber, D.C., Lundgren, J.G., 2009a. Detection of predation using qPCR: effect of prey quantity, elapsed time, chaser diet, and sample preservation on detectable quantity of prey DNA. *Journal of Insect Science* 9, 41.
- Weber, D.C., Lundgren, J.G., 2009b. Assessing the trophic ecology of the Coccinellidae: Their roles as predators and as prey. *Biological Control* 51, 199–214.
- Weber, R.G., Holman, M.V., 1976. *Coleomegilla maculata* (DeGeer), (Coleoptera: Coccinellidae), a new coleopteran predator of the elm leaf beetle, *Pyrrhalta luteola* (Mueller), (Coleoptera: Chrysomelidae). *Journal of the Kansas Entomological Society* 49, 160.
- Whitehead, D.R., Duffield, R.M., 1982. An unusual specialized predator prey association (Coleoptera: Coccinellidae, Chrysomelidae): failure of a chemical defense and possible practical application. *The Coleopterists Bulletin* 36, 96–97.
- Wiebe, A.P., Obrycki, J.J., 2002. Prey suitability of *Galerucella pusilla* eggs for two generalist predators, *Coleomegilla maculata* and *Chrysoperla carnea*. *Biological Control* 23, 143–148.
- Wiebe, A.P., Obrycki, J.J., 2004. Quantitative assessment of predation of eggs and larvae of *Galerucella pusilla* in Iowa. *Biological Control* 31, 16–28.
- Yadava, C.P., Shaw, F.R., 1968. The preferences of certain coccinellids for pea aphids, leafhoppers, and alfalfa weevil larvae. *Journal of Economic Entomology* 61, 1104–1105.
- Yakhontov, V.V., 1934. The alfalfa weevil *Phytonomus* (*Phytonomus variabilis* Hbst.). *Review of Applied Entomology Series A* 22, 334–336.
- Yakhontov, V.V., 1938. Practical results of an experiment. A biological method of controlling pests of lucerne and cotton. *Review of Applied Entomology Series A* 26, 238–239.
- Yasuda, H., Ohnuma, N., 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomologia experimentalis et applicata* 93, 63–67.
- Yasuda, H., Shinya, K., 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42, 153–163.