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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.

Keywords: biological control, Coccinellidae, functional response, numerical response, prey selection, reproductive strategy, predation

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 (Hodek 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.

1. Range of prey consumed

1.1. 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 et al., 1970), Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Groden 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 & 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) (Elliot 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 Yeargan, 1998a; Schellhorn and Andow, 1999; Snyder, 2009, this issue).

1.2. Gut and frass analyses. Methods that augment field observations also have revealed frequent coccinellid consumption of insect prey other than Sternorrhyncha (Weber and Lundgren, 2009, this issue). The remarkable nineteenth century ecologist S. A. 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 nematocerous 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. Rodriguez 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, in press) that are not well detected by their remains in gut or frass analysis (Triltsch, 1999).

1.3. 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 outbreaks 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 *Chrysophtharta 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 *Plagiodera 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 *Plagiodera 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.

2. Impact of lady beetles on prey populations

2.1. 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.

2.1.1. Coleomegilla maculata *and lepidopteran prey.* Most attention has focused on *Coleomegilla 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 Bottrell, 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 eight-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 three 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 hours), 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-hour 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% vs 25% every 3 hours). 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).

2.1.2. Coleomegilla 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 (Groden 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 (Groden 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 (Groden 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 *G. 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 hours 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).

2.1.3 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 *Hippodamia 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. Hippa et al. (1976) judged from field observations that feeding by larvae and adults of *Coccinella 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 *A. hexaspilota* (= *mirabilis*) Hope attacking the chrysomelid, *Gastrolina depressa*, on walnuts in Japan. De Little et al. (1990) estimated that 66-84% of *Chysophtharta bimaculata* eggs and young larvae died, primarily from predation by *Cleobara 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 argrillacea* (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, 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).

2.2 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, this issue; Weber and Lundgren, 2009, this issue). 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 *Coleomegilla 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 Yeargan, 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).

3. 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.

3.1. Larval growth and development.

3.1.1. 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 *Pharoscymnus semiglobosus* Karsch (coccidophagous). In subsequent studies, larval rates of development and survival, and weights of newly eclosed *Harmonia axyridis* (Schanderl et al., 1988), *Hippodamia convergens* (Kato et al., 1999) and *Propylea japonica* (Thunberg) (Hamasaki and Matusi, 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 *A. pisum* before switching the larvae thereafter to a diet of grain moth eggs. Abdel-Salam and Abdel-Baky (2001) reared *Harmonia 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.

3.1.2. 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 (Munyaneza and Obrycki, 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 *Harmonia conformis* readily completed development in the laboratory on a diet of eggs of the Tasmanian eucalypt defoliator

Chrysophtharta 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 *Aiolocaria hexaspilota* Hope, a specialist predator of leaf beetles, initially with eggs and subsequently with larvae of the willow leaf beetle *Plagiodera 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 *Coccinella 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. calmariensis*, larvae of this lady beetle perform poorly on these prey. Wiebe and Obrycki (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. calmariensis* eggs or larvae (Matos and Obrycki, 2006). Larvae of *H. axyridis* also failed to survive on a diet of *G. calmariensis* eggs, and only

27% survived on a diet of *G. calmariensis* larvae, with slow development and reduced size as adults (Matos and Obrycki, 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, this issue; Weber and Lundgren, 2009, this issue). 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, 2002; 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.

3.1.3. 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.

3.1.4. 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.

3.2. 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 Clerq 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 *Coccinella 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 *Chrysophtharta 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 *Paropsis 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 *C. 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).

3.3 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, 2009, this issue). 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 that 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.

4. 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; Kajita et al., 2000; Musser and Shelton, 2003; Lucas et al., 2004a; 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).

4.1. Prey choice

4.1.1. 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 *D. 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; Ouayagode 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.

4.1.2. Preferences among non-hemipteran prey. Other studies indicate that lady beetles may be subtly selective in their consumption of non-hemipteran prey. Hippa et al. (1982) found that adults of *C. hieroglyphica* ate conspecific eggs and eggs of *Galerucella 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.

4.2 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.

4.3. 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.

4.4 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).

5. 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, this issue; Obrycki et al., 2009, this issue), 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 *Semiadalia 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 (*Galerucella nymphaeae* complex) that attack cloudberries and cultivated strawberry in northern Finland, Hippa and Koponen (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.

5.1. 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 2009) 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; 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 *Chrysophtharta 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.

5.2 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 *B. 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.

6. 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, this issue), 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, this issue). 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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