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Review

Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds

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ABSTRACT

This review surveys the literature dealing with food relationships of coccidophagous, aleurodophagous and psyllophagous coccinellids. While in the cold temperate climate aphids are the dominant prey group (68% of ladybird species), globally, coccids are the dominant prey group of 36% of coccinellid species, and only 20% prey primarily on aphids. Special attention is given to the physiological and environmental factors that affect the nutritive suitability of prey. In particular, the physiological states and development stages of the predators and prey species, sensory cues used in foraging, interspecific differences in the suitability of prey, the effects of host plants on predator–prey interactions, and climatic and seasonal effects on predation are discussed. Considerably more research has been conducted on the utility of coccinellids as predators of coccids than on aleyrodids and psyllids, in part because of the characteristics of whiteflies that restrict their consumption by polyphagous species. A major conclusion is that the assumption that coccinellids (and other predators) are of limited value in managing these non-aphid sternorrhynchans is premature, and that more research is sorely needed on these prey groups from predator ecologists.

1. Introduction

Coccinellidae feed on a wide variety of prey species (Hodek, 1996), e.g. mites (Biddinger et al., 2009), aphids (Obrycki et al., 2009), Coleoptera and Lepidoptera (Evans, 2009), and non-prey food (Lundgren, 2009; Sutherland and Parrella, 2009). This review focuses on three kinds of prey: coccids (scales and mealybugs), aleyrodids (whiteflies), and psyllids, i.e. Hemiptera Sternorrhyncha other than aphids. Coccids are essential food for a large proportion (36%) of coccinellid species globally, especially in the tropics and subtropics.

Although prey specialization occurs even within individual tribes of coccinellids, such as Coccinellini, there is a tendency for coccinellids to feed on common prey groups at the tribal level. Coccidophagy is likely the ancestral condition for the family Coccinellidae (Giorgi et al., 2009), and coccidophagous coccinellids belong to several tribes (and genera), including Sukunahikonini, Sticholotini, Scymnini (*Cryptolaemus*, *Diomus*, *Nephus*, *Sidis*), Hyperaspini (*Hyperaspis*), Telsimiini, Chilocorini (*Chilocorus*, *Exochomus*), Coccidulini (*Rhyzobius*), Azyini, Exoplectrini, Noviini (*Novius*, *Rodolia*), and Coccinellini (*Neda*). Psyllids are consumed preferentially by coccinellids in the tribe Ortaliini, and occasionally Coccinellini. Species from Serangiini, Scymnini (*Clitostethus*), and Scymnillini prefer aleyrodids as prey. (For a table of all groups of preys of ladybirds see Hodek, 1996, pp. 144–145.)

An exact evidence of trophic ecology of coccinellids can only been gained by a systematic, preferably experimental study. The finding that some food may be eaten by ladybirds in spite of its low suitability or even toxicity (Hodek, 1956; Blackman, 1965) led to the principal distinction between essential food promoting successful preimaginal development and reproduction, while alternative foods only enable survival (Hodek, 1962, 1996). Here, we discuss some of the trophic ecology of lady beetles that specialize on non-aphid, hemipteran insects.

2. Scale insects (Coccoidea)

2.1. Economic importance of coccids and coccidophagous ladybirds

While globally, coccids are the dominant prey group for 36% of coccinellid species, and while only 20% consume primarily

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aphids, 68% of temperate ladybird species consume aphids (Klausnitzer and Klausnitzer, 1997). Majerus (1994) gives a very useful list of principal and secondary foods of British coccinellids (without defining these two categories), where coccids are listed as secondary prey for 16 primarily aphidophagous species, including, among others, *Adalia bipunctata* (L.) and *Coccinella septempunctata* L. The helpful food list of Klausnitzer and Klausnitzer (1997) for central-European Coccinellidae gives examples of prey consumed by ladybirds in the field under authors' observations (for a world perspective, see Giorgi et al., 2009).

Coccids damage many crops of economic importance, particularly woody species. However, eco- and ethological studies on coccidophagous ladybirds are scarce. In our view, this is due in part to their much greater success in "classical" biological control. Attempts at much more difficult augmentative and conservation biological control of aphids have apparently incited more intensive ecological and behavioral research of this guild of lady beetles (Obrycki et al., 2009). Two case studies, involving *Rodolia cardinalis* (Mulsant) and *Cryptolaemus montrouzieri* Mulsant, demonstrate that coccidophagous ladybirds can be excellent biological control agents.

2.1.1. *Rodolia cardinalis*

A textbook case of classical biological control occurred in the USA, when *R. cardinalis* was introduced in 1888 to California to reduce populations of the invasive *Icerya purchasi* Maskell in citrus groves (DeBach and Schlinger, 1964; Caltagirone and Doutt, 1989). The scarce occurrence of *I. purchasi* in its native Australia was correctly believed to be caused by the top-down regulation of this species by natural enemies. This led to the historical introduction of *R. cardinalis* and the parasitoid *Cryptochaetum* sp. to California, and the subsequent successful reduction of *I. purchasi* populations there and elsewhere around the world (DeBach and Schlinger, 1964). However, it was not until 100 years later that the role of natural enemies of *R. cardinalis* in Australia was definitively established when they were experimentally excluded from *Acacia* trees (Prasad, 1989).

The basic reason for the success of this biological control program was explained by Thorpe (1930, p. 937) and Hodek (1973, p. 215): the "rate of increase ratio between the (introduced) predator and prey was in favour of the coccinellid" and stressed also later (Hagen, 1974; Hodek and Honěk, 1996; Kindlmann and Dixon, 1999; Dixon, 2000; Hodek and Michaud, 2008). Many other coccidophagous ladybirds have similar favorable rates of increase relative to those of their coccid prey, and have thus been successfully established as efficient classical biological control agents, particularly in warm temperate or subtropical regions such as Hawaii, West Africa, Kenya, and Fiji (DeBach and Schlinger, 1964).

2.1.2. *Cryptolaemus montrouzieri*

The mealybug destroyer *Cryptolaemus montrouzieri* failed to become established after its introduction into the USA in 1892, except along the southern California coast, probably because it cannot survive winters and has a limited ability to spread (DeBach and Hagen, 1964). It has to be mass-cultured on mealybugs reared on potato sprouts and periodically released inoculatively in citrus groves. *Cryptolaemus montrouzieri* has successfully controlled *Pseudococcus citri* (Risso) in citrus groves, and both *Pseudococcus citri* and *Phenacoccus gossypii* Townsend & Cockerell in California glasshouses on gardenias and chrysanthemums, respectively (DeBach and Schlinger, 1964). On citrus on the northern Black Sea coast, *C. montrouzieri* controlled *Pseudococcus gahani* Green and *Pulvinaria aurantii* Cockerell (DeBach and Schlinger, 1964).

2.1.3. Other coccid biological control agents

The impact of coccinellid predators of scales is not limited to the above two well-known species. *Chilocorus stigma* (Say) and *Microweisea misella* (Le Conte) killed on average 70% of pine needle scales, *Chionaspis pinifoliae* (Fitch) and *Chionaspis heterophyllae* Cooley, in unsprayed Christmas tree plantations in lower Michigan (Fondren and McCullough, 2005). Early instars of the soft scales, *Toumeyella pini* (King) and *T. parvicornis* (Cockerell), on *Pinus* spp. in Colorado, were preyed upon by *Coccinella septempunctata* L. and *Hippodamia convergens* (Guerin-Meneville), coccinellid species that are generally regarded as aphidophagous (Cooper and Cranshaw, 2004). *Fiorinia externa* Ferris (Diaspididae), an introduced pest of the eastern hemlock, *Tsuga canadensis* (L.) Carriere, was preyed upon by five coccinellid species in eastern Tennessee and western North Carolina. Three species, *Chilocorus stigma* (Say), *Rhyzobius lophantae* Blaisdell and *Scymnillus horni* (Gordon), were dominant while two others were found in low numbers (*Harmonia axyridis* Pallas, *Scymnus loweii* Mulsant). Lynch et al. (2006) considered the natural abundance of predators sufficient to reduce *F. externa* significantly in the region. The efficacy of coccinellids *Nephus bilucernarius* Mulsant and *Sticholotis rufipes* Weise (present at 0.1–1.8 and 0.05–0.2 individuals per plant, respectively) on Oahu and Maui in pineapple fields infested with the mealybugs *Dysmicoccus brevipes* (Cockerell) and *D. neobrevipes* Beardsley, was lowered by the interference of the ant *Pheidole megacephala* (F.) (Gonzáles-Hernández et al., 1999).

2.2. Food specificity of coccidophagous ladybirds

2.2.1. Non-coccid food

Many coccinellids consume non-prey foods as a critical part of their diet (Hodek, 1996, chapter 6.1.1.2; Lundgren, 2009). For example, gut dissections confirmed that adults of the introduced coccidophagous *Chilocorus kuwanae* Silvestri were observed feeding on the nectar and pollen of two *Euonymus* spp. in North Carolina, USA (Nalepa et al., 1992).

To improve the economy of mass production of coccidophagous lady beetles, scientists have employed factitious prey with notable success. In many cases, eggs of Lepidoptera are a good factitious prey for coccidophagous lady beetles, as with the larvae of mealybug predator, *Cryptolaemus montrouzieri*, which can be successfully reared on the eggs of *Sitotroga cerealella* (Olivier). Neither preimaginal survival, nor weight at eclosion were reduced on this factitious prey (Pilipjuk et al., 1982). Diets developed by Okada (1970) for *Chilocorus* spp. were based on honeybee brood. However, the most satisfactory honeybee-brood diets also contained royal jelly and other supplements (Hattingh and Samways, 1993).

Reports on cannibalism in coccidophagous ladybirds are almost nonexistent, in contrast to aphidophagous species. It does not seem surprising, as the population dynamics of coccids are much more stable than those of aphids. Cannibalism has generally been considered as an adaptation to the highly variable abundance of prey (Osawa, 1992; Hodek, 1996).

2.2.2. Plant mediated effects on prey quality

Almost all reported cases of unsuitable coccid prey concern herbivores that derive chemical protection from their host plants. An early observation on the rejection by *Rodolia cardinalis* of *Icerya purchasi*, that fed on *Spartium* (Fabaceae) or *Genista* (Fabaceae) was not explained satisfactorily. Shortage of shade to the eggs of the predator (Savastano, 1918), or smell of the plants (Balachovsky, 1930) were the suspected causes. However, the ladybirds also rejected the coccids, isolated from the host plants (Poutiers, 1930). Hodek (1996) supposed that substances sucked from plants (e.g. the alkaloid spartein) render *I. purchasi* unpalatable for *R. cardinalis*.

Host-plant derived toxicity of coccid prey was revisited more recently by measuring survival and development time of *R. cardinalis*, *Chilocorus bipustulatus* (L.) and *Cryptolaemus montrouzieri* (Mendel et al., 1992). The coccinellids were reared on the margarodid *I. purchasi*, diaspidid *Lepidosaphes ulmi* (L.) and pseudococcid *Planococcus citri* (Risso), or on *Aphis craccivora* Koch (Hemiptera: Aphididae). These scales and aphids were reared on alkaloid-containing legumes *Erythrina corallodendrum* L. and *Spartium junceum* L. (both Fabaceae) or on non-toxic plants (*Citrus sinensis* (L.), *Cucurbita moschata* (Duchesne ex Lamarck), *Euphorbia tirucalli* L.) (Mendel et al., 1992). Survival of *R. cardinalis* and *C. bipustulatus* was significantly reduced and the development time of *R. cardinalis* increased when they ate insects from the toxic plants. However, this was not the case with *C. montrouzieri*. In the field, the population density of the scales and aphids was conspicuously higher on toxic plants (Mendel et al., 1992). The negative prey-mediated, tritrophic effect of *E. corallodendrum* and *S. junceum* is also implicated in the failure of *Rodolia iceryae* Jenson to establish in Israel (Mendel and Blumberg, 1991).

Host-plant derived effects on the polyphagous ladybird *Exochomus flaviventris* Mader, indigenous to sub-Saharan Africa, were demonstrated with the cassava mealybug *Phenacoccus manihoti* Matile-Ferrero (Pseudococcidae). In this laboratory assay, cassava (*Manihota esculenta* Crantz) varieties and a weed (*Talinum triangulare* (Jacquin) Willdenow), varied in their susceptibility to cassava mealybug. Resistance to mealybugs in the cassava varieties stems from flavonoid cyanogenic glycosides. *Exochomus flaviventris* had the longest oviposition period, highest fecundity, and low preimaginal mortality when fed on mealybugs that were reared on the less resistant cassava variety (Le Rü and Mitsipa, 2000). The greatest negative effects on preimaginal duration and survival of the predator occurred when they were fed mealybugs reared on the cassava with an intermediate (surprisingly not the highest) level of glycosides. A similar relationship was experienced with DIMBOA in wheat, where the coccinellid *Eriopis connexa* (Germar) was most affected when fed aphid prey reared on plants with an intermediate level of secondary phytochemicals (for details see Hodek, 1996).

The effects of herbivore-specific interactions with defensive plant chemistry on coccinellids are well illustrated with the insect community on oleander. Aphids from oleander are poisonous to coccinellids, but the scale *Aspidiotus nerii* Bouche from the same plant is suitable prey for the coccinellid *Chilocorus infernalis* Mulsant (compared to *Asterolecanium* sp. on giant bamboo *Dendrocalamus giganteus* Munro; Hattingh and Samways, 1991). It is unclear why the aphids, but not the scales, are made unpalatable to coccinellids via the glycosides contained in oleander.

2.2.3. Interspecific variation in prey quality

In addition to plant-mediated effects, coccids inherently vary in their suitability as prey for ladybirds (Muma, 1955; Huffaker and Doutt, 1965). Before the release of *R. cardinalis* to Galapagos, a hazard assessment was conducted of this species' propensity to prey on non-target sternorrhynchans, some of them already threatened by extinction. Predation by neonates, 3rd instars and adults of *R. cardinalis* on members of several coccid families (Margarodidae [*Margarodes*], Pseudococcidae [*Paracoccus*, *Pseudococcus*], Eriococcidae [*Eriococcus*], and Coccidae [*Ceroplastes*]) was tested in laboratory trials. *Rodolia cardinalis* was unable to complete development on any of the tested non-target prey. It fed only on *Margarodes similis* Morrison, a species closely related to *I. purchasi*, but this subterranean prey is not exposed to *R. cardinalis* under field conditions (Causton et al., 2004).

Finally, the parasitism status of a prey item may affect its acceptability (and, presumably, suitability) to coccidophagous ladybirds. An example comes from *R. cardinalis*, which avoids its prey, *I. purchasi*, when it is parasitized by *Cryptochaetum iceryae* (Williston). The beetles starve if only parasitized scales are available as food (Quezada and DeBach, 1973).

2.2.4. Essential prey

Prey found in experiments to be suitable for development and reproduction of coccidophagous ladybirds are listed in Table 1. Often, it is the case that several prey are equally capable of supporting development and reproduction (the definition of an essential food; Hodek, 1962, 1996) in a coccidophagous ladybird species. For example, *Coccus hesperidum* L. (Coccidae) and *Abgrallaspis cyanophyli* (Signoret) (Diaspididae) were equally suitable for the development and reproduction of *Chilocorus nigritus* (F.). Indeed, *Ch. nigritus* is a promising biological control agent of scales in temperate glasshouses (Ponsonby and Copland, 2007a).

Sometimes different life stages of an essential prey species vary in their suitability as food for a ladybird, and a heterogeneous mixture of different developmental stages of one-species prey may be most suitable for the predator. Transfer of females of *Ch. nigritus* after 10 d feeding on a heterogeneous mixture of all stages of the diaspidid *A. cyanophyli* to a homogeneous diet consisting of only adult females or 1st or 2nd instars of this diaspidid, was followed by a dramatic decrease in oviposition (Ponsonby and Copland, 2007b).

2.2.5. Differences in prey specificity in congeneric species

Two species of the genus *Coelophora*, both endemic to New Caledonia, show a different level of prey specificity. Larvae of the aphidophagous species *C. mulsanti* (Montrouzier), preying on more mobile prey, are more active than larvae of the coccidophagous *C. quadrivittata* Fauvel, suggesting that dietary breadth may be related to the mobility of the preferred prey. While the latter species appears to be rather stenophagous (only one prey is known – *Coccus viridis* [Green]), the euryphagous *C. mulsanti* was reared on several aphids and is reported to feed in the field also on cicadellid larvae (Sallée and Chazeau, 1985).

2.3. Patterns in prey consumption rates

Both larval stage and environmental conditions, particularly temperature, affect prey consumption by coccidophagous coccinellids (Hodek, 1996). Larval age has a large effect on the amount of food consumed: 4th instar larvae consume most prey, but a different proportion in individual species. For example, 4th instar of *Chilocorus bipustulatus* fed *Chrysomphalus aonidum* (L.) consumed less than 50% of total larval diet (Yinon, 1969), whereas *Exochomus flavipes* (Thunberg) fed *Dactylopius opuntiae* (Cockerell) ate almost 75% of their total larval diet during the same instar (Geyer, 1947).

The consumption of the eggs of the coccid *Pulvinaria regalis* Canard by *Exochomus quadripustulatus* (L.) varied under three temperature regimens: two alternating (9/19 and 12/24 °C) and one constant at 25 °C. The total mass of *P. regalis* eggs consumed by larvae was lowest (40 mg) at the high, constant temperature, which shortened the developmental duration to 50% of that at the lowest temperature regimen (Sengonca and Arnold, 2003).

2.4. Foraging behavior of coccidophagous ladybirds

2.4.1. Foraging cues

There is substantial evidence that foraging by coccinellids is not an entirely random process, and that it is at least partly guided by visual and olfactory cues (Seagraves, 2009). Many coccidophagous ladybeetles change their searching behavior from extensive to intensive when they encounter prey or at least its residues (e.g., honeydew, exuviae, etc.) (Podoler and Henen 1986; van den Meiracker et al., 1990). Foraging cues may be stage specific, 4th instars

Table 1
Coccids as essential prey of coccinellids.

Coccinellid species	Prey species	References
Adalia decempunctata (L.)	*Matsucoccus josephi* Bodenheimer	Bodenheimer and Neumark (1955)
Azya orbigera Mulsant	*Coccus viridis* (Green)	Liere and Perfecto (2008)
Brumoides suturalis (F.)	*Ferrisia virgata* (Cockerell) (better for development)	Gautam (1990)
	Planococcus pacificus Cox (better for oviposition)	Gautam (1990)
Chilocorus baileyi (Blackburn)	*Aonidiella orientalis* (Newstead)	Elder and Bell (1998)
Chilocorus bipustulatus (L.)	*Aspidiotus nerii* Bouche	Uygun and Elekcioglu (1998)
	Chrysomphalus aonidum (L.)	Yinon (1969)
Chilocorus circumdatus Gyllenhal	*Aonidiella orientalis* (Newstead)	Elder and Bell (1998)
Chilocorus kuwanae (Silvestri)	*Chionaspis salicis* (L.)	Kuznetsov and Pantyuchov (1988)
	Chrysomphalus bifasciculatus Ferris	Tanaka (1981)
	Phenacaspis alnus Borchsenius	Kuznetsov and Pantyuchov (1988)
	Unaspis yanonensis (Kuwana)	Nohara (1963) and Tanaka (1981)
	Unaspis euonymi (Comstock)	Van Driesche et al. (1998) and Ricci et al. (2006)
Chilocorus nigritus (F.)	*Abgrallaspis cyanophylli* (Signoret)	Ponsonby and Copland (1996, 2000, 2007b)
	Acutaspis umbonifera (Newstead)	Ponsonby and Copland (2007a)
	Aonidiella aurantii (Maskell)	Samways (1986)
	A. aurantii (Maskell) (preferred by adults)	Samways and Tate (1986) and Samways and Wilson (1988)
	Aspidiotus nerii Bouche	Erichsen et al. (1991) and Hattingh and Samways (1993)
	A. nerii Bouche (preferred by larvae)	Samways and Wilson 1988
	Asterolecanium miliaris (Boisduval)	Hattingh and Samways 1993
	Coccus hesperidum L.	Ponsonby and Copland (2007a)
	Pinnaspis buxi (Bouche)	Ponsonby and Copland (2007a)
	Saissetia coffeae (Walker)	Ponsonby and Copland (2007a)
Chilocorus renipustulatus Scriba	*Chionaspis salicis* (L.) [L]	Mills (1981)
Chilocorus rubidus Hope	*Eulecanium caraganae* Borchsenius (eggs for larvae, eggs and larvae for adults)	Pantyukhov (1968)
Chilocorus stigma (=bivulnerus) (Say)	*Chrysomphalus aonidum* (L.)	Muma (1955)
	Chionaspis heterophyllae Cooley	Fondren and McCullough (2005)
Coelophora quadrivittata Fauvel	*Coccus viridis* (Green)	Chazeau (1981)
Cryptognatha nodiceps Marshall	*Aspidiotus destructor* Signoret	Lopez et al. (2004)
Cryptolaemus montrouzieri Mulsant	*Chloropulvinaria psidii* (Maskell) (eggs)	Mani and Krishnamoorthy (1990)
	Maconellicoccus hirsutus Green	Persad and Khan (2002)
	Planococcus citri (Risso)	Garcia and O'Neil (2000)
Diomus austrinus Gordon	*Phenacoccus madeirensis* Green	Chong et al. (2005)
	Planococcus citri (Risso)	Chong et al. (2005)
Exochomus flavipes (Thunberg)	*Dactylopius opuntiae* (Cockerell)	Geyer (1947)
	Matsucoccus josephi Bodenheimer	Bodenheimer and Neumark (1955)
Exochomus quadripustulatus (L.)	*Chionaspis salicis* (L.) [L]	Mills (1981)
	Planococcus citri (Risso)	Katsoyannos and Laudeho (1977)
	Pseudochermes fraxini (Kaltenbach) [L]	Mills (1981)
	Saissetia oleae Olivier	Laudeho and Katsoyanos (1977)
Hyperaspis desertorum Weise	*Orthezia urticae* (L.) [L]	Savoiskaya (1983) (p. 152)
Hyperaspis lateralis Mulsant	*Pseudococcus aurilanatus* (Maskell)	McKenzie (1932)
	Pseudococcus sequoiae Coleman (eggs, young larvae preferred prey)	McKenzie (1932)
Hyperaspis notata Mulsant	*Phenacoccus manihoti* Matile-Ferrero	Stäubli Dreyer et al. (1997a)
	Phenacoccus madeirensis Green	Stäubli Dreyer et al. (1997b)
Hyperaspis raynevali (Mulsant)	*Phenacoccus herreni* Cox & Williams	Kiyindou and Fabres (1987)
Hyperaspis senegalensis hottentotta Mulsant	*Phenacoccus manihoti* Matile-Ferrero	Fabres and Kiyindou (1985)
Lindorus lophantae Blaisdell	*Phoenicococcus marlatti* Cockerell	Gomez Vives (1999)
Microweisea misella (LeConte)	*Chionaspis heterophyllae* Cooley	Fondren and McCullough (2005)
Nephus bilucernarius Mulsant	*Dysmicoccus brevipes* (Cockerell)	Gonzáles-Hernández et al. (1999)
	Dysmicoccus neobrevipes Beardsley	Gonzáles-Hernández et al. (1999)
Nephus bisignatus (Boheman)	*Planococcus citri* (Risso)	Kontodimas et al. (2004)
Nephus includens (Kirsch)	*Planococcus citri* (Risso)	Kontodimas et al. (2004)
Pharoscymnus numidicus Pic	*Parlatoria blanchardi* Targioni Tozzetti	Kehat (1968)
Pullus mediterraneus F.	*Saissetia oleae* Olivier (eggs)	Ba M'Hamed and Chemseddine (2001)
Rhyzobius lophantae Blaisdell	*Aspidiotus nerii* Bouche	Cividanes and Gutierrez (1996) and Stathas (2000)
Rhyzobius ventralis (Erichson)	*Eriococcus coriaceus* Maskell	Richards (1981)
Rodatus (*Rhyzobius*) *major* (Blackburn)	*Monophlebulus pilosior* (Maskell) (eggs)	Richards (1985)
Rodolia cardinalis (Mulsant)	*Icerya purchasi* Maskell	DeBach and Schlinger (1964)
Scymnus coccivora Ayyar	*Maconellicoccus hirsutus* Green	Persad and Khan (2002)
Serangium parcesetosum Sicard	*Coccus hesperidum* L.	Yigit et al. (2003)
Sticholotis rufipes Weise	*Dysmicoccus brevipes* (Cockerell)	Gonzáles-Hernández et al. (1999)
	Dysmicoccus neobrevipes Beardsley	Gonzáles-Hernández et al. (1999)
Synharmonia (*Oenopia*) *conglobata* (L.)	*Matsucoccus josephi* Bodenheimer	Bodenheimer and Neumark (1955)

Essential prey enables successful completion of development to adults and oviposition (for details see text).
[L] rating as essential prey is based on observations of predator larvae together with the listed prey.

of *Cryptolaemus montrouzieri* perceive prey only through physical contact, but adults can detect their mealybug prey at a distance of 14 mm (Heidari and Copland, 1992). Searching behavior may also be intensified by prey sex pheromones; *Rhyzobius* sp. responded to the sex pheromones of two matsucoccids, *Matsucoccus feytaudi* Ducasse and *M. matsumurae* Kuwana (Branco et al., 2006).

A high population density of the prey may deter the predator from foraging, perhaps due to the resulting copious amounts of honeydew (Samways, 1986; Seagraves, 2009). Significantly fewer *Chilocorus nigritus* (F.) adults were found on *Cucurbita* fruits highly infested (>60 scales per cm^2) with *Aspidiotus nerii* Bouche than on less infested fruits (24 scales per cm^2) (Erichsen et al., 1991).

2.4.2. Prey intake

Many coccids are physically protected from predation, and require physical or behavioral adaptations in predators that consume them; the feeding process of coccidophagous coccinellids has been described in detail in two instances. The coccid, *Eriococcus coriaceus* Maskell, is protected by an outer covering. In spite of a posterior hole in the covering through which crawlers escape, the larvae of *Rhyzobius ventralis* usually make a hole in the lower part of the sac, and curl themselves around the protective covering until the coccid has been completely consumed (Richards, 1981). *Rodatus major* (Blackburn) larvae and adults specialize on the eggs of *Monophlebulus pilosior* (Maskell) (Margarodidae). The 4th instar "feeds almost continuously throughout the day, lying with its mouth close to the margarodid's genital opening so that it can eat the eggs" as they are laid (Richards, 1985).

2.4.3. Role of ants

Ants may kill or disrupt the foraging of both adult and larval coccinellids (Majerus et al., 2007). Even the wax-producing larvae of *Cryptognatha nodiceps* Marshall, *Azya trinitatis* (Marshall) and *Scymnus aeneipennis* Sicard are eaten by several species of ants attending the coccid *Aspidiotus destructor* Signoret in Vanuatu (Cochereau, 1969).

Not all ladybirds suffer from their interactions with ants. The predation rate of the myrmecophilous coccinellid *Azya orbigera* Mulsant, an important predator of the green coffee scale, *Coccus viridis* (Green), was not decreased in the presence of the mutualistic scale-tending ant *Azteca instabilis* F.Smith (Formicidae). Furthermore, the ant showed aggressive behaviour toward *A. orbigera*'s parasitoids and its presence decreased parasitism of the ladybird (Liere and Perfecto, 2008). It has generally been assumed that the Argentine ant, *Linepithema humile* (Mayr), tends honeydew-excreting hemipterans and that its presence negatively impacts natural enemy foraging. Daane et al. (2007) tested this assumption using exclusion experiments in two Californian regions where vineyards were infested by the grape mealybug, *Pseudococcus maritimus* (Ehrhorn), and the obscure mealybug *Pseudococcus viburni* (Signoret). While the ants lowered densities of encyrtid parasitoids, they increased the densities of the ladybird *Cryptolaemus montrouzieri* on ant-tended vines. Argentine ants increase the population density of mealybugs primarily by removing the honeydew that impedes the movement of the mealybug crawlers. Meanwhile, the larvae of *C. montrouzieri* successfully forage in patches of high mealybug density. One hypothesis is that larvae of *C. montrouzieri*, being also covered with waxy structures, successfully mimic mealybugs and avoid detection by ants. Furthermore, when approached by an ant, the coccinellid larva stops moving and lowers its body against substrate, thus better resembling a sessile mealybug. The ants move around the larva, stroke it with their antennae like they stroke the mealybug. After failing to obtain honeydew, the ant moves away (Daane et al., 2007).

3. Whiteflies (Aleyrodoidea)

Whiteflies are another group of important non-aphid sternorrhynchan pests that afflict crops worldwide. Although considerable research has focused on their parasitoids, there are only a few reviews on biological control of whiteflies by predators, all dealing with *Bemisia tabaci* (Gennadius) (Gerling, 1986; Nordlund and Legaspi, 1996; Gerling et al., 2001; Gould et al., 2008).

3.1. Prey specificity

Although detailed studies are limited to only a few coccinellid species, it appears that predation of whiteflies evolved independently several times in a handful of tribes. Thus for instance seven coccinellid species associated with four aleyrodid prey species in Turkey belong to four tribes: Coccinellini, Chilocorini, Scymnini, and Serangiini (Ulusoy et al., 1996). Under field conditions, 17 specialist coccinellids have been associated with 16 whitefly species (Table 2). An additional 15 presumed aphidophagous or coccidophagous coccinellid species were observed to consume eight whitefly species (Table 2), sometimes in large quantities. Methods used for detecting predation include establishing correlations of predator and prey abundances (Dreistadt and Hagen, 1994; Leite et al., 2005) in the field as well as gut content analysis. Biochemical techniques used to detect whitefly remnants in the guts of coccinellids include ELISA (Hagler and Durand, 1994; Hagler and Naranjo, 1994) and PCR-based gut analyses (Zhang et al., 2007a,b).

Whiteflies are a fairly unique type of prey, and once a coccinellid comes to specialize upon this group, whiteflies can be replaced by few other prey types. Artificial food media and factitious prey, eggs of *Helicoverpa zea* (Boddie) or *Manduca sexta* (L.), were rejected by the coccinellid *S. parcesetosum*, a specialist on *Bemisia argentifolii* Bellows and Perring (Legaspi et al., 1996), which only reluctantly consumed thrips and mites and aphids (AlZyoud and Sengonca, 2004). The whitefly specialist, *Clithostethus arcuatus* (Rossi) cannibalizes conspecific eggs and pupae under food limitation in mass cultures (Liotta, 1981b; Bellows et al., 1992). Thus, cannibalism may help supplement the diet of coccinellids when whiteflies are scarce.

Whiteflies are poor prey for those coccinellids that do not specialize on this prey group (Deligeorgidis et al., 2005; Zhang et al., 2007c). Larvae and adults of coccidophagous *Cryptognatha nodiceps* Marshall failed to survive on a diet of three whitefly species (Lopez et al., 2004). Results with aphidophagous species were similar. Also, larvae of *Coccinella undecimpunctata* L. were unable to complete development and died in the fourth instar when reared on *Aleyrodes proletella* L. Although adults of *C. undecimpuncatata* consumed 30–40 aleyrodids per day, they lost body mass and died sooner than those fed aphids (Cabral et al., 2006).

3.2. Prey consumption

Coccinellid predators can consume a staggering number of whiteflies over their lifespan. *Serangium parcesetosum* consumed 1012 nymphs of *T. vaporariorum* during their larval stage and 3842 nymphs during their 71 d adult life (AlZyoud et al., 2005a, 2005b). This coccinellid also consumes numerous *B. tabaci* nymphs over its life (one estimate is approximately 4910 nymphs over the life of one predator) (Legaspi et al., 1996; Sengonca et al., 2005). Larvae of *Serangium* sp. consumed more than 1000 nymphs of *B. tabaci* over their 13 d life (Asiimwe et al., 2007).

3.2.1. Physiological status of the predator and prey

The usefulness of whiteflies as prey for specialist coccinellids is dependent on the physiological status of the predator and whitefly examined (AlZyoud and Sengonca, 2004; Sengonca et al., 2005). Whiteflies differ in their suitability as they age (Huang et al., 2006). For example, *Delphastus catalinae* (Horn) adults eat significantly more eggs than small (L1 and L2) or large (L4) nymphs of *B. argentifolii* (Legaspi et al., 2006). *Delphastus pusillus* (LeConte) consume more *B. tabaci* eggs as the predator ages. First instars consumed 72 eggs, second instars consumed 217 eggs, and during the

Table 2
Coccinellid species associated with whitefly species (probably essential prey) in the field.

Coccinellid species	Prey species	References
Specialist species		
Axinoscymnus cardilobus Ren & Pang	*Bemisia tabaci* (Gennadius)	Huang et al. (2006)
Brumoides suturalis (F.)	*Aleurolobus barodensis* (Maskell)	Inayatullah (1984)
Clitostethus arcuatus (Rossi)	*Aleurothrixus floccosus* (Maskell)	Katsoyannos et al. (1997) and Liotta (1981a)
	Aleurotrachelus jelinekii (Frauenfeld)	Mills (1981)
	Aleyrodes proletella L.	Bathon and Pietrzik (1986) and Silvestri (1934)
	Dialeurodes citri (Ashmead)	Agekian (1977), Liotta (1981b), Loi (1981), Priore (1969), Soylu (1980), Ulu (1985)
	Siphoninus immaculata (Heeger)	Kirkaldy (1907)
	Siphoninus phillyreae (Haliday)	Mentzelos (1967) and Tremblay (1969)
	Trialeurodes vaporariorum (Westwood)	Agekian (1977)
Cryptognatha cordiceps (Marshall)	*Aleurocanthus woglumi* Ashby	Dowell and Cherry (1981)
Delphastus nebulosus Chapin	*Aleurocanthus woglumi* Ashby	Medina-Gaud et al. (1991)
Delphastus pallidus LeConte	*Aleurocanthus woglumi* Ashby	Dowell and Cherry (1981)
	Bemisia tabaci (Gennadius)	Castineiras (1995)
Delphastus pusillus LeConte	*Aleurocanthus woglumi* Ashby	Cherry and Dowell (1979), Dowell and Cherry (1981) and Quezada (1974)
	Aleurothrixus floccosus (Maskell)	Meyerdirk et al. (1980)
	Aleurotrachelus socialis Bondar	Gold et al. (1989)
	Bemisia argentifolii Bellows & Perring	Heinz and Parrella (1994a) and Hoelmer et al. (1994)
	Paraleyrodes citri Bondar	Meyerdirk et al. (1980)
	Trialeurodes abutilonea (Haldeman)	Watve and Clower (1976)
	Trialeurodes variabilis (Quaintance)	Gold et al. (1989)
Delphastus sp.	*Aleurocanthus woglumi* Ashby	Elizondo and Quezada (1990)
Nephaspis amnicola Wingo	*Aleurodicus dispersus* Russell	Kumashiro et al. (1983)
	Paraleyrodes citri Bondar	Meyerdirk et al. (1980)
Nephaspis bicolor Gordon	*Aleurodicus dispersus* Rusell	Lopez and Kairo (2003)
	Aleurothrixus floccosus (Maskell)	Lopez and Kairo (2003)
Nephaspis gorhami Leconte	*Aleurocanthus woglumi* Ashby	Dowell and Cherry (1981)
Nephaspis oculatus (Blatchley)	*Bemisia tabaci* (Gennadius)	Ren et al. (2002)
Oenopia sauzeti Mulsant	*Aleurolobus barodensis* (Maskell)	Inayatullah (1984)
Scymnus hoffmani Weise	*Bemisia tabaci* (Gennadius)	Zhang et al. (2007b)
Scymnus nubilus Mulsant	*Aleurolobus barodensis* (Maskell)	Inayatullah (1984)
Serangium japonicum Chapin	*Bemisia tabaci* (Gennadius)	Yao et al. (2005)
Serangium parcesetosum (Sicard)	*Aleurolobus barodensis* (Maskell)	Inayatullah (1984) and Shah et al. (1986)
	Bemisia tabaci (Gennadius)	Kapadia and Puri (1992)
	Dialeurodes citri (Ashmead)	Malausa et al. (1988), Timofeeva and Nhuan (1978) and Yigit (1992)
Stethorus minutalus Gordon & Chapin	*Bemisia tabaci* (Gennadius)	Silva and Bonani (2008) (an error; see Biddinger et al. (2009)
Stethorus gilvifrons (Mulsant)	*Bemisia tabaci* (Gennadius)	Al-Duhawi et al. (2006)
Generalist species		
Chilocorus stigma (Say)	*Aleurocanthus woglumi* Ashby	Dowell and Cherry (1981)
Coccinella novemnotata Herbst	*Trialeurodes abutilonea* (Haldeman)	Watve and Clower (1976)
Coccinella septempunctata bruckii Mulsant	*Trialeurodes vaporariorum* (Westwood)	Kajita (1979)
Coelophora inaequalis (F.).	*Aleurodicus dispersus* Russell	Kajita et al. (1991)
Coleomegilla maculata lengi Timberlake	*Trialeurodes abutilonea* (Haldeman)	Watve and Clower (1976)
Cycloneda sanguinea (L.)	*Aleurocanthus woglumi* Ashby	Dowell and Cherry (1981)
	Bemisia tabaci (Gennadius)	Leite et al. (2005, 2003) and Yigit (1992)
Exochomus bimaculosus Mulsant	*Bemisia tabaci* (Gennadius)	Leite et al. (2003) and Yigit (1992)
Harmonia axyridis (Pallas)	*Bemisia tabaci* (Gennadius)	Zhang et al. (2007b)
Harmonia sedecimnotata (F.)	*Aleurodicus dispersus* Russell	Kajita et al. (1991)
Hippodamia convergens Guerin-Meneville	*Bemisia tabaci* (Gennadius)	Hagler and Naranjo (1994)
Megalocaria dilatata F.	*Aleurocanthus* sp.	Ginting et al. (1992)
	Aleurodicus sp.	Ginting et al. (1992)
Menochilus sexmaculatus (F.)	*Aleurodicus dispersus* Russell	Kajita et al. (1991)
Olla abdominalis (Say)	*Trialeurodes abutilonea* (Haldeman)	Watve and Clower (1976)
Propylea japonica Thunberg	*Bemisia tabaci* (Gennadius)	Zhang et al. (2007a,b,c)
	Trialeurodes vaporariorum (Westwood)	Kajita (1979)
Psyllobora lenta (Mulsant)	*Bemisia tabaci* (Gennadius)	Leite et al. (2005)

rest of development, larvae consumed 688 eggs each. Daily consumption by adult *D. pusillus* varied with the stage of prey (167, 138, 71, 35, and 12 individuals were eaten of *B. tabaci* eggs, 1st, 2nd, 3rd, and 4th instars, respectively). *Delphastus pusillus* laid no eggs when fed 50 or 100 *B. tabaci* eggs per day and the number of eggs laid increased when daily feeding rates were higher (Hoelmer et al., 1993). Similar patterns of increasing oviposition with increasing food intake were observed in other species as well (Liu et al., 1997; AlZyoud et al., 2005a, 2005b).

Consumption rates differ among species in part because of differences in searching behavior, mainly walking speed and prey handling times (Liu and Stansly, 1999). Other important factors determining consumption rates may be the dietary requirement for a deficient nutrient (e.g. an amino acid which is scarce in the food). A case in point is *S. parcesetosum* which preys on *B. argentifolii*. The low methionine content of this prey requires that the coccinellid consume a greater number than it would to simply satisfy its requirements for other nutrients (Cohen and Brummett, 1997).

The suitability of a particular prey is frequently manifested as preferences by the predator under choice conditions. *Delphastus catalinae* fed *B. tabaci* presented on *Lycopersicum esculentum* Miller only ate eggs and glabrous nymphs younger than 3rd instars (Simmons and Legaspi, 2004; Guershon and Gerling, 2006). *Delphastus pusillus* on poinsettia preferred *B. tabaci* nymphs over eggs (Heinz and Parrella, 1994a).

Parasitization and infection can have important implications for prey quality, and thus it is not surprising that coccinellids respond differently to affected prey. *Serangium parcesetosum* larvae (L2 and L4) and adults rejected *B. tabaci* parasitized by *Encarsia formosa* Gahan (AlZyoud and Sengonca, 2004). *Delphastus catalinae* rejected *B. tabaci* mummified by *Encarsia sophia* (Girault and Dodd). However, non-mummified parasitized 2nd and 3rd instar prey and unparasitized prey of the same instars were equally accepted by *D. catalinae* (Zang and Liu, 2007). In contrast, *Hippodamia convergens* Guerin-Meneville preferred *B. tabaci* parasitized by *Eretmocerus* sp. nr. *emiratus* (Naranjo, 2007). Longevity of *D. pusillus* was reduced by 49% and fecundity by 91% when they were fed *T. vaporariorum* infected with *Lecanicillium lecanii* (Zimmermann) (Perez et al., 2007).

3.2.2. Effects of host plants on predation

Host plants also affect the predation rate of whiteflies (Legaspi et al., 1996; AlZyoud et al., 2005a, 2005b). When *D. catalinae* was fed *B. argentifolii* from excised leaf discs of five cultivated host plant species, consumption rates differed significantly. Whiteflies on cotton were eaten the most, followed by collards, cowpea, tomato and hibiscus (*Hibiscus rosa-sinensis* L.). In addition to tri-trophic effects, predation rates may be influenced bi-trophically by volatile compounds emitted by foliage (Legaspi et al., 2006), or through the effects of plant architecture on foraging coccinellids. Tomentose leaf hairs decreased the search speed and area covered by *D. catalinae* foraging for *B. tabaci*, and increased its rate of emigration from the plant (Guershon and Gerling, 2006). Leaf pubescence also lowered the foraging and/or predation rates of *Coleomegilla maculata lengi* Timberlake and *D. pusillus* on pubescent poinsettia (*Euphorbia pulcherrima* Willd ex Klotzch, cv. Dark Red Annette Hegg) (Heinz and Parrella, 1994b; Heinz and Zalom, 1996; Lucas et al., 2004). But pubescence had no measurable effects on *D. catalinae* in this system (Lucas et al., 2004).

3.2.3. Seasonal and climatic effects

Predation of whiteflies is strongly affected by temperataure. The optimum predation temperature for *D. catalinae* is greater than 35 °C, at which temperature they consume up to 181 *B. tabaci* nymphs per day (Simmons and Legaspi, 2004). Larvae and adults of *S. parcesetosum* have different optimum predation temperatures; larvae ate 29–33% fewer *B. tabaci* at 30 °C than at 18 °C, while adults consumed 44–57% fewer prey at 18 °C than at 30 °C (Sengonca et al., 2004, 2005). Cumulative lifetime consumption by the same coccinellid species fed *B. argentifolii* decreased as temperature increased to 40 °C (Legaspi et al., 1996).

In part, temperature affects predation indirectly by affecting the life processes and activity levels of the predator. Developmental duration, adult longevity and oviposition vary with temperature and may be associated with variation in food consumption. Oviposition may be the best indicator of food consumption because it requires a large amount of energy and nutrients, greater than other activities performed during the adult stage. Food consumption therefore can be inferred from coccinellid life tables. *Axinoscymnus cardilobus* fed *B. tabaci* from *Codiaeum variegatum* (L.) performed best at temperatures between 20 and 26 °C, with maximum oviposition at 23 °C (Huang et al., 2008). *Clithostethus arcuatus* fed *Aleyrodes proletella* reared on *Brassica oleracea* L. var. *costata* had a temperature optimum for fecundity at 25 °C combined with 75% humidity (Mota et al., 2008). *Delphastus catalinae* fed *B. argentifolii* had highest fecundity at 26 °C (Legaspi et al., 2008). For the same species fed *B. tabaci* on cotton, the highest oviposition and longest lifespan occurred at 25 °C (Kutuk and Yigit, 2007) and in *Nephaspis oculatus* (Blatchley) fed *B. tabaci*, optimum temperature for oviposition was 26 °C (Ren et al., 2002). Provided that number of eggs laid by the coccinellid is positively correlated with number of its whitefly food, maximum predation rate for both species should be expected at 25–26 °C.

Humidity also affects performance and presumably food consumption in coccinellids. In *D. catalinae* fed *B. tabaci*, maximum egg production, shortest development and greatest adult weight occurred at 85% relative humidity (Simmons et al., 2008).

Since predation is determined by many factors, under natural conditions it may differ between years. Preferences of *C. arcuatus* larvae for developmental stages of *D. citri* differed among years. Eggs were the preferred prey in 1974, whereas more 1st instars were consumed in 1975 (Agekian, 1977).

3.2.4. Predation under natural conditions

Despite their ability to consume whiteflies under controlled laboratory conditions, coccinellids probably have a minimal effect on whitefly populations under field conditions (Gould et al., 2008). Using cages with different mesh size, Lin et al. (2008) established the importance of medium-sized predators as contributors to *B. tabaci* mortality. However, coccinellids contributed little to the overall predation of the pest. In another experiment (Gold et al., 1989), abundance of *Aleurotrachelus socialis* Bondar and *Trialeurodes variabilis* (Quaintance) on cassava intercropped with cowpea was lower than in monoculture. However, abundance of *D. pusillus* was higher in monoculture than in the diversified system, and predator–prey ratios were so low that coccinellid predation could not have caused the observed reductions in pest density.

In some cases, however, coccinellids were efficient agents for inundative releases in glasshouses. *Serangium parcesetosum* was efficient in control of *B. argentifolii* on poinsettia (*Euphorbia pulcherrima*) (Ellis et al., 2001).

4. Psyllids (Psylloidea)

4.1. Prey specificity

Psyllids are less important as prey for coccinellids compared to other sternorrhynchans, and data on predation are correspondingly scarce. Predation of psyllids was documented by direct observation and also by establishing correlations between prey and coccinellid abundance (Michaud, 2001; Pluke et al., 2005). Philogene and Chang (1978) provided a list of 14 coccinellid species associated with *Cacopsylla pyricola* (Foerster). Recent work reveals that psyllids were associated with and probably eaten by 18 primarily aphidophagous and cocccidophagous coccinellid species (Table 3).

Several studies suggest that psyllids are not frequent prey of coccinellids. Pear psyllids *Cacopsylla bidens* (Sulc) and *C. pyricola* were not consumed by coccinellids in the field (Shaltiel and Coll, 2004; Agustí et al., 2003). In the laboratory, psyllids were rejected by the coccidophagous specialist *Cryptognatha nodiceps* Marshall (Lopez et al., 2004).

4.2. Prey consumption

Some psyllids may be essential prey of ladybirds. Recently, Michaud and Olsen (2004) found that the invasive Asian citrus psyllid, *Diaphorina citri* Kuwayama, was essential prey for four coccinellid species: *Olla v-nigrum* (Mulsant), *Exochomus childreni* Mulsant, *Curinus coeruleus* Mulsant and *H. axyridis*. However, *Cycloneda sanguinea* (L.) females ceased oviposition within 2 d of being transferred to this prey.

5. Conclusions and future directions

Experimental (ecological and behavioral) research on coccinellids feeding on non-aphid sternorrhynchans receives less attention than that for aphidophagous ladybirds, in spite of the importance of these prey (especially coccids) both evolutionarily and in terms

Table 3
Coccinellid species associated with psyllid species (probably essential prey) in the open.

Coccinellid species	Prey species	References
Chilocorus cacti L.	*Diaphorina citri* Kuwayama	Pluke et al. (2005)
	Heteropsylla cubana Crawford	Valenciaga et al. (1999)
Cladis nitidula F.	*Diaphorina citri* Kuwayama	Pluke et al. 2005
Cleobora mellyi (Mulsant)	*Ctenarytania thysanura* Ferris & Klyver	Mensah and Madden (1993)
Coccinella transversalis (F.)	*Ctenarytania thysanura* Ferris & Klyver	Mensah and Madden (1993)
Coelophora inaequalis F.	*Diaphorina citri* Kuwayama	Pluke et al. (2005)
Coleomegilla innotata Mulsant	*Diaphorina citri* Kuwayama	Pluke et al. (2005)
Cryptolaemus montrouzieri Mulsant	*Diaphorina citri* Kuwayama	Pluke et al. (2005)
Curinus coeruleus Mulsant	*Diaphorina citri* Kuwayama	Michaud and Olsen (2004)
	Heteropsylla cubana Crawford	Follett and Roderick (1996) and Valenciaga et al. (1999)
Cycloneda sanguinea limbifer L.	*Diaphorina citri* Kuwayama	Michaud (2004) and Pluke et al. (2005)
	Heteropsylla cubana Crawford	Valenciaga et al. (1999)
Diomus pumilio Weise	*Acizzia uncatoides* (Ferris & Klyver)	Dreistadt and Hagen (1994)
Exochomus childreni Mulant	*Diaphorina citri* Kuwayama	Michaud (2004) and Michaud and Olsen (2004)
Harmonia axyridis Pallas	*Diaphorina citri* Kuwayama	Michaud (2004) and Michaud and Olsen (2004)
Harmonia conformis (Boisduval)	*Ctenarytania thysanura* Ferris & Klyver	Mensah and Madden (1993)
Hippodamia convergens Guerin	*Diaphorina citri* Kuwayama	Pluke et al. (2005)
Menochilus sexmaculatus (F.)	*Heteropsylla cubana* Crawford	Gopalan et al. (1988)
Olla v-nigrum Mulsant	*Diaphorina citri* Kuwayama	Michaud (2004) and Michaud and Olsen (2004)
	Heteropsylla cubana Crawford	Chazeau et al. (1991)
Scymnus gracilis Motschulsky	*Heteropsylla cubana* Crawford	Gopalan et al. (1988)
Scymnus sp.	*Diaphorina citri* Kuwayama	Pluke et al. (2005)

of the number of extant species of coccinellids that consume them. Nevertheless, coccinellids as predators of coccids play vital roles in classical and augmentative biological control programs. Research on these prey groups illustrates several recent themes in the foraging of coccinellids. First, coccinellids do not only forage randomly, but they use a range of sophisticated cues to detect their prey (van den Meiracker et al., 1990; Heidari and Copland, 1992; Branco et al., 2006; Seagraves, 2009). Nutritional value of essential prey varies with coccinellid species. Prey quality depends on its host plant (Hattingh and Samways, 1991; Mendel et al. 1992; Le Rü and Mitsipa, 2000), and the physiological and developmental states of the insects. Also, mixed diets involving different developmental stages of the prey species may be superior for coccinellids over homogeneous ones (Ponsonby and Copland, 2007a,b).

The role of coccinellids in biological control of whiteflies and psyllids is less studied than for coccids. Coccinellids are likely important in suppressing the outbreaks of these sternorrhynchans, but the importance of coccinellids as biological control agents of endemic whiteflies is only beginning to be recognized as a result of the spectacular invasions of these sternorrhynchan pests. Also interesting is the quality that whiteflies present as prey; there appears to be a strong fidelity between coccinellid specialists and whiteflies as prey that is not easily breached by polyphagous coccinellids. Unlike in coccids, the study of factors involved in detection of whiteflies and psyllids is still in its early phase and thus further research is desirable. In general, there is a great need to intensify experimental research on the ecology and ethology of the coccinellid predators of non-aphid Sternorrhyncha.

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