

Chapter 7

INTRAGUILD INTERACTIONS

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7.1 SCOPE

This chapter deals with **interactions between coccinellid species**, and **between coccinellids and other intraguild organisms**. Intraspecific predation (cannibalism; 5.2.8), interactions with the extraguild prey (Chapters 5 and 11), interactions with non-guild natural enemies (Chapter 8) and intraspecific competition will not be discussed here.

7.2 COCCINELLIDS AS GUILD MEMBERS

A **guild** is a group of species in a community that **share similar resources** (food or space) regardless of differences in tactics of resource acquisition and in taxonomic position (Polis et al. 1989). More than **4000** coccinellid **species** belong to guilds according to their **essential food**, ensuring the completion of larval development and oviposition (Hodek 1996; 5.2.1 and 5.2.11; Fig. 5.1). However, most predaceous coccinellid species also exploit **alternative food** sources. *Har. axyridis* for example consumes not only aphids and coccids, but also non-hemipteran prey (McLure 1986, Lucas et al. 1997b, 1998b, 2002, 2004a; 5.2.7) and material of plant origin such as pollen and nectar (Kovach 2004, Lucas et al. 2007a; 5.2.9). This species is also an intraguild predator (Alhmedi et al. 2010; 7.8).

The guild of a coccinellid species may change with season (Triltsch 1997). In Eastern Canada, most temperate aphidophagous species are **pollinivorous** during spring (when animal prey is scarce) and later become **zoophagous**. Several species, such as *Har. axyridis*, become **frugivorous** in autumn (Kovach 2004, Lucas et al. 2007a). *Col. maculata* is a **zoophytrophagous** species completing its life cycle on plant or animal material (5.2.9).

Apart from ladybirds (e.g. Evans 1991, Loevei et al. 1991, Lucas et al. 2007b), the guilds include also **non-coccinellid predators, parasitoids, and pathogens** (e.g. Obrycki & Tauber 1985, Coderre & Tourneur 1986, Brown 2004).

7.3 COCCINELLIDS AS NEUTRALISTS

Coccinellids avoid interacting with other intraguild members by **evolutionary** or **ecological mecha-**

nisms. Partition of the niche allows **coexistence** of species exploiting the same resource.

7.3.1 Temporal guild partition

Temporal guild partition has often been reported (Lövei & Radwan 1988, Musser & Shelton 2003, Brown 2004, Dixon 2007). The **activity** of predators exploiting *Adelges tsugae* varies **diurnally**, some being more active at night (Flowers et al. 2007). Also Interactions between *A. bipunctata* and *Har. axyridis* in Japan may be avoided by **desynchronisation** of their occurrences (Toda & Sakuratani 2006).

7.3.2 Spatial guild partition

Adults and larvae of co-occurring species commonly exploit **different plant parts/heights** (Coderre & Tourneur 1986, Coderre et al. 1987, Chang 1996, Schellhorn & Andow 1999a, Lucas et al. 2002, Musser & Shelton 2003, Hoogendoorn & Heimpel 2004, Evans & Toler 2007, Flowers et al. 2007). They may also avoid interactions by changing their **within-plant distribution** (Hoogendoorn & Heimpel 2004). **Plant and habitat characteristics** may have an impact on foraging efficiency or influence contact between intraguild competitors (Lucas & Brodeur 1999, Lucas et al. 2004c, Janssen et al. 2007). *Coccinella transversoguttata* and *Scymnus lacustris* dominate in younger red pine stands, whereas *Mulsantina picta* and *Anatis mali* do so in older stands (Gagne & Martin 1968). Coccinellids were more abundant on yellow (nutrient-stressed) maize plants than on control (greener) plants, while lacewings were more numerous on control (Lorenzetti et al. 1997). Spatial guild partition occurs also at a **larger scale**, when different species exploit **different crops** in a landscape (Colunga-Garcia et al. 1997).

7.3.3 Thermal guild partition

Coccinellidae, Syrphidae and Chrysopidae differ in their **lower developmental threshold** and **speed of development** (Honěk & Kocourek 1988, 1990), and in their **resource exploitation efficiency** (Dixon et al. 2005). In northern regions, different **tolerance to cold** leads to different **overwintering strategies**

and reduces interaction opportunities. In Eastern Canada, *Har. axyridis* does not survive outside and overwinters in buildings, while the indigenous *Col. maculata* overwinters outside (Labrie et al. 2008).

7.3.4 Body size guild partition

The **body size** of ladybirds also determines a partition in resource exploitation as the size imposes **geometrical** and **physiological constraints** in term of resource density needed (Dixon & Hemptinne 2001, Dixon 2007, Sloggett 2008). Smaller species would thus exploit lower aphid population densities more successfully than larger species (but see Evans 2004).

7.4 COCCINELLIDS AS INTERACTING ORGANISMS

In spite of guild partition, coccinellids are repeatedly involved in **intraguild interactions** at different periods of their life cycle (Fig. 7.1). These interactions are promoted by the fact that (i) many other insects share the **same guilds with many coccinellid species**; (ii) the extraguild prey of most predaceous coccinellids have an **aggregated distribution in time and space** leading to natural enemies aggregation; and (iii) coccinellid eggs and early instars occur **close to their food source** (Lucas 2005). For example, the large **temporal overlap** of *P. japonica*, *Har. axyridis*, and *C. septempunctata brucki* exploiting *Aphis gossypii* on *Hibiscus* trees in Japan (Kajita et al. 2006) enhances interaction opportunities.

All types of **classical ecological interactions** (mutualism, commensalism, competition, and predation) might occur within the guild. For any of these interactions, many **direct effects** (from direct physical interactions) and **indirect effects** (through intermediary species) (Wootton 1994, Abrams et al. 1996) may impact the focal species, its intraguild competitors, its principal (extraguild) food source and its higher-order (extraguild) natural enemies (Fig. 7.1). These interactions may affect the density (**density-mediated effects**) of the species considered, or any morphological, physiological or behavioural traits (**traits-mediated effects**).

History of the protagonists is one of key factors in intraguild interactions (Lucas 2005) that are frequently sudden and **ephemeral events** occurring at

specific times and stages. The size, morphology, physiology, behaviour, vigour and autonomy, as well as the competitive, defensive and predatory aptitudes of an individual **change drastically throughout its life cycle**. All traits affecting the ladybird's **stage** at the time of a potential interaction (such as **time of colonization, life cycle length, voltinism**, etc.) influence the probability of its occurrence, its type, and its outcome. For instance, phoretic mites will use specific stages of ladybirds (7.5). Also, a third ladybird instar may be an intraguild prey of a chrysopid larva, whereas in the fourth instar it could be the predator of a similar size chrysopid larva (Fig. 7.2).

7.5 COCCINELLIDS AS INTRAGUILD COMMENSALISTS AND MUTUALISTS

Direct or indirect commensalism occurs whenever an organism derives a **benefit from** a second organism while the latter is not affected (Wootton 1994). **Phoresy** is an example: an organism is transported (dispersed) by an unaffected host (Holte et al. 2001). The coccinellid acts as a **vector** of hemisarcoptid mites when the non-feeding hypopal stage attaches itself to the elytra of the coccinellid adults (O'Connor & Houck 1989). Several predatory phoretic mites belong to the same guild as their coccinellid carrier (e.g. Houck & O'Connor 1991, Hurst et al. 1997, Holte et al. 2001).

Coccinellids may similarly act as **vectors of intraguild pathogens** (Pell et al. 1997, Roy et al. 1998, 2001, Thomas et al. 2006). This interaction is considered commensalism when the pathogens have negligible direct effects on ladybirds. If the coccinellids are infested by the pathogens, the interaction is detrimental (7.9.2).

Coccinellids may **indirectly benefit other guild members** through their action on the shared resource (Losey & Denno 1998, 1999, Aquilino et al. 2005), an interaction known as '**predator facilitation**' (Charnov 1976). For instance, the foliar-foraging *C. septempunctata* generates a strong dropping response in *Acyrtosiphon pisum* increasing its availability for the ground-foraging carabid *Harpalus pennsylvanicus* (Losey & Denno 1998, 1999; Fig. 7.3).

Direct or indirect mutualism is **mutually beneficial** for two different populations/species (Wootton 1994, Abrams et al. 1996) that share the same resource. Hypopodes of the astigmatid mite *Hemisarcoptes*

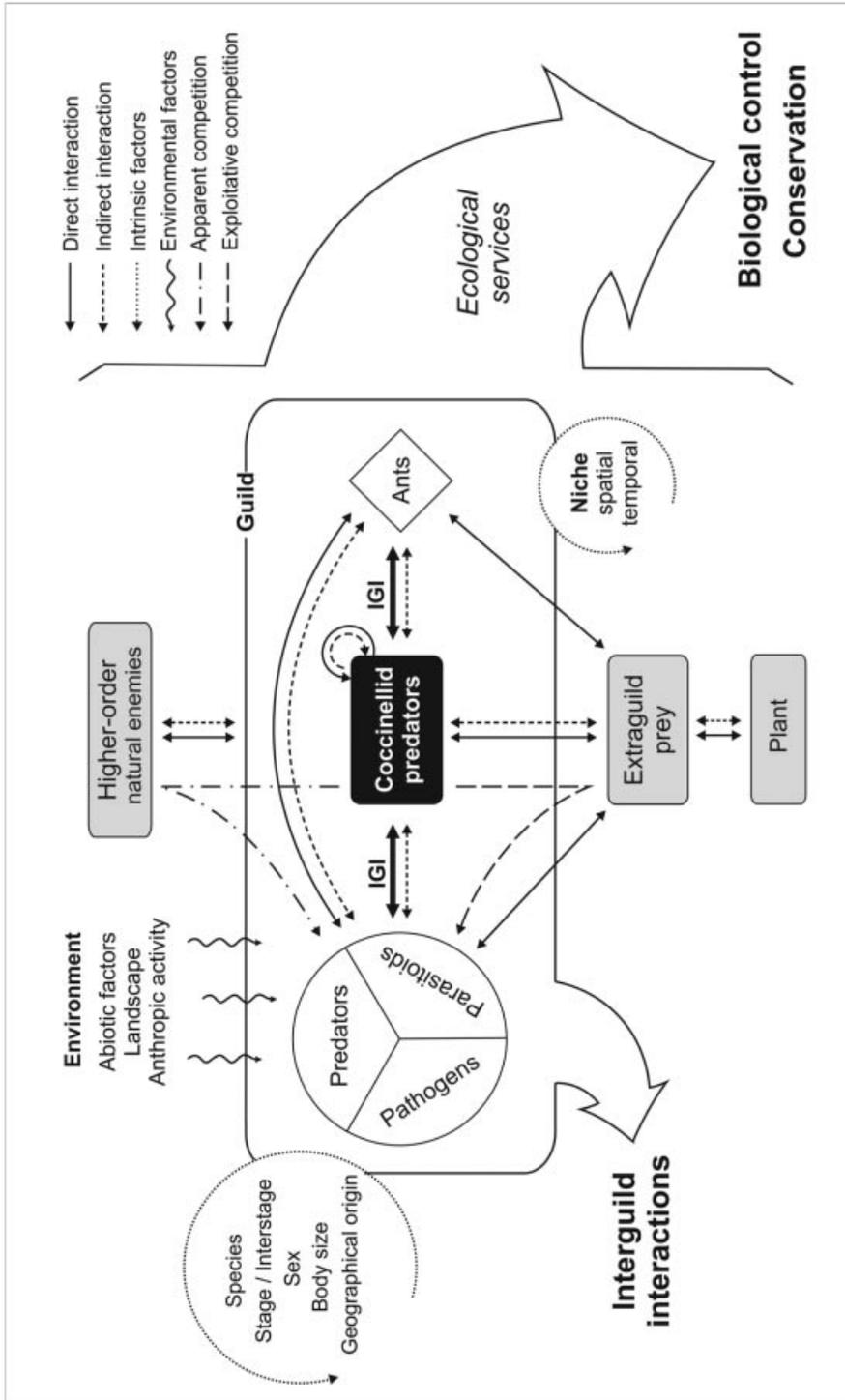


Figure 7.1 Schematic representation of intraguild interactions (IGI) involving predatory ladybirds. Any type of interaction may generate indirect effects on other protagonists within and outside the guild.

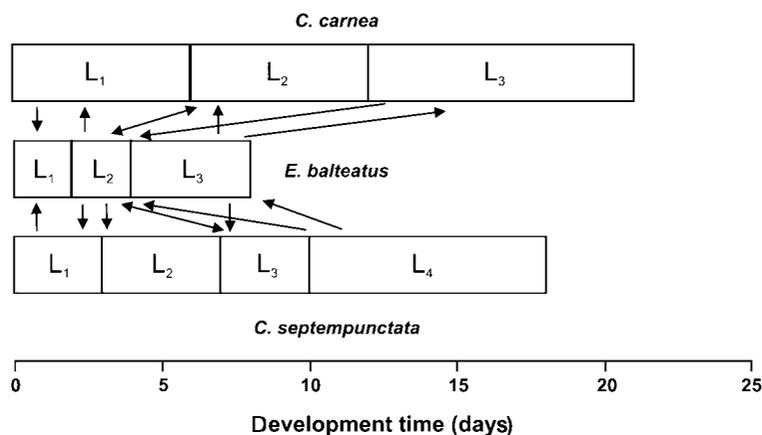


Figure 7.2 Linkage between developmental time of larval instars and occurrence of intraguild predation between *Episyrphus balteatus*, *Chrysoperla carnea* and *Coccinella septempunctata* in a perfectly synchronized community. Arrows point toward intraguild prey. (After Hindayana et al. 2001, with permission).

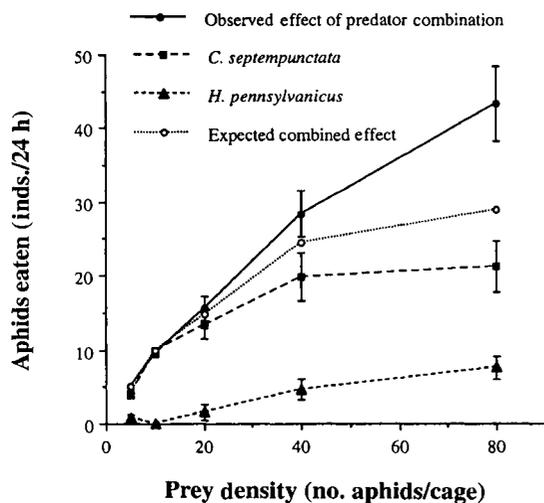


Figure 7.3 Coccinellids as commensalists. Effect of aphid prey density and predator treatment on the consumption of prey aphids. Predator treatments: foliar-foraging predator only (*Coccinella septempunctata*); ground-foraging predator only (*Harpalus pennsylvanicus*); both predators in combination (*C. septempunctata* plus *H. pennsylvanicus*). The expected effect is based on the sum of the foliar and ground predators acting in isolation. (After Losey & Denno 1998, with permission).

cooremani benefit from *Chil. cacti* by phoretic dispersal and resource acquisition. The ladybird may benefit by acquiring resources from the hypopode and thus the interaction was assumed to be potentially mutualistic (Holte et al. 2001). The boundary between parasitism, mutualism and commensalism remains to be clarified.

7.6 COCCINELLIDS AS COMPETITORS

7.6.1 Exploitative competition

Exploitative competition is an **indirect interaction** between individuals of two competing species: one species reduces the abundance of a shared resource and consequently affects the second species (Wootton 1994, Abrams et al. 1996). For example, a coccinellid larva or adult affects another intraguild member by **consuming** or **disturbing** their shared prey. Smaller coccinellids with lower food requirements have a competitive advantage over larger species at low aphid densities (Obrycki et al. 1998b).

The recruitment of coccinellid predators is described by the **aggregative numerical response**, the

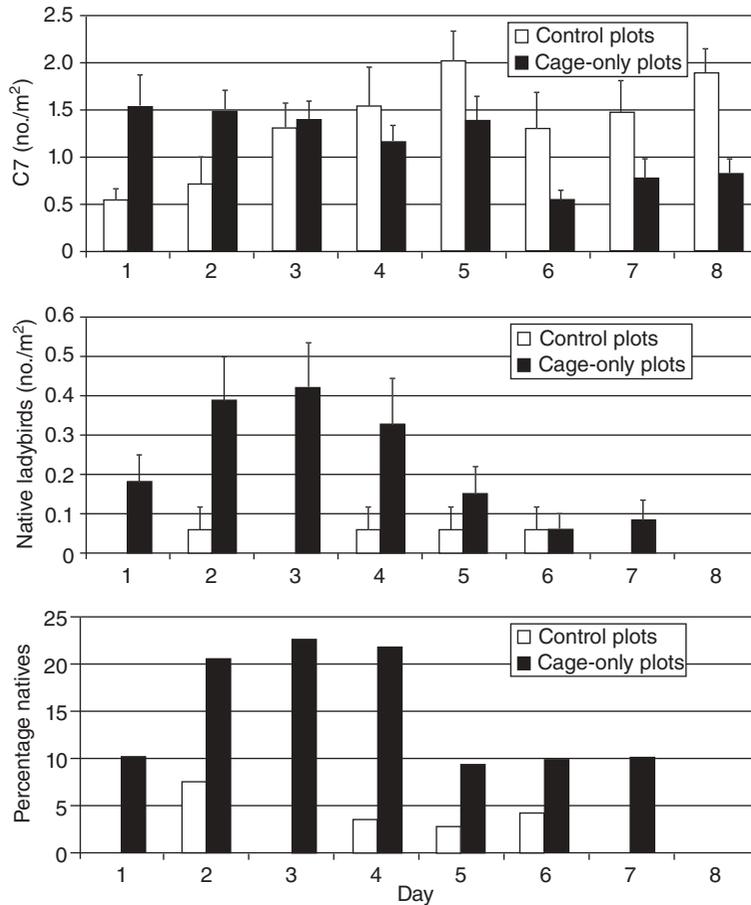


Figure 7.4 Coccinellids as exploitative competitors. Numbers of adults of *Coccinella septempunctata* (C7) and native ladybirds observed in visual censuses on successive days (x-axis) of experimental plots that had either been caged previously (cage-only plots) or left uncaged (control plots) in lucerne (top and middle panels; means + 1 SE), and percentage of all individuals (of C7 or natives) observed that belonged to native species (bottom panel). Day 1 is the day after cage removal. (After Evans 2004, with permission).

threshold of which is species specific (5.3.5). Evans (2004) showed that the arrival of the Palearctic *C. septempunctata* in Utah (USA) lucerne fields caused a decline in pea aphid populations and then a decline in native coccinellids (1992–2001) (Fig. 7.4). An artificial increase in aphid densities stimulated the return of native coccinellids to the focal crop. Evans proposed that *C. septempunctata* prevented aphid outbreaks, reducing the level at which lucerne crops retain native coccinellids.

Whitefly egg consumption in multi-specific treatments (one *Delphastus catalinae* adult and one *Col. maculata* adult) was significantly lower than the

individual consumptions of the two coccinellid species, even though no behavioural interference was observed (Lucas et al. 2004c).

Exploitative competition may also take the form of **induced defensive responses and dispersion of a shared prey** following ladybird attacks (Dixon 1958, Nelson & Rosenheim 2006). These responses can affect **subsequent predation efficiency** by intraguild competitors (conspecifics or heterospecifics). Aphid dropping induced by *Har. axyridis* reduced its predation efficiency by approximately 40% (Francke et al. 2008) and potentially also that of other foliar-dwelling guild members. On apple saplings, *C. septempunctata* caused

significantly greater dispersion of mite colonies than did *Har. axyridis* (Lucas et al. 2002).

7.6.2 Apparent competition

This indirect interaction arises when **two prey** species share a **common natural enemy** and when an increase in one prey leads to an increase in the shared natural enemy so as to cause a decline in the other prey species (Holt 1977, Wootton 1994). The invasion of *Har. axyridis* provided the potential for such an interaction. *Harmonia axyridis* is a low-quality host for the generalist parasitoid *Dinocampus coccinellae* that does not seem to discriminate between coccinellid species; the abundance of this new host may thus constitute an **egg sink**, leading to a decrease in *D. coccinellae* populations and consequently to a **reduction of the parasitism on the native coccinellids** (Hoogendoorn & Heimpel 2002, Firliej et al. 2005, 2006, Koyama & Majerus 2007; also 8.3.2.1).

7.7 COCCINELLIDS AS VECTORS OF MALE-KILLING BACTERIA

Coccinellids are suspected of transmitting **male-killing bacteria, such as *Wolbachia***, although clear empirical data are lacking (Hurst et al. 2003, Tinsley & Majerus 2007; see also 8.4.5.2). This interaction may have **detrimental or beneficial** effects (Majerus et al. 1998, Engelstadter & Hurst 2007) on the other coccinellids and on infected competitors, but is positive for the bacteria. These bacteria are transmitted **vertically** from mother to daughter, but **horizontal transmission is strongly suspected** in coccinellids (Hurst et al. 2003). Horizontal transfer is more likely to occur by direct transfer of infective material (e.g. predation) between closely related species and organisms in close confinement (Tinsley & Majerus 2007).

7.8 COCCINELLIDS AS INTRAGUILD PREDATORS

7.8.1 General rules of intraguild predation involving coccinellid predators

Intraguild predation (IGP), defined as **predation on a competitor** (Polis et al. 1989, Polis & Holt 1992),

includes (i) **effective IGP**: prey is killed and consumed (IGP *sensu stricto*); (ii) **interspecific killing**: prey is killed but not consumed; and (iii) **IGP risk**: prey is at risk of being killed and/or consumed (Lucas 2005). IGP usually involves an **intraguild predator**, an **intraguild prey** and a shared resource (**extraguild prey**). IGP is a widespread force **structuring animal assemblages** (Arim & Marquet 2004). IGP is also important in **biological control** systems (Rosenheim et al. 1993, 1995; 7.11.2, Chapter 11).

IGP by or on predaceous coccinellids is quite common (Dixon 2000, Lucas 2005, Gagnon 2010) due to **aggregations** of the shared prey (mainly gregarious Sternorrhyncha) (Dixon 1985, 1987), **richness and abundance** of competitors (Frazer 1988, Drea & Gordon 1990), and **drastic changes in body size and mobility** during the **life cycle**. IGP involving coccinellids is common in the field even at high extraguild prey densities (Gardiner & Landis 2007, Gagnon 2010, but see Hemptinne & Dixon 2005).

IGP is **described** by its (i) **intensity (probability of occurrence)**, (ii) **direction** (mutual or unidirectional), and (iii) **symmetry** (dominance or not of a species). IGP was mostly demonstrated in microcosm where the intraguild prey cannot escape so that the **real IGP intensity** in the field remained **uncertain** until recently (e.g. Hindayana et al. 2001, Kindlmann & Houdkova 2006). Using molecular tools, Gagnon (2010) detected coccinellid intraguild prey in 52.9% of the coccinellid intraguild predators in Quebec soybean crops. Direct observations on cotton revealed that 6.6% of **neonate lacewings died from IGP** in a period equivalent to about **1.4% of their total life cycle** (Rosenheim et al. 1999). Such results indicate **IGP** as a **major source of mortality** for lacewing neonate larvae and also for young instars of coccinellids.

Studies tend to demonstrate that the intensity of IGP involving aphidophagous coccinellids is possibly higher than in other systems such as those involving aleyrodophagous mirids (Lucas & Alomar 2002a, b) due to the active searching of coccinellids and to their low mobility compared to mirids.

Five general rules on IGP involving coccinellids can be established **at species level**:

1 IGP intensity decreases as extraguild prey density increases (Sengonca & Frings 1985, Lucas et al. 1998a, Schellhorn & Andow 1999b, Hindayana et al. 2001, Yasuda et al. 2004, Gagnon 2010). For exceptions see Lucas et al. (1998a), Phoofolo

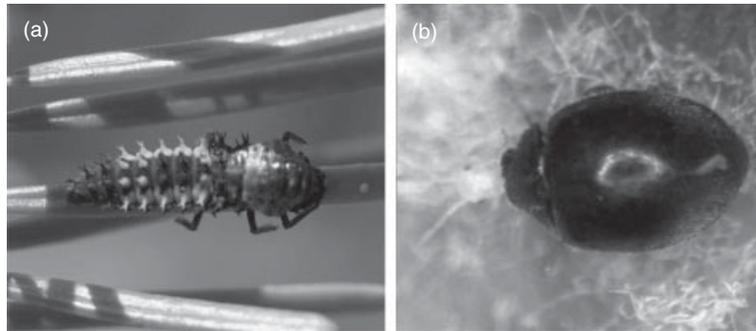


Figure 7.5 Coccinellids as intraguild predators. (a) Intraguild predation by a fourth instar larva of *Harmonia axyridis* preying upon a pupa of *Adalia bipunctata*. Picture by Serge Laplante; (b) Intraguild predation by an adult of *Stethorus punctillum* preying upon a first instar of the mullein bug *Campylomma verbasci*. Picture by Olivier Aubry (Laboratoire de Lutte biologique, UQAM, 2008). (See colour plate.)

and Obrycki (1998), and Snyder et al. (2004b), IGP is frequently motivated by **nutritive needs**, which decrease in the presence of alternative food. Furthermore, an increase in extraguild prey density can generate a **dilution effect** protecting furtive intraguild prey (Lucas & Brodeur 2001).

2 IGP intensity increases as intraguild prey density increases (Noia et al. 2008), thus increasing the **probability of encounters**. These first two rules may theoretically be compensatory depending on the numerical response of intraguild prey to extraguild prey density (but see Lucas & Rosenheim 2011).

3 IGP is unidirectional (the predator and prey status of each protagonist remain constant; Polis et al. 1989) **and directed toward a specialist organism** (predator, parasitoid or pathogen) (Lucas et al. 1998a, Yasuda & Ohnuma 1999, Hindayana et al. 2001).

4 IGP is mutual (each species may prey on the other one during its life cycle; Polis et al. 1989) **when two non-specialized species are involved** (Lucas et al. 1998a, Felix & Soares 2004, but see Mallampalli et al. 2002 and de Clercq et al. 2003 for exceptions). Due to drastic changes in size, mobility, vigour and defensive capacity during the life cycle, each species may at specific times be the intraguild prey or the intraguild predator (Lucas 2005).

5 Mutual IGP is asymmetrical (i.e. one species acts as the predator significantly more often than does the other; Lucas 2005) **in favour of the larger species** that are generally more successful in

confrontations (Lucas et al. 1998a, Obrycki et al. 1998a, Hindayana et al. 2001), but exceptions may occur (Sengonca & Frings 1985, Lucas et al. 1998a, Snyder et al. 2004b).

7.8.2 Occurrence of intraguild predation by coccinellids

Most coccinellid species may prey upon intraguild competitors (Fig. 7.5). **Older larval instars** (third and fourth) and **adults** are more often **intraguild predators** than younger stages. Because of **an important (at least 5-fold) increase in body size** during immature development, an encounter between small, young larval stages (or eggs), and larger, more powerful older larvae (or adults) often results in antagonistic interactions. In contrast, an encounter between **similar sized** ladybird and/or lacewing larvae usually generates a **low intensity of IGP** even at low extraguild prey densities (Chang 1996, Lucas et al. 1998a, Obrycki et al. 1998a). Older larvae interact with each other more strongly than young larvae (Yasuda et al. 2004).

The **significant benefits** of IGP for coccinellids include: (i) **elimination of a potential predator**, (ii) **elimination of a competitor**, (iii) **consumption of a protein-rich meal** (Polis et al. 1989), and (iv) **acquisition of toxins from intraguild prey** (Hautier et al. 2008). Four hypotheses have been built (Lucas 2005):

1 Protective IGP hypothesis: the predator attacks the IG prey to **protect itself before a period of**

high vulnerability (Fig. 7.7). The consumption of the prey is facultative.

- 2 **Competitive IGP hypothesis:** the predator **eliminates a competitor** and the consumption of the IG prey is facultative. Neither protective nor competitive IGP have yet been reported in coccinellids.
- 3 **Nutritional IGP hypothesis:** IGP occurs during **extraguild food shortage** or when the **alternative food is scarce** or has a lower nutritive value than the IG prey (e.g. Lucas et al. 2009). In temperate areas, pollen is used as a food source at the beginning of the season, but does not allow maturation of ovaries in most predatory ladybird species (5.2.9); at this time, any predation event would be highly beneficial. Also, *Har. axyridis* is among the last insects to be found in autumn in maize fields of Eastern Canada (as larvae and pupae); third and fourth instars are highly aggressive at this time, and IGP/cannibalism is extremely common (Lucas, unpublished). For *Har. axyridis*, supplementing a limited aphid diet with *A. bipunctata* eggs provides **nutritional benefits during extraguild prey shortages** (Ware et al. 2009). Such ability to effectively exploit coccinellid intraguild prey as food (**specialization**) may be related to a **lower efficiency in extraguild prey exploitation** (Sato et al. 2008). Based on the fact that **nitrogen content** is generally higher in predatory insects than in herbivores, Kagata and Katayama (2006) tested and rejected the hypothesis that nitrogen shortages promote IGP between aphidophagous coccinellids.
- 4 **Opportunistic IGP hypothesis:** the predator **selects the prey according to its size**, regardless of its guild. The lacewing *Chrysoperla rufilabris* seems to show **no preference** for intra- or extraguild prey, and IGP occurrence is mainly determined by the **encounter rate** (Lucas et al. 1998a). Many coccinellids species are polyphagous and prey selection is greatly influenced by **capture efficiency**, which is directly related to **predator and prey relative sizes** (Dixon 1959, Klingauf 1967; 5.2.3) and to the **prey defensive abilities** (Provost et al. 2006).

Preying upon a competitor which is also a predator can be **risky**: the intraguild predator **may be injured** or may itself **become the prey** (Polis et al. 1989, Dixon 2000). However, such a situation seems rare in

the field since coccinellids usually avoid confrontation with prey of similar size (Lucas et al. 1998a). Ladybirds may also **be contaminated by generalist entomopathogens** infesting their intraguild prey. Also, IGP may increase a predator exposure to pesticides (Provost et al. 2003). Finally, many coccinellids are protected by **toxic alkaloids** (7.9.1, 5.2.6.1, 9.2).

All in all, the **cost/benefit ratio of IGP** by coccinellid predators would depend whether the **intraguild prey are** predators, parasitoids, or pathogens.

7.8.3 Intraguild predation on intraguild coccinellids (by coccinellids)

Most extraguild prey are exploited by an assemblage of ladybird species (Chazeau 1985, Frazer 1988, Drea & Gordon 1990). Potential for antagonistic interactions and IGP between ladybird predators is therefore high (e.g. Takahashi 1989, Schellhorn & Andow 1999a, b, Yasuda & Ohnuma 1999, Yasuda et al. 2001, 2004, Michaud & Grant 2003, Felix & Soares 2004, Snyder et al. 2004a, Kajita et al. 2006, Majerus et al. 2006, Hodek & Michaud 2008).

Since morphology and development are relatively similar among ladybirds, **IGP between coccinellids** follows **six general rules**:

- 1 **IGP intensity is usually high among predaceous coccinellid species** due to their **great voracity, their similar foraging strategies**, and to a **contagious distribution of their resource** (Hodek 1996).
- 2 **IGP is mutual.** A ladybird is an **intraguild predator at old larval/adult stages** or **intraguild prey at young larval/egg stages**.
- 3 **The larger individual usually preys upon the smaller.**
- 4 **Polyphagous species are less affected by alkaloids** of their intraguild prey than specialists (Yasuda & Ohnuma 1999).
- 5 **Eggs, pupae, and moulting individuals are highly susceptible to IGP** (exceptions are linked to chemical protection; 7.9.1).
- 6 **Adults are never successfully attacked.**

Important **differences among species** modulate the above rules. The **attack rates** (the number of attacks divided by the number of individuals contacted) of *Har. axyridis* toward *C. septempunctata* exceeded 50%, while the **attack rates** of *C. septempunctata* toward *Har.*

axyridis was less than 20% (Yasuda et al. 2001). The average **escape rates** (escapes divided by attacks) of *Har. axyridis* following *C. septempunctata* attacks was higher than the escape rates of *C. septempunctata* following *Har. axyridis* attacks. In the pair *Har. axyridis* and *C. undecimpunctata*, a smaller advantage in body weight was required for *Har. axyridis* to become an intraguild predator of *C. undecimpunctata* than vice versa (Felix & Soares 2004). Snyder et al. (2004) found that the **exotic** species *C. septempunctata* and *Har. axyridis* had a significant advantage in IGP confrontations over the **native** *Hip. convergens* and *C. transversoguttata*. Especially *Har. axyridis* attacked more successfully and escaped more frequently when attacked. In contrast to native species, **cannibalism** was a **greater threat for *Har. axyridis*** than IGP (5.2.8).

As intraguild predators, coccinellids frequently have **sub-lethal effects** on intraguild prey. The presence of *Har. axyridis* **slowed *A. bipunctata* larval development** at high extraguild prey density, whereas IGP by *Har. axyridis* or by *C. septempunctata* occurred at low extraguild prey density (Kajita et al. 2000). In a cage experiment, *Har. axyridis* caused a **decrease in *C. undecimpunctata* fecundity**, even when the extraguild resource was abundant (Soares & Serpa 2007). In field cages, *Har. axyridis* larvae (intraguild predator) had no effect on survival or weight gain of *Col. maculata* larvae (intraguild prey) (Hoogendoorn & Heimpel 2004), but the intraguild prey **modified its distribution**, possibly to avoid interactions with the predator. Adult *Col. maculata*, *C. septempunctata* or *Har. axyridis* did not modify their **distribution** when in presence of adults of the other species (Lucas et al. 2002).

Finally, **key factors** influencing IGP among coccinellids are (i) **time of colonisation, voltinism**, and **speed of development** which determine the intraguild prey/intraguild predator status of the protagonists at a specific time, and (ii) **oviposition, moulting and pupation site**, since the susceptibility of **non-mobile stages/periods** is strongly linked to their position (e.g. distance from the shared resource) (Lucas et al. 2000, Lucas 2005).

7.8.4 Intraguild predation on intraguild non-coccinellid predators

Significant mortality from IGP by coccinellid predators has been demonstrated on lacewings (e.g. Michaud

& Grant 2003, Gardiner & Landis 2007), syrphids (Hindayana et al. 2001), and cecidomyiids (e.g. Lucas et al. 1998a, Gardiner & Landis 2007).

7.8.4.1 Intraguild neuropterans

Green/brown lacewings and ladybirds often **co-occur spatially and temporally** in the fields (Phoofolo & Obrycki 1998). **Mutual IGP** has been reported both in the laboratory and in the field (Sengonca & Frings 1985, Lucas et al. 1998a, Phoofolo & Obrycki 1998). For example, **lacewing eggs**, despite the presence of the pedicel and a tough chorion, were easily eaten by all stages of *Col. maculata* (Lucas 1998). However, when **reared** on lacewing eggs, coccinellids did not complete their pre-imaginal development (*C. septempunctata*) or developed into smaller adults (*Col. maculata* and *Har. axyridis*) (Phoofolo & Obrycki 1998). **Lacewing pupae** were not successfully attacked by *Col. maculata* (Lucas et al. 1998a).

In the presence of a *C. septempunctata* first instar, first instars of *Chrysoperla plorabunda* sheltered themselves in axils after feeding (Chang 1996). *Chrysopa perla* and *Chrysopa oculata* **avoided oviposition** on substrates with **tracks** of *Har. (=Leis) dimidiata* first instars and *Col. maculata* third instars, respectively. Tracks of first instars of some other coccinellid species had no impact on *C. perla* and *C. oculata* oviposition (Ruzicka 2001b, Chauhan & Weber 2008).

7.8.4.2 Intraguild dipterans

Vermiform dipteran larvae seem **highly susceptible** to IGP by coccinellids (Lucas et al. 1998a, Gardiner & Landis 2007). *Harmonia axyridis* caused 40% direct mortality of the cecidomyiid *Aphidoletes aphidimyza* larvae after 2 hours in a microcosm experiment (Voynaud 2008). The aphidophagous chamaemyiid *Leucopis* spp. larvae are occasionally victims of IGP by ladybird and lacewing larvae (Sluss & Foote 1973). Both cecidomyiid and chamaemyiid larvae are **furtive predators** that exploit aphid colonies without generating aphid **defensive response** (Lucas et al. 1998a, Lucas & Brodeur 2001, Frechette et al. 2008). They benefit thus from a **dilution effect** (the probability of being attacked by a predator decreases as colony size increases; Edmunds 1974), in large aphid colonies which reduces their susceptibility to IGP (Lucas & Brodeur 2001).

Coccinellids have an **indirect effect** by reducing aphid density through predation and aphid dispersion (Voynaud 2008). In addition to having less food available, midges suffer from a reduced **dilution effect** that increases IGP risks (Lucas & Brodeur 2001).

Leaf **trichomes** provide **refuges** for *A. aphidimyza* eggs against IGP by *Col. maculata* and play a role in **oviposition site selection** (Lucas & Brodeur 1999). Also, *A. aphidimyza* laid fewer eggs on plants previously exposed to second instar *C. septempunctata* (Ruzicka & Havelka 1998; but see Lucas & Brodeur 1999).

When attacked by coccinellids (Hindayana et al. 2001), older syrphid larvae defend themselves by **oral secretions (slime)** or rarely by **counter-attacks**. *Episyrphus balteatus* **pupae** were **never attacked** by *C. septempunctata* adults or larvae (Hindayana et al. 2001). In Petri dishes, *E. balteatus* laid fewer eggs in presence of *Har. axyridis* larval tracks (Almohamad et al. 2010).

7.8.4.3 Intraguild hemipterans

The **great mobility** of mirids should severely lower interactions with intraguild members as well as the possibility of relevant observations. **Asymmetrical IGP** in favour of the coccinellid was observed between *Har. axyridis* and the mirid *Hyaliodes vitripennis*. A **low intensity** of IGP was also noted when compared to coccinellid–coccinellid interactions. The presence of less mobile extraguild prey (phytophagous mites), to which the attacks of mirids were directed, further reduced IGP intensity (Provost et al. 2005, 2006).

Small acarophagous ladybirds also attack young stages of acarophagous bugs, such as *Stethorus pusillus* preying on first instar mirid *Campylomma verbasci* (Fig. 7.5). IGP by coccinellids on eggs, young larvae, or moulting individuals of other intraguild heteropterans is highly probable but has not yet been documented.

7.8.4.4 Other intraguild predators

Predatory mites of the phytoseiid *Amblyseius andersoni* are frequently found in **acarodomatia** (tufts of hair or invaginations on the leaf surface of several plants). These structures protect the mites against IGP by *C. septempunctata* and *Hip. variegata* adults, but not against second instar lacewings (*Chrysoperla rufilabris*) (Norton et al. 2001).

IGP by ladybirds on eggs of the **derodontid** beetle *Laricobius nigrinus* has also been reported (Flowers et al. 2005). IGP by coccinellids could also affect **other predators** (Cantharidae, Dermaptera, spiders, etc.).

7.8.5 Intraguild predation on intraguild parasitoids

Coccinellids can affect **intraguild parasitoids**: (i) by **direct predation** of parasitized extraguild prey, or (ii) by **non-lethal impact** on adult parasitoids. Ladybirds often **avoid eating parasitized extraguild prey**, or **prefer unparasitized prey** (5.2.7.1).

The coccidophagous *Rodolia* sp. was reluctant to consume parasitized coccids (Quezada & DeBach 1974). *Cryptolaemus montrouzieri* **feeds on** citrus mealybugs **parasitized** by *Anagyrus pseudococci* but not on individuals older than 4 days (Mutsu et al. 2008).

The aleyrophagous *Serangium parcesetosum* larvae and adults tended to **avoid** *Bemisia tabaci* pupae parasitized by *Eretmocerus mundus* (Al-Zyoud 2007). *Delphastus catalinae* adults **did not discriminate** whiteflies parasitized by *Encarsia sophia*, while second instars **preferred unparasitized** whiteflies (Zang & Liu 2007).

In the aphidophagous *Col. maculata*, larvae did not discriminate between healthy *Trichoplusia ni* eggs and those parasitized by *Trichogramma evanescens* (Roger et al. 2001) and *C. septempunctata* did not discriminate *Lysiphlebus testaceipes* mummies from unparasitized *Schizaphis graminum* (Royer et al. 2008). Despite intense (98–100%) predation on *L. testaceipes* mummies, *Hip. convergens* exhibited a **partial preference for unparasitized** hosts (Colfer & Rosenheim 2001; but see Ferguson & Stiling 1996). *Coccinella undecimpunctata* larvae had no preference for parasitized or healthy aphids even though **parasitized aphids had inferior nutritive values** (Bilu & Coll 2009). Coccinellids **destroyed more than 95%** of the immature parasitoids of the psyllid, *Diaphorina citri*, in Florida citrus groves (Michaud 2004).

The larvae of *C. undecimpunctata* disturbed *A. colemani* **adults** and **reduced parasitization** (Bilu & Coll 2007). Adults of the parasitoid *Lysiphlebus fabarum*, **avoided** plants with coccinellids (Raymond et al. 2000). Nakashima et al. (2004, 2006) also demonstrated that three aphid parasitoid species **avoided leaves previously visited by adult ladybirds**.

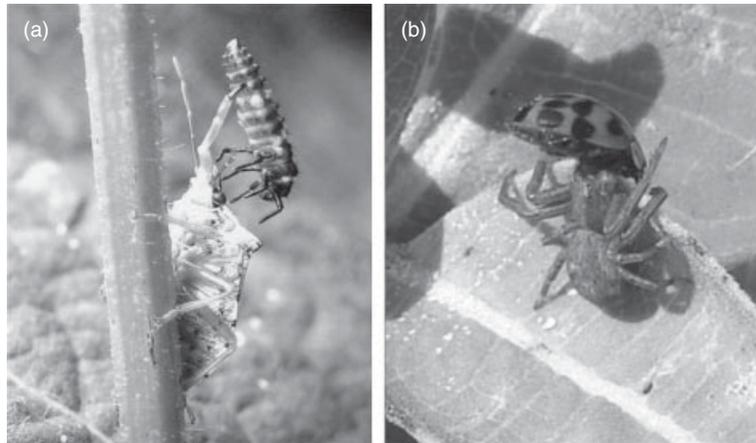


Figure 7.6 Coccinellids as intraguild prey. (a) Intraguild predation by an adult *Podisus maculiventris* on a larva of *Coleomegilla maculata lengi* in a soybean field. Picture by Florent Renaud, 2007; (b) Intraguild predation by a *Thanatus* sp. spider on an adult of *Harmonia axyridis* in an apple orchard. Picture by Jennifer de Almeida, 2008 (Both pictures from Laboratoire de Lutte biologique, UQAM). (See colour plate.)

7.8.6 Intraguild predation on intraguild pathogens

Coccinellids interact with intraguild **entomopathogens** when eating infected prey and the outcome depends whether **the pathogen is specific** to the extraguild prey or **able to infect coccinellids** as well. For instance, aphids (or aphid cadavers) infected by aphidopathogenic fungus *Pandora neophidis* are preyed upon by *Har. axyridis* and *C. septempunctata* adults and larvae (Roy et al. 1998, 2003, 2008a, Roy & Pell 2000). Despite an overall **preference** by both predators for uninfected aphids, *C. septempunctata* is **more selective** than *Har. axyridis*, the Japanese population of *Har. axyridis* is more selective than the UK population, and satiated individuals are more selective than starved ones (8.4).

7.8.7 Coccinellids as top predators

Among coccinellids, *Har. axyridis*, is considered a top predator, dominating both the aphidophagous and coccidophagous guilds (Dixon 2000, Majerus et al. 2006, Pervez & Omkar 2006). A **top (or apex) predator** is largely **free from predation pressure** and is regulated more by **bottom-up** than **top-down** forces

(Gittleman & Gompper 2005). It should have a **stronger impact** on **intermediate predators** (the intraguild prey) than on the **shared prey** (the extraguild prey) (Dixon 2007). Indeed, numerous (mainly laboratory) studies confirm that *Har. axyridis* **dominates confrontations** with most coccinellid species (Pell et al. 2008, Alhmedi et al. 2010). This is explained by a **large body size**, **strong larval spines**, **chemical protection**, **rapid larval development**, great **nutritional plasticity** and high **aggressiveness** (Labrie et al. 2006, Majerus et al. 2006, Pervez & Omkar 2006, Sato et al. 2008). The predator could also have a better capacity to process ingested defence chemicals (Kajita et al. 2010). Labrie et al. (2006) reported the development of a **fifth larval instar** in laboratory conditions.

An alternative assumption is that *Har. axyridis* is **one species among other** large generalist aphidophagous coccinellids (Soares et al. 2008):

- 1 Generalist aphidophagous species are a threat to *Har. axyridis* younger/smaller instars (Felix & Soares 2004, Burgio et al. 2008). Furthermore, *Har. axyridis* is **sometimes dominated** in intraguild interactions, for example, by the pentatomid *Podisus maculiventris* (de Clercq et al. 2003), by spiders (Yasuda & Kimura 2001, Fig. 7.6b) or by the

ladybird *Anatis ocellata* (Ware & Majerus 2008). Thus it is **not** always **free from significant predation**;

- 2 Its stronger impact on the intermediate predator than on the shared prey remains to be demonstrated (Lucas et al. 2007a);
- 3 Also other **eurytopic** and/or **euryphagous** species, such as *C. septempunctata* (Hodek & Michaud 2008) and *P. quatuordecimpunctata* (Lucas et al. 2007b) have achieved success in invasion.

According to still another view, **IGP does simply not determine predator dominance**. IGP between ladybird species has no significant impact on their abundance, since **defensive traits evolved to avoid IGP** (Kindlmann & Houdkova 2006, Dixon 2007). **Cannibalism** may be the **key factor regulating coccinellid abundance**.

7.9 COCCINELLIDS AS INTRAGUILD PREY

Any predatory ladybird risks being attacked by **intraguild generalists (predators, parasitoids, or pathogens)** (Figs. 7.1 and 7.6). This vulnerability to IGP is **species- and stage-dependent**: some species are more protected by **size, unpalatability, behaviour** or other **protective devices** (Dixon 2000, de Clercq et al. 2003, Lucas 2005, Ware & Majerus 2008).

Even though all developmental stages are **potential intraguild prey, non-mobile stages** (eggs and pupae), **young instars** and **molting individuals** are much more vulnerable (Sengonca & Frings 1985, Lucas et al. 1997a, 1998a, 2000, Obrycki et al. 1998a, Hindayana et al. 2001; Fig. 7.7).

Finally, apart from **direct attacks** (e.g. death or injury), coccinellid intraguild prey may also suffer from **IGP risks** (e.g. **retarded development**) and respond by defensive mechanisms (7.9.1).

7.9.1 Defensive mechanisms of coccinellids against intraguild predation

Defensive mechanisms protect individuals during **susceptible periods**, some developed specifically against intraguild threats, while others against several

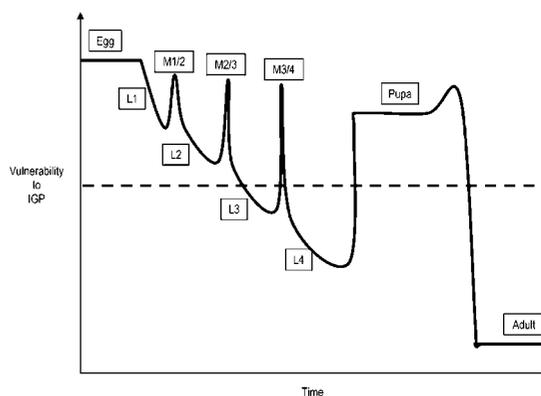


Figure 7.7 Susceptibility of a coccinellid to intraguild predation during its life cycle. The horizontal line refers to a threshold of vulnerability linked to a potential intraguild predator. M1/2, Molt from first to second larval instar; L1, first larval instar. (After Lucas 2005).

types of enemies. Protection is achieved by **successive lines of defence** (Lucas 2005).

7.9.1.1 Defence of all stages

Many coccinellid species are protected by **toxic compounds** either **synthesized *de novo***, or **sequestered** from their food (**chemical piracy**) (Pasteels 2007, Kajita et al. 2010; 9.3); the **trade-off between the cost (production, toxicity) and the benefits (defence)** is not clear (Pasteels 2007). **Biparental endowment** of chemical defences into eggs is possible: in *Epilachna paenulata*, males transfer alkaloids to females at mating (Camarano et al. 2009).

The toxic compounds may be encountered **passively** by the attacker, or may be **actively released** (reflex bleeding; 8.2.1.2 and 9.2.1) in response to attacks (Cuenot 1896, Pasteels et al. 1973, Eisner et al. 1986, Holloway et al. 1991, de Jong et al. 1991, Attygalle et al. 1993). As a rule, these compounds seem to have a **limited effect against cannibalism** but a **significant one against IGP** (Agarwala et al. 1998, Hemptinne et al. 2000b). Reflex bleeding of larvae could have a cost on the weight of resulting adults (Sato et al. 2009).

Another type of defence is exploiting a **protected habitat** (such as aphid galls or **ant-attended aphid colonies**; 7.10) that provides an **intraguild enemy-free space**.

7.9.1.2 Defence of eggs

Defence of eggs has been extensively studied (e.g. Agarwala & Dixon 1993, Yasuda & Shinya 1997, Hemptinne & Dixon 2000, Cottrell 2005). The first line of defence is the **selection of an enemy-free space** for laying eggs (5.4.1.3). **This behaviour** reflects the trade-off between **egg susceptibility** to intraguild predators and cannibals, and **starvation risk in neonates** (Schellhorn & Andow 1999a, Magro et al. 2007, Seagraves 2009).

Females may **avoid oviposition sites** where intraguild predators are present (e.g. Iablokoff-Khnzorian 1982). Adult females are able to detect **oviposition-detering semiochemicals (ODS)** from **consppecific larval tracks** (e.g. Ruzicka 1997, 2001a, 2003, Doumbia et al. 1998, Hemptinne et al. 2000b, Frechette et al. 2003; 5.4.1.3). For **heterospecific ODS**, several studies failed to detect any response (Doumbia et al. 1998, Yasuda et al. 2000, Oliver et al. 2006), while others demonstrated a significant heterospecific effect (Ruzicka 1997, 2001a, 2006, Michaud & Jyoti 2007) or inconsistent results (Ruzicka 2001b, Ruzicka & Zemek 2003).

Faeces of *Har. axyridis* (intraguild predator) represented cues that **reduced feeding and oviposition** in *P. japonica* (intraguild prey) (Agarwala et al. 2003). However, *Har. axyridis* behaviour was not affected by *P. quatuordecimpunctata* faeces.

In the presence of the intraguild predator *Chrysoperla carnea*, *Serangium parcesetosum* laid more eggs between the plant veins (Al-Zyoud et al. 2005).

The presence of **immobilized individuals of the coccinellid intraguild predator** *C. leonina transversalis* (but not the smaller *Scymnus pyrocheilus*) **reduced oviposition** in *Menochilus sexmaculatus* (Agarwala et al. 2003).

A second line of defence of ladybird eggs is the **chemical protection** (9.6) that varies according to the intraguild prey and the intraguild predator species (Sato & Dixon 2004, Flowers et al. 2005, Rieder et al. 2008, Ware et al. 2008). The chemicals involved may be partially or totally **repellent**, and may involve **nutritive costs** (Agarwala & Dixon 1992, Hemptinne et al. 2000a, Cottrell 2007, Kajita et al. 2010). For example, chemical protection efficiently protects *Calvia quatuordecimguttata* against *Har. axyridis* (Ware et al. 2008), *Har. quadripunctata* (Dyson 1996), *A. bipunctata*, *P. quatuordecimpunctata*, *Calvia decemguttata* and *A. decempunctata* (Vanhove 1998). Eating **heterospecific**

eggs may slow the predator's **development**, **decrease larval weight gain** and **adult size**, and even **cause death** (Phoofolo & Obrycki 1998, Hemptinne et al. 2000a, b, Cottrell 2004, Rieder et al. 2008). Egg chemical defence could be linked to **co-evolution of defences against sympatric** ladybird species (Agarwala & Yasuda 2001, Rieder et al. 2008).

Despite chemical defence, eggs remain highly **susceptible to cannibalism** (e.g. Agarwala et al. 1998, Omkar et al. 2004, Rieder et al. 2008, Sato & Dixon 2004). **Larvae prefer** (and are less affected by) consuming **consppecific eggs** (but see Cottrell 2005). In situations of aphid scarcity, egg cannibalism may help starving larvae to survive (Agarwala & Yasuda 2001). **Cannibalizing eggs may protect larvae against IGP**, either by **additional toxin acquisition**, or by **acceleration of their development**, thus reducing the time they are susceptible to IGP (Gagne et al. 2002, Michaud & Grant 2004, Omkar et al. 2007).

Another defensive trait of ladybird eggs is linked to the fact that they are laid in **clusters** and are thus less vulnerable to predation than when laid singly (due to a **dilution effect**) (Agarwala & Yasuda 2001). Furthermore, the **cluster may concentrate the toxic compounds** of eggs at a single point, increasing efficiency (Agarwala & Yasuda 2001, Omkar et al. 2004).

7.9.1.3 Defence of larvae

The susceptibility of young instars to IGP is linked to the **oviposition site** often **selected** by the female close to resources (5.4.1.3). Older larvae may **actively avoid** sites occupied by potential predators (Hoogenboom & Heimpel 2004).

Morphological characteristics, such as abdominal **spines** or **wax**, may provide defence for coccinellid larvae against IGP (Voelkl & Vohland 1996, Ware & Majerus 2008). Such traits are well developed in some species and absent in others (Pope 1979, Michaud & Grant 2003, Ware & Majerus 2008).

Large body size remains one of the most effective defences of coccinellid larvae against IGP (Lucas et al. 1997a, 1998a, Felix & Soares 2004, Ware & Majerus 2008). Thus any mechanism able to provide a **larger size** at the time of the intraguild confrontation (e.g. an earlier time of colonization) will **increase the potential intraguild prey survival probability**. Also **diet** can significantly affect the growth of the larvae. The **slow-growth-high-mortality (SGHM) hypothesis**,

which predicts that prolonged development results in greater exposure to natural enemies and in a subsequent increase in mortality (Clancy & Price 1987), applies to IGP involving coccinellids. Furthermore, one can implicitly propose a second hypothesis: as a result of prolonged development, the body size of an individual at any particular time is expected to be smaller and therefore its susceptibility to IGP should be higher (Fig. 7.2).

Following an encounter, coccinellid larvae frequently **escape** by different means (Hough-Goldstein et al. 1996, Lucas et al. 1997a, 1998a, de Clercq et al. 2003; 5.4.2). The susceptibility of *Col. maculata lengi* larvae to IGP by chrysopid third instar (*C. rufilabris*) is **age specific** and is influenced by the coccinellid **behavioural defensive strategies** (Lucas et al. 1997a): young larvae exhibited escape reactions (**dropping, fleeing and retreating**) but did not survive once caught by the lacewings, while older larvae used **wriggling** or **biting** representing 7.5% to 11% of all successful defences (Lucas et al. 1997a). A **drastic difference in dropping** from the plant was observed between *A. bipunctata* and *C. septempunctata* when facing *Har. axyridis* larvae: 43.3% of the *C. septempunctata* first instars dropped and 54.5% were killed by IGP whereas <2% of the *A. bipunctata* first instars dropped. The mortality of the latter from IGP was therefore 95% (Sato et al. 2005). Since IGP is influenced by extraguild prey density, **emigration when food is scarce** has a potential defensive value. Emigration tendency varies among species: 80% of *C. septempunctata brucki* larvae emigrated prior to aphid population extinction, whereas less than 20% of *Har. axyridis* and *P. japonica* did so (Sato et al. 2003).

Protection of coccinellid larvae by **alkaloids** differs according to intraguild predators and prey (Yasuda & Ohnuma 1999). For example, both *Cycloneda sanguinea* and *Har. axyridis* larvae preferred to feed on dead *C. sanguinea* larvae than on dead *Har. axyridis* larvae. Moreover, *Har. axyridis* larvae that fed on *C. sanguinea* larvae reached the adult stages, while no *C. sanguinea* larvae completed development on *Har. axyridis* larvae (Michaud 2002).

7.9.1.4 Defence of moulting individuals and pupae

Site selection for pupation and ecdysis influences ladybird **susceptibility to IGP**. In *Col. maculata lengi*,

vulnerability of pupae and newly moulted larvae to IGP by *Chrysopa rufilabris* larvae depended on **site selection**, leaves with aphid colonies being the most risky sites (Lucas et al. 2000; also Osawa 1992, Michaud & Jyoti 2007; 5.4.1.3). Larval ecdysis generally occurs (60%) near the aphid colonies exploited by the larvae (Lucas et al. 2000); by doing so, the larvae stay close to the resources and reduce the risk of encountering an intraguild predator during displacement. Since the moulting process lasts less than 20 min (except the later sclerotization of the cuticle), **IGP risk** is relatively low.

In contrast, 90% of the larvae **left the plant to pupate**; this reflects predation risks on the plant. In *Col. maculata*, pupation lasts about 20% of preimaginal developmental time (Warren & Tadić 1967). Remaining on the plant would thus expose pupae to natural enemies for a longer period than moulting larvae. Furthermore, the proximity of a food source is less important since the emerging adults are alate and can **disperse**. Finally, when searching for a pupation site, IGP risks are lower for fourth instar larvae than it would be in younger instars.

Microhabitat selection for ecdysis and pupation thus reflects a **trade-off between the advantages of remaining close to resources and the costs of being exposed to IGP** (Lucas et al. 2000).

Pupae may also reduce IGP risk through **flipping behaviour, 'gin traps'** (sclerotized teeth along junctions of movable abdominal segments; e.g. Eisner & Eisner 1992), and **warning colouration** (Majerus 1994). **Gregarious pupation** (of 2–5 pupae) has been reported for some species (*Har. axyridis*, *C. septempunctata*) in the field (G. Labrie, unpublished) and may also provide defence against IGP through a passive **dilution effect**. Specific defences such as **hair cover** is a protection against intraguild ants (Voelkl 1995). In some species, these hairs secrete **defensive droplets** (Attygalle et al. 1993). **Anachoresis**, the selection of shelters (holes, crevices etc.) (Edmunds 1974), also protects pupae against predation (Richards 1985).

7.9.1.5 Defence of adults

Adults are better defended than any other stage (Sengonca & Frings 1985, Lucas et al. 1998a, Mallampalli et al. 2002, de Clercq et al. 2003), but may be preyed upon by intraguild predators such as chrysopids (Lucas

et al. 1998a), pentatomids (de Clercq et al. 2003; Fig. 7.6a), reduviids (E. Lucas, unpublished) or spiders (Fig. 7.6b).

Adults may **avoid sites** with intraguild natural enemies (7.9). Adults may escape by **fleeing, dropping or flying away** (Hough-Goldstein et al. 1996, de Clercq et al. 2003). The shape (rounded, compact) of coccinellid adults and body sclerotization should contribute to the low susceptibility of adults to IGP (de Clercq et al. 2003).

Unpalatability of adults linked to the presence of **greater concentrations of toxic alkaloids** than in larvae may also lower the susceptibility of adults to IGP, even though this is species-specific (Mallampalli et al. 2002, de Clercq et al. 2003).

The **aposematic colouration** (bright and contrasting patterns) of adults is considered a **warning signal** (for toxicity) and an effective defence against visual predators (8.2). This aposematic pattern is common to many sympatric species, which may **reinforce the strength of the warning message (Mullerian mimicry)** (Holloway et al. 1991, Dolenska et al. 2009). However, no study has demonstrated any impact of aposematism against IGP.

7.9.2 Intraguild predation on coccinellids

Intraguild predators of ladybirds belong to a variety of groups (especially chrysopids, Hemiptera, syrphids and coccinellids). **Coccinellids** represent possibly the most dangerous intraspecific (cannibalism) and interspecific (IGP) threat for other coccinellids (7.8.3). Intraguild predation may also come from generalist parasitoids or pathogens.

7.9.2.1 Intraguild predation by intraguild predators

Chrysopid larvae frequently attack all ladybird stages (Sengonca & Frings 1985, Lucas et al. 1998a) and are usually reported to be **superior in confrontations** with similar-size coccinellid larvae (Sengonca & Frings 1985, Lucas et al. 1997a, 1998a, Phoofolo & Obrycki 1998, Michaud & Grant 2003). This superiority may be linked to their more **elongated mouthparts** allowing chrysopids to keep coccinellids at a safe distance (Lucas et al. 1997a, 1998a, Michaud & Grant 2003). *Coccinella septempunctata* females detected the presence

of **ODS** and laid fewer eggs on sites previously exposed to second lacewing instars (Ruzicka 1997).

Syrphid larvae preyed upon coccinellid larvae (Hindayana et al. 2001): in small arena, 1.1% of *C. septempunctata* larvae were killed and eaten by *Episyrphus balteatus* larvae and 7.4% were killed but **not consumed**. Coccinellids **avoided** pea plants when *E. balteatus* eggs or larvae were present (Alhmedi et al. 2007a, b).

Pentatomids also preyed on intraguild coccinellids, the interaction being **asymmetrical** in favour of the bugs (Mallampalli et al. 2002, de Clercq et al. 2003; Fig. 7.6a). By contrast, the **anthocorid** bug *Orius laevigatus* was not able to feed on *A. bipunctata* or *Har. axyridis* eggs (Santi & Maini 2006). However, **molecular gut-content analysis** showed that 2.5% of immature *Orius insidiosus* had consumed *Har. axyridis* material in the field (Harwood et al. 2009). IGP by **mirids** on coccinellids has not been reported and may be rare since mirids select slow-moving easy and safe prey (Kullenberg 1944, Frechette et al. 2007). It is not known whether coccinellid eggs can be attacked by mirids.

Spiders are important ladybird predators (Ceryngier & Hodek 1996, Yasuda & Kimura 2001; Fig. 7.6b). Most spiders are generalists and frequently share a common prey with generalist coccinellids. The **crab spider** *Misumenops tricuspidatus* attacked larvae of aphidophagous coccinellids (Yasuda & Kimura 2001).

IGP by the **derodontid** beetle *Laricobius nigrinus* on eggs of the ladybird *Sasajiscymnus tsugae* has also been reported, both species preying on the hemlock woolly adelgid (Flowers et al. 2005).

7.9.2.2 Intraguild predation by intraguild parasitoids

IGP on coccinellids can result from parasitism by **generalist parasitoids** also attacking extraguild prey. Babendreier et al. (2003) investigated the impact on natural enemies of **mass releases of *Trichogramma brassicae*** against the European corn borer *Ostrinia nubilalis*. No parasitoid emerged from *C. septempunctata* and *A. bipunctata* eggs; however, **young larval instars of *Trichogramma*** were recorded in *A. bipunctata* eggs and **egg mortality increased**. Since several coccinellids have been reported as predators of *O. nubilalis* eggs (Musser & Shelton 2003), the interaction is considered as IGP (or **intraguild parasitism**).

7.9.2.3 Intraguild predation by intraguild pathogens

IGP on coccinellids can result from **contamination by a generalist pathogen** infesting both the extraguild prey and the coccinellid hosts. Contamination by the fungus *Beauveria bassiana* has been observed in **hibernation sites** (Iperti 1964, 1966, Cottrell & Shapiro-Ilan 2003). In **biological control programmes**, contamination by generalist pathogens of both coccinellids and the target pests has been extensively demonstrated with **fungi** (Hodek 1973, Todorova et al. 1996, 2000, Cottrell & Shapiro-Ilan 2003, 2008), **bacteria/by-products of bacteria** (e.g. Giroux et al. 1994) and **nematodes** (Mracek & Ruzicka 1990, Lemire et al. 1996, Shapiro-Ilan & Cottrell 2005). Impacts are highly variable according to the **strain/species** considered (Krieg et al. 1984, Lucas et al. 2004b, Cottrell & Shapiro-Ilan 2008).

Some coccinellid species **avoid** preying upon **sporulating cadavers** of extraguild prey, **reducing contamination risks** (Roy et al. 2008b).

7.10 COCCINELLIDS INTERACTING WITH INTRAGUILD ANTS

Intraguild interactions between **ants** and ladybirds mainly result from **aphid-attending by ants**, but also may include **ant predation by coccinellids** (Majerus et al. 2007; see also 5.4.1.6 and 8.2.4).

Ants attend **honeydew** producing Hemiptera; 40% of aphid species are obligatorily tended by ants (Kunkel & Kloft 1985). Since they feed on honeydew and sometimes on the hemipterans producing it, ants belong to the **same guilds** as aphidophagous or coccidophagous coccinellids. Ants **protecting honeydew** against predators and parasitoids (e.g. Way 1963, Bradley 1973, Addicott 1979, Ceryngier & Hodek 1996) are frequently **keystone species** (producing disproportionately large effects on the abundance of interacting species in a community). Consequently the **natural enemy guild structure** is **drastically changed** by the presence of ants (e.g. Paine 1969, Sloggett & Majerus 2000, Eubanks & Styrsky 2006, Guenard 2007, Majerus et al. 2007).

Interactions between coccinellids and ants depend on: **species and density of** (i) **honeydew-producers**, (ii) **ants**, and (iii) **coccinellids** (Sloggett & Majerus

2000, Harmon & Andow 2007, Majerus et al. 2007). The **aggressiveness** of the ants and the **ants-hemipteran relative density** determine the **protection intensity** or **bodyguard effect** (Harmon & Andow 2007). The **numerical response** of ants and natural enemies will be related to the attractiveness of the resource (chemicals produced and insect density).

The aptitude to exploit ant-tended aphid colonies reflects the degree of **myrmecophily** of ladybirds. Per definition, myrmecophilous species would take more benefits when exploiting colonies tended by ants than unattended ones, which would not be the case for non-myrmecophilous species.

7.10.1 Non-myrmecophilous coccinellid species

Ants mostly show **aggressiveness toward non-myrmecophilous coccinellids** (e.g. Way 1963, Tedders et al. 1990, Eubanks 2001, Herbert & Horn 2008). In extreme cases, ants may even kill all coccinellid developmental stages (Voelkl 1995, Ceryngier & Hodek 1996, Kaplan & Eubanks 2002, Eubanks & Styrsky 2006, Oliver et al. 2008).

Ladybird larvae appear to be **more susceptible** to ant attacks **than adults**, and Sternorrhyncha are usually exploited only by adult ladybirds (Reimer et al. 1993, Guenard 2007). Ant-attended sternorrhynchans may provide **enemy-free space for potential intraguild prey** of non-myrmecophilous coccinellids, such as **myrmecophilous coccinellids** (7.10.2), **furtive predators** (Guenard 2007) or **parasitoids** (Voelkl 1992, Fischer et al. 2001).

Mutualism between ants and honeydew-producers may include alarm signals for the attention of ants. The treehopper *Publilia concava* produces an **acoustic vibration alarm signal** when in contact with *Har. axyridis*: this signal increases both ant activity and the probability of the ants detecting the ladybird (Morales et al. 2008).

Consequently, non-myrmecophilous coccinellids frequently leave ant-attended aphid colonies, and may also **avoid laying eggs** in these patches (Oliver et al. 2008).

According to Sloggett and Majerus (2000), there is a **great variability in the degree of association** between non-myrmecophilous coccinellids and ants, co-occurrence being linked to an extreme food

specialization and/or to a scarcity of non-attended colonies.

7.10.2 Myrmecophilous coccinellid species

Myrmecophilous ladybirds possess **morphological, behavioural or chemical traits** that efficiently protect them from attacks by ants (Pontin 1960, Majerus 1989, Voelkl 1995, 1997, Voelkl & Vohland 1996, Sloggett et al. 1998, Majerus et al. 2007). Some species are also able to **follow ant trails** (Godeau et al. 2003). These species are usually **restricted to ant-attended systems** during at least a part of their life cycle. The **benefits** of being able to exploit ant-attended prey include: (i) **avoiding competition with non-myrmecophilous competitors** and (ii) **avoiding predation/IGP/parasitism in an enemy-free space** (Guenard 2007).

For example, the myrmecophilous ladybird *Azya orbigera* is a predator of the green coffee scale, *Coccus viridis*. When these coccids are attended by the ant *Azteca instabilis*, **the ants attack the parasitoids** of *A. orbigera*, **reducing the parasitization rate** on the ladybird (Liere & Perfecto 2008).

The myrmecophilous *Scymnus posticalis* is never attacked by ants and is found within aphid colonies together with another ladybird, *Phymatosternus lewisii* (Kaneko 2007a). Furthermore, *S. posticalis* is an intraguild predator of the aphid parasitoid *Lysiphlebus japonicus* within ant-attended aphid colonies (Kaneko 2007b). This means that ants can **protect** myrmecophilous coccinellids (Voelkl 1995) and other intraguild prey such as furtive predators **against non-myrmecophilous** intraguild predators and/or intraguild parasitoids (Guenard 2007), but do not protect them against other myrmecophilous species.

7.11 APPLIED ASPECTS OF INTRAGUILD INTERACTIONS

7.11.1 Conservation

Intraguild interactions may affect **coccinellid co-existence** and consequently **coccinellid diversity** conservation. This is illustrated by **biological invasions** that occurred in North America, notably with *C. septempunctata*, *Har. axyridis*, and *P. quatuordecimpunctata*, but also *Hip. variegata* (Day et al. 1994, Coderre

et al. 1995, Brown & Miller 1998, Brown 2003, Turnock et al. 2003, Alyokhin & Sewell 2004, Lucas et al. 2007a, b). These **invasions** have greatly **modified** the structure and dynamics of the **coccinellid assemblages** (e.g. Evans 1991, Elliott et al. 1996, Horn 1996, Brown & Miller 1998, Michaud 2002, Turnock et al. 2003, Lucas et al. 2007b; but see Brown 2003). In Eastern Canada, for example, the **exotic species** *P. quatuordecimpunctata*, *C. septempunctata*, and *Har. axyridis* are **dominant** in most agricultural ecosystems that have aphids (Lucas et al. 2007b). By the end of the 1970s, the dominant species in Quebec maize fields was *Hip. tredecimpunctata tibialis*. Following the invasion of exotic ladybirds this species **disappeared completely** from maize ecosystem (Coderre & Tournear 1986, Lucas et al. 2007b), but it is **still present in wild environments** (S. Laplante, unpublished).

In northeastern USA, **successive invasions** by the same exotic species caused a significant decline in *Hip. tredecimpunctata* and *C. transversoguttata* **abundances**, but increased coccinellid **diversity** (Alyokhin & Sewell 2004). A positive correlation between the densities of the three invaders was possibly a result of **biotic facilitation**. Similarly, populations of *Cycloneda sanguinea*, the dominant aphidophagous coccinellid in Florida citrus ecosystems, decreased in this system following *Har. axyridis* establishment (Michaud 2002). **Interactions** can also occur **between invasive species**: in the midwestern USA, *Har. axyridis* replaced *C. septempunctata*, allowing **the return** of several **native** coccinellid species to American orchards (previously excluded by *C. septempunctata*) (Horn 1996, Brown 1999, 2003).

If biological invasions are **detrimental to ladybird specialists**, they probably result in **local displacement of euryphagous species** (Evans 2004, Mills 2006). Evans (2004) verified the **shifting habitat hypothesis** in Utah alfalfa fields: native coccinellids abandoned the crop when an invading species (*C. septempunctata*) kept aphid populations at low densities, but returned to that crop when aphid densities were artificially increased (see Fig. 7.4).

In order to **co-exist, the intraguild prey should be more efficient in resource exploitation than the intraguild predator** (Holt & Polis 1997, Mylius et al. 2001, Arim & Marquet 2004, Borer et al. 2007). However, the predictions of most **models** are not valid in the field, due to the presence of more than two natural enemy species, of alternative resources, of

other interactions such as cannibalism, of a temporal sequence of predators, of refuges, of anti-predatory mechanisms, or others (Okuyama & Ruyle 2003, Kindlmann & Houdkova 2006, Amarasekare 2007, Borer et al. 2007, Holt & Huxel 2007, Janssen et al. 2007, Rudolf 2007).

Obrycki et al. (1998b) proposed that **smaller coccinellid species** would have a **competitive advantage** over **larger** ones at **low aphid densities** because of their lower food requirements. At **higher aphid densities**, large species might have an advantage by IGP-interference. This may promote **co-existence** between species.

Which mechanisms cause changes in coccinellid assemblages? It is very difficult to clearly **establish the link** between **field studies** demonstrating modifications in terms of composition, abundance, and dynamics, and **laboratory studies** on interaction processes. The reality is complex, with changes involving **direct interactions** (e.g. IGP), **indirect interactions** (e.g. exploitative competition) and **interguild effects** (7.12).

Finally, **intraguild interactions may also prevent biological invasion**. It has been proposed that the failure of *A. bipunctata* to invade Japan (Sakuratani et al. 2000) could be due to **heavy mortality from IGP** by *Har. axyridis* and *C. septempunctata* (Kajita et al. 2006; but see Toda & Sakuratani 2006).

7.11.2 Biological control

Intraguild interactions may affect **biological control** of pests. Coccinellids act as **natural control agents** of herbivorous pests and several species are **used commercially** as **biocontrol agents**. Intraguild interactions may affect pest control **synergistically**, **additively**, or **antagonistically** and influence biocontrol mainly by: (i) **intraguild predation**, (ii) **predator facilitation** and (iii) **ant interference**.

7.11.2.1 Intraguild predation and biocontrol

In a **meta-analysis of literature**, the effects on herbivorous pest control depended on the type of IGP involved (Rosenheim & Harmon 2006).

Observations recorded **opposite effects of IGP by/on coccinellids on biological control**. IGP may **disrupt** biological control by ladybirds. Adding the spider *M. tricuspidatus* (IGP of coccinellid larvae)

generated a lower level of aphid control than by ladybirds alone (Yasuda & Kimura 2001). On the other hand, Invasion of West Virginia (USA) apple orchards by *Har. axyridis* drastically modified the coccinellid community, but **improved *Aphis spiraecola* natural control** (Brown & Miller 1998). Snyder et al. (2004a), Aquilino et al. (2005) and Bilu and Coll (2007) suggest a **complementarity** of ladybirds and other natural enemies. Similarly, Weisser (2003) reported an **additive effect of coccinellids and parasitoids** against the pea aphid.

In an aphidophagous guild, IGP by *Har. axyridis* on *Aphidoletes aphidimyza* and *Chrysoperla carnea* did not affect the control of soybean aphids, *Aphis glycines*, either in the laboratory or in field cages (Costamagna et al. 2007, Gardiner & Landis 2007). The authors explained this by the fact that *Har. axyridis* and *C. septempunctata* had such a **strong impact on aphids that IGP did not disrupt biological control**.

In Florida citrus groves *Har. axyridis*, *Olla v-nigrum*, *Cycloneda sanguinea*, and *Exochomus childreni* were responsible for more than 95% mortality of immature stages of the psyllid parasitoid, *Tamarixia radiata* (Michaud 2004). Removing the ladybirds improved *Diaphorina citri* maturation success by 120-fold; IGP did not decrease biocontrol.

Despite high IGP in greenhouse cages by the coccinellid *Delphastus pusillus* on two parasitoids (*Encarsia formosa* and *Encarsia pergandiella*), **no disruption** of whitefly control occurred (Heinz & Nelson 1996).

When considering IGP between coccinellids and pathogens, the negative impact of the predator (consumption of infested pests) may be reduced by the **transportation of infective material** by the coccinellid (such as conidia) and **subsequent contamination** of uninfected hosts (Thomas et al. 2006).

7.11.2.2 Facilitation and biocontrol

Predator facilitation may occur when the activity of one predator increases the susceptibility of a shared prey to another predator (Losey & Denno 1998, 1999). In the complex of *Col. maculata*, *Har. axyridis*, and *Nabis* sp., the proportion of pea aphids consumed was increased by 0.14 when **enemy richness** increased from one to three, due to predator facilitation and potentially to a **decrease in intraspecific competition** (Aquilino et al. 2005). Nevertheless, predator facilitation may be rare in the field, since **three key elements are required** for this interaction:

(i) **synchrony** of the predatory species, (ii) **predator-induced escape behaviour** of the prey resulting in **habitat switching** and encounters with **new predators**, and (iii) **minimal negative interaction** between the predatory species (Losey & Denno 1999).

7.11.2.3 Ants and biocontrol

Ants exert **disruptive impact** on the biological control of honeydew-producing pests by coccinellids (Ceryngier & Hodek 1996, Kaplan & Eubanks 2002, Herbert & Horn 2008). For instance, the presence of the ant *Pheidole megacephala* prevented effective control of *Coccus viridis* by coccidophagous coccinellids, mainly *Azya luteipes* and *Curinus coeruleus* in Hawaiian coffee trees (Reimer et al. 1993).

The mutualism between ants and honeydew-producers leads to an increase of both taxa but also to a greater **suppression of other herbivorous species** such as caterpillars and phytophagous bugs, and may thus have an **overall beneficial effect** (Eubanks & Styrsky 2006).

7.11.2.4 Intraguild interactions and biocontrol approaches

Intraguild interactions involving ladybirds may have more or less significant impacts depending on the **type of biocontrol** implemented. In **classical biological control**, the main effect of intraguild interaction would be **biotic interference** between local and released agents (Goeden & Louda 1976, Stiling 1993). Introduced coccinellid species rarely lowered the pest control levels. For example, the **introductions** of *Har. axyridis*, *C. septempunctata* or *P. quatuordecimpunctata* in North America did not reduce the natural control of agricultural pests, despite strong effects on native ladybird species (Gardiner & Landis 2007, Lucas et al. 2007a), but see the case of *Aphis spiraeicola* above. **As local species**, ladybirds can also interact with the released agent through competition and IGP. Releases of *Aphidius colemani* improved the control of soybean aphids, despite IGP by *Har. axyridis* and *Chrysoperla carnea* (Chacón et al. 2008).

Contrasting effects of IGP have been reported in **augmentative biocontrol**. IGP may influence **inundative biological control** when released agents (i) attack local intraguild members, (ii) are attacked by local intraguild members, (iii) are attacked by other released agents. Heavy predation upon released agents

(and **biocontrol disruption**) has been observed in some experiments (that do not involve ladybirds) (e.g. Rosenheim et al. 1993, 1999). By contrast, despite intense IGP, aphid **control was greatest** in treatments using both *Hip. convergens* and the parasitoid *L. testaceipes*, probably due to a **partial preference** of the coccinellid for unparasitized aphids (Colfer & Rosenheim 2001).

In a **conservation biocontrol** approach, most programmes tend to diversify the environment, in order to increase natural enemy **biodiversity/abundance** and/or to **anticipate their colonization** of focal crops (Thomas et al. 1992, Landis et al. 2000). A more complex environment may, for example, provide more **refuges** for intraguild prey and reduce **encounter frequencies** (Fincke & Denno 2002). Increasing the richness of natural enemies may also enable **predator facilitation**.

The **impact of management** on crop **colonization** by natural enemies is of critical importance. For example, **colonization sequence** may determine the **intraguild predator/prey status** of each guild member and consequently could lead to avoidance mechanisms. In rape, pea and wheat crops, the **aphidophagous guild** in the margin strips of stinging nettle differed from that of the crops (Alhmedi et al. 2007a, c): while *Har. axyridis* was more common in the **field margins** than in the crops, *C. septempunctata* showed the reverse pattern.

7.12 INTERGUILD EFFECTS

Because of a wide range of food, predaceous coccinellids **belong to different guilds**. Ladybirds respond **numerically** (Evans & Toler 2007; 5.3.5) or **functionally** (Lucas et al. 2004a; 5.3.2) to the simultaneous presence of several prey species. Intraguild interactions affecting coccinellid populations would thus affect the different guilds concerned. For example the honeydew produced by the aphid *Rhopalosiphum maidis* on maize plants in the laboratory drastically increased the longevity and parasitism performance of the parasitoid *Trichogramma ostrinae*. Since this parasitoid is released in **augmentative control** programmes against the European corn borer, any impact on aphid populations by aphidophagous predators (such as coccinellids) would decrease honeydew production and consequently reduce the **parasitoid efficiency** against the target pest (Fuchsberg et al.

2007). The situation is even more complicated since several predatory coccinellids belong both to the aphidophagous guild and to the guild that exploit corn borers (Musser & Shelton 2003). Additionally, *Trichogramma* spp. can theoretically parasitize aphidophagous insect eggs (Babendreier et al. 2003, Mansfield & Mills 2004).

7.13 CONCLUSION

In the previous books on ladybirds, no chapter was specifically dedicated to **intraguild interactions** (Hodek 1973, Hodek & Honěk 1996). Studies on interactions involving ladybirds focussed mainly on **vertical interactions** (such as predaceous coccinellids versus prey). In the last 20 years, **horizontal (intraguild) interactions** have been studied increasingly and it is now clear that these interactions dramatically influence the **composition, structure and dynamics** of guilds and consequently of entomological **communities**. Intraguild interactions have generated **ecological and evolutionary responses** by ladybirds such as **defensive responses**, etc.

Despite this recent interest, intraguild interactions remain difficult to study and many questions are pending. At the **methodological** level, intraguild interactions (specifically IGP) are **difficult to detect and quantify** in the field. **Traditional methods** in the laboratory, in field cages or in the field provide a rough estimate of the interactions. The **intensity** of the interaction (Hindayana et al. 2001), as well as its **direction** (Frechette et al. 2007), can change according to complexity and size of the experimental arena. Alternative, but very time-consuming methods include **gut dissection** (Triltsch 1997; 5.2.1) and **direct observations** (e.g. Rosenheim et al. 1999; Chapter 10) that provide **precise and realistic information** on the interaction and permit **impact quantification**. Fortunately, **powerful new tools** (such as molecular methods) have been developed (Chapter 10).

At the **conceptual** level, studies considering the complexity of the **whole system** are needed. It is crucial that future studies consider not only the intraguild organisms, but also other **co-occurring species**, other **potential prey**, and **higher-order natural enemies**. Since most coccinellid species studied are **generalist predators** (i.e. belong to multiple guilds) future studies should thus also consider **interguild effects**. Doing this may lead to a different

interpretation of the impact of an interaction on **species coexistence** or on **biological control efficiency** (Eubanks & Styrsky 2006, Straub & Snyder 2006).

Future studies should also consider the **multiple co-occurring types of interactions**, e.g. IGP and defences and their **indirect effects**.

There is crucial need to consider intraguild interactions at **larger temporal** (covering several generations) and **spatial (landscape)** scales, and to consider **individual, population, community and ecosystem** levels. The real impact of an intraguild interaction remains very difficult to assess at a large spatial scale. Alternatively, it is speculative to link an **ecological phenomenon evaluated at a large scale** with a specific **intraguild interaction**. For example, it is extremely difficult to establish if a species is excluding another one via IGP at the landscape scale. Furthermore, most studies on intraguild interactions are carried out over **short temporal scales**.

Finally, even if **biotic** (e.g. biological invasion), **abiotic** (e.g. global climatic change) or **anthropic** factors (e.g. biological control programmes) have been studied by focussing on vertical interactions, their impact on intraguild interactions remains poorly understood.

Studies on intraguild interactions are **concentrated** on just a few systems and some guilds are poorly studied; the present chapter is consequently **biased toward aphidophagous guilds**. The literature available is also **biased toward laboratory results** and considers only a **few species**. Sloggett (2005) showed that, from 1995 to 2004, 76% of the available literature on intraguild relations of aphidophagous ladybirds was **concentrated on five species**: *C. septempunctata* 33%, *Har. axyridis* 19%, *Col. maculata* 12%, *A. bipunctata* 7% and *Hip. convergens* 5%. Thus there is a great need for studies on **less-studied species** or within **less-studied guilds**, and especially **in the field**.

An interesting result from Sloggett's analysis is that **before 1974, no study on intraguild interactions was available**, whereas 108 studies out of a total of 623 (>17%) were reported in the 1995–2004 period (Sloggett 2005).

To conclude, it can be claimed that intraguild interactions now **retain the attention of the scientific community** and generate a huge amount of literature. Intraguild interactions are fascinating and yet remain mainly **terra incognita**.

REFERENCES

- Abrams, P. A., B. A. Menge, G. G. Mittlebach, D. A. Spiller and P. Yodzis. 1996. The role of indirect effects in food webs. In G. A. Polis and K. O. Winemiller (eds). *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, New York. pp. 371–399.
- Addicott, J. F. 1979. A multispecies aphid–ant association: density dependence and species–specific effects. *Can. J. Zool.* 57: 558–569.
- Agarwala, B. K. and A. F. G. Dixon. 1992. Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecol. Entomol.* 17: 303–309.
- Agarwala, B. K. and A. F. G. Dixon. 1993. Kin recognition: egg and larval cannibalism in *Adalia bipunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 90: 45–50.
- Agarwala, B. K. and H. Yasuda. 2001. Overlapping oviposition and chemical defense of eggs in two co-occurring species of ladybird predators of aphids. *J. Ethol.* 19: 47–53.
- Agarwala, B. K., S. Bhattacharya and P. Bardhanroy. 1998. Who eats whose eggs? Intra- versus inter-specific interactions in starving ladybird beetles predaceous on aphids. *Ethol. Ecol. Evol.* 10: 361–368.
- Agarwala, B. K., H. Yasuda and Y. Kajita. 2003. Effect of conspecific and heterospecific feces on foraging and oviposition of two predatory ladybirds: role of fecal cues in predator avoidance. *J. Chem. Ecol.* 29: 357–376.
- Alhmedi, A., F. Francis, B. Bodson and E. Haubruge. 2007a. Évaluation de la diversité des pucerons et de leurs ennemis naturels en grandes cultures à proximité de parcelles d'orties. *Notes fauniques Gembloux* 60(4): 147–152.
- Alhmedi, A., F. Francis, B. Bodson and E. Haubruge. 2007b. Intraguild interactions of aphidophagous predators in fields: effect of *Coccinella septempunctata* and *Episyrphus balteatus* occurrence on aphid infested plants. *Comm. Agric. Appl. Biol. Sci.* 72(3) 381–390.
- Alhmedi, A., E. Haubruge, B. Bodson and F. Francis. 2007c. Aphidophagous guilds on nettle (*Urtica dioica*) strips close to fields of green pea, rape and wheat. *Insect Sci.* 14: 419–424.
- Alhmedi, A., E. Haubruge and F. Francis. 2010. Intraguild interactions implicating invasive species: *Harmonia axyridis* as a model species. *Biotechnol. Agron. Soc. Environ.* 14(1): 187–201.
- Almohamad, R., F. J. Verheggen, F. Francis and E. Haubruge. 2010. Intraguild interactions between the predatory hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) and the Asian ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae): effect of larval tracks. *Eur. J. Entomol.* 107: 41–45.
- Alyokhin, A. and G. Sewell. 2004. Changes in lady beetle community following the establishment of three alien species. *Biol. Invasions* 6: 463–471.
- Al-Zyoud, F. A. 2007. Prey species preferences of the predator *Serangium parcesetosum* Sicard (Col., Coccinellidae) and its interaction with another natural enemy. *Pak. J. Biol. Sci.* 10: 2159–2165.
- Al-Zyoud, F. A., N. Tort and C. Segonca. 2005. Influence of leaf portion and plant species on the egg-laying behaviour of the predatory ladybird *Serangium parcesetosum* Sicard (Col., Coccinellidae) in the presence of a natural enemy. *J. Pest Sci.* 78: 167–174.
- Amarasekare, P. 2007. Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. *Ecology* 88: 2720–2728.
- Aquilino, K. M., B. J. Cardinale and A. R. Ives. 2005. Reciprocal effects of host plant and natural enemy diversity on herbivore suppression: an empirical study of a model tri-trophic system. *Oikos* 108: 275–282.
- Arim, M. and P. A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecol. Letters* 7: 557–564.
- Attygalle, A. B., K. D. McCormick, C. L. Blankespoor, T. Eisner and J. Meinwald. 1993. Azamacrolides: a family of alkaloids from the pupal defensive secretion of a ladybird beetle (*Epilachna varivestis*). *Proc. Nat. Acad. Sci. USA* 90: 5204–5208.
- Babendreier, D., M. Rostas, M. C. J. Hofte, S. Kuske and F. Bigler. 2003. Effects of mass releases of *Trichogramma brassicae* on predatory insects in maize. *Entomol. Exp. Appl.* 108: 115–124.
- Bilu, E. and M. Coll. 2007. The importance of intraguild interactions to the combined effect of a parasitoid and a predator on aphid population suppression. *BioControl* 52: 753–763.
- Bilu, E. and Coll, M. 2009. Parasitized aphids are inferior prey for a coccinellid predator: implications for intraguild predation. *Environ. Entomol.* 38: 153–158.
- Borer, E. T. C. J. Briggs and R. D. Holt. 2007. Predators, parasitoids, and pathogens: a cross-cutting examination of intraguild predation theory. *Ecology* 88: 2681–2688.
- Bradley, G. A. 1973. Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator–prey relationship between *Hyperaspis congressis* (Coleoptera: Coccinellidae) and *Toumeyella numismaticum* (Homoptera: Coccidae). *Can. Entomol.* 105: 1113–1118.
- Brown, M. W. 1999. Temporal changes in the aphid predator guild in eastern North America. *Integrated Plant Protection in Orchards, IOBC/WPRS Bull.* 22(7): 7–11.
- Brown, M. W. 2003. Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl* 48: 141–153.
- Brown, M. W. 2004. Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA. *Biol. Control* 29: 189–198.
- Brown, M. W. and S. S. Miller. 1998. Coccinellidae (Coleoptera) in apple orchards of eastern West Virginia and the

- impact of invasion by *Harmonia axyridis*. *Entomol. News* 109: 143–151.
- Burgio, G., A. Lanzoni, G. Accinelli and S. Maini. 2008. Estimation of mortality by entomophages on exotic *Harmonia axyridis* versus native *Adalia bipunctata* in semi-field conditions in northern Italy. In H. E. Roy and E. Wajnberg (eds). *From Biological Control to Invasion: the Ladybird Harmonia axyridis as a Model Species*. Springer, Netherlands. pp. 277–287.
- Camarano, S., A. Gonzalez and C. Rossini. 2009. Biparental endowment of endogenous defensive alkaloids in *Epilachna paenulata*. *J. Chem. Ecol.* 35: 1–7.
- Ceryngier, P. and I. Hodek. 1996. Enemies of Coccinellidae. In I. Hodek and A. Honěk (eds). *Ecology of Coccinellidae*. Kluwer Academic Publishers, Boston. pp. 319–350.
- Chacón, J. M., D. A. Landis and G. E. Heimpel. 2008. Potential for biotic interference of a classical biological control agent of the soybean aphid. *Biol. Control* 46: 216–225.
- Chang, G. C. 1996. Comparison of single versus multiple species of generalist predators for biological control. *Environ. Entomol.* 25: 207–622.
- Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biology* 9: 126–136.
- Chauhan, K. R. and D. C. Weber. 2008. Lady beetle (Coleoptera: Coccinellidae) tracks deter oviposition by the golden-eyed lacewing. *Chrysopa oculata*. *Biocontrol Sci. Technol.* 18: 727–731.
- Chazeau, J. 1985. Predaceous insects. In W. Helle and M. W. Sabelis (eds). *World Crop Pests, Spider Mites. Their Biology, Natural Enemies and Control. Vol. 1B*. Elsevier, New York. pp. 211–246.
- Clancy, K. M. and P. W. Price. 1987. Rapid herbivore growth enhances enemy attack: sublethal plant defenses remain a paradox. *Ecology* 68: 736–738.
- de Clercq, P., I. Peters, G. Vergauwe and O. Thas. 2003. Interaction between *Podisus maculiventris* and *Harmonia axyridis*, two predators used in augmentative biological control in greenhouse crops. *BioControl* 48: 39–55.
- Coderre, D. and J. C. Tourneur. 1986. Vertical distribution of aphids and aphidophagous insects on maize. In: Hodek I (ed) *Ecology of Aphidophaga*, Academia, Prague. pp. 291–296.
- Coderre, D., E. Lucas and I. Gagné. 1995. The occurrence of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Canada. *Can. Entomol.* 127: 609–611.
- Coderre, D., L. Provencher and J. C. Tourneur. 1987. Oviposition and niche partitioning in aphidophagous insects on maize. *Can. Entomol.* 119: 195–203.
- Colfer, R. G. and J. A. Rosenheim. 2001. Predation on immature parasitoids and its impact on aphid suppression. *Oecologia* 126: 292–304.
- Colunga-Garcia, M., S. H. Gage and D. A. Landis. 1997. The response of an assemblage of Coccinellidae (Coleoptera) to a diverse agricultural landscape. *Environ. Entomol.* 26: 797–804.
- Costamagna, A. C., D. A. Landis and C. D. Difonzo. 2007. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecol. Appl.* 17: 441–451.
- Cottrell, T. E. 2004. Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biol. Control* 31: 362–371.
- Cottrell, T. E. 2005. Predation and cannibalism of lady beetle eggs by adult lady beetles. *Biol. Control* 34: 159–164.
- Cottrell, T. E. 2007. Predation by adult and larval lady beetles (Coleoptera: Coccinellidae) on initial contact with lady beetle eggs. *Environ. Entomol.* 36: 390–401.
- Cottrell, T. E. and D. I. Shapiro-Ilan. 2003. Susceptibility of a native and an exotic lady beetle (Coleoptera: Coccinellidae) to *Beauveria bassiana*. *J. Invert. Pathol.* 2: 137–144.
- Cottrell, T. E. and D. I. Shapiro-Ilan. 2008. Susceptibility of endemic and exotic North American ladybirds to endemic fungal entomopathogens. *Eur. J. Entomol.* 105: 455–460.
- Cuenot, L. 1896. Sur la saignée réflexe et les moyens de défense de quelques insectes. *Arch. Zool. Exp. Gen.* 4: 655–680.
- Day, W. H., D. R. Prokrym, D. R. Ellis and R. J. Chianese. 1994. The known distribution of the predator *Propylea quatuordecimpunctata* (Coleoptera, Coccinellidae) in the United States, and thoughts on the origin of this species and five other exotic lady beetles in Eastern North America. *Entomol. News* 105: 244–256.
- Dixon, A. F. G. 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). *Trans. R. Entomol. Soc. Lond.* 110: 319–334.
- Dixon, A. F. G. 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J. Anim. Ecol.* 28: 259–281.
- Dixon, A. F. G. 1985. *Aphid Ecology*. Blackie and Son Ltd., New York. 157 pp.
- Dixon, A. F. G. 1987. The way of life of aphids: host specificity, speciation and distribution. In A. K. Minks and P. Hanewin (eds), *World Crop Pests Aphids: Their Biology, Natural Enemies and Control. Vol. 2A*. Elsevier, Amsterdam. pp. 197–207.
- Dixon, A. F. G. 2000. *Insect Predator–Prey Dynamic: Ladybird Beetles and Biological Control*. Cambridge University Press, Cambridge, UK. 257 pp.
- Dixon, A. F. G. 2007. Body size and resource partitioning in ladybirds. *Popul. Ecol.* 49: 45–50.
- Dixon, A. F. G. and J. L. Hemptinne. 2001. Body size distribution in predatory ladybird beetles reflects that of their prey. *Ecology* 82: 1847–1856.
- Dixon, A. F. G., V. Jarosik and A. Honěk. 2005. Thermal requirements for development and resource partitioning in aphidophagous guilds. *Eur. J. Entomol.* 102: 407–411.
- Dolenska, M., O. Nedvĕd, P. Vesely, M. Tesarova and R. Fuchs. 2009. What constitutes optical warning signals of ladybirds (Coleoptera: Coccinellidae) towards bird predators: colour, pattern or general look? *Biol. J. Linn. Soc.* 98: 234–242.

- Doumbia, M., J. L. Hemptinne and A. F. G. Dixon. 1998. Assessment of patch quality by ladybirds: role of larval tracks. *Oecologia* 113: 197–202.
- Drea, J. J. and R. D. Gordon. 1990. Coccinellidae. In D. Rosen (ed). *World Crop Pests, Armored Scale Insects. Vol. 4B*. Elsevier Science Publishers, New York. pp. 19–40.
- Dyson, E. 1996. An investigation of *Calvia quatuordecimpunctata*: egg cannibalism, egg predation and evidence for a male-killer. Undergraduate dissertation, University of Cambridge.
- Edmunds, M. 1974. *Defence in Animals*. Longman Inc., New York. 358 pp.
- Eisner, T. and M. Eisner. 1992. Operation and defensive role of 'gin traps' in a coccinellid pupa (*Cycloneda sanguinea*). *Psyche* 99: 265–273.
- Eisner, T., M. Goetz, D. Aneshansley et al. 1986. Defensive alkaloid in blood of Mexican bean beetle (*Epilachna varivestis*). *Experientia* 42: 204–207.
- Elliott, N., R. Kieckhefer and W. Kauffman. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* 105: 537–544.
- Engelstadter, J. and G. D. D. Hurst. 2007. The impact of male-killing bacteria on host evolutionary processes. *Genetics* 175: 245–254.
- Eubanks, M. D. 2001. Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. *Biol. Control* 21: 35–43.
- Eubanks, M. D. and J. D. Styrsky. 2006. Ant–hemipteran mutualism: keystone interactions that alter food web dynamics and influence plant fitness. In J. Brodeur and G. Boivin (eds). *Progress in Biological Control: Trophic and Guild Interactions in Biological Control*. Springer, Netherland. pp. 171–190.
- Evans, E. W. 1991. Intra versus interspecific interactions of ladybeetles (Coleoptera: Coccinellidae) attacking aphids. *Oecologia* 87: 401–408.
- Evans, E. W. 2004. Habitat displacement of North American ladybirds by an introduced species. *Ecology* 85: 637–665.
- Evans, E. W. and T. R. Toler. 2007. Aggregation of polyphagous predators in response to multiple prey: ladybirds (Coleoptera: Coccinellidae) foraging in alfalfa. *Popul. Ecol.* 49: 29–36.
- Felix, S. and A. O. Soares. 2004. Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of bodyweight. *Eur. J. Entomol.* 101: 237–242.
- Ferguson, K. I. and P. Stiling. 1996. Non-additive effects of multiple natural enemies on aphid populations. *Oecologia* 108: 375–379.
- Fincke, D. L. and R. F. Denno 2002. Intraguild predation diminished in complex-structured vegetation: implication for prey suppression. *Ecology* 83: 643–652.
- Firlej, A., G. Boivin, E. Lucas and D. Coderre. 2005. First report of parasitism of *Harmonia axyridis* parasitism by *Dinocampus coccinellae* Schrank in Canada. *Biol. Invasions* 7: 553–556.
- Firlej, A., E. Lucas, D. Coderre and G. Boivin. 2006. Teratocytes growth pattern reflects host suitability in a host–parasitoid assemblage. *Physiol. Entomol.* 32: 181–187.
- Fischer, S., J. Samietz, F. L. Wäckers and S. Dorn. 2001. Interaction of vibrational and visual cues in parasitoid host location. *J. Comp. Physiol. (A)* 187: 785–791.
- Flowers, R. W., S. M. Salom and L. T. Kok 2005. Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, *Adelges tsugae* (Hemiptera: Adelgidae), in the laboratory. *Environ. Entomol.* 34: 664–675.
- Flowers, R. W., S. M. Salom, L. T. Kok and D. E. Mullins 2007. Behavior and daily activity patterns of specialist and generalist predators of the hemlock woolly adelgid, *Adelges tsugae*. *J. Insect Sci.* 7(44): 1–20.
- Francke, D. L., J. P. Harmon, C. T. Harvey and A. R. Ives. 2008. Pea aphid dropping behavior diminishes foraging efficiency of a predatory ladybeetle. *Entomol. Exp. Appl.* 127: 118–124.
- Frazer, B. D. 1988. Coccinellidae. In A. K. Minks, P. Harrewijn and W. Helle (eds). *World Crop Pests, Aphids. Vol. 2B*. Elsevier, New York. pp. 231–247.
- Fréchette, B., C. Alauzet and J.-L. Hemptinne. 2003. Oviposition behaviour of the two spots ladybird beetle *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) on plants with conspecific larval tracks. In: Soares AO, Ventura MA, Garcia V and Hemptinne J-L (eds). *Proc. 8th Int. Symp. Ecol. Aphidophaga. Arquipélago, Life Mar. Sci. (Suppl.)* 5: 73–77.
- Fréchette, B., S. Rojo, O. Alomar and E. Lucas. 2007. Intraguild predation among mirids and syrphids. Who is the prey and who is the predator? *BioControl* 52: 175–191.
- Fréchette, B., Larouche, F. and E. Lucas. 2008. *Leucopis annulipes* larvae (Diptera: Chamaemyiidae) use a furtive predation strategy within aphid colonies. *Eur. J. Entomol.* 105: 399–403.
- Fuchsberg, J. R., T. H. Yong, J. E. Losey, M. E. Carter and M. P. Hoffmann. 2007. Evaluation of corn leaf aphid (*Rhopalosiphum maidis*; Homoptera : Aphididae) honeydew as a food source for the egg parasitoid *Trichogramma ostrinia* (Hymenoptera : Trichogrammatidae). *Biol. Control* 40: 230–236.
- Gagne, I., D. Coderre and Y. Mauffette. 2002. Egg cannibalism by *Coleomegilla maculata lengi* neonates: preference even in the presence of essential prey. *Ecol. Entomol.* 27: 285–291.
- Gagne, W. C. and J. L. Martin. 1968. The insect ecology of red pine plantations in central Ontario. V. The Coccinellidae (Coleoptera). *Can. Entomol.* 100: 835–846.
- Gagnon, A. E. 2010. Prédation intraguild chez les coccinellidae : impact sur la lutte biologique au puceron du soya. Unpubl. PhD dissertation, Université Laval, Québec, Canada.

- Gardiner, M. M. and D. A. Landis. 2007. Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biol. Control* 40: 386–395.
- Giroux, S., J. C. Cote, C. Vincent, P. Martel and D. Coderre. 1994. Bacteriological insecticide M-One effects on predation efficiency and mortality of adult *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). *J. Econ. Entomol.* 87: 39–43.
- Gittleman, J. L. and M. E. Gompper. 2005. Plight of predators: the importance of carnivores for understanding patterns of conservation and biodiversity and extinction risks. In Barbosa P and Castellanos I (eds) *Ecology of Predator–Prey Interactions*. Oxford University Press, USA, pp. 370–388.
- Godeau, J. F., J. L. Hemptinne and J. C. Verhaeghe. 2003. Ant trail: a highway for *Coccinella magnifica* Redtenbacher (Coleoptera: Coccinellidae). In A. O. Soares, M. A. Ventura, V. Garcia and J.-L. Hemptinne (eds). *Proc. 8th Int. Symp. Ecol. Aphidophaga. Arquipélago, Life Mar. Sci. (Suppl.)* 5: 79–83.
- Goeden, R. D. and S. M. Louda. 1976. Biotic interference with insects imported for weed control. *Annu. Rev. Entomol.* 21: 325–342.
- Guenard, B. 2007. Mutualisme fourmis pucerons et guildes aphidophage associée : le cas de la prédation furtive. Unpubl. MSc dissertation, Université du Québec à Montréal, Québec, Canada.
- Harmon, J. P. and D. A. Andow. 2007. Behavioral mechanisms underlying ants' density-dependent deterrence of aphid-eating predators. *Oikos* 116: 1030–1036.
- Harwood, J. D., H. J. S. Yoo, M. H. Greenstone, D. L. Rowley and R. J. O'Neil. 2009. Differential impact of adults and nymphs of a generalist predator on an exotic invasive pest demonstrated by molecular gut-content analysis. *Biol. Invasions* 11: 895–903.
- Hautier, L., J.-C. Grégoire, J. De Schauwers et al. 2008. Intraguild predation by *Harmonia axyridis* on coccinellids revealed by exogenous alkaloid sequestration. *Chemoecology* 18: 191–196.
- Heinz, K. M. and J. M. Nelson. 1996. Interspecific interactions among natural enemies of *Bemisia* in an inundative biological control program. *Biol. Control* 6: 384–393.
- Hemptinne, J. L. and A. F. G. Dixon. 2000. Defence, oviposition and sex: semiochemical parsimony in two species of ladybird beetles (Coleoptera: Coccinellidae)? A short review. *Eur. J. Entomol.* 97: 443–447.
- Hemptinne, J. L. and A. F. G. Dixon. 2005. Intraguild predation in aphidophagous guilds: does it exist? *Proc. Int. Symposium Biol. Control Aphids Coccids. Tsuruoka, Japan.* (http://72.14.205.104/search?q=cache:ROmacSkS6_gj:www.net.sfsi.co.jp/shoko-travel/symposium/symPDF/S5/Hemptinne.pdf+hemptinne+dixon+IGPandhl=frandct=clnkandcd=1andgl=ca.)
- Hemptinne, J. L., A. F. G. Dixon and C. Gauthier. 2000a. Nutritive cost of intraguild predation on eggs of *Coccinella septempunctata* and *Adalia bipunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 97: 559–562.
- Hemptinne, J. L., G. Lognay, C. Gauthier and A. F. G. Dixon. 2000b. Role of surface chemical signals in egg cannibalism and intraguild predation in ladybirds (Coleoptera: Coccinellidae). *Chemoecology* 10: 123–128.
- Herbert, J. J. and D. J. Horn. 2008. Effect of ant attendance by *Monomorium minimum* (Buckley) (Hymenoptera: Formicidae) on predation and parasitism of the soybean aphid *Aphis glycines* Matsumura (Hemiptera: Aphididae). *Environ. Entomol.* 37: 1258–1263.
- Hindayana, D., R. Meyhofer, D. Scholz and H. M. Poehling. 2001. Intraguild predation among the hoverfly *Episyrphus balteatus* de Geer (Diptera: Syrphidae) and other aphidophagous predators. *Biol. Control* 20: 236–246.
- Hodek, I. 1973. *Biology of Coccinellidae*. Academia Press, Prague. 292 pp.
- Hodek, I. 1996. Food relationships. In I. Hodek and A. Honěk (eds). *Ecology of Coccinellidae*. Kluwer Academic Publishers, Boston, USA, pp. 143–238.
- Hodek, I. and A. Honěk. 1996. *Ecology of Coccinellidae*. Kluwer Academic Publishers, Netherlands. 480 pp.
- Hodek, I. and J. P. Michaud. 2008. Why is *Coccinella septempunctata* so successful? (A point-of-view). *Eur. J. Entomol.* 105: 1–12.
- Holloway, G. J., P. W. de Jong, P. M. Brakefield and H. de Vos. 1991. Chemical defence in ladybird beetles (Coccinellidae). I. Distribution of coccinelline and individual variation in defence in 7-spot ladybirds (*Coccinella septempunctata*). *Chemoecology* 2: 7–14.
- Holt, R. D. 1977. Predation, apparent competition and the structure of prey communities. *Theor. Popul. Ecol.* 12: 197–229.
- Holt, R. D. and G. R. Huxel. 2007. Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology* 88: 2706–2712.
- Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. *Am. Nat.* 149: 745–764.
- Holte, A. E., M. A. Houck and N. L. Collie. 2001. Potential role of parasitism in the evolution of mutualism in astigmatid mites: *Hemisarcoptes cooremani* as a Model. *Exp. Appl. Acarol.* 25: 97–107.
- Honěk, A. and F. Kocourek. 1988. Thermal requirements for development of aphidophagous Coccinellidae (Coleoptera), Chrysopidae, Hemerobiidae (Neuroptera), and Syrphidae (Diptera): some general trends. *Oecologia* 76: 455–460.
- Honěk, A. and F. Kocourek. 1990. Temperature and development time in insects: a general relationship between thermal constants. *Zool. Jahrb. Abt. Syst. Ökol. Geogr. Tiere* 117: 401–439.
- Hoogendoorn, M. and G. E. Heimpel. 2002. Indirect interactions between and introduced and a native ladybird beetle species mediated by a shared parasitoid. *Biol. Control* 25: 224–230.

- Hoogendoorn, M. and G. E. Heimpel. 2004. Competitive interactions between an exotic and a native ladybeetle: a field cage study. *Entomol. Exp. Appl.* 111: 19–28.
- Horn, D. J. 1996. Impact of introduced Coccinellidae on native species in nontarget ecosystems. (Abstract.) Symposium of the IOBC working group 'Ecology of Aphidophaga'. University of Agriculture, Gembloux (unpaginated).
- Houck, M. A. and B. M. O'Connor. 1991. Phoresy in the acariform acari. *Annu. Rev. Entomol.* 36: 611–636.
- Hough-Goldstein, J., J. Cox and A. Armstrong. 1996. *Podisus maculiventris* (Hemiptera: Pentatomidae) predation on ladybird beetles (Coleoptera: Coccinellidae). *Fla. Entomol.* 79: 64–68.
- Hurst, G. D. D., M. E. N. Majerus and A. Fain. 1997. Coccinellidae (Coleoptera) as vectors of mites. *Eur. J. Entomol.* 94: 317–319.
- Hurst, G. D. D., J. H. Graf von der Schulenburg, T. M. O. Majerus et al. 2003. Invasion of one insect species, *Adalia bipunctata*, by two different male-killing bacteria. *Insect Mol. Biol.* 8: 133–139.
- Iablokoff-Khnzorian, S. M. 1982. *Les coccinelles; Coléoptères-Coccinellidae*. Société Nouvelle des Éditions Boubée, Paris. 568 pp.
- Iperti, G. 1964. Les parasites des coccinelles aphidiphages dans les Alpes-Maritimes et les Basses-Alpes. *Entomophaga* 9: 153–180.
- Iperti, G. 1966. Comportement naturel des coccinelles aphidiphages du sud-est de la France: leur type de spécificité, leur action prédatrice sur *Aphis fabae* L. *Entomophaga* 11: 203–210.
- Janssen, A., M. W. Sabelis, S. Magalhães, M. Montserrat and T. van der Hammen. 2007. Habitat structure affects intraguild predation. *Ecology* 88: 2713–2719.
- de Jong, P. W., G. J. Holloway, P. M. Brakefield and H. de Vos. 1991. Chemical defence in ladybird beetles (Coccinellidae). II. Amount of reflex fluid, the alkaloid adaline and individual variation in defence in 2-spot ladybirds (*Adalia bipunctata*). *Chemoecology* 2: 15–19.
- Kagata, H. and N. Katayama. 2006. Does nitrogen limitation promote intraguild predation in an aphidophagous ladybird? *Entomol. Exp. Appl.* 119: 239–246.
- Kajita, Y., J. J. Obrycki, J. J. Sloggett and K. F. Haynes. 2010. Intraspecific alkaloid variation in ladybird eggs and its effects on con- and hetero-specific intraguild predators. *Oecologia* 163: 313–322.
- Kajita, Y., F. Takano, H. Yasuda and B. K. Agarwala. 2000. Effects of indigenous ladybird species (Coleoptera: Coccinellidae) on the survival of an exotic species in relation to prey abundance. *Appl. Entomol. Zool.* 35: 473–479.
- Kajita, Y., F. Takano, H. Yasuda and E. W. Evans. 2006. Interactions between introduced and native predatory ladybirds (Coleoptera, Coccinellidae): factors influencing the success of species introductions. *Ecol. Entomol.* 31: 58–67.
- Kaneko, S. 2007a. Larvae of two ladybirds, *Phymatosternus lewisii* and *Scymnus posticalis* (Coleoptera: Coccinellidae), exploiting colonies of the brown citrus aphid *Toxoptera citricidus* (Homoptera: Aphididae) attended by the ant *Pristomyrmex pungens* (Hymenoptera: Formicidae). *Appl. Entomol. Zool.* 2: 181–187.
- Kaneko, S. 2007b. Predator and parasitoid attacking ant-attended aphids: effects of predator presence and attending ant species on emerging parasitoid numbers. *Ecol. Res.* 22: 451–458.
- Kaplan, I. and M. D. Eubanks. 2002. Disruption of cotton aphid (Homoptera: Aphididae) – natural enemy dynamics by red imported fire ants (Hymenoptera: Formicidae). *Environ. Entomol.* 31: 1175–1183.
- Kindlmann, P. and K. Houdkova. 2006. Intraguild predation: fiction or reality? *Popul. Ecol.* 48: 317–322.
- Klingauf, F. 1967. Abwehr- und Meidreaktionen von Blattläusen (Aphididae) beim Bedrohung durch Räuber und parasiten. *Z. Angew. Entomol.* 60: 269–317.
- Kovach, J. 2004. Impact of the multicolored Asian lady beetle as a pest of fruit and people. *Am. Entomol.* 50: 165–167.
- Koyama, S. and M. E. N. Majerus. 2007. Interactions between the parasitoid wasp *Dinocampus coccinellae* and two species of coccinellid from Japan and Britain. In H. E. Roy and E. Wajnberg (eds). *From Biological Control to Invasion: The Ladybird Harmonia axyridis as a Model Species*. Springer, Netherlands. pp. 253–264.
- Krieg, A., A. Huger, G. Langenbruch and W. Schmetter. 1984. New results on *Bacillus thuringiensis* var. *tenebrionis* with special regard to its effects on the Colorado potato beetle (*Leptinotarsa decemlineata*). *Anz. Schaedlkd. Pflanzenschutz Umweltschutz* 57: 145–150.
- Kullenberg, B. 1944. Studien über die Biologie der Capsiden. *Zool. Bidrag Från Uppsala (Suppl.)* 23: 1–522.
- Kunkel, H. and W. J. Kloft. 1985. Die Honigtauerzeuger des Waldes. In W. J. Kloft and H. Kunkel (eds). *Waldtracht und Waldhonig in der Imkerei*. Ehrenwirth, Munich. pp. 48–264.
- Labrie, G., E. Lucas and D. Coderre. 2006. Can developmental and behavioral characteristics of the multicolored Asian lady beetle *Harmonia axyridis* explain its invasive success? *Biol. Invasions* 8: 743–754.
- Labrie, G., D. Coderre and E. Lucas. 2008. Overwintering strategy of the multicolored Asian lady beetle (Coleoptera: Coccinellidae): cold-free space as a factor of invasive success. *Ann. Entomol. Soc. Am.* 101: 860–866.
- Landis, D. A., S. D. Wratten and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- Lemire, S., D. Coderre, C. Vincent and G. Bélair. 1996. Lethal and sublethal effects of the entomogenous nematode, *Steinernema carpocapsae*, on the coccinellid *Harmonia axyridis*. *Nematropica* 26: 284–285.
- Liere, H. and I. Perfecto. 2008. Cheating on a mutualism: indirect benefits of ant attendance to a coccidophagous coccinellid. *Ecol. Entomol.* 37: 143–149.

- Lorenzetti, F., J. T. Arnason, B. J. R. Philogène and R. I. Hamilton. 1997. Différentiation spatiale de niche chez des aphidiphages prédateurs: la couleur de la plante comme critère de sélection. *BioControl* 42: 49–56.
- Losey, J. E. and R. F. Denno. 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79: 2143–2152.
- Losey, J. E. and R. F. Denno. 1999. Factors facilitating synergistic predation: the central role of synchrony. *Ecol. Appl.* 9: 378–386.
- Lövei, G. L. and Z. A. Radwan. 1988. Seasonal dynamics and microhabitat distribution of coccinellid developmental stages in apple orchard. In E. Niemezyk and A. F. G. Dixon (eds). *Ecology and Effectiveness of Aphidophaga*. SPB Academic Publishing, The Hague. pp. 275–277.
- Loevei, G. L., M. Sároszpatáki and Z. A. Radwan. 1991. Structure of ladybird (Coleoptera: Coccinellidae) assemblage in apple: changes through developmental stages. *Environ. Entomol.* 20: 1301–1308.
- Lucas, E. 1998. How do ladybirds (*Coleomegilla maculata lengi*, Coleoptera: Coccinellidae) feed on green lacewing eggs (*Chrysoperla rufilabris*, Neuroptera: Chrysopidae). *Can. Entomol.* 130: 547–548.
- Lucas, E. 2005. Intraguild predation among aphidophagous predators. *Eur. J. Entomol.* 102: 351–364.
- Lucas, E. and O. Alomar. 2002a. Impact of *Macrolophus caliginosus* presence on damage production by *Dicyphus tamaninii* (Heteroptera: Miridae) on tomato fruits. *J. Econ. Entomol.* 95: 1123–1126.
- Lucas, E. and O. Alomar. 2002b. Impact of the presence of *Dicyphus tamaninii* Wagner (Heteroptera: Miridae) on whitefly (Homoptera: Aleyrodidae) predation by *Macrolophus caliginosus* (Wagner) (Heteroptera: Miridae). *Biol. Control.* 25: 123–128.
- Lucas, E. and J. Brodeur. 1999. Oviposition site selection by *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae). *Environ. Entomol.* 28: 622–627.
- Lucas, E. and J. Brodeur. 2001. A fox in a sheep-clothing: dilution effect for a furtive predator living inside prey aggregation. *Ecology* 82: 3246–3250.
- Lucas, E. and J. A. Rosenheim. 2011. Influence of extraguild prey density on intraguild predation by heteropteran predators: A review of the evidence and a case study. *Biol. Control.* 59: 61–67.
- Lucas, E., D. Coderre and J. Brodeur. 1997a. Instar-specific defense of *Coleomegilla maculata lengi* (Coccinellidae): influence on attack success of the intraguild predator *Chrysoperla rufilabris* (Chrysopidae). *Entomophaga* 42: 3–12.
- Lucas, E., D. Coderre and C. Vincent 1997b. Voracity and feeding preferences of *Coccinella septempunctata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Tetranychus urticae* and *Aphis citricola*. *Entomol. Exp. Appl.* 85: 151–159.
- Lucas, E., D. Coderre and J. Brodeur. 1998a. Intraguild predation among three aphid predators: Characterization and influence of extra-guild prey density. *Ecology* 79: 1084–1092.
- Lucas, E., S. Lapalme and D. Coderre. 1998b. Voracité comparative de trois coccinelles aphidiphages sur le tétranyque rouge du pommier (Acarina: Tetranychidae). *Phytoprotection* 78: 117–123.
- Lucas, E., D. Coderre and J. Brodeur. 2000. Selection of molting and pupating site by *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae): avoidance of intraguild predation? *Environ. Entomol.* 29: 454–459.
- Lucas, E., I. Gagne and D. Coderre. 2002. Impact of the arrival of *Harmonia axyridis* on adults *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera : Coccinellidae). *Eur. J. Entomol.* 99: 457–463.
- Lucas, E., B. Frechette and O. Alomar. 2009. Resource quality, resource availability, and intraguild predation among omnivorous mirids. *Biocontrol Sci. Technol.* 19: 555–572.
- Lucas, E., S. Demougeot, C. Vincent and D. Coderre. 2004a. Predation upon the oblique-banded leafroller, *Choristoneura rosaceana* (Lepidoptera: Tortricidae), by two aphidophagous coccinellids (Coleoptera: Coccinellidae) in the presence and absence of aphids. *Eur. J. Entomol.* 101: 37–41.
- Lucas, E., S. Giroux, S. Demougeot, R. M. Duchesne and D. Coderre 2004b. Compatibility of a natural enemy, *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae) and four insecticides used against the Colorado Potato Beetle (Coleoptera: Chrysomelidae). *J. Appl. Entomol.* 128: 233–239.
- Lucas, E., C. Labrecque and D. Coderre. 2004c. *Delphastus catalinae* and *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae) as biological control agents of the greenhouse whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae). *Pest Manag. Sci.* 60: 1073–1078.
- Lucas, E., G. Labrie, C. Vincent and J. Kovach. 2007a. The multicoloured Asian ladybeetle: beneficial or nuisance organism? In C. Vincent, M. Goettel and G. Lazarovits (eds.). *Biological Control: A Global Perspective*. CABI International, UK. pp. 38–52.
- Lucas, E., C. Vincent, G. Labrie et al. 2007b. The multicolored Asian ladybeetle *Harmonia axyridis* in Quebec agroecosystems ten years after its arrival? *Eur. J. Entomol.* 104: 737–743.
- Magro, A., J. N. Tene, N. Bastin, A. F. G. Dixon and J. L. Hemptinne. 2007. Assessment of patch quality by ladybirds: relative response to conspecific and heterospecific larval tracks a consequence of habitat similarity? *Chemoecology* 17: 37–45.
- Majerus, M. E. N. 1989. *Coccinella magnifica* (Redtenbacher): A myrmecophilous ladybird. *Br. J. Entomol. Nat. Hist.* 2: 97–106.
- Majerus, M. E. N. 1994. *Ladybirds. New Naturalist Series 81*. Harper Collins, London. 368 pp.
- Majerus, T. M. O., M. E. N. Majerus, B. Knowles et al. 1998. Extreme variation in the prevalence of inherited male-killing microorganisms between three populations of

- Harmonia axyridis* (Coleoptera: Coccinellidae). *Heredity* 81: 683–691.
- Majerus, M. E. N., J. J. Slogett, J. F. Godeau and J. L. Hemptinne. 2007. Interactions between ants and aphidophagous and coccidophagous ladybirds. *Popul. Ecol.* 49: 15–27.
- Majerus, M. E. N., V. Strawson and H. Roy. 2006. The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. *Ecol. Entomol.* 31: 207–215.
- Mallampalli, N., I. Castellanos and P. Barbosa. 2002. Evidence for intraguild predation by *Podisus maculiventris* on a ladybeetle, *Coleomegilla maculata*: implications for biological control of Colorado potato beetle, *Leptinotarsa decemlineata*. *BioControl* 47: 387–398.
- Mansfield, S. and N. J. Mills. 2004. A comparison of methodologies for the assessment of host preference of the gregarious egg parasitoid *Trichogramma platneri*. *Biol. Control* 29: 332–340.
- McLure, M. S. 1986. Role of predators in regulation of endemic populations of *Matsucoccus matsumurae* (Homoptera: Margarodidae) in Japan. *Environ. Entomol.* 15: 976–983.
- Michaud, J. P. 2002. Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environ. Entomol.* 31: 827–835.
- Michaud, J. P. 2004. Natural mortality of Asian psyllid (Homoptera: Psyllidae) in central Florida. *Biol. Control* 29: 260–269.
- Michaud, J. P. and A. K. Grant. 2003. Intraguild predation among ladybeetles and a green lacewing: do the larval spines of *Curinus coeruleus* (Coleoptera: Coccinellidae) serve as a defensive function? *Bull. Entomol. Res.* 93: 499–505.
- Michaud, J. P. and A. K. Grant. 2004. Adaptive significance of sibling egg cannibalism in Coccinellidae: comparative evidence from three species. *Ann. Entomol. Soc. Am.* 97: 710–719.
- Michaud, J. P. and J. L. Jyoti. 2007. Repellency of conspecific and heterospecific larval residues to *Hippodamia convergens* (Coleoptera: Coccinellidae) ovipositing on sorghum plants. *Eur. J. Entomol.* 104: 399–405.
- Mills, N. 2006. Interspecific competition among natural enemies and single versus multiple introductions in biological control. In J. Brodeur and G. Boivin (eds) *Progress in Biological Control: Trophic and Guild Interactions in Biological Control*. Springer, The Netherlands, pp. 191–220.
- Morales, M. A., J. L. Barone and C. S. Henry. 2008. Acoustic alarm signalling facilitates predator protection of treehoppers by mutualist ant bodyguards. *Proc. R. Soc. Lond. (Biol)* 275: 1935–1941.
- Mracek, Z. and Z. Ruzicka. 1990. Infectivity and development of *Steinernema* sp. strain Hylobius (Nematoda, Steinernematidae) in aphids and aphidophagous coccinellids. *J. Appl. Entomol.* 110: 92–95.
- Musser, F. R. and A. M. Shelton. 2003. Predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. *Environ. Entomol.* 32: 1131–1138.
- Mutsu, M., N. Kilinçer, S. Ulgenturk and M. B. Kaydan. 2008. Feeding behavior of *Cryptolaemus montrouzieri* on mealybugs parasitized by *Anagyrus pseudococci*. *Phytoparasitica* 36: 360–367.
- Mylius, S. D., K. Klumpers, A. M. de Roos and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am. Nat.* 158: 259–276.
- Nakashima, Y., M. A. Birkett, B. J. Pye, J. A. Pickett and W. Powell. 2004. The role of semiochemicals in the avoidance of the seven-spot ladybird, *Coccinella septempunctata*, by the aphid parasitoid, *Aphidius ervi*. *J. Chem. Ecol.* 30: 1103–1116.
- Nakashima, Y., M. A. Birkett, B. J. Pye and W. Powell. 2006. Chemically mediated intraguild predator avoidance by aphid parasitoids: interspecific variability in sensitivity to semiochemical trails of ladybird predators. *J. Chem. Ecol.* 32: 1989–1998.
- Nelson, E. H. and J. A. Rosenheim. 2006. Encounters between aphids and their predators: the relative frequencies of disturbance and consumption. *Entomol. Exp. Appl.* 118: 211–219.
- Noia, M., I. Borges and A. O. Soares. 2008. Intraguild predation between the aphidophagous ladybird beetles *Harmonia axyridis* and *Coccinella undecimpunctata* (Coleoptera: Coccinellidae): the role of intra and extraguild prey densities. *Biol. Control* 46: 140–146.
- Norton, A. P., G. English-Loeb and E. Belden. 2001. Host plant manipulation of natural enemies: leaf domatia protect beneficial mites from insect predators. *Oecologia* 126: 535–542.
- Obrycki, J. J. and M. J. Tauber. 1985. Seasonal occurrence and relative abundance of aphid predators and parasitoids on pubescent potato plants. *Can. Entomol.* 117: 1231–1237.
- Obrycki, J. J., K. L. Giles and A. M. Ormord. 1998a. Experimental assessment of interactions between larval *Coleomegilla maculata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae) in field cages. *Environ. Entomol.* 27: 1280–1288.
- Obrycki, J. J., K. L. Giles and A. M. Ormord. 1998b. Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* 117: 279–285.
- O'Connor, B. M. and M. A. Houck. 1989. Two new genera of Hemisarcoptidae (Acari: Astigmata) from the Huron Mountains of Northern Michigan. *Gt Lakes Entomol.* 22: 1–10.
- Okuyama, T. and R. L. Ruyle. 2003. Analysis of adaptive foraging in an intraguild predation system. *Web Ecol.* 4: 1–6.
- Oliver, T. H., J. E. L. Timms, A. Taylor and S. R. Leather. 2006. Oviposition responses to patch quality in the larch ladybird

- Aphidecta oblitterata* (Coleoptera: Coccinellidae): effects of aphid density, and con- and heterospecific tracks. *Bull. Entomol. Res.* 96: 25–34.
- Oliver, T. H., I. Jones, J. M. Cook and S. R. Leather. 2008. Avoidance responses of an aphidophagous ladybird *Adalia bipunctata*, to aphid-tending ants. *Ecol. Entomol.* 33: 523–528.
- Omkar, G. M., A. Pervez and A. K. Gupta. 2004. Role of surface chemicals in egg cannibalism and intraguild predation by neonates of two aphidophagous ladybirds, *Propylea dissecta* and *Coccinella transversalis*. *J. Appl. Entomol.* 128: 691–695.
- Omkar, G. M., A. Pervez, A. K. Gupta. 2007. Sibling cannibalism in aphidophagous ladybirds: its impact on sex-dependent development and body weight. *J. Appl. Entomol.* 131: 81–84.
- Osawa, N. 1992. Effect of pupation site on pupal cannibalism and parasitism in the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). *Jap. J. Entomol.* 60: 131–135.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *Am. Nat.* 103: 91–93.
- Pasteels, J. M. 2007. Chemical defence, offence and alliance in ants–aphids–ladybirds relationships. *Popul. Ecol.* 49: 5–14.
- Pasteels, J. M., C. Deroe, B. Tursch et al. 1973. Distribution et activités des alcaloïdes défensifs des Coccinellidae. *J. Insect Physiol.* 19: 1771–1784.
- Pell, J. K., R. Pluke, S. J. Clark, M. G. Kenward and P. G. Alderson. 1997. Interactions between two aphid natural enemies, the entomopathogenic fungus *Erynia neoaphidis* Remaudière and Hennebert (Zygomycetes: Entomophthorales) and the predatory beetle *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *J. Invert. Pathol.* 69: 261–268.
- Pell, J. K., J. Baverstock, H. E. Roy, R. L. Ware and M. E. N. Majerus. 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. In H. E. Roy and E. Wajnberg (eds), *From Biological Control to Invasion: The Ladybird Harmonia axyridis as a Model Species*. Springer, Netherlands. pp. 147–168.
- Pervez, A. and Omkar. 2006. Ecology and biological control application of multicolored asian ladybird, *Harmonia axyridis*: a review. *Biocontrol Sci. Tech.* 16: 111–128.
- Phoofolo, M. W. and J. J. Obrycki. 1998. Potential for intraguild predation and competition among predatory Coccinellidae and Chrysopidae. *Entomol. Exp. Appl.* 89: 47–55.
- Polis, G. A. and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends Ecol. Evol.* 7: 151–154.
- Polis, G. A., C. A. Myers and R. D. Holt. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297–330.
- Pontin, A. J. 1960. Some records of predators and parasites adapted to attack aphids attended by ants. *Entomol. Mon. Mag. Lond.* 95: 154–155.
- Pope, R. D. 1979. Wax production by coccinellid larvae (Coleoptera). *Syst. Entomol.* 4: 171–196.
- Provost, C., D. Coderre, E. Lucas, G. Chouinard and N. Bostanian. 2003. Impact d'une dose sub létale de lambda-cyhalothrin sur les prédateurs intraguïdes d'acariens phytophages en vergers de pommiers. *Phytoprotection* 84: 105–113.
- Provost, C., D. Coderre, E. Lucas, G. Chouinard and N. Bostanian. 2005. Impact of Intraguild predation and lambda-cyhalothrin on predation efficiency of three acarophagous predators. *Pest Manag. Sci.* 61: 532–538.
- Provost, C., E. Lucas, D. Coderre and G. Chouinard. 2006. Prey selection by the lady beetle *Harmonia axyridis*: the influence of prey mobility and prey species. *J. Insect Behav.* 19: 265–277.
- Quezada, J. R. and P. DeBach. 1974. Bioecological and population studies of the cottony cushion scale, *Icerya purchasi* Mask. and its natural enemies, *Rodolia cardinalis* Mulsant and *Chrysochaeta iceryae* Will., in Southern California. *Hilgardia* 41: 631–688.
- Raymond, B., A. C. Darby and A. E. Douglas. 2000. Intraguild predators and the spatial distribution of a parasitoid. *Oecologia* 124: 367–372.
- Rieder, J. P., T. A. S. Newbold, S. Sato, H. Yasuda and E. W. Evans. 2008. Intra-guild predation and variation in egg defence between sympatric and allopatric populations of two species of ladybird beetles. *Ecol. Entomol.* 33: 53–58.
- Reimer, N. J., M. L. Cope and G. Yasuda. 1993. Interference of *Pheidole megacephala* (Hymenoptera: Formicidae) with biological control of *Coccus viridis* (Homoptera: Coccidae) in coffee. *Environ. Entomol.* 22: 483–488.
- Richards, A. M. 1985. Biology and defensive adaptations in *Rodatus major* (Coleoptera: Coccinellidae) and its prey, *Monophlebulus pilosior* (Hemiptera: Margarodidae). *J. Zool.* 205: 287–295.
- Roger, C., D. Coderre, C. Vigneault and G. Boivin. 2001. Prey discrimination by a generalist coccinellid predator: effect of prey age or parasitism? *Ecol. Entomol.* 26: 163–172.
- Rosenheim, J. A. and J. P. Harmon. 2006. The influence of intraguild predation on the suppression of a shared prey population: an empirical reassessment. In J. Brodeur and G. Boivin (eds), *Progress in Biological Control: Trophic and Guild Interactions in Biological Control*. Springer, Netherland. pp. 1–20.
- Rosenheim, J. A., R. Wilhoit and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96: 439–449.
- Rosenheim, J. A., H. K. Kaya, L. E. Ehler, J. J. Marois and B. A. Jaffee. 1995. Intraguild predation among biological control agents: theory and evidence. *Biol. Control* 5: 303–335.
- Rosenheim, J. A., D. D. Limburg and R. G. Colfer. 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. *Ecol. Appl.* 9: 409–417.

- Roy, H. E. and J. K. Pell. 2000. Interactions between entomopathogenic fungi and other natural enemies: implications for biological control. *Biocontrol Sci. Tech.* 10: 737–752.
- Roy, H. E., J. K. Pella, S. J. Clark and P. G. Alderson. 1998. Implications of predator foraging on aphid pathogen dynamics. *J. Invert. Pathol.* 71: 236–247.
- Roy, H. E., J. K. Pell and P. G. Alderson. 2001. Targeted dispersal of the aphid pathogenic fungus *Erynia neoaphidis* by the aphid predator *Coccinella septempunctata*. *Biocontrol Sci. Tech.* 11: 99–110.
- Roy, H. E., P. G. Alderson and J. K. Pella. 2003. Effect of spatial heterogeneity on the role of *Coccinella septempunctata* as an intra-guild predator of the aphid pathogen *Pandora neoaphidis*. *J. Invert. Pathol.* 82: 85–95.
- Roy, H. E., J. Baverstock, R. L. Ware et al. 2008a. Intraguild predation of the aphid pathogenic fungus *Pandora neoaphidis* by the invasive coccinellid *Harmonia axyridis*. *Ecol. Entomol.* 33: 175–182.
- Roy, H. E., J. Brown, P. Rothery, R. L. Ware and M. E. N. Majerus 2008b. Interactions between the fungal pathogen *Beauveria bassiana* and three species of coccinellid: *Harmonia axyridis*, *Coccinella septempunctata* and *Adalia bipunctata*. In H. E. Roy and E. Wajnberg (eds). *From Biological Control to Invasion: the Ladybird Harmonia axyridis as a Model Species*. Springer, The Netherlands. pp. 265–276.
- Royer, T. A., K. L. Giles, M. M. Lebusa and M. E. Payton. 2008. Preference and suitability of greenbug, *Schizaphis graminum* (Hemiptera: Aphididae) mummies parasitized by *Lysiphlebus testaceipes* (Hymenoptera: Aphididae) as food for *Coccinella septempunctata* and *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biol. Control* 47: 82–88.
- Rudolf, V. H. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. *Ecology* 88: 2697–2705.
- Ruzicka, Z. 1997. Recognition of oviposition-detering allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *Eur. J. Entomol.* 94: 431–434.
- Ruzicka, Z. 2001a. Oviposition responses of aphidophagous coccinellids to tracks of ladybird (Coleoptera: Coccinellidae) and lacewing (Neuroptera: Chrysopidae) larvae. *Eur. J. Entomol.* 98: 183–188.
- Ruzicka, Z. 2001b. Responses of chrysopids (Neuroptera) to larval tracks of aphidophagous coccinellids (Coleoptera). *Eur. J. Entomol.* 98: 283–285.
- Ruzicka, Z. 2003. Perception of oviposition-detering larval tracks in aphidophagous coccinellids *Cycloneda limbifer* and *Ceratomegilla undecimnotata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 100: 345–350.
- Ruzicka, Z. 2006. Oviposition-detering effects of conspecific and heterospecific larval tracks on *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 103: 757–763.
- Ruzicka, Z. and J. Havelka. 1998. Effects of oviposition-detering pheromone and allomones on *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *Eur. J. Entomol.* 95: 211–216.
- Ruzicka, Z. and R. Zemek. 2003. Effects of conspecific and heterospecific larval tracks on mobility and searching patterns of *Cycloneda limbifer* Say (Coleoptera: Coccinellidae) females. In A. O. Soares, M. A. Ventura, V. Garcia and J.-L. Hemptinne (eds). *Proc. 8th Int. Symp. Ecol. Aphidophaga. Arquipélago, Life Mar. Sci. (Suppl.)* 5: 85–93.
- Sakuratani, Y., Y. Matsumoto, M. Oka et al. 2000. Life history of *Adalia bipunctata* (Coleoptera: Coccinellidae) in Japan. *Eur. J. Entomol.* 97: 555–558.
- Santi, F. and S. Maini. 2006. Predation upon *Adalia bipunctata* and *Harmonia axyridis* eggs by *Chrysoperla carnea* larvae and *Orius laevigatus* adults. *Bull. Insectol.* 59: 53–58.
- Sato, S. and A. F. G. Dixon. 2004. Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. *Agric. Forest Entomol.* 6: 21–24.
- Sato, S., A. F. G. Dixon and H. Yasuda. 2003. Effect of emigration on cannibalism and intraguild predation in aphidophagous ladybirds. *Ecol. Entomol.* 28: 628–633.
- Sato, S., H. Yasuda and E. W. Evans. 2005. Dropping behaviour of larvae of aphidophagous ladybirds and its effects on incidence of intraguild predation: interactions between the intraguild prey, *Adalia bipunctata* (L.) and *Coccinella septempunctata* (L.), and the intraguild predator, *Harmonia axyridis* Pallas. *Ecol. Entomol.* 30: 220–224.
- Sato, S., R. Jimbo, H. Yasuda and A. F. G. Dixon. 2008. Cost of being an intraguild predator in predatory ladybirds. *Appl. Entomol. Zool.* 43: 143–147.
- Sato, S., K. Kushibuchi and H. Yasuda. 2009. Effect of reflex bleeding of a predatory ladybird beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), as a means of avoiding intraguild predation and its cost. *Appl. Entomol. Zool.* 44: 203–206.
- Schellhorn, N. A. and D. A. Andow. 1999a. Cannibalism and interspecific predation: role of oviposition behavior. *Ecol. Appl.* 9: 418–428.
- Schellhorn, N. A. and D. A. Andow. 1999b. Mortality of coccinellid (Coleoptera: Coccinellidae) larva and pupae when prey become scarce. *Popul. Ecol.* 28: 1092–1100.
- Seagraves, M. P. 2009. Lady beetle oviposition behavior in response to the trophic environment. *Biol. Control* 51: 313–322.
- Sengenon, C. and B. Frings. 1985. Interference and competitive behaviour of the aphid predators, *Chrysoperla carnea* and *Coccinella septempunctata* in the laboratory. *Entomophaga* 30: 245–251.
- Shapiro-Ilan, D. I. and T. E. Cottrell 2005. Susceptibility of lady beetles (Coleoptera: Coccinellidae) to entomopathogenic nematodes. *J. Invert. Pathol.* 2: 150–156.

- Sloggett, J. J. 2005. Are we studying too few taxa? Insights from aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 102: 391–398.
- Sloggett, J. J. 2008. Weighty matters: body size, diet and specialization in aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 105: 381–389.
- Sloggett, J. J. and M. E. N. Majerus 2000. Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. *Biol. J. Linn. Soc.* 70: 63–88.
- Sloggett, J. J., R. A. Wood and M. E. N. Majerus. 1998. Adaptations of *Coccinella magnifica* Redtenbacher, a myrmecophilous coccinellid, to aggression by wood ants (*Formica rufa* group). I. Adult behavioral adaptation, its ecological context and evolution. *J. Insect Behav.* 11: 889–904.
- Sluss, T. P. and B. A. Foote. 1973. Biology and immature stages of *Leucopis verticalis* (Diptera: Chamaemyiidae). *Can. Entomol.* 103: 1427–1434.
- Snyder, W. E., S. N. Ballard, S. Yang et al. 2004a. Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoids *Aphelinus asychis* on greenhouse roses. *Biol. Control.* 30: 229–235.
- Snyder, W. E., G. M. Clevenger and S. D. Eigendrode. 2004b. Intraguild predation and successful invasion by introduced ladybird species. *Oecologia* 140: 559–565.
- Soares, A. O. and A. Serpa. 2007. Interference competition between ladybird beetle adults (Coleoptera: Coccinellidae): effects on growth and reproductive capacity. *Popul. Ecol.* 49: 37–43.
- Soares, A. O., I. Borges, P. A. V. Borges, G. Labrie and E. Lucas. 2008. *Harmonia axyridis*: what will stop the invader? In H. E. Roy and E. Wajnberg (eds). *From Biological Control to Invasion: The Ladybird Harmonia axyridis as a Model Species*. Springer, The Netherlands. pp. 127–146.
- Stiling, P. 1993. Why do natural enemies fail in classical biological control programs? *Am. Entomol.* 39: 31–37.
- Straub, C. S. and W. E. Snyder. 2006. Experimental approaches to understanding the relationship between predator biodiversity and biological control. In J. Brodeur and G. Boivin (eds) *Progress in Biological Control: Trophic and Guild Interactions in Biological Control*. Springer, The Netherlands. pp. 221–240.
- Takahashi, K. 1989. Intra- and inter-specific predations by lady beetles in spring alfalfa fields. *Jap. J. Entomol.* 57: 199–203.
- Tedders, W. L., C. C. Reilly, B. W. Wood, R. K. Morrison and C. S. Lofgren. 1990. Behavior of *Solenopsis invicta* (Hymenoptera: Formicidae) in pecan orchards. *Environ. Entomol.* 19: 44–53.
- Thomas, M. B., S. D. Wratten and N. W. Sotherton 1992. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *J. Appl. Ecol.* 29: 524–531.
- Thomas, M. B., S. P. Arthurs and E. L. Watson. 2006. Trophic and guild interactions and the influence of multiple species on disease. In J. Brodeur and G. Boivin (eds). *Progress in Biological Control: Trophic and Guild Interactions in Biological Control*. Springer, The Netherlands: pp. 101–122.
- Tinsley, M. C. and M. E. N. Majerus 2007. Small steps or giant leaps for male-killers? Phylogenetic constraints to male-killer host shifts. *BMC Evol. Biol.* 7: 238.
- Toda, Y. and Y. Sakuratani. 2006. Expansion of geographical distribution of an exotic ladybird beetle, *Adalia bipunctata* (Coleoptera: Coccinellidae), and its interspecific relationships with native ladybird beetles in Japan. *Ecol. Res.* 21: 292–300.
- Todorova, S. I., D. Coderre and J. C. Cote. 2000. Pathogenicity of *Beauveria bassiana* isolates toward *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae), *Myzus persicae* (Homoptera: Aphididae) and their predator *Coleomegilla maculata lengi* (Coleoptera: Coccinellidae). *Phytoprotection* 81: 15–22.
- Todorova, S. I., J. C. Cote and D. Coderre. 1996. Evaluation of the effects of two *Beauveria bassiana* (Balsamo) Vuillemin strains on the development of *Coleomegilla maculata lengi* Timberlake (Col., Coccinellidae). *J. Appl. Entomol.* 120: 159–163.
- Triltsch, H. 1997. Gut contents in field sampled adults of *Coccinella septempunctata* (Col.: Coccinellidae). *Entomophaga* 42: 125–131.
- Turnock, W. J., I. L. Wise and F. O. Matheson 2003. Abundance of some native coccinellines (Coleoptera: Coccinellidae) before and after the appearance of *Coccinella septempunctata*. *Can. Entomol.* 135: 391–404.
- Vanhove, F. 1998. Impact de la défense des oeufs sur la structure des communautés de Coccinellidae. Unpubl. Master dissertation, University of Gembloux, Belgium.
- Voelkl, W. 1992. Aphids or their parasitoids: who actually benefits from ant-attendance? *J. Anim. Ecol.* 61: 273–281.
- Voelkl, W. 1995. Behavioral and morphological adaptations of the coccinellid, *Platynaspis luteorubra* for exploiting ant-attended resources (Coleoptera: Coccinellidae). *J. Insect Behav.* 8: 653–670.
- Voelkl, W. 1997. Interactions between ants and aphid parasitoids: patterns and consequences for resource utilization. *Ecol. Stud.* 130: 225–240.
- Voelkl, W. and K. Vohland. 1996. Wax cover in larvae of *Scymnus* species: do they enhance coccinellid larval survival? *Oecologia* 107: 498–503.
- Voynaud, L. 2008. Prédation intraguilde entre prédateurs actif et furtif au sein d'une guilde aphidophage. Unpubl. MSc dissertation, Université du Québec à Montréal, Québec, Canada.
- Ware, R. L. and M. E. N. Majerus. 2008. Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird *Harmonia axyridis*. In H. E. Roy and E. Wajnberg (eds). *From Biological Control to Invasion: The Ladybird Harmonia axyridis as a Model Species*. Springer, The Netherlands. pp. 169–188.

- Ware, R. L., B. Ygel and M. E. N. Majerus. 2009. Effects of competition, cannibalism and intra-guild predation on larval development of the European coccinellid *Adalia bipunctata* and the invasive species *Harmonia axyridis*. *Ecol. Entomol.* 34: 12–19.
- Ware, R. L., F. Ramon-Portugal, A. Magro et al. 2008. Chemical protection of *Calvia quatuordecimpunctata* eggs against intraguild predation by the invasive ladybird *Harmonia axyridis*. In H. E. Roy and E. Wajnberg (eds). *From Biological Control to Invasion: The Ladybird Harmonia axyridis as a Model Species*. Springer, The Netherlands. pp. 189–200.
- Warren, L. O. and M. Tadić. 1967. Biological observations on *Coleomegilla maculata* and its role as a predator of the fall webworm. *J. Econ. Entomol.* 60: 1492–1496.
- Way, M. J. 1963. Mutualism between ants and honeydew-producing homoptera. *Annu. Rev. Entomol.* 8: 307–344.
- Weisser, W. W. 2003. Additive effects of pea aphid natural enemies despite intraguild predation. In A. O. Soares, M. A. Ventura, V. Garcia and J.-L. Hemptinne (eds). *Proc. 8th Int. Symp. Ecol. Aphidophaga. Arquipélago, Life Mar. Sci. (Suppl.)* 5: 11–15.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.* 25: 443–466.
- Yasuda, H. and T. Kimura. 2001. Interspecific interactions in a tritrophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Entomol. Exp. Appl.* 98: 17–25.
- Yasuda, H. and N. Ohnuma. 1999. Effect of cannibalism and predation on the larval performance of two ladybird beetles. *Entomol. Exp. Appl.* 93: 63–67.
- Yasuda, H. and K. Shinya. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. *Entomophaga* 42: 153–163.
- Yasuda, H., T. Takagi and K. Kogi. 2000. Effects of conspecific and heterospecific larval tracks on the oviposition behavior of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 97: 551–553.
- Yasuda, H., T. Kikuchi, P. Kindlmann and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and predation in larvae of two predatory ladybirds. *J. Insect Behav.* 14: 373–384.
- Yasuda, H., E. W. Evans, Y. Kajita, K. Urakawa and T. Takizawa. 2004. Asymmetric larval interactions between introduced and indigenous ladybirds in North America. *Oecologia* 141: 722–731.
- Zang, L. S. and T. X. Liu. 2007. Intraguild interactions between an oligophagous predator, *Delphastus catalinae* (Coleoptera: Coccinellidae), and a parasitoid, *Encarsia sophia* (Hymenoptera: Aphelinidae), of *Bemisia tabaci* (Homoptera: Aleyrodidae). *Biol. Control* 41: 142–150.