Chapter 7

INTRAGUILDL 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 zoophytophagous 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 mechanisms. 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 _Acyrthosiphon 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.
Intraguild interactions

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
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.

Whitely 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

**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).
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, Firlej 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 aleyrodaphagous 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:


For exceptions see Lucas et al. (1998a), Phoofolo
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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 & Ohnnuma 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

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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).

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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 matura-

tion 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)


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

1 **IGP intensity is usually high among preda-

cceous coccinellid species due to their great voracity, their similar foraging strategies, and 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 alka-

loids** 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, volitnism, 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 (Voinnaud 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** (Canntharidae, 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 montouzieri* **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 (Collier & 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 (Michauda 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.
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 neoaphidis 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, Obyrcké 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 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**) (Pastels 2007, Kajita et al. 2010; 9.3): the **trade-off between the cost** (production, toxicity) and the **benefits** (defence) is not clear (Pastels 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, Pastels 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**.

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**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, Moult from first to second larval instar; L1, first larval instar. (After Lucas 2005).
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. lablokkof-Khnzorian 1982). Adult females are able to detect oviposition-deterring semiochemicals (ODS) from conspecific 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. leo ina transversalis (but not the smaller Scymnus pyrochelitus) 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 quatuordecimpunctata 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 conspecific 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 (Hoogen-doorn & 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 *be*ahavioural 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 moult*ing* 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 & Tadi´c 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 chrysopterids (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). 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). 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). 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). 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. 2007). 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).

Sympatric species, which may reinforce the strength of the warning message (Mullerian mimicry) (Holloway et al. 1991, Dolenska et al. 2007). However, no study has demonstrated any impact of aposematism against IGP.

Spiders are important ladybird predators (Cernyger & 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 (Hoděk 1973, Todorova et al. 1996, 2000, Cottrell & Shapiro-Ilan 2003, 2008), bacteria/by-products of bacteria (e.g. Giroux et al. 1994) and nematodes (Mrácek & Ruzicka 1990, Lemire et al. 1996, Shapiro-Ilan & Hoděk 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 & Hoděk 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


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 sternorrhynchs 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 *Pubillia 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 orbignyana 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. orbignyana, reducing the parasitization rate on the ladybird (Lière & Perfecto 2008).

The myrmecophilous Scymnus posticalis is never attack by ants and is found within aphid colonies together with another ladybird, Phymatosternus lewisi (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 & Tourneur 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 Cycloneura 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

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 spiraceola* 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 whitely 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 (Cerynghier & 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 luticeps* and *Curinus coeruleus* in Hawaiin 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* and *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 spiraecola* 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 inductive 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 ostriniae*. 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.
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 & Honček 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 (Trütsch 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*. 
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