Chapter 5

FOOD RELATIONSHIPS

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5.1 INTRODUCTION

Studies of food relations in coccinellids were among the earliest fields of research on this family, because of the evident interest in ladybirds as natural enemies of aphid, coccid and mite pests. The history of studies of coccinellid food relations can be divided into three periods. In the earliest period, studies focussed on what the ladybirds eat and lists of the prey species eaten were compiled. In the middle phase, hypotheses and models were constructed that were based on only fragmentary experiments, usually executed in extremely artificial settings. This remained characteristic well into the end decades of the last century. In agreement with Burk (1988), the need for empirical hypothesis testing in future decades was stressed by Hodek (1996).

Fortunately a new generation of researchers has undertaken more comprehensive causal studies in several branches of coccinellid food research and important progress has been achieved within a relatively short period. Here, in the introduction, we briefly call attention to some of the studies that are discussed in this chapter.

In 5.2, Sloggett's (2008b) prey size–density hypothesis, based on concrete observations, opens a new dimension of prey specificity: size relation between the prey and predator instead of (or together with) physiological suitability and/or chemical composition of the prey. Body size may be more important than prey chemistry as a universal factor underlying dietary specialization.

New light has been thrown on nutritional complementarity by Evans and co-authors (Kalaskar & Evans 2001, Evans et al. 2004, Evans & Gunther 2005) and Michaud & Jyoti (2008), and differences in the larval versus adult food specificity was stressed by Michaud (2005). Some problems of food ecology are being solved by detailed field experiments, often using the addition of artificial food and sometimes the mark–recapture techniques (Evans & Toler 2007, Honěk et al. 2008a, b, Sloggett 2008a, b, Sloggett et al. 2008; 5.2.7).

Important recent advances have also been made concerning patterns and processes of food consumption (5.3). Close study has revealed new insights, for example, as to how prey limitation early in life affects ladybird performance later on (Dmitriew & Rowe 2007), and how the biochemical properties of prey versus predator may influence a ladybird's ability to balance its nutritional needs (Specty et al. 2003, Kagata & Katayama 2006).

The importance of behavioural studies and their relative shortage in relation to insect predators has recently been stressed (Mills & Kean 2010). However, in these studies (5.4) decisive, qualitative progress has been made. Sensory responses, which were previously questioned, have not only been repetitively documented by many teams in several countries, but also the chemical composition of some attracting volatiles has been revealed; thus the volatiles produced by herbivore-injured plants have been found to attract enemies to those herbivores. The adaptive phenomenon of oviposition deterring substances, left on the substrate by crawling larvae, has been discovered (Ruzicka 1997) and then recorded in a number of coccinellid species, and one chemical responsible has already been identified (Klewer et al. 2007).

Under the pressure of the typically discontinuous occurrence of aphid prey, the evolution of coccinellid feeding behaviour evidently has not led to development of **gustatory discrimination** in generalists, at least in aphidophagous coccinellids. It has been recorded repeatedly that the ladybirds do not avoid less suitable or even toxic food. They even do not prefer better food when given a choice (e.g. Nielsen et al. 2002, Nedvěd & Salvucci 2008, Snyder & Clevenger 2004; 5.2.1.1, 5.2.5, 5.2.6.1).

We compile the findings in this chapter in the optimistic expectation that they represent just the beginning of a new fruitful period for studies of coccinellid food and feeding.

5.2 FOOD SPECIFICITY

5.2.1 Food range

Although a tendency to feed on the same or similar prey can be observed in taxonomic groups of coccinellids, one may find prey **specialists** even **within** individual **tribes**. Thus, for example, in the generally aphidophagous tribe Coccinellini there are also non-predaceous species, such as the phytophagous *Bulaea lichatschovi* (Capra 1947, Dyadechko 1954, Savoiskaya 1966, 1970a) and the pollinivorous and mycophagous *Tytthaspis sedecimpunctata* (Dauguet 1949, Turian 1969, Ricci 1982, Ricci et al. 1983; 5.2.6). Within this tribe there are further species which specialize on immature stages of Coleoptera, such as *Aiolocaria* spp.

(Iwata 1932, 1965, Savoiskaya 1970a, 1983, Kuznetsov 1993), *Calvia quindecimguttata* (Kanervo 1940) and *Coccinella hieroglyphica* (Hippa et al. 1984; Table 5.1) which feed on pre-imaginal stages of Chrysomelidae, or *Neocalvia* spp. which prey on larvae of mycophagous coccinellids of the tribe Psylloborini (Camargo 1937). Thus, not only entomophagy, but also phytophagy and mycophagy are represented within the tribe Coccinellini. Phytophagy is typical for the subfamily Epilachninae, mycophagy in the tribe Psylloborini (Sutherland & Parrella 2009) and feeding on mites in Stethorini (Biddinger et al. 2009). The classification of coccinellids is still partially artificial (Giorgi et al. 2009; Chapter 1) and thus discussing the food specialization of a whole tribe cannot but have its limitations (Hodek 1996).

Predaceous coccinellids have a wide range of **accepted food**. Apart from feeding on sternorrhynchan Hemiptera and phytophagous mites, they often prey also on Thysanoptera and young instars of holometabolan insects (Evans 2009) and even food of plant origin as well as fungi. Taxonomic differences in the rate of coccinellid development are related to the predominant type of food consumed (Table 5.2).

Table 5.1 Larval mortality and pupal weight of *Coccinella hieroglyphica* fed on aphids or chrysomelids (Hippa et al. 1984).

	Larval mortality		Fresh weight of ♀ pupae (mg)		
Prey	**%**	**n**	**mean**	**S.E.**	**n**
*Myzus persicae**	20.9	43	9.78	0.13	12
*Symydobius oblongus**	22.9	70	9.89	0.12	25
Galerucella sagittariae†	—	—	—	—	—
eggs	67.7	31	10.19	0.72	5
larvae	10.8	74	12.47	0.22	17

*Aphidoidea.
†Chrysomelidae.

Table 5.2 Rate of natural increase (r_m) of acariphagous, aphidophagous and coccidophagous coccinellid species (after Roy et al. 2003).

Species	Prey relationship	Temp (°C)	r_m (d^{-1})
Parastethorus nogripes	Acariphagous	25.0	0.152
Stethorus madecassus	Acariphagous	25.0	0.155
Stethorus punctum picipes	Acariphagous	24.0	0.121
Stethorus pusillus	Acariphagous	24.0	0.100
Coccinella septempunctata	Aphidophagous	26.0	0.190
Coleomegilla maculata lengi	Aphidophagous	25.0	0.110
Olla v-nigrum	Aphidophagous	25.7	0.160
Propylea quatuordecimpunctata	Aphidophagous	26.0	0.140
Diomus hennesseyi	Coccidophagous*	25.0	0.103
Exochomus flaviventris	Coccidophagous*	25.0	0.050
Hyperaspis notata	Coccidophagous*	25.0	0.081
Hyperaspis raynevali	Coccidophagous*	25.0	0.081
Hyperaspis senegalensis hottentotta	Coccidophagous*	26.0	0.070
Rodolia iceryae	Coccidophagous*	27.0	0.064

*Coccidophagous ladybirds have characteristically slower development: 5–10 % per day.

The great variety of food consumed led to the assumption that food specificity in coccinellids concerns only major taxonomic groupings: e.g. aphidophagous ladybirds only eat aphids. Observed **acceptance** has been **mistaken for suitability** of prey, even by experienced workers. For example Balduf (1935) concluded, on the basis of a survey of accepted food, that no special groups of aphids are selected by ladybirds of the tribes Hippodamiini and Coccinellini. Kanervo (1940) treated the six species of aphid prey as a single complex because coccinellids did not show any great preference for individual species of aphids. Such an assumption has long been perpetuated even though contradictory evidence has been reported. This is notably the case in the incorrect characterization of prey of *Adalia bipunctata*. Although habitat preference is important, overgeneralizations may often be erroneous. The conclusion that all aphids living on shrubs or trees represent suitable prey for *A. bipunctata*, while aphids from other habitats are unfavourable prey for this ladybird (Pruszynski & Lipa 1971), has already been refuted by earlier data on *Aphis sambuci* (Hodek 1956, Blackman 1965) as well as by more recent data discussed in this chapter.

Early studies of predator–prey relationships were mostly limited to compiling lists of observed feeding in the field or concurrent presence of predator and prey on the same plant (Hodek 1996 for references). The reliability of such lists was questioned quite early by Thompson (1951): 'The various species of ladybirds do not actually feed . . . the host insects with which they are associated in the records'. Thompson warned further that: 'The gradual accumulation of such records in the literature finally gives a picture which may be completely inaccurate in so far as the real behaviour and food habits of the species are concerned.'

However, when experimental analysis of the food relationships of particular species of coccinellids is missing, the lists of **observed associated occurrence** of predator and prey can be useful. They provide preliminary orientation on the relations of ladybird species to natural prey and habitats. Lists of **accepted** prey have been published for the eight most common aphidophagous coccinellid species from Far East Russia (Kuznetsov 1975, 1993) and for 36 species of aphidophagous Coccinellidae in India (Agarwala & Ghosh 1988). Agarwala et al. (1987) discriminated between the 'accepted' and 'common' aphid prey of four coccinellid species from northeastern India. The data is based on examinations of gut contents and field observations.

Majerus (1994) gives a useful list of principal and secondary foods of British coccinellids (although without defining these two categories). Another helpful food list of Klausnitzer and Klausnitzer (1997) for central European Coccinellidae does not differentiate the suitabilities of different prey, but just gives examples of prey consumed by ladybirds based on the authors' observations. Species of psyllids and aleyrodids observed to be preyed on by coccinellids have recently been listed, while an other compilation in the same paper lists essential coccid prey (Hodek & Honěk 2009).

After the invasion of the soybean pest *Aphis glycines* to the USA, Wu et al. (2004) compiled a list of its natural enemies (including seven coccinellid species) in China and southern Korea. *Propylea japonica* (62%) and *Har. axyridis* (10%) were earlier reported as dominant ladybeetles on *A. glycines* in China (Wang & Ba 1998).

5.2.1.1 Methods for detection of food range

The **natural food range** of coccinellids can be ascertained in several ways (Weber & Lundgren 2009). The classical method is the microscopic detection and identification of **prey remnants** from the guts or excreta (e.g. Agarwala et al. 1987, Triltsch 1999, Ricci & Ponti 2005, Ricci et al. 2005, Davidson & Evans 2010) which can be compared with the whole specimens of insects from the same community.

In **serological assays** (also Chapter 10.7) the specific proteins of the prey are identified by their reaction with the serum of a sensitized mammal (usually a rabbit). In the 1980s, the most popular assays were ELISAs (e.g. Crook & Sunderland 1984, Sunderland et al. 1987, Hagley & Allen 1990). A double antibody method that can be scored by eye (Stuart & Greenstone 1990, Greenstone & Trowell 1994) is still used (Santos et al. 2009).

The interpretation of **molecular gut-content** data depends on the rate of decay in their detectability, expressed as DNA half-life. The predators with longer period of prey-detectability might be wrongly considered as more important, when compared with predators that have short detectability. **DNA half-life** depends on types of ingestion and digestion. When one egg of *Leptinotarsa decemlineata* was used as prey, DNA half-life was 7.0 hours in *Col. maculata* and 50.9 hours in the spined soldier bug, *Podisus maculiventris* (Greenstone et al. 2007). Two serological methods have recently been used to prove that eggs of a noctuid are prey of *Hip. variegata* (Mansfield et al. 2008). The **polymerase chain reaction** technique (PCR) effectively amplifies DNA prey residues in the gut contents of arthropod predators by use of specific primers. Species can be identified based on gene amplification fragments which are observed as bands in the stained agarose gel following electrophoresis. The use of data obtained by PCR-based methods requires careful evaluation of all possible factors that may affect interpretation. *Hip. variegata* had the shortest median detection success 17 hours at 20°C, while it was 36 hours in a nabid bug and 50 hours in a spider. The rate of detection decreases with increasing temperature in *Hip. variegata*, but not in the spider, although sex and weight of *Hip. variegata* did not influence detection of prey DNA (Hosseini et al. 2008). PCR can only be used to detect prey DNA in the gut if the predator was captured shortly before testing. In the case of *Rhopalosiphum padi* as prey and *A. bipunctata* as predator, temperature (21 or 14°C) had no significant effect on *R. padi* detection (McMillan et al. 2007). For a novel use of **chromatographic analysis** see Sloggett et al. (2009b; also Chapter 10).

5.2.2 Nutritional suitability of food

In spite of their considerable polyphagy as regards **accepted food**, many coccinellid species are specialists as far as **nutritionally suitable** food is concerned. Predator–prey relationships should be viewed in this sense to rightly assess the possible impact of a coccinellid on any given pest.

Different criteria of food suitability have been used in food research in coccinellids. As stressed above and in 5.2.1, **acceptance** has been an invalid criterion of food suitability. **Preference** for certain prey seemed to provide useful evidence: Strauss' (1982) linear index of prey selection was used in the analysis of prey preference in *Stethorus punctum* (Houck 1986). However, experiments with *Megoura viciae* (Blackman 1967a) and *Aphis sambuci* (Hodek 1956, Nedvěd & Salvucci 2008) have shown that ladybirds feed on toxic aphids even if provided with a better alternative.

The **presence of larvae** of the predator in association with a prey species is considered to be good evidence for evaluating food specificity in the field, although it may be misleading in a habitat with several potential prey species. Mills (1981) warned that, in early and late season, the adults can be observed in association with prey types and habitats that are not used during reproduction, and the presence of larvae served as criterion for his list of essential prey for *A. bipunctata*. A great advantage of this list (Mills 1981) is the inclusion of the type of **habitat** and **host plant**. Most listed prey would be essential prey. *A. bipunctata*, however, develops on the listed *Aphis sambuci* with a significantly lower larval survival and weight of emerging adults, compared with good essential prey (Blackman 1965, 1967b; Table 5.3). *Aphis sambuci* is thus a rather unsuitable prey for *A. bipunctata*. In terms of the fecundity of *A. bipunctata* females, *Drepanosiphum platanoidis* on sycamore and *Chaitophorus capreae* on sallow were the least suitable prey (Mills 1981). In rare cases the predator–prey relationship has been safely

Table 5.3 Larval development and oviposition of *Adalia bipunctata* on different aphids (Blackman 1965, 1967b).

Aphid species	Larval development (days)	Larval mortality (%)	Weight of adults at emergence (mg)	Fecundity (total eggs laid)	Fertility (% of viable eggs)
Myzus persicae	10.4	17.8	11.8	676.2	89.4
Neomyzus circumflexus	9.5	16.7	11.9	—	—
Acyrthosiphon pisum	10.8	13.9	12.6	—	—
Microlophium carnosum	10.6	9.1	12.4	—	—
Aphis fabae	13.0	27.6	7.9	249.6	55.9
Aphis sambuci	13.4	25.0	8.0	—	—
*Brevicoryne brassicae**	21; 23	(66.7)	5.1; 6.1	—	—

*Only 2 out of 6 larvae completed development.

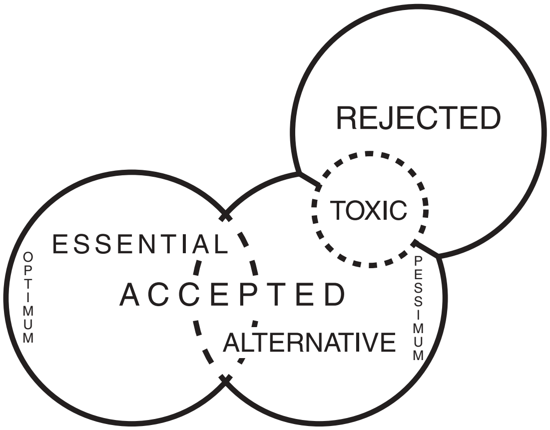

Figure 5.1 Types of physiological suitability of coccinellid foods (modified from Hodek 1996).

identified by another indirect method: that of systematic and **long term observation**. In the course of 5 years, Eastop and Pope (1966, 1969) found 99% of specimens of *Scymnus auritus* on oaks infested with *Phylloxera glabra*.

In most cases only **experimental evidence**, when main life history parameters of predators are measured on a prey species, is an entirely safe way to assess physiological suitability. This became apparent when it was found that a toxic aphid, *Aphis sambuci*, was eaten by *C. septempunctata*, but exerted detrimental effects (Hodek 1956). It was then suggested that physiological parameters, such as growth, reproduction and mortality, should be used as the decisive criterion. It was proposed to discriminate between two principal kinds of food: **essential** (Fig. 5.1; 5.2.11) that ensure oviposition and the completion of larval development, and **alternative** that serve only as a source of energy and thus prolong survival in comparison with starvation (Hodek 1962, 1967, 1973, 1993). This approach has been widely accepted (e.g. Mills 1981, Evans et al. 1999, Giorgi et al. 2009, Berkvens et al. 2010).

The experimental evaluation of the suitability of prey does have some disadvantages, however. If the prey is offered to the predator in a small space, the escape and defence behaviour of prey is limited and predator's searching behaviour may be modified. By such experiments a prey species can be ascertained as essential, although in the field it does not coincide with the predator in space and time (Iperti 1965, 1966, Brun & Iperti 1978). It appears that alternative feeding on various foods is advantageous for predatory ladybirds (5.2.5). The listing of 'unnatural' essential prey (in 5.2.11) can be useful information for culturing ladybirds. However, it is important not to overestimate the records on nutritive quality of the prey (5.2.6, 5.2.11). Complex predator–prey relations have recently been discussed in a comprehensive and novel way (Sloggett 2008a; 5.2.3).

Ideally, to characterize 'natural' essential prey, observational and experimental approaches should be combined. The relationships of 11 strains of five coccinellid species (*C. septempunctata*, *Hip. tredecimpunctata*, *Hip. variegata*, *P. quatuordecimpunctata* and *Cer. undecimnotata*) with two species of essential aphid prey (*Diuraphis noxia* and *Schizaphis graminum*) were evaluated by Michels and Flanders (1992). The comparison of the main life-history parameters indicated important differences in prey suitability, between both coccinellid species and strains of the same species. Thus, for example, in the Moldavian strain of *P. quatuordecimpunctata* the number of eggs laid with *D. noxia* as food was only a fraction of that with *S. graminum*. The Ukrainian strain of the same coccinellid species, however, had twice the fecundity when fed on *D. noxia* than on *S. graminum*. Michaud (2000) compared the performance of seven coccinellid species fed on *Aphis spiraecola* and *Toxoptera citricidus* and Ozder and Saglam (2003) evaluated *A. bipunctata* on four and *C. septempunctata* on five aphid species (Table 5.4).

In Europe, the effect of a range of aphid species on life history parameters has been compared in *A. bipunctata* (Kalushkov 1998), *Anatis ocellata* and *Calvia quatuordecimguttata* (Kalushkov & Hodek 2001), *C. septempunctata* (Kalushkov & Hodek 2004) and *P. quatuordecimpunctata* (Kalushkov & Hodek 2005). In all four papers the laboratory experiments were complemented by observation of predator–prey relations in the field. In India, Omkar and his colleagues made comparative studies for four species: *C. septempunctata* (Omkar & Srivastava 2003), *C. leonina transversalis* (Omkar & James 2004), *Menochilus sexmaculatus* (Omkar & Bind 2004), and *P. dissecta* (Pervez & Omkar 2004). They compared the performance of ladybirds when reared on seven aphid species as prey. In these four experiments the sequence of suitability of all aphids used appeared surprisingly regular when measured by survival of larvae, survival of adults and fecundity

Table 5.4 Total development time and survival of two coccinellid species as affected by aphid prey (recorded at 25 ± 1°C, 16L:8D in Tekirdag, Turkey) (modified after Ozder & Saglam 2003).

	Aphid species				
	S. avenae	***R. padi***	***M. cerasi***	***H. pruni***	***M. dirhodum***
	Adalia bipunctata				
Total development (days)	20.7 ± 1.03 (19–22) c	16.7 ± 0.76 (16–18) a	17.9 ± 0.80 (17–20) b	19.8 ± 1.14 (18–21) c	—
Survival (%)	67 ab	78 ab	82 a	50 b	—
	Coccinella septempunctata				
Total development (days)	18.9 ± 1.07 (16–21) a	19.0 ± 1.15 (18–21) a	17.5 ± 0.84 (16–18) a	20.8 ± 1.60 (19–23) b	18.6 ± 0.89 (18–20) a
Survival (%)	84 a	70 ab	60 ab	37 b	63 a

Within rows, means followed by a common letter do not differ significantly ($P < 0.05$).
Values are means ± SE; the range between minimum and maximum values is given in parentheses ($n = 30$).
Sitobion avenae, *Rhopalosiphum padi*, *Myzus cerasi*, *Hyalopterus pruni*, *Metopolophium dirhodum.*

(Tables 5.5, 5.6). In other studies the effect of prey on the parameters was more variable (see next paragraph). When Omkar and co-authors experimented with *Aphis nerii*, it was always the least suitable prey. *Aphis craccivora* and *A. gossypii* were optimal for three ladybird species, but not for *C. septempunctata. Lipaphis pseudobrassicae* was optimal prey for this species, while this aphid was the second worst prey for *M. sexmaculatus*. For *C. leonina transversalis* and *P. dissecta*, *L. pseudobrassicae* was the third optimal prey. Earlier Indian papers also recorded *L. pseudobrassicae* as a very good prey for *C. septempunctata*, but it was unsuitable for the reproduction of *Micraspis discolor* (Atwal & Sethi 1963, Agarwala et al. 1987).

More variable effects of aphids on coccinellids' parameters have been recorded by other workers. A high percentage of *Har. axyridis* larvae survived to adult (70%) when reared on *Aphis spiraecola* (Table 5.7), but the females did not lay eggs on this diet (Michaud 2000). Similarly the fecundity of *C. septempunctata* was optimum on *Acyrthosiphon pisum* and *Sitobion avenae*, but the male longevity was lower on these two aphids than on *A. fabae* and *A. craccivora* – although the fresh weight of emerged males, reared on the former two aphids, was among the highest (Kalushkov & Hodek 2004).

For the sake of easier orientation, differences in the nutritive suitability of foods will be discussed in particular subchapters. Alternative food will be discussed in the sections on low quality prey (5.2.6), non-insect food (5.2.9), and non-hemipteran prey (5.2.7). There are overlapping cases; the categories of food should never be used dogmatically and inflexibly.

5.2.3 Prey size–density hypothesis

In almost the entirety of Section 5.2 the discussion of food specificity is based on the nutritional and chemical qualities of prey, i.e. mostly on the nature of allelochemicals derived from host plants. The research has stressed these aspects for the past several decades, and the contents of the chapter reflect this.

However, prey specificity has recently begun to be viewed from another angle: the relation between the **body size** of aphidophagous ladybirds and aphid prey is considered as more important (or at least similarly important) than chemistry. The turning point may be represented by the concept of Sloggett (2008b): 'body size trade-offs are the likely most important universal factor underlying dietary specialization in aphidophagous coccinellids'. As our short explanation here will necessarily remain a simplification, the reader is advised to study directly the two recent papers by Sloggett (2008a, b), which contain many stimulating thoughts.

Sloggett's (2008a) **prey size–density hypothesis** has been formulated in response to a related hypothesis

Table 5.5 Life-history parameters of *Coccinella septempunctata* as affected by aphid prey (modified after Omkar and Srivastava 2003).

Aphid species		***L. erysimi***	***M. persicae***	***A. craccivora***	***A. gossypii***	***U. compositae***	***A. nerii***
Development duration (days)		13.9 ± 0.1 a	15.2 ± 0.1 b	16.8 ± 0.1 c	17.9 ± 0.1 d	21.0 ± 0.1 e	22.9 ± 0.1 b
Weight (mg)	Male	38.2 ± 0.3 a	33.9 ± 0.1 b	29.9 ± 0.2 c	27.1 ± 0.2 d	23.8 ± 0.1 e	20.8 ± 0.2 b
	Female	40.6 ± 0.2 a	37.7 ± 0.2 b	33.4 ± 0.1 c	31.3 ± 0.2 d	25.9 ± 0.1 e	22.3 ± 0.4 b
Immature survival (%)		73.5 ± 0.9 a	66.6 ± 0.8 b	64.2 ± 2.2 bc	61.2 ± 3.1 cd	52.1 ± 2.4 e	43.9 ± 1.3 f
Adult emergence (%)		90.1 ± 1.4 a	88.5 ± 1.2 ab	85.0 ± 1.5 ab	81.1 ± 2.1 ab	80.2 ± 2.9 bc	71.7 ± 2.8 d
Consumption (aphids/female/day)		72.1 ± 1.4 a	65.3 ± 1.5 b	59.2 ± 1.3 c	53.8 ± 1.6 cd	34.8 ± 1.5 e	26.3 ± 2.1 f
Female longevity (days)		85.7 ± 1.5	80.0 ± 1.0	76.6 ± 1.4	73.7 ± 1.8	62.5 ± 1.3	53.5 ± 1.0
Relative growth rate (RGR)		1.52 ± 0.02	1.27 ± 0.03	0.99 ± 0.01	0.86 ± 0.02	0.57 ± 0.01	0.49 ± 0.02
Oviposition period (days)		69.8 ± 1.3 a	57.9 ± 1.0 b	50.7 ± 1.1 c	44.8 ± 1.6 d	30.2 ± 1.1 e	16.4 ± 0.6 f
Fecundity (eggs/female)		1764 ± 8.46 a	1198.5 ± 0.1 b	1060.7 ± 25.8 c	739.2 ± 32.0 d	488.1 ± 16.4 c	203.2 ± 11.8 d
Egg viability (%)		87.9 ± 1.1 a	79.9 ± 0.6 b	74.7 ± 0.73 c	71.12 ± 0.9 d	58.6 ± 1.3 e	48.7 ± 2.1 f

Lipaphis erysimi, *Myzus persicae*, *Aphis craccivora*, *Aphis gossypii*, *Uroleucon compositae*, *Aphis nerii.*
Mean ± SE followed by the same letters in the same row are not significantly different at $P < 0.001$.
$n = 10$, 25 ± 2°C

Table 5.6 Life-history parameters of *Propylea dissecta* as affected by aphid prey (modified after Pervez and Omkar 2004).

Aphid species	***A. gossypii***	***A. craccivora***	***L. erysimi***	***U. compositae***	***B. brassicae***	***R. maidis***	***M. persicae***
Immature survival (%)	77.1 ± 1.1 a	74.1 ± 1.3 ab	71.8 ± 1.5 b	67.7 ± 1.9 bc	67.2 ± 1.9 c	65.3 ± 1.3 cd	63.0 ± 1.9 d
Adult emergence (%)	93.2 ± 0.8 a	92.0 ± 0.9 ab	88.9 ± 1.5 bc	85.3 ± 1.0 c	84.9 ± 1.0 d	82.8 ± 1.5 e	81.7 ± 1.8 e
Female longevity (days)	62.4 ± 1.9 a	58.4 ± 0.9 ab	53.0 ± 2.6 bc	51.9 ± 1.4 c	51.0 ± 1.4 cd	50.9 ± 2.3 d	49.4 ± 2.3 d
Oviposition period (days)	50.3 ± 2.0 a	44.8 ± 0.9 b	34.0 ± 1.6 c	29.0 ± 1.3 c	27.0 ± 1.5 cd	24.2 ± 1.3 d	18.0 ± 1.4 e
Fecundity (eggs/female)	856.0 ± 30.0 a	750.0 ± 36.7 b	506.0 ± 24.1 c	456.8 ± 21.5 d	414.0 ± 17.7 de	374.6 ± 16.8 e	212.0 ± 18.2 f
Egg viability (%)	96.4 ± 0.3 a	95.4 ± 0.4 a	87.0 ± 1.4 b	83.9 ± 1.7 bc	81.2 ± 1.8 c	76.1 ± 1.7 cd	72.5 ± 2.8 d

Aphis gossypii, *Aphis craccivora*, *Lipaphis erysimi*, *Uroleucon compositae*, *Brevicoryne brassicae*, *Rhopalosiphum maidis*, *Myzus persicae.*
$n = 10$; mean ± SE in the same row not followed by the same letter are significantly different at $P < 0.001$.

Table 5.7 Survival rates for larvae of seven coccinellid species fed on *Aphis spiraecola* and *Toxoptera citricida* (modified after Michaud 2000).

	Larvae surviving to adult (%)		
	A. spiraecola	***T. citricida***	***P***
Coccinella septempunctata	5.0	0.0	ns*
Coelophora inaequalis	0.0	0.0	—
Coleomegilla maculata fuscilabris	0.0	45.0	0.01†
Cycloneda sanguinea	60.0	100.0	0.001*
Harmonia axyridis	70.0	95.0	ns*
Hippodamia convergens	68.0	0.0	0.001†
Olla v-nigrum	0.0	0.0	—

Larvae (n = 20) were fed from eclosion on either *A. spiraecola* or *T. citricida*.

*Significant differences based on one-way ANOVA; ns indicates no significant difference.

†Significant differences based on Mann-Whitney *U* test; ns indicate no significant difference.

(Dixon 2007, see also Dixon & Stewart 1991, Stewart et al. 1991, Dixon & Hemptinne 2001). From calculations of minimum mass of prey needed for egg laying and the surface searched within a time unit, both of which scale with body weight, Dixon (2007) maintained that ‘there appears to be no association between the size of aphidophagous predators and that of the species or the age structure of the aphid colonies they exploit’.

In Dixon’s hypothesis (Fig. 5.2a) smaller ladybirds reproduce at lower total aphid densities (thus earlier in the season). The idea that the body of aphidophagous ladybirds and the size of their aphid prey are unrelated has become embedded in the literature, based on the absence of correlation between the weight of seven species of aphidophagous ladybirds of different sizes and the weight of their prey (Dixon & Stewart 1991, Stewart et al. 1991). Furthermore, comparisons between the largest and smallest species showed no difference (Stewart et al. 1991). Comparisons were based on species-specific prey lists from the literature where typical prey was not differentiated from rarely eaten prey. Furthermore, nymphs of early instars are much smaller than adult aphids, and large and small ladybirds evidently exploit them differently. Particularly in the case of large aphid species the relative size affects capture efficiency. This was described by Klingauf (1967) in coccinellid larvae and observed by Sloggett (2008b), when e.g. adults of large *Cinara* conifer aphids were easily caught by adults of the large *Anatis ocellata*, but kicked away the small *Myrrha octodecimguttata*.

A further size-related dilemma commented upon by Sloggett (2008b) is that of the relation between body size of aphidophagous ladybirds and aphid density and size. While Dixon’s (2007) model considers only prey density (Fig. 5.2a), Sloggett (2008b) argues that the relationship is more complex and comprises **both prey size and prey density** (Fig. 5.2b, c). Dixon’s (2007) model holds true when the prey is a small aphid species: large and small ladybirds have the same chance of catching the prey. This is not the case with large aphid species. A small ladybird can only catch young instars (Fig. 5.2b, c). Thus it exploits only a proportion of aphids and needs a higher prey density to catch the same number of aphids (Fig. 5.2b). The largest aphids caught by large ladybirds represent most energy. Small ladybirds are many times less efficient and are likely to need a higher prey density for reproduction (Fig. 5.2c). Simply put, **small ladybirds** can exploit lower densities of small aphid species because they need less food. By contrast, **large ladybirds** can exploit lower densities of large aphid species because they are more efficient at capture. Thus there is a relationship between predator size and prey size, but it is not the rigid relationship as tested by Stewart et al. (1991). In such a situation, with large aphid species, small ladybirds will not reproduce earlier, but later (or not at all) (Sloggett 2008b).

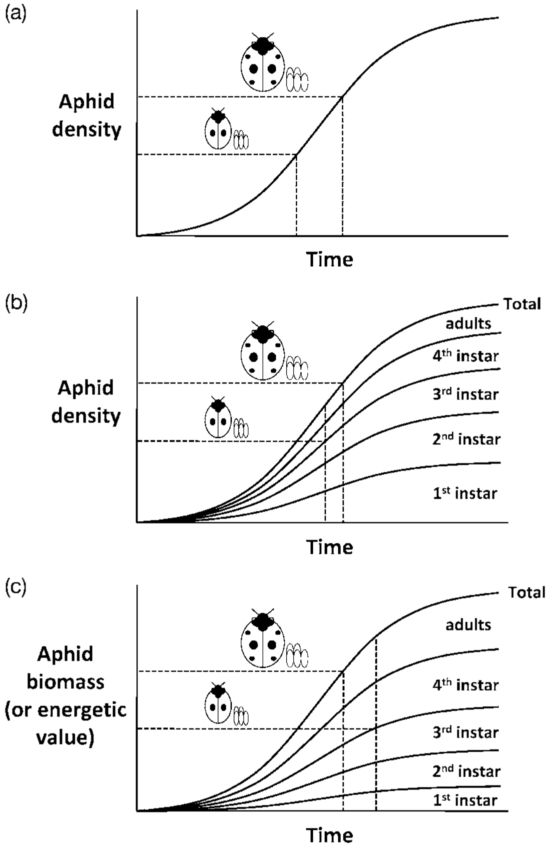

Figure 5.2 Relationship between prey abundance and ladybird body size. In each case the horizontal dashed lines represent the prey threshold necessary for reproduction by the large (upper line) and small (lower line) ladybirds. The vertical dashed lines show the total aphid abundance and the time at which reproduction is possible for each of the species. (a) The established view of Dixon (2007): here there is no relationship between ladybird body size and capture efficiency as might occur with small aphid species. Small ladybirds require a lower density of aphids for reproduction on account of their lower energetic requirements (see text for details) and can thus reproduce earlier in the development of an aphid population. (b) Total aphid density required by a small ladybird is increased if the small ladybird, on account of its size, is unable to catch larger aphid instars (in this case fourth instars and adults); this might occur with large aphid species. Aphid density is broken down into the proportions of the different instars occurring, and does not take into account the differences in size and energetic content of the different aphid instars but only their numerical abundance. (c) A similar, but more realistic graph than (b) taking into account the different energetic values of different instars. Because the small aphid instars which can be caught by a small ladybird are less energy rich than the average aphid, this acts to make the total abundance of aphids necessary for reproduction higher still, leading to a situation where a small ladybird reproduces later than a large one (from Sloggett 2008b).

Sloggett (2008b) quotes several pieces of evidence, supporting his prey size–density hypothesis. These include: (i) Banks (1955) recorded on nettles (*Urtica dioica*) infested by the larger aphid *Microlophium carnosum*, earlier arrival of large numbers of *C. septempunctata* and only later appearance of *A. bipunctata* and *P. quatuordecimpunctata*. (ii) Evans (2004) reported that *C. septempunctata* can exploit the large pea aphids (*A. pisum*) on alfalfa at lower densities than can the smaller native ladybirds. The topic was revisited in Honěk et al. (2008a, b), when aphids were rather small and ladybirds thus followed Dixon's (2007) argument.

5.2.4 Euryphagous and stenophagous species / Generalist and specialist species

In most of 5.2 the discussion is focussed on specific prey types. In this section the focus is on the characteristics of the coccinellid species, in particular the contrast between those that can successfully develop and reproduce on only a narrow range of foods, that is specialist or stenophagous species, and those with a rather wide range of essential prey / foods – generalist or euryphagous (polyphagous) species. The latter species may be more easily manipulated when used in biological control (Chapter 11) as they can be more easily mass-produced on artificial diets (5.2.10) for periodic colonization, or their numbers augmented in the field by providing alternative foods.

In relation to prey, the terms generalists versus specialists have naturally remained rather vague, because, as Sloggett (2008b) rightly points out 'dietary breadth is a continuum, rather than a dichotomy'. Thus we have hesitated (Hodek & Michaud 2008) over which of these terms to use for *A. bipunctata* to indicate its difference from *C. septempunctata*: we considered

Table 5.8 Dichotomization of the British aphidophagous Coccinellini into dietary generalists and specialists. For discussion on conifer specialists see Sloggett and Majerus (2000) (modified after Sloggett 2008b).

Generalists	Specialists (habitat)
Adalia bipunctata	*Adalia decempunctata* (trees and shrubs)
Calvia quatuordecimguttata	*Anatis ocellata* (conifers)
Coccinella magnifica	*Anisosticta novemdecimpunctata* (reed beds)
Coccinella quinquepunctata	*Aphidecta obliterata* (conifers)
Coccinella septempunctata	*Harmonia quadripunctata* (conifers)
Coccinella undecimpunctata	*Hippodamia tredecimpunctata* (reed beds, marsh)
Hippodamia variegata	*Myrrha octodecimguttata* (conifers)
Propylea quatuordecimpunctata	*Myzia oblongoguttata* (conifers)

C. septempunctata to be a habitat generalist, but more specialized to prey (24 essential prey in Hodek's 1996 list). *A. bipunctata* seems to us more habitat specialized, with a clear preference for shrubs and trees, but less specialized towards prey (40 essential prey in Hodek's 1996 list). Both *A. bipunctata* and *C. septempunctata* appeared in the same group of generalists in a recent paper (Sloggett 2008b), where 16 British aphidophagous Coccinellini are divided into eight generalists and eight specialists (Table 5.8).

As underlined by Sloggett (2008b) evolution of specialization in predators operates by fitness trade-offs between types of prey. Adaptations enabling high fitness on one type cause a decrease in fitness with other prey types. Such a trade-off holds also for generalist versus specialist predators. Specialists are very successful on only a few types of prey, but perform poorly on many others, while for generalists there is less variation in performance on a wider range of prey. More specialised aphidophagous ladybirds are less mobile due to their greater tolerance of lower aphid densities (Sloggett et al. 2008).

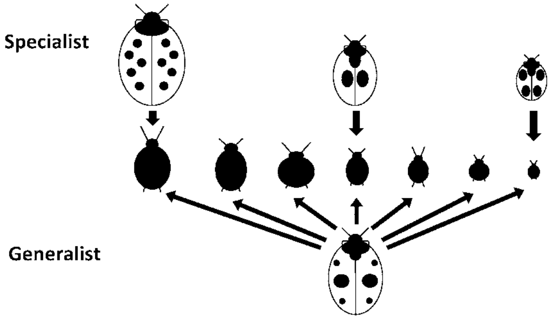

Figure 5.3 Body sizes of ladybirds which are dietary specialists and generalists in relation to aphid size. Specialists will closely match their prey in size whereas generalists, which feed on prey of a diversity of sizes, will be medium sized. As a result, specialists are expected to display a wider diversity of sizes than generalists (from Sloggett 2008b).

Interest has always been concentrated on trade-offs related to prey nutritive suitability, as affected by allelochemicals derived from prey host plants. However, no unequivocal demonstration of such a chemical trade-off has been made for aphidophagous ladybirds (Sloggett 2008a) (see also discussion at the end of 5.2.5). Sloggett (2008b) therefore suggests that body size may play such a role (5.2.3). A specialist is likely to have the right size to perform well on the special prey: it is big enough to catch the old aphid instars (and adults), but not so big as to need too high a prey density for reproduction, i.e. its size will fit the prey. A generalist will, by contrast, tend to be of medium size and therefore prey on a wide range of aphid sizes (Fig. 5.3, Sloggett 2008b).

Sloggett (2008b) tested his **'body size–dietary breadth' hypothesis** on 16 native British aphidophagous Coccinellini (Table 5.8, Sloggett 2008a). He compared sizes between eight specialists and eight generalists (Fig. 5.4, Sloggett 2008a). The size range of specialists is greater and both the largest (*Anatis ocellata*, *Myzia oblongoguttata*) and the smallest two species (*Anisosticta novemdecimpunctata*, *Aphidecta obliterata*) are specialists. In conclusion the author argues that 'body size is a trade-off of likely considerable importance in determining prey specialization due to its relationship with both prey size and density'. He is right to invite a re-evaluation of the hypotheses on body size, such as those claiming that there is no relationship between predator body size and prey size (5.2.3).

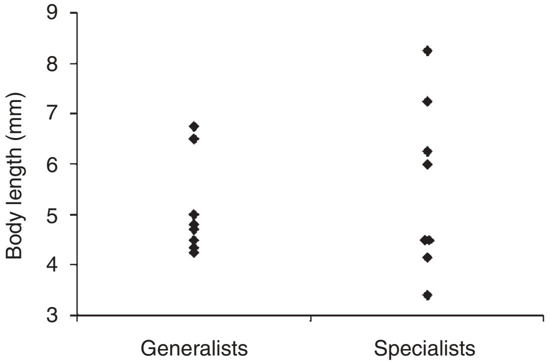

Figure 5.4 The distribution of body sizes in dietary generalists and specialists belonging to the native British aphidophagous Coccinellini (from Sloggett 2008b).

5.2.4.1 Generalists

Coleomegilla maculata

A number of papers have indicated that *Col. maculata* is a widely polyphagous species. Early data on its polyphagy were reported by Putman (1957). The rate of larval development was not decreased by feeding on the **mite** *Tetranychus urticae* compared with feeding on aphids; all larvae completed development, adult survival was very high and oviposition was not inhibited. Another mite, *Panonychus ulmi* also appeared to be suitable food for larvae of *Col. maculata*, and the adults fed much more extensively on crawlers of *Pulvinaria vitis* than did the other coccinellids in the study. Three *Coccinella* spp., *Cycloneda munda* and *A. bipunctata* were less euryphagous.

Studies of this type are also used to imply broad dietary breadth within individual groups of prey, particularly across aphid species. Some such data have been supplied for *C. septempunctata* and *A. bipunctata* by Blackman (1967a, b) and for *Har. axyridis* and *C. s. brucki* by Japanese authors (Okamoto 1961, 1966, Hukusima & Sakurai 1964, Takeda et al. 1964, Hukusima & Kamei 1970). Other examples are also discussed in 5.2.2.

Coleomegilla maculata preys so intensively on **eggs** of some pest insects that it has been studied in the control of the lepidopterans *Heliothis virescens* (Ables et al. 1978) and *Ostrinia nubilalis* (Risch et al. 1982) as well as the Colorado potato beetle *Leptinotarsa decemlineata* (Hazzard & Ferro 1991, Hilbeck et al. 1997, Nault & Kennedy 2000, Mallampalli et al. 2005). Wiebe and Obrycki (2004) reported *Col. maculata* feeding on eggs of another chrysomelid, *Galerucella pusilla*, but the larvae did not thrive well on this prey. The functional response of *Col. maculata* to eggs of *L. decemlineata* was modified by the presence of aphids, but not maize pollen.

An important aspect of euryphagy of *Col. maculata* is its **pollinivory** (5.2.9 for recent data) and an apparent preference for **powdered food**. The preference for lower strata of corn plants discussed in Chapter 4 is apparently related to the pollinivory of this species (Ewert & Chiang 1966). Laboratory tests have proved that pollen of several plants is essential food for *Col. maculata*. The pollens of *Betula populifolia* and *Carpinus caroliniana* were found to be superior to pollen of *Zea mays*, *Cannabis sativa*, *Juglans cinerea* and *Typha latifolia*, but all of these pollens enabled the completion of larval development in *Col. maculata*. By contrast, the pollen of coniferous trees, and also of *Quercus rubra* and *Ambrosia artemisiifolia* was unsuitable (Smith 1960, 1961). When Atallah and Newsom (1966) used stamens of cotton as a source of pollen, *Col. maculata* larvae failed to develop and died within 4 days. Pollinivory of coccinellids, including *Col. maculata*, has been reviewed by Lundgren (2009).

Although *Col. maculata* can develop satisfactorily on mites and coccids (Putman 1957), live aphids (Smith 1965b), and on holometabolan eggs and larvae, its specific relationship to powdered food was shown by preference for aphids in such a form. Only 30% of the larvae completed development if fed with live *Acyrthosiphon pisum*, and the resulting adults weighed only 8.5 mg; the same prey in a dry powdered state, however, gave a much higher survival (90%) and larger adults (12.0 mg) (Smith 1965b). Dry aphids appeared marginally more suitable than pollen (Smith 1965b). In another study, however, *Col. maculata* adults had a doubled pre-oviposition period and a halved fecundity when fed on corn (*Zea mays*) pollen in comparison with live aphids *A. pisum* (Hodek et al. 1978).

A limit to the polyphagy of *Col. maculata* was shown when both adults and larvae refused nymphal leafhoppers of several species, which were, however, eaten by larvae of *C. novemnotata* and adults of *C. trifasciata* (Yadava & Shaw 1968). The nutritional suitability of this prey was not determined.

Harmonia axyridis

Already before the invasion of *Har. axyridis* to the Nearctic region several Japanese authors had reported its polyphagy in relation to aphids (Okamoto 1961, 1966, Hukusima & Sakurai 1964, Takeda et al. 1964, Hukusima & Kamei 1970) and particularly to a substitutive food, represented by a lyophilized powder of drone honey bee larvae (Niijima et al. 1986; 5.2.7). Very high (100%, the same as in *C. septempunctata*) successful completion of larval development was recorded on *Aphis fabae* on sugar beet in California (Ehler et al. 1997). Also after the arrival to Europe, *Har. axyridis* appears to have remained a generalist predator. In Belgium, for example, three aphid species have recently been reported as its prey with *Microlophium carnosum* on *Urtica* preferred before *Acyrthosiphon pisum* on *Pisum* and *Sitobion avenae* on *Triticum* (Alhmedi et al. 2008). *Har. axyridis* was also reported as the most abundant predator of the hemlock wooly adelgid *Adelges tsugae* on *Tsuga* species in southeastern United States (Wallace & Hain 2000). For feeding on psyllids see Hodek and Honěk (2009).

Adalia bipunctata

Wide polyphagy was documented by Mills (1979, 1981, Hodek 1993). Mills reported 28 aphid species as the prey of adults; with seven of them not accepted by the larvae (Table 5.9). An experimental analysis of predation in the field has shown a great variation in the suitability of prey aphids. In terms of the number of coccinellid eggs produced, *Eucallipterus tiliae* on lime appeared the most beneficial, with *Euceraphis punctipennis* on birch as the second best, while *Drepanosiphum platanoidis* on sycamore and *Chaitophorus capreae* on sallow were the least beneficial. Mills concluded that the suitability of an aphid species as prey was most influenced by capture efficiency. This amounted to 58% for the most suitable prey, *E. tiliae*, but only to 21% for the least suitable *D. platanoidis*. The nutritive value of the aphids for *A. bipunctata* was also considered to play a role in prey selection in the field (Mills 1979). Hodek (1996) listed 40 species as essential prey of *A. bipunctata* and this list has not increased much (5.2.11).

Rhopalosiphum padi was less suitable than *Aphis pomi* for egg laying in overwintered females of *A. bipunctata* (Semyanov 1970). Overwintered females had a much greater fecundity than the first generation on the problematic prey *H. pruni*. The host plants of the prey for the two coccinellid generations were not specified. Also the successful rearing of *A. bipunctata* on an artificial diet (Kariluoto 1980) or on *Ephestia kuehniella* eggs (de Clercq et al. 2005) is an indication of polyphagy. In a more recent experiment, *A. bipunctata* larvae developed with highest mortality on *H. pruni* (50%); *Sitobion avenae* was less detrimental (33%), while *R. padi* (22%) and *Myzus cerasi* (18%) might be considered essential larval prey (Ozder & Saglam 2003).

Table 5.9 Aphids on which *Adalia bipunctata* was observed to feed by Mills (1979).

Host plant		Aphid
Alnus glutinosa	—	*Pterocallis alni*
Fagus sylvatica	—	*Phyllaphis fagi*
Betula alba	—	*Euceraphis punctipennis*
Prunus spinosa	—	*Brachycaudus helichrysi*
Sarothamnus scoparius	A	*Aphis* sp.
Prunus cerasus	—	*Myzus cerasi*
Rumex obtusifolius	A	*Aphis* sp.
Sambucus nigra	—	*Aphis sambuci*
Viburnum opulus	A	*Aphis* sp.
Crataegus monogyna	A	*Dysaphis* sp.
Corylus avellana	—	*Myzocallis coryli*
Larix decidua	—	Adelgid sp.
Tilia europaea	—	*Eucallipterus tiliae*
Acer platanoides	A	*Periphyllus testudinaceus*
Urtica dioica	—	*Microlophium carnosum*
Quercus robur	—	*Tuberculatus annulatus*
Vinca major	A	*Aulacorthum solani*
Phragmites communis	A	*Hyalopterus pruni*
Rosa canina	—	*Macrosiphum rosae*
Salix caprea	—	*Chaitophorus capreae*
Pinus sylvestris	—	Adelgid sp.
Castanea sativa	—	*Myzocallis castanicola*
Acer pseudoplatanus	—	*Drepanosiphum platanoidis*
Cirsium arvense	—	*Uroleucon cirsii*
Quercus cerris	—	*Myzocallis boerneri*
Juglans regia	—	*Chromaphis juglandicola*
Salix fragilis	—	*Cavariella* sp.
Salix fragilis	—	*Tuberolachnus salignus*

A, Adults but not larvae of *A. bipunctata* were observed feeding on these prey species.

Hippodamia *spp.*

The relative euryphagy of these species is very favourable for natural biological control on sorghum. On the Texas High Plains, *Rhopalosiphum maidis* provides an early season food source for native coccinellids, mostly *Hip. convergens* (57.0%) and *Hip. sinuata* (36.6%), that lay eggs there. The 'captive' larval population then feeds on the later arriving *Schizaphis graminum*. For the prevention of damaging levels of *S. graminum*, the presence of *R. maidis* is therefore a key factor (Michels & Matis 2008).

Other generalists

Oenopia* (= *Synharmonia*) *conglobata (Kanervo 1940, 1946) and ***Coccinella hieroglyphica*** (Hippa et al. 1984, Sloggett & Majerus 1994) show tendencies towards polyphagy; both aphids and pre-imaginal stages of chrysomelids were found to be essential prey for these species. Kanervo (1940, 1946) claimed that ***Calvia quindecimguttata*** was a specialized feeder on chrysomelids and that aphids were accepted merely as alternative prey. ***Calvia quatuordecimguttata*** can develop well both on psyllids and aphids, while psyllids (particularly *Psylla mali*) appear to be their preferred food, enabling faster larval development, greater weight of pupae and higher fecundity (Semyanov 1980). Feeding and reproduction on all stages of psyllids, mainly *Psylla jucunda* on *Acacia*, was recorded in ***Harmonia conformis*** in Australia over a period of 2 years (Hales 1979). Indications of polyphagy in ***Propylea quatuordecimpunctata*** are discussed in relation to non-insect food in 5.2.9.

Two species of ***Coelophora*** both endemic to New Caledonia, exhibit specificity to different prey groups, namely aphids and coccids. Larvae of the aphidophagous *C. mulsanti*, which feed on the more mobile prey, are more active than larvae of the coccidophagous *C. quadrivittata*. Thus even between congenerics the typical differences in behaviour-related prey mobility are maintained. While the coccidophagous species appears to be rather stenophagous (only one prey is known, *Coccus viridis*), the aphidophagous *C. mulsanti* was euryphagous, being reared on several aphids (*Rhopalosiphum padi*, *Hyperomyzus lactucae*, *Aphis gossypii*); it is also reported to feed on cicadellid larvae in the field (Sallée & Chazeau 1985).

5.2.4.2 Specialists

The thermophilous coccinellid ***Clitostethus arcuatus*** (tribus Scymnini) appears to be a specialized predator of aleyrodids (Hodek & Honěk 2009), ovipositing e.g. on *Aleurodes proletella* (Bathon & Pietrzik 1986). A study of prey specificity of ***Rodolia cardinalis*** before its release to Galapagos confirmed its stenophagy: it feeds specifically on Margarodidae and did not complete development on scale insects from the families Pseudococcidae, Eriococcidae and Coccidae (Causton et al. 2004).

The stenophagy of the genus ***Coccinella*** was already indicated by the findings of Putman (1957) and Smith (1965a; 5.2.10). Of three *Coccinella* spp., two (*C. novemnotata* and *C. trifasciata*) could not complete their larval development on dry powdered aphids. *C. transversoguttata* succeeded at least on one of the three aphids tested (on dry *Acyrthosiphon pisum*) (Smith 1961). Whereas Hodek (1996) listed 24 species of essential prey for *C. septempunctata*, i.e. much less than the 40 species for *A. bipunctata*, both species are often considered as generalists (e.g. Sloggett 2008a, b). Reduced values of *C. septempunctata* life-history parameters on low quality foods are discussed in 5.2.6. The strange report that the larvae of ***Coccinella undecimpunctata*** can complete their development when fed solely on fresh manure (Hawkes & Marriner 1927) has been rightly questioned by Benham & Muggleton (1970) with the plausible explanation that cannibalism was overlooked. The attraction to manure is evidently related to halophily of *C. undecimpunctata* (Hodek et al. 1978 as *Cer. undecimnotata* (sic)). Harpaz (1958) in Israel achieved complete larval development of *C. undecimpunctata* on *Aphis pomi*.

Adelgidae and Lachnidae have been reported as favoured prey of ***Aphidecta obliterata*** (Majerus & Kearns 1989, Klausnitzer & Klausnitzer 1997).

Non-abundant nutrient concept

A novel view of the relation between prey and a ladybird was suggested by Cohen and Brummett (1997). They criticized the '**rule of sameness**' (House 1974) which maintains that nutritional requirements of insects are in principle (i.e. excluding consideration of allelochemical content) 'similar regardless of systematic position or feeding habit of the species'. Despite caveats expressed by House (1974), his rule has been interpreted broadly to imply that nutritional differences are negligible between various prey species. Cohen and Brummett (1997) point out that this liberal interpretation has resulted in a neglect of important differences in the nutritional composition of various prey. Inspired by Liebig's 'law of the minimum', Cohen and Brummett measured the body content of **methionine** (the least abundant amino acid) in three predators and three prey. Thus *E. kuehniella* eggs contain 11.2 ng/mg, while *Bemisia* larvae only have 0.2 ng/mg of methionine. The adult ladybird *Serangium parcesetosum* contains only 6.1 ng/mg, while *Chrysopa* or *Geocoris* have 10.0 ng/mg of methionine. *S. parcesetosum*, with its lower carcass methionine content but also smaller size, shorter handling time and shorter life span, is more suited to be a successful, long-term predator of *Bemisia* than are either *Chrysopa* or *Geocoris*.

This principle does not only apply to methionine. Other substances, such as other essential amino acids as well as sterols, polyunsaturated fatty acids or vitamins, may be limiting. Cohen and Brummett (1997) stress that 'explanation of fitness of predators to their prey is more likely to be found in considering nutrients that are non-abundant rather than energy'.

5.2.5 Mixed and combined diet

The role of **mixing** of different dietary resources has been studied quite frequently in phytophagous insects and has been found to be positive in most cases (for references see Unsicker et al. 2008). The favourable effect of mixed diets, more often documented in non-coccinellid predators (recently e.g. by Harwood et al. 2009) has been explained by several theories: either by the necessity to get a more complete and balanced range of the nutrients needed (Pulliam 1975, Raubenheimer & Simpson 1999), or to dilute allelochemicals present in individual host plants and therefore to decrease their toxic effect (Freeland & Janzen 1974, Behmer et al. 2002).

In predaceous ladybirds this approach has long been neglected. Feeding on several kinds of food has been interpreted as a rather emergency feature, compelled by shortage of the 'right' food. Frequently this is true and we may then rightly speak about alternative, or substitution food. In particular cases, in species such as *Tytthaspis sedecimpunctata* (Ricci 1982; 1986a; Ricci et al. 1983), *Rhyzobius litura* (Ricci 1986b), *Illeis galbula* (Anderson 1982) and perhaps also *Propylea* spp. (Turian 1971, Hukusima & Itoh 1976) and other polyphagous species, when even taxonomically distant organisms serve as food (5.2.7, 5.2.9), mixed feeding appears favourable, and is a usual phenomenon.

The coccinellids may select a favourable balance of important nutrients from pollen and conidia of mildew, or pollen and aphids etc., as is assumed by the model of **self-selection** of optimal diets (Waldbauer & Friedman 1991). Some workers have already attempted to check by experiments the suitability of **food combinations** for coccinellids. The simultaneous presence of two prey has been found to increase the predation rate of *Har. axyridis* (Lucas et al. 2004; Fig. 5.5). A positive effect of coccinellid feeding on curculionid larvae in

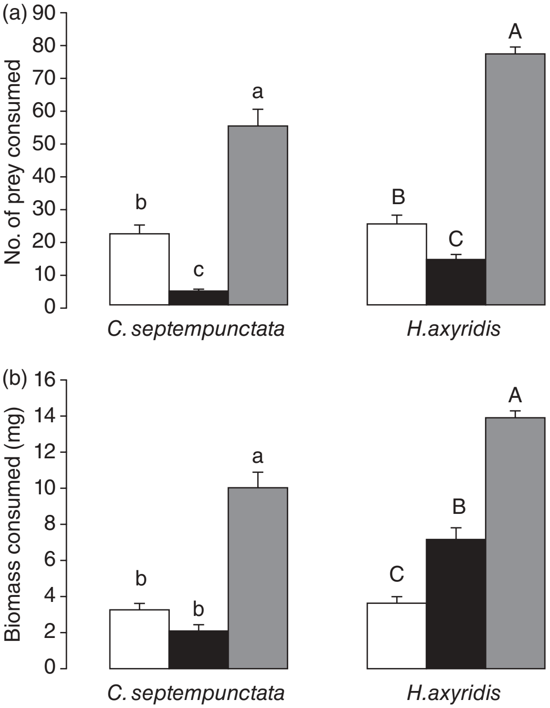

Figure 5.5 Overall predator voracity (mean ± SE) of *Coccinella septempunctata* and *Harmonia axyridis* in 24 hours, when offered 100 *Aphis pomi* (white bars), 30 larvae of *Choristoneura rosaceana* (black bars) or both prey species (grey bars). (a) Total number of prey predated. (b) Total biomass consumed. Different letters indicate a significant ($P < 0.05$) difference among the different treatments for the same coccinellid species (modified from Lucas et al. 2004).

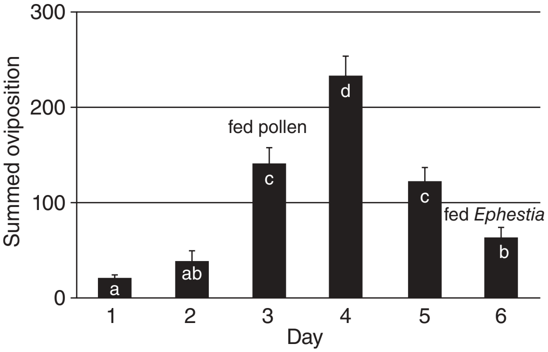

Figure 5.6 Total egg production (mean ± SEM) by *Hippodamia convergens* females ($n = 113$) over 135 days as a function of food provisioning showing the peak in oviposition every fourth day following provision with animal protein. Females paired with males were held on a 6-day feeding cycle (eggs of *Ephestia kuehniella* once every 6 days followed by pollen 3 days later) with continuous access to sunflower petioles). Means bearing the same letter were not significantly different (Tukey test, $\alpha > 0.05$) (modified from Michaud & Qureshi 2006).

fields of alfalfa, when essential aphid prey is available only at low levels, was studied by Evans and collaborators (5.2.7). The importance of animal protein from *E. kuehniella* for egg laying was documented in *Hip. convergens* (Michaud & Qureshi 2006; Fig. 5.6). Related findings by Snyder et al. (2000) are discussed in 5.2.8.2.

In some experiments, however, no benefit from mixing was observed. Four species of ladybirds, reared on the mixture of *Myzus persicae* and eggs of *Leptinotarsa decemlineata*, had lower survival and development rate than the controls reared on aphids alone (Snyder & Clevenger 2004). They did not avoid eating the chrysomelid eggs, although there was a surplus of aphids. Similarly *C. septempunctata* did not benefit from a mixed diet of three aphid species, *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi*. The value of this mixture was intermediate between the higher quality single species diets of one of the first two species and the lower quality *R. padi*. The cause of quality differences, either nutrient content (Cohen & Brummett 1997) or presence of allelochemicals (Hauge et al. 1998), remained unknown. It is most interesting that in the studies cited above the authors found that the same ranking of the three aphid prey for quality also applied for spiders and carabids. Nielsen et al. (2002) used a mix of very good essential prey (the aphid *Metopolophium dirhodum*) and two slightly lower quality essential prey (*Myzus persicae* and *Sitobion avenae*) for *C. septempunctata*. Again no benefit of mixing was recorded although the mixed diet contained entirely essential aphid prey, whether the aphids had been raised on the same or different host plants. Inclusion in the mix of a toxic aphid (*A. sambuci*) considerably decreased the larval fitness of *C. septempunctata*. This result again demonstrates the inability of coccinellids to avoid toxic prey. A similar finding for the same predator and prey (Nedvěd & Salvucci 2008) is discussed in 5.2.6.1.

Males of *Har. axyridis* showed a consistent feeding preference for *Myzus persicae* versus *A. fabae*, while the females did not show any preference. Mixing the aphids in varying ratios of *M. persicae* to *A. fabae* did not affect oviposition rate (Soares et al. 2004). Similarly Phoofolo et al. (2007) did not find any difference between a one-species diet and a mixed diet of *Schizaphis graminum* and *Rhopalosiphum padi* for larvae of *Hip. convergens*.

One-species prey, but a **mixture of different developmental stages**, may appear more suitable for the predator than a homogeneous prey consisting of only one stage. Transfer of females of *Chil. nigritus* after 10 days feeding on a heterogeneous mixture of all stages of the diaspid *Abgrallaspis cyanophyli* to homogeneous prey resulted in an important decrease in oviposition during the next days (Ponsonby & Copland 2007b; Table 5.10). It has also been suggested for other insects that treating a prey population as a homogenous entity can lead to erroneous conclusions (Rudolf 2008).

5.2.5.1 Complementation across stages

By changing the diet between larvae and adults of the highly polyphagous *Col. maculata*, Michaud and Jyoti (2008) revealed what they called 'dietary complementation across life stages'. Coccinellid larvae appear to process some types of food more efficiently than adults. Eggs of the pyralid *Ephestia kuehniella* were the best diet for the larvae and resulted in the largest adults, with highest fecundity (182 eggs) and shortest preoviposition period when the adults were then fed on aphids (*Schizaphis graminum*). This combination thus led to higher fecundity than continuous feeding on aphids (139 eggs) or continuous feeding on

Table 5.10 Decrease in total egg laying after a change in prey population structure in *Chilocorus nigritus* fed on *Abgrallaspis cyanophyli* at 26°C ($n = 5$) (modified after Ponsonby & Copland 2007b).

Prey stage	No. of eggs laid (±SD)
Treatment 1 control	
10 days on all stages	165.0 (57.6)
10 days on all stages	174.2 (26.4)
Treatment 2	
10 days on all stages	141.2 (33.4)
10 days on first-instar nymphs	91.0 (37.6)
Treatment 3	
10 days on all stages	138.6 (48.1)
10 days on second-instar nymphs	69.6 (41.3)
Treatment 4	
10 days on all stages	135.8 (37.8)
10 days on adult females	71.4 (57.1)

Table 5.11 Mean values for the reproductive performance of female *Coleomegilla maculata* revealing interactions between larval and adult diets. Larvae were fed one of three diets and the adults obtained in each treatment further subdivided into two groups, each got one of two adult diets (after Michaud & Jyoti 2008).

	Adult diet	
Larval diet	Greenbug*	Flour moth eggs†
	Pre-reproductive period (days)	
Greenbug	14.9	14.9
Flour moth eggs	10.9	16.4
Pollen	15.8	14.3
	Reproductive period (days)	
Greenbug	30.1	20.1
Flour moth eggs	22.2	23.1
Pollen	28.5	23.7
	Fecundity (number of eggs/female)	
Greenbug	138.7	161.3
Flour moth eggs	182.4	146.3
Pollen	125.8	106.5
	Fertility (percentage of egg hatch)	
Greenbug	42.4	65.8
Flour moth eggs	48.8	68.1
Pollen	49.1	46.7
	Fertility (number of larvae/female)	
Greenbug	58.0	108.1
Flour moth eggs	129.4	101.1
Pollen	66.8	50.3

**Schizaphis graminum.*
†*Ephestia kuehniella.*

lepidopteran eggs (146 eggs) (Table 5.11). The authors conclude that both foods are essential, but nutritional demands for larval growth and development versus adult dispersal and reproduction may differ. *E. kuehniella* eggs were also combined with *Acyrthosiphon pisum* in similar experiments on *P. japonica* (Hamasaki & Matsui 2006; Table 5.12).

5.2.5.2 Prey switching

Can switching of prey have a significant effect on the predator? *Chilocorus nigritus* larvae can switch from feeding on *Coccus hesperidum* (Coccidae) to *Abgrallaspis cyanophyli* (Diaspididae) and vice versa with only minor detrimental effects. Subsequent generations proved that both these prey were essential (Ponsonby & Copland 2007a).

5.2.5.3 Prey specialization through selection

The performance gradually increased over six *A. bipunctata* generations when they were reared and selected on *Aphis fabae*, a rather poor prey (5.2.6.3); e.g. the mortality decreased from 58 to 0%. The achieved specialization to *A. fabae* resulted in poorer performance on the previously (and generally) highly suitable prey, *Acyrthosiphon pisum*. The authors assume that this ability to adapt enables *A. bipunctata* to 'switch' from the more suitable tree-dwelling aphids, such as e.g. lime aphid *Eucallipterus tiliae*, to field aphids occurring later in the season (Rana et al. 2002). While the results of such apparent selection are very important, the general validity of this interpretation is contentious (Sloggett 2008b). Furthermore, tree aphids are poor prey, while some field aphids (such as *A. pisum*) are excellent prey. Also some aphids return from fields to primary hosts (trees, shrubs) in late season.

5.2.6 Lower quality prey (mostly aphids)

5.2.6.1 Toxic prey

The reasons why particular prey species are harmful to particular coccinellids have not yet been fully explained.

Table 5.12 Reproductive traits of *Propylea japonica* reared on *Acyrthosiphon pisum* or *Ephestia kuehniella* eggs (modified after Hamasaki and Matsui 2006).

Larval diet	***A. pisum***	***E. kuehniella* eggs**	***A. pisum***	***E. kuehniella* eggs**	***A. pisum***	***E. kuehniella* eggs**
Adult diet	**Pre-oviposition period (d)**		**Eggs laid per 20 d***		**Egg hatchability (%)†**	
A. pisum	3.9 ± 1.4 (15)	3.7 ± 1.5 (19)	184.4 ± 106.8 (15)	210.9 ± 95.9 (19)	60.8 ± 9.2 (15)	63.7 ± 20.0 (19)
E. kuehniella eggs	6.8 ± 3.6 (13)	5.3 ± 1.4 (15)	58.0 ± 33.8 (13)	76.5 ± 52.1 (15)	77.5 ± 15.5 (13)	66.5 ± 21.0 (15)

Mean ± SD. Values in parentheses indicate the number of samples.
*Total number of eggs laid per female for 20 d after emergence.
†Percentage of hatched larvae.

That death is caused by starvation, resulting from a low feeding rate on unsuitable food, may be discounted because in experiments comparably reduced feeding on other, essential food did not cause a substantial rise in mortality (e.g. Hodek 1957a). There remain two other possibilities. Either the unsuitable aphids contain some special **substances** (**allelochemicals derived from the plants**) **poisonous** to coccinellids, or such aphids are deficient in nutritive value. Most studies have focussed on the former possibility.

Aphis sambuci

Jöhnssen (1930) observed a marked increase in feeding by *C. septempunctata*, when he switched it from *Aphis sambuci* to *A. hederae*. In two experiments, Hodek (1956) also found a rather low intake of *A. sambuci* by *C. septempunctata* and showed that this aphid is inadequate food for both larvae and adults of *C. septempunctata*; the larvae could not complete their development and died within 25–26 days. In the first experiment (started 24 June) two-thirds of the larvae died in the fourth instar after a higher feeding rate, while in the second experiment (started 22 July) all but one died in the third instar after a much lower feeding rate (Fig. 5.7). This difference may have been caused by differing chemical compositions in different phenological phases of the host plant and consequently also in the aphids.

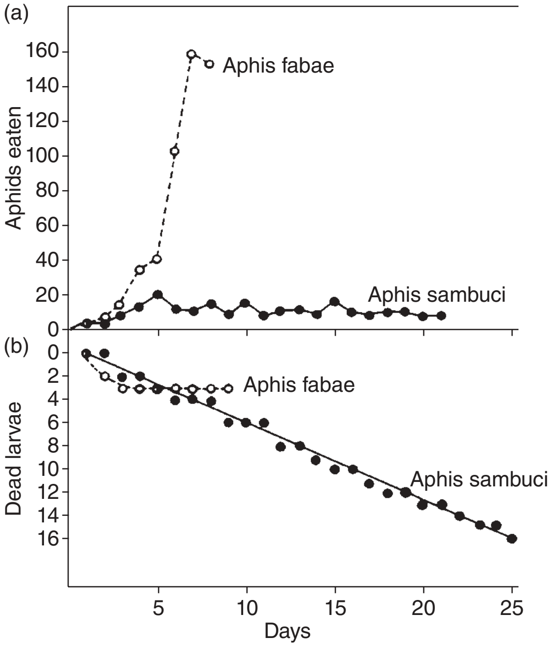

Figure 5.7 Effect of *Aphis sambuci* in comparison with *Aphis fabae* on the larval development of *Coccinella septempunctata*. (a) Daily feeding rate of larvae. (b) Mortality of larvae (from Hodek 1956).

All **freshly emerged** *C. septempunctata* adults died on average after 17.5 days when fed only on *A. sambuci*. The control adults, fed on *Aphis fabae* (= *A.cirsiiacanthoidis*) or on *Uroleucon aeneus* had at most a mortality of 16.6%. Compared to the control, the survival of **overwintered adults** on *A. sambuci* was not decreased, but egg laying was inhibited (Hodek 1957b) and ovaries did not mature. Not until suitable food had been provided for 9 days, did the adults begin to oviposit. As the aphid host plant *Sambucus nigra* often

Table 5.13 Larvae of *Coccinella septempunctata* fed on reduced daily rates of *Aphis fabae* (Hodek 1957a).

Daily feeding rate in 4th instar (number of aphids)	Duration of development (days)					Mortality (%)	*n*
	Larval instars						
	1 + 2 + 3	4	Prepupa	Pupa	Total		
surplus (aver. consumed 70)	5.2	2.6	1.0	4.0	12.8	8	13
30	4.8	3.7	0.8	4.2	13.5	0	18
10	4.9	5.9	0.9	4.2	15.9	10	20

Table 5.14 Survival to adulthood, larval times, total developmental times and adult weights of *Coccinella septempunctata* larvae on different aphid diets (modified after Nielsen et al. 2002).

Aphid diets	*n*	No. survived*	Larval time (days)[†]	Total developmental time (days)[†]	Adult weight (mg)[‡]
Experiment 1					
Metopolophium dirhodum	30	26 a	11.27 ± 0.20 a	15.27 ± 0.22 a	25.54 ± 0.84 a
Myzus persicae	30	20 ab	12.95 ± 0.17 b	16.70 ± 0.15 b	18.88 ± 0.67 b
Aphis sambuci	30	0 c	—	—	—
M. dirhodum and *M. persicae*	30	18 b	11.22 ± 0.21 a	15.06 ± 0.12 a	25.44 ± 0.81 a
M. dirhodum and *A. sambuci*	30	2 c	13.50 ± 0.50 ab	17.00 ± 0.00 b	14.58 ± 1.78 b
M. persicae and *A. sambuci*	30	0 c	—	—	—
M. dirhodum, *M. persicae* and *A. sambuci*	30	5 c	17.80 ± 0.38 b	21.60 ± 0.51 c	16.14 ± 1.21 b
Experiment 2					
M. dirhodum	50	27 a	11.26 ± 0.17 a	15.33 ± 0.19 a	27.57 ± 0.95 a
Sitobion avenae	50	35 a	12.09 ± 0.26 b	16.11 ± 0.27 b	28.09 ± 0.73 a
M. dirhodum and *S. avenae*	50	34 a	11.41 ± 0.20 c	15.18 ± 0.17 a	28.63 ± 0.90 a

Mean ± SE; within columns and experiments the same letters indicate no significant difference between treatments.

*χ^2 test; numbers in this column are sample sizes for next three columns.

[†] Multiple comparisons after Kruskal–Wallis tests.

[‡] Fisher LSD test.

grows at or near *C. septempunctata* hibernation sites, the adults may be found in colonies of *A. sambuci* in the spring, but they do not lay eggs there.

The possibility that the insufficient feeding rate on *A. sambuci* (Fig. 5.7) might cause the mortality of *C. septempunctata* larvae by starvation was excluded by rearing the most voracious fourth instar (Hodek 1957a) on substantially reduced food rations of the suitable food – *A. fabae* (Table 5.13). The reduction of feeding rate to one-seventh prolonged the fourth instar, but there was no increase in mortality. Development was completed with only about one-third of the total larval food intake, with a surplus of aphids. If only some larval instars were fed with *A. sambuci* (Hodek 1957a), most (68–76%) larvae pupated and larval development was prolonged. In a later study in England *A. sambuci*, although a very poor food, enabled half the specimens of *C. septempunctata* to develop to extremely small adults (Blackman 1965, 1967b). A negative effect of *A. sambuci* on *C. septempunctata* was also documented by Nielsen et al. (2002; Table 5.14), and on *C. magnifica* by Sloggett et al. (2002).

The larvae of *A. bipunctata* completed development on *A. sambuci*, although at a slower rate than on *A. fabae* (Hodek 1957a). This was confirmed by Blackman (1965, 1967b). In central Europe this species breeds mostly on shrubs and trees, i.e. in the same habitat as *A. sambuci*. The larvae of *Scymnus subvillosus* seem

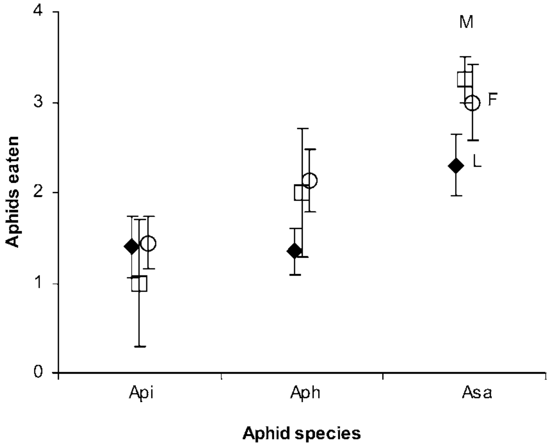

Figure 5.8 Consumption rates (mean ± SE) per 4 hours by *Coccinella septempunctata* larvae (L, solid diamonds), males (M, open squares), and females (F, open circles) on three aphid species. Api, *Acyrthosiphon pisum*; Aph, *Aphis cirsiiacanthoidis*; Asa, *Aphis sambuci* (from Nedvěd & Salvucci 2008).

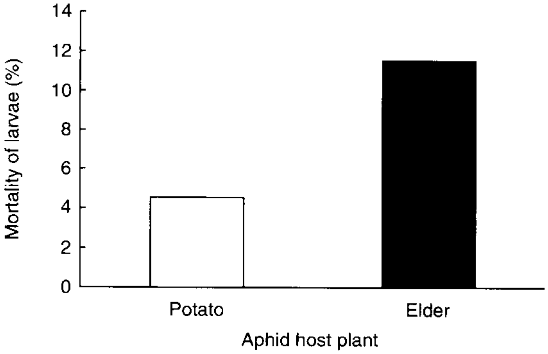

Figure 5.9 Mortality of *Harmonia axyridis* larvae 7 days after rearing began, when they were fed with *Aulacorthum magnoliae* reared on potato ($n = 243$) or elder ($n = 243$) (from Fukunaga & Akimoto 2007).

to be adapted to feeding on *A. sambuci*; Klausnitzer (1992) was able to rear late instar larvae to adults on this diet.

For *Aphis sambuci* we may assume passage of the **glycoside sambunigrin**, contained in the host plant *Sambucus nigra*, from the plant into the aphid. This glycoside may be split enzymatically into hydrocyanic acid in the body of the coccinellid, for enzymes which split glycosides have been identified in the body of *Coccinella* spp. (Kuznetsov 1948).

Contrary to expectation, *Aphis sambuci* was preferred in a preliminary, 4-hour choice experiment to *Aphis cirsiiacanthoidis* and *Acyrthosiphon pisum* (Nedvěd & Salvucci 2008; Fig. 5.8). Starved fourth instar or adult *C. septempunctata* consumed twice as many *A. sambuci* as of the two other aphid species. These preference tests again show how misleading observations of prey acceptance can be for evaluating prey suitability. Nedvěd & Salvucci (2008) recorded *C. septempuctata* fourth instars dying when fed on *A. sambuci*, thus confirming the earlier findings of Hodek (1956), Blackman (1965) and Nielsen et al. (2002).

Aulacorthum magnoliae

Similar or identical allelochemical substances are also the likely lethal agent in *A. magnoliae*. This aphid, also from an elder (*Sambucus racemosa* ssp. *sieboldiana*), was found to be toxic to *C. septempunctata brucki* and *Har. axyridis* (Okamoto 1966). This was confirmed by Fukunaga and Akimoto (2007; Fig. 5.9) who found high larval mortality of *Har. axyridis* that preyed on *A. magnoliae* fed on *S. r. sieboldiana*. The authors consider that the aphid absorbs toxic substances or their precursors from *Sambucus*.

Aphis craccivora

Aphis craccivora from a number of different host plants was recorded as unsuitable food for *Har. axyridis* already in early studies (Okamoto 1966, 1978, Hukusima & Kamei 1970 in Hodek 1996) and again more recently by Ueno (2003; Table 5.15), who however found lower toxicity than were reported in the earlier studies. Hukusima & Kamei (1970) found that *Har. axyridis* larvae did not develop on this prey, and adults also died within 4–6 days if the aphid was collected from *Robinia pseudoacacia* or six other host plants. However, *A. craccivora* was a favourable food when fed on *Vicia sativa* or *Vigna unguiculata* subsp. *cylindrica*. In contrast to *Har. axyridis*, both larvae and adults of *P. japonica* were resistant to the detrimental effect of *A. craccivora* from *R. pseudoacacia*. In Okamoto's (1966) experiments, *Har. axyridis* larvae also died when *A. craccivora* was reared on *Vicia faba* instead of *R. pseudoacacia*.

Hukusima & Kamei (1970) suggested **allelochemicals** as the explanation for the probably toxic effect of

Table 5.15 Larval period and pupal mass of *Harmonia axyridis* reared on *Acyrthosiphon pisum*, *Aphis craccivora*, or artificial diet (after Ueno 2003).

	Food		
	A. pisum	***A. craccivora***	**Artificial diet**
	Larval period (days)		
Male	13.8 ± 0.5 (44)	18.8 ± 0.7 (32)	19.7 ± 0.6 (32)
Female	13.1 ± 0.3 (45)	20.6 ± 0.8 (22)	21.1 ± 0.6 (41)
	Pupal mass (mg)		
Male	27.2 ± 0.5 (44)	19.6 ± 0.6 (32)	20.9 ± 0.9 (32)
Female	28.5 ± 0.7 (45)	22.0 ± 0.9 (22)	23.1 ± 0.7 (41)

Mean ± SE. Sample sizes are given in parentheses.
Both aphids were reared on bean plant seedlings in glass tubes.

A. craccivora on *Har. axyridis*. The authors reported that aphids from *R. pseudoacacia* contained two extra amino acids (glycine and arginine) in contrast to aphids from other host plants, though these are not normally considered to be toxic substances. In later experiments, also in Japan, the lethal effect of *A. craccivora* fed on *R. pseudoacacia* was ascribed to the **amines canavanine** and **ethanolamine** isolated both from the host plant and the aphid by Obatake and Suzuki (1985).

Cer. undecimnotata can neither complete larval development nor oviposit when fed on *Aphis craccivora* (from *Vicia faba*), though on the same host plant *A. craccivora* is an essential food for *C. septempunctata* (Hodek 1960). Azam and Ali (1970) reported *A. craccivora* as lethal for *C. septempunctata* when the aphid was fed on *Glycinidia*. The effect of host plant chemistry on the unsuitability of prey might explain an earlier observation that the larvae of *C. septempunctata brucki* and *P. japonica* die when fed on *A. craccivora* in spring, but not in summer (Takeda et al. 1964). Different host plants were probably involved. **Different concentrations of allelochemical substances** in the same plant but in different seasons of the year might be another plausible explanation, indicated by findings from another aphidophagous insect, *Chrysopa perla*. When the lacewings were fed on *Aphis nerii* from *Nerium oleander* in June, none survived, but the survival was much higher (78%) in winter (Canard 1977).

Megoura viciae

While **gradual poisoning** is one of the possible explanations of the detrimental effect of some unsuitable aphids (as *A. sambuci* or *A. craccivora*), in some instances an **acute toxic effect** has been proven or at least strongly indicated.

Larvae of *A. decempunctata* attacked and ate *Aphis fabae* and *M. viciae*, but after about 2 minutes the larvae released the prey and vomited and 50% of larvae provided with *M. viciae* died (Dixon 1958). The toxicity of *M. viciae* to *A. bipunctata* was studied in detail by Blackman (1965, 1967b) who found this aphid to be lethal to all larval stages and to adults. Neither larvae nor adults avoid attacking this aphid when mixed with suitable prey. Even when *M. viciae* and the non-toxic *Acyrthosiphon pisum* were provided in the ratio of 1:9, all the larvae failed to reach the pupal stage. The first instar larvae, when fed on this prey, perished more rapidly than those starved. The fourth instars accepted *M. viciae* readily, but after about 4 min. of feeding they suddenly rejected their prey and vomited. When fed on this prey, all adults died within a week of emergence. Frechette et al. (2006; Table 5.16) have more recently confirmed the toxicity of *M. viciae* for *A. bipunctata*. Even the larvae of the polyphagous *Har. axyridis* cannot develop when fed exclusively on *M. viciae*. They succeeded only when at least the first instar larvae were fed on *Aphis gossypii* that evidently is essential prey for this coccinellid (Tsaganou et al. 2004). *M. viciae* is toxic to *Exochomus quadripustulatus*: the larvae died within 2 days (Radwan & Lövei 1983), and the aphid is very unsuitable for *Cycloneda sanguinea* (Isikber & Copland 2002; Table 5.17).

The rapid response of *A. bipunctata* and *A. decempunctata* to *M. viciae* indicates a toxic effect. A toxic substance suspected (Dixon 1958) was, however, not found in chemical analysis of the aphid (Dixon et al. 1965). In contrast to the results from the

Table 5.16 Number of eggs laid by *Adalia bipunctata* females that oviposited after 8 and 24 hours, and the percentage of mortality after 24 hours in the presence of three aphid species, *Acyrthosiphon pisum*, *Aphis fabae* and *Megoura viciae* (modified after Frechette et al. 2006).

	Previously fed on	Treatment	*n*	No. of eggs		Mortality (%)
				8 h	24 h	
Experiment 1	*A. pisum*	*A. pisum*	17	13.00 ± 1.94 (*n* = 9)	14.40 ± 1.33 (*n* = 15)	0
	A. pisum	*A. fabae*	17	11.40 ± 1.69 (*n* = 10)	13.92 ± 1.76 (*n* = 13)	0
	A. pisum	*M. viciae*	20	7.63 ± 1.80 (*n* = 8)	9.63 ± 1.38 (*n* = 16)	20
Experiment 2	*A. fabae*	*A. pisum*	18	13.10 ± 1.80 (*n* = 10)	15.79 ± 2.17 (*n* = 14)	0
	A. fabae	*A. fabae*	18	12.88 ± 1.76 (*n* = 8)	16.58 ± 2.56 (*n* = 12)	0

Mean ± SE; negative effect of *M. viciae* was shown by both parameters, egg laying and mortality.

Table 5.17 Developmental time and survival rate of *Cycloneda sanguinea* on four aphid species (modified after Isikber & Copland 2002).

	A. gossypii	*A. fabae*	*M. persicae*	*M. viciae*	P value
Overall development*	14.6 ± 0.2 b (12)	15.2 ± 0.2 b (13)	14.5 ± 0.3 b (10)	16.7 ± 0.8 a (7)	P < 0.01
Overall survival†	0.86 a (14/12)	0.81 a (16/13)	0.77 a (13/10)	0.39 b (18/7)	P = 0.012

Aphis gossypii, *Aphis fabae*, *Myzus persicae*, *Megoura viciae*

Values within rows with the same letter are not significantly different (LSD at 1% level). One way ANOVA was applied for data analysis.

*Overall development (larva + prepupa + pupa). Figures in brackets show the number of individuals as replicates.

†Overall survival (larva + prepupa + pupa). Figures in brackets show the numbers of individuals at the start and at the end of development, respectively.

aforementioned species, more than 60% of *C. septempunctata* larvae successfully completed development on *M. viciae*, although a slightly negative effect was shown on the length of development and weight of emerged adults (Blackman 1965, 1967b; Table 5.18).

Aphis nerii

Aphis nerii infests host plants in the families Asclepiadaceae (milkweeds) and Apocyanaceae (oleander). Oleanders are toxic due to high levels of the **cardiac glycoside cardenolides**, particularly **oleandrin** and **neriin**. The cardenolides are ingested by the aphid, sequestered and excreted in the honeydew (Rothschild et al. 1970, Malcolm 1990). Malcolm identified 25 cardenolides in *Nerium oleander* and 17 of them in the aphids; 20 were detected in the honeydew. *A. nerii* on *N. oleander* is poisonous to most coccinellids that have been tested, including *C. septempunctata*, *Cer. undecimnotata*, *P. quatuordecimpunctata* and *A. bipunctata* (Iperti 1966), and *Harmonia dimidiata*, *C. septempunctata brucki* and *C. leonina* (Tao & Chiu 1971). An exception is *Hip. variegata*, which developed normally on this prey (Iperti 1966). Bristow (1991) observed that honeydew produced by leaf-feeding *A. nerii* was less palatable to ants (*Linepithema humile*) than honeydew from floral colonies. She also offered aphids from these two plant parts to *Hip. convergens* adults, and these consumed significantly more leaf than floral aphids. The ladybirds often failed to consume the aphid entirely and

Table 5.18 Development of *Coccinella septempunctata* larvae on different aphids (Blackman 1965, 1967b).

Aphid species	Development (days)	Mortality (%)	Weight of adult at emergence (mg)
Myzus persicae	13.0	12.5	36.4
Aphis fabae	13.6	9.1	36.3
Acyrthosiphon pisum	13.3	18.6	37.2
Megoura viciae	14.8	13.4	33.5
Brevicoryne brassicae	16.1	26.1	30.9
*Aphis sambuci**	19.5	50.0	18.4

*Only 6 out of 12 larvae completed development.

spent 1–10 minutes cleaning their mouthparts after each attack. The parallel response of the ants and coccinellids may indicate a lower content of cardenolides in the floral tips.

Rather surprising, therefore, are the reports that larvae of three coccinellid species completed their development with quite a high survival on *A. nerii*, reared in this experiment, however, on *Calotropis procera*. Survival was as follows: *C. septempunctata*, 43.9% (Omkar & Srivastava 2003); *C. leonina transversalis*, 37.8% (Omkar & James 2004); *Menochilus sexmaculatus*, 32.3% (Omkar & Bind 2004).

Whereas the aphids from oleander are poisonous for coccinellids, the scale *Aspidiotus nerii* from oleander is a more suitable prey for the coccinellid *Chilocorus infernalis* than *Asterolecanium* sp. on giant bamboo *Dendrocalamus giganteus* (Hattingh & Samways 1991). It is not clear whether the scales avoid taking in glycosides, or whether they are or are not sequestered by the coccinellid.

Macrosiphum albifrons

Macrosiphum albifrons, the lupin aphid, feeding on *Lupinus mutabilis* plants with a high content of **quinolizidine alkaloids** (>0.1% alkaloids in fresh matter), was toxic to *C. septempunctata* larvae and adults (Gruppe & Roemer 1988). The aphids themselves preferred plants with high alkaloid content. Adults of *A. bipunctata* survived longer (max. 15 days) than *C. septempunctata* (10 days) when fed on aphids from high alkaloid plants. Other *Lupinus* spp. cultivars with a high content of the alkaloid lupanin were 100% lethal to the larvae of *C. septempunctata*. The only exception was *L. luteus*, although its total alkaloid content is similar. This host plant contains 70% **spartein** and only 30% **lupanin** (Emrich 1991).

Toxoptera citricidus

Toxoptera citricidus caused the death of larvae in all coccinellid species studied in Taiwan: *Har. dimidiata*, *Har. axyridis*, *C. septempunctata brucki*, *C. leonina*, *Menochilus sexmaculatus* and *Synonycha grandis* (Tao & Chiu 1971). The lethal effect was also recorded in Venezuela on the larvae of *Cycloneda sanguinea*, while *Uroleucon ambrosiae* served as an essential prey (Morales & Burandt 1985). In contrast, Michaud (2000) found that *C. sanguinea* from Florida citrus groves completed larval development on *T. citricidus* as did *Har. axyridis*, with respectively 100 and 95% survival. The adults of *C. sanguinea* were also found to oviposit when they were fed on *T. citricidus* and their voracity was so high that they had the potential to control the aphid. Larvae of four other coccinellid species, *C. septempunctata*, *Coelophora inaequalis*, *Olla v-nigrum* and *Hip. convergens*, did not complete development on *T. citricidus*; however, the females of these four species produced viable eggs on the same diet (Michaud 2000). This is one of the observations that call for more precision in the definition of essential food, along with other cases in which prey suitability for larvae and adults differs (5.2.11). Similar complex interrelations were recorded by Michaud (2000) for *Aphis spiraecola* on citrus.

Aphis jacobaeae

Feeding of *C. septempunctata* on *A. jacobaeae* containing **pyrolizidine alkaloids** apparently differs from the intoxication of coccinellids by other toxic aphids mentioned above. *A. jacobaeae* feeds on several species of *Senecio* where a large range of pyrolizidine alkaloids are present in the form of N-oxides. A high content of **senecionine**, **seneciphylline**, **jacobine** and

erucifoline was found in *S. jacobaea*, and similarly in *A. jacobaeae* and its predator *C. septempunctata* (Witte et al. 1990). The aphid contained 0.8–3.5 mg of pyrolizidine alkaloids per 1 g fresh weight and the adult coccinellid 0.3–4.9 mg. The **precoccinellines** (alkaloids which the coccinellids produce) amounted to a mean of 10.5 mg/g fresh weight (Chapter 9).

Both aphids and coccinellids store their pyrrolizidine alkaloids as tertiary alkaloids, while other insects (*Tyria*, *Arctia*) store them as N-oxides (Witte et al. 1990). These authors proposed that the high pyrrolizidine alkaloid content may protect ladybirds against birds. This probably was the first reported case of coccinellids obtaining defence chemicals from their prey, but it was not measured to what extent the alkaloid content affected development and oviposition of the coccinellids.

The **hydroxamic acid DIMBOA** (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) present in wheat extracts is associated with resistance of wheat to aphids. The effect of this secondary metabolite on larvae of the coccinellid *Eriopis connexa* was examined by feeding them on aphids (*Rhopalosiphum padi*) that had fed for 24 hours on wheat cultivars with differing DIMBOA content (Martos et al. 1992). The allelochemical was less deleterious than the toxic compounds discussed above. The greatest negative effect was paradoxically achieved by intermediate levels of DIMBOA (Table 5.19). Aphids feeding on wheat seedlings with an intermediate DIMBOA level accumulated most DIMBOA in their bodies because aphids on the high DIMBOA varieties could detect the compound and this deterred their feeding. Thus high DIMBOA concentrations, which would increase the resistance to aphids, would actually reduce the effect of the secondary metabolite on the predator (Martos et al. 1992).

Some authors have attempted to explain the unsuitability of certain foods in terms of **nutrient deficiency**. Atwal & Sethi (1963) suggested that the higher protein content of *Lipaphis pseudobrassicae* makes this aphid more favourable than *Aphis gossypii* for *C. septempunctata*. Hariri (1966b) similarly supposed that *Acyrthosiphon pisum* is more nutritious for *A. bipunctata* than is *Aphis fabae*. The low suitability of *A. fabae* for larvae of *A. bipunctata* is explained by Blackman (1967b) as due to two factors: difficulty in ingesting the food and low nutritive value. The two may be related; nutritive value may be low because some essential nutrients are left behind in the non-ingested carcass.

General remarks on toxic prey

As described above, there are several examples of aphids which, like many other herbivores, protect themselves by toxins sequestered from their host plants. Pasteels (2007) calls this method 'chemical piracy' to stress its difference from the synthesis of toxins *de novo* in animal bodies (for specific coccinellid alkaloids see Chapter 9).

The toxicity of certain prey operates selectively. For example, *Megoura viciae* is toxic to *Adalia* spp. and *Exochomus quadripustulatus*, but most *C. septempunctata* larvae develop on this prey. *Aphis sambuci* is toxic for *C. septempunctata*, but much less so to *A. bipunctata*. The differences are often related to habitat specificity: *Coccinella septempunctata* prefer habitats with low plants, which is where *M. viciae* occurs, while *Adalia* spp. and

Table 5.19 Effect of DIMBOA levels in cultivars of wheat on development of *Eriopis connexa*. Aphids (*Rhopalosiphum padi*) were allowed to feed on the plants for 24 hours before they were given as prey to coccinellid larvae (Martos et al. 1992).

Content of DIMBOA* in wheat plants (μg/g fresh weight)	***n***	**Development duration (days)**		**Survival (%)**	
		larvae†	**pupae†**	**larvae**	**pupae**
140	10	10.4 a	4.0 a	98	100
270	10	10.7 b	4.0 a	93	100
440	10	9.1 c	3.8 a	100	100

*DIMBOA = 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one is a secondary metabolite found in cereal extracts; its level indicates resistance to aphid.

†Means within a column followed by the same letter are not significantly different ($P = 0.05$).

E. quadripustulatus, which prefer shrubs and trees, come into contact with *A. sambuci* more frequently, but not with *M. viciae*.

In the relationship between aphids (and prey in general) and coccinellids we are witnessing a similar process of evolution of specificity that has been intensively studied in phytophages and plants. In fact, we may witness here a further level of the evolutionary process within tritrophic relations. Moreover, in the case of the tritrophic chain *Senecio jacobaea–Aphis jacobaeae–C. septempunctata*, we may see additional evolutionary elements: *C. septempunctata* not only seems unaffected by pyrrolizidine alkaloids in aphids, but keeps the chemicals in their body and probably uses them as a defensive chemical, together with their own alkaloids. It is a pity that this interesting model has not been studied in more detail since 1990.

In general, much research is needed on the adaptive mechanisms in individual species of coccinellids to toxic prey. Are the toxic compounds detoxified or excreted in a non-sequestered state or are they stored in a transformed inert form? *Har. axyridis* appears to detoxify the alkaloids of intraguild coccinellid prey (Sloggett & Davis 2010). An important message emerges for further studies: because the prey insect mostly gets toxins from the host plant, not only the plant species should be recorded, but also other aspects, the season, plant variety or cultivar etc., because the concentration of allelochemicals will vary.

5.2.6.2 Rejected prey

While certain accepted prey do not facilitate development (5.2.6.3) or can even be toxic (5.2.6.1), other prey are rejected and not eaten. The placement of unsuitable prey into these three groups remains rather arbitrary. However, in some prey species considered to be rejected prey due to unknown factors (e.g., *Icerya purchasi* or *Brevicoryne brassicae*), toxic substances have been found in later analyses. These relations have most often been described for aphids and aphidophagous coccinellids, but also occur between other prey and predators (Fig. 5.1).

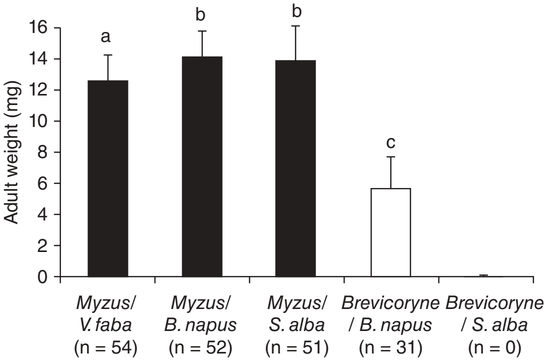

Figure 5.10 Effect of the aphid host plant (*Sinapis alba*, *Brassica napus* and *Vicia faba*) on adult weight of *Adalia bipunctata* fed with *Myzus persicae* or *Brevicoryne brassicae*. n, number of individuals reaching the adult stage. Different letters indicate significant differences at P = 0.001 (from Francis et al. 2000).

Delphiniobium junackianum feeds on *Aconitum* which contains the poisonous compound **aconitin**. This allelochemical may be the reason why coccinellids reject this prey, although Hawkes (1920) suspected that the intense colour of the aphid was probably a warning. In other examples, unpalatability is connected with a **waxy surface**, as in ***Brevicoryne brassicae*** or, to a lesser extent, in *Hyalopterus pruni*. Telenga and Bogunova (1936) observed that the coccinellid *Har. axyridis* refused *B. brassicae* in the field, and in the laboratory the females ceased oviposition when transferred from *H. pruni* to *B. brassicae*. George (1957) also noticed that *B. brassicae* was avoided by Coccinellidae.

The effect of **glucosinolates**, the main **allelochemicals of Brassicaceae**, on *A. bipunctata* was studied in a tritrophic context (other tritrophic studies in 5.2.12.). Two aphid species, the generalist *Myzus persicae* and the brassica specialist *B. brassicae* were fed on two brassicas: white mustard, *Sinapis alba*, with a high glucosinolate content and oil seed rape, *Brassica napus*, where the level of glucosinolates is six times lower. Four types of prey were fed to *A. bipunctata* and survival, adult weight, developmental rate and reproduction were recorded (Francis et al. 2000; Figs. 5.10, 5.11). *Myzus persicae* from *S. alba* gave low larval mortality of *A. bipunctata* but negatively affected oviposition. *Brevicoryne brassicae* from *S. alba* was clearly a toxic food, causing prolonged development of early instars; and no individual completed development.

This difference was explained by gas chromatographic analysis: significant amounts of glucosinolates were detected in *M. persicae*, but no degradation products. However, these highly toxic degradation products, **isothiocyanates**, were identified in *B. brassicae*. Moreover, myrosinase, which catalyses

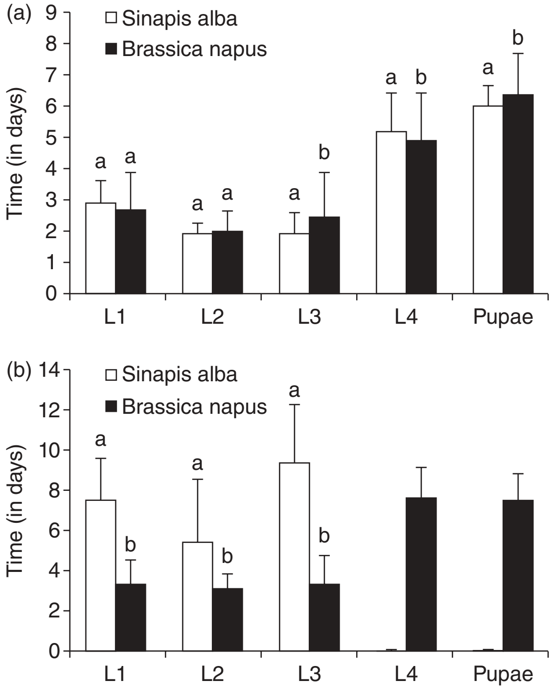

Figure 5.11 Effect of the aphid host plant (*Sinapis alba*, *Brassica napus*) on larval and pupal development of *Adalia bipunctata* fed with *Myzus persicae* (a) and *Brevicoryne brassicae* (b). Different letters indicate significant differences at P = 0.001 for pairwise comparisons (from Francis et al. 2000).

glucosinolate degradation, was detected in *B. brassicae* but not in *M. persicae* (Francis et al. 2000). When fed exclusively on *B. brassicae*, *Har. axyridis* larvae also did not complete development (Tsaganou et al. 2004). Aphid diet containing glucosinolates affects first instar *A. bipunctata* more seriously than *C. septempunctata*. As little as 0.2% of sinigrin in the diet leads to 100% mortality in the former species; by contrast, first instars of *C. septempunctata* survived when fed with *B. brassicae* reared on *Brassica nigra* or artificial diet containing up to 1% sinigrin. However, development rate was decreased (Pratt et al. 2008; Table 5.20).

We see here a similar relation between allelochemical tolerance and habitat as with *Aphis sambuci*. Again the common occurrence of the coccinellid species in the preferred habitat with the toxic aphid appears to lead to **evolution of adaptive resistance** to the allelochemical. *Coccinella septempunctata* comes in contact with brassicas and therefore their glucosinolates more often than *A. bipunctata*, which prefers tree and shrub habitats.

Hyalopterus pruni was described as unsuitable for *A. bipunctata* by Hawkes (1920). It was rejected by larvae of *A. decempunctata* immediately on piercing the body wall. In subsequent attacks this aphid was rejected as soon as the larva touched it with its palps (Dixon 1958). By contrast, Hodek (1959) found this aphid to be essential larval prey for *C. septempunctata* in spite of the waxy covering. Ozder & Saglam (2003) recorded 63% larval mortality in *C. septempunctata* and

Table 5.20 Survival of *Adalia bipunctata* or *Coccinella septempunctata* first instar larvae to second instar (a) fed *Brevicoryne brassicae* or *Myzus persicae* reared on *Brassica nigra*, (b) fed *Brevicoryne brassicae* reared on artificial diets containing a range of concentrations of sinigrin (modified after Pratt et al. 2008).

(a) Survival to second instar (%)	Aphid species	
	Myzus persicae	***Brevicoryne brassicae***
Adalia bipunctata	90	0
Coccinella septempunctata	90	90

(b) Survival to second instar (%)	Sinigrin content in aphid artificial diet					
	0%	**0.2%**	**0.4%**	**0.6%**	**0.8%**	**1.0%**
Adalia bipunctata	90	0	0	0	0	0
Coccinella septempunctata	100	90	90	80	70	80

n = 9–10.

50% in *A. bipunctata* when *H. pruni* was the prey, while in *Parexochomus nigromaculatus* the larval mortality was only 26% (Atlıhan & Kaydan 2002, Atlıhan & Ozgokce 2002). A marshland species *Anisosticta bitriangularis* preferred starvation to feeding on an unusual prey ***Schizolachnus piniradiatae*** (Gagné & Martin 1968).

An interesting study was made about 80–90 years ago on the famous ***Rodolia cardinalis***. This coccidophagous ladybird refused to feed on its normal host ***Icerya purchasi*** when the scale fed on *Spartium* or *Genista*. It was thought that such plants with sparse leaves failed to provide shade (Savastano 1918) or that the smell of the plants repelled the ladybirds (Balachowsky 1930). However, even if the coccids which had fed on *Spartium* or *Genista* were offered to the ladybirds without host plants they were still rejected (Poutiers 1930). These unsuitable host plants contain respectively the yellow pigment **genistein** and the alkaloid **spartein**. It has therefore been hypothesized (Hodek 1956) that substances imbibed by *I. purchasi* from the plants make them unpalatable for *Rodolia*, similar to the toxic effects of alellochemicals to other coccinellids. Thus the unsuitability of *I. purchasi* from *Spartium* or *Genista* was considered another case of acquired toxicity (Hodek 1973; 5.2.6.1).

In a later study, the survival and development time of *R. cardinalis* and *Chilocorus bipustulatus* was measured when they were reared on four prey. These were three scale insects (a margarodid *I. purchasi*, a diaspidid *Lepidosaphes ulmi* and a pseudococcid *Planococcus citri*) and *Aphis craccivora*. The prey were reared on the alkaloid-bearing legumes *Erythrina corallodendron* and *Spartium junceum* and on non-toxic plants as a control. Survival of both ladybirds was significantly reduced and the development time of *R. cardinalis* increased by preying on insects from the toxic plants (Mendel et al. 1992). However, this was not the case with *Cryptolaemus montrouzieri*. This negative effect of *E. corallodendron* and *S. junceum* rendering *I. purchasi* toxic, prevented colonization of these plants by this ladybird (Mendel & Blumberg 1991).

Aiolocaria hexaspilota, a specialized **predator of chrysomelids**, has been reported as feeding both as larvae and adults on the pre-imaginal stages of several chrysomelids (Iwata 1932, 1965, Savoiskaya 1970a, 1983, Kuznetsov 1975), but rejected another chrysomelid, *Agelastica coerulea* from *Alnus japonica* (Iwata 1965) and two central-Asiatic chrysomelids, (vernacular names in Savoiskaya 1970a). In Kazakhstan, its essential prey is the chrysomelid *Melasoma populi*. In later experiments *A. hexaspilota* accepted larvae and pupae of *Galeruca interrupta armeniaca* rather reluctantly (Savoiskaya 1983).

5.2.6.3 'Problematic' prey

Coccinellids accept some food which is not adequate and worsens life-history parameters, although it is not toxic.

This can occur when coccinellids, specialized to certain taxonomic groups of prey, are fed **prey from other groups**. Although adults and larvae of *A. bipunctata* were occasionally found feeding on tetranychid mites (Robinson 1951) and the gut of *A. bipunctata* and of three *Coccinella* spp. contained remains of the mite *Panonychus ulmi* (Putman 1964), the coccinellids could not develop on this prey (Robinson 1951, Putman 1957). Conversely, the adults of the acarophagous *Stethorus pusillus* did not oviposit when fed on aphids, and the larvae could not complete their development (Putman 1955). Also **other prey of the generally appropriate group** may be inadequate. This acarophagous coccinellid refuses the mite *Bryobia praetiosa*. If *Stethorus gilvifrons* preys on *Bryobia rubrioculus*, the adults do not oviposit and the larvae die in the second or third instar (Dosse 1967).

Aphis fabae poses quite a problem because of its taxonomy. Its host-plant-adapted biotypes have been redefined as different species, and thus the authors quoted below probably worked with a variety of species. When the host plant is not reported, one can only guess at the exact aphid used. This may explain why the suitability of *A. fabae* differs between the studies. An aphid used by Hodek (1956, 1957a, b) is what is now probably *A. cirsiiacanthoidis*, while Ehler et al. (1997) defined their prey as the '*A. fabae* complex on sugar beet'.

As early as 1954, Dyadechko found *A. fabae* somewhat less suitable than *Toxoptera graminum* for *Coccinula quatuordecimpustulata*. Nine out of ten species of coccinellids including the polyphagous *Col. maculata* tested by Smith (1965b) failed to complete their larval development when fed on *Aphis fabae*. The 10th species, *Hip. tredecimpunctata*, reached the adult stage, but

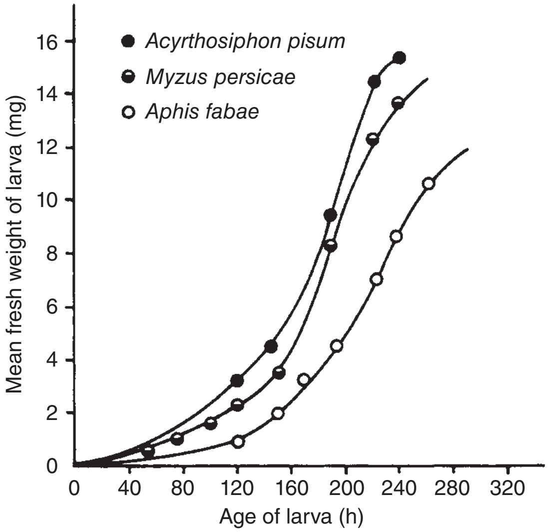

Figure 5.12 Development of *Adalia bipunctata* larvae on different aphid foods (from Blackman 1967a).

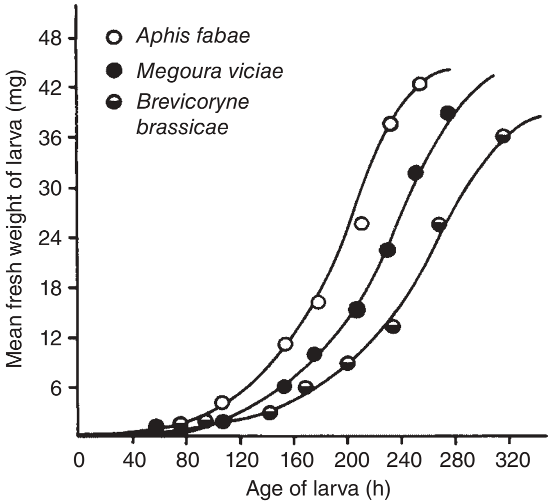

Figure 5.13 Development of *Coccinella septempunctata* larvae on different aphid foods (from Blackman 1967b).

the beetles were smaller and their development was significantly slower than when fed on *Acyrthosiphon pisum* or *Rhopalosiphum maidis*.

In a thorough study, Blackman (1965, 1967b) tested the suitability of several aphid foods for *A. bipunctata* and *C. septempunctata* (Tables 5.3 and 5.18, Figs. 5.12 and 5.13). Although *A. fabae* and *A. sambuci* are natural prey for *A. bipunctata* in the field, they were relatively unsuitable food for this coccinellid, as was shown by the longer larval development and the greater larval mortality. *A. bipunctata* also had a lower fecundity and fertility when fed on *A. fabae*. Hariri (1966a, b) reported similar results. When the larvae were fed on this aphid the resulting adults weighed less, they contained less fat and glycogen and their fecundity was halved. Iperti (1966) ascertained an adverse effect of *A. fabae* on vitellogenesis in *A. bipunctata*.

In contrast to *A. bipunctata*, larvae of *C. septempunctata* are able to develop on *A. fabae* successfully. Hodek, Blackman and Ehler recorded almost 100% successful completion of larval development by *C. septempunctata* on *A. fabae*: Hodek (1956, 1957a), 92–100%; Blackman (1965, 1967b), 91%; Ehler et al. (1997), 100%. *Aphis fabae* is toxic to the larvae of *Exochomus quadripustulatus* (Radwan & Lövei 1983), but rather suitable for *Cer. undecimnotata* (under the wrong name *Hip. undecimnotata*) (Papachristos & Milonas 2008).

Atwal and Sethi (1963) found that the larvae and resulting pupae of *C. septempunctata* were heavier when fed on *Lipaphis pseudobrassicae* than on ***Sitobion avenae*** and ***Aphis gossypii***. When studying food specificity in *Harmonia axyridis*, Hukusima and Kamei (1970) found three aphids (***Aphis pomi***, ***Brevicoryne brassicae*** and ***Hyalopterus pruni***) out of nine to be less suitable for the larvae, prolonging development by about one-third, compared with diets of six more suitable species, including *Acyrthosiphon pisum* and *Myzus persicae*. *Aphis pomi* was the least suitable of four essential aphid prey for *Exochomus quadripustulatus*: the mortality of larvae was 19% (vs. 7–11%) and the adult fresh weight 8 mg (vs. 12–14 mg) (Radwan & Lövei 1983). Olszak (1988) found *A. pomi* highly detrimental for larvae of *C. septempunctata* (100% mortality), *A. bipunctata* (94%) and *P. quatuordecimpunctata* (73%).

Chilocorus bipustulatus is unable to reproduce when feeding on the olive scale ***Saissetia oleae*** (Huffaker & Doutt 1965). *Chilocorus stigma* has a markedly lower fecundity and survival and a prolonged pre-oviposition period if fed on the mussel scale *Lepidosaphes beckii* (Muma 1955), whereas the scale *Chrysomphalus aonidum* is a suitable prey.

Table 5.21 Effect of four different host plants of the mealybug *Phenacoccus manihoti* on life-history parameters in *Exochomus flaviventris* (modified after Le Rü & Mitsipa 2000).

	Cassava (*Manihot esculenta*)			
	Incoza var.	Zanaga var.	hybrid[1)]	*Talinum*
Glycosides	*n* = 11 high content	*n* = 10 low content	*n* = 11 —	*n* = 11 lacks glycosides
Immature mortality (%)	24.4	15.9	23.1	14.8
Oviposition time (days)	28.9	47.4	25.8	38.6
Total fecundity (eggs/female)	265.1	384.5	199.5	269.0

[1)] Hybrid of *M. esculenta* and *M. glaziovii*.

The adults of the coccidophagous *Cryptognatha nodiceps* also feed on the **aleurodid** *Aleurodicus cocois*, but the females do not lay eggs (Lopez et al. 2004).

Prey feeding on resistant plants

Aphis fabae feeding on a partially resistant cultivar of *Vicia faba* (that reduced aphid numbers by 63%) was not a favourable prey for *C. septempunctata*: fecundity, fertility and oviposition period were decreased while the pre-oviposition period was prolonged compared to feeding on prey from the susceptible cultivar. The combined action of the partial resistance of the crop and the slightly handicapped predator was more effective in lessening aphid numbers than either effect alone (Shannag & Obeidat 2008).

Similar observations were made on cassava. A host plant effect on the polyphagous African ladybird *Exochomus flaviventris* was recorded when it fed on the cassava mealybug ***Phenacoccus manihoti***, when reared on varieties of cassava (*Manihot esculenta*) and a weed (*Talinum triangulare*) that sometimes hosted large populations of the mealybug. Cassava varieties contained different levels of **cyanogenic glycosides** that were associated with their resistance to mealybugs. The mealybugs that fed on the low-resistance variety 'Zanaga' appeared to be the most suitable for *E. flaviventris* (Table 5.21). The worst effects on the duration and survival in larval development of ladybirds were caused by mealybugs from host plants with intermediate levels of glycosides and surprisingly not those with the highest (Le Rü & Mitsipa 2000). Similar greatest negative effects of intermediate allelochemical content on coccinellids were observed with DIMBOA in wheat, where the aphid prey found higher DIMBOA levels deterrent (5.2.6.1).

5.2.7 Prey other than aphids/coccids

5.2.7.1 Developmental stages of Holometabola

The rearing of specific prey for aphidophagous or coccidophagous coccinellids requires a large amount of space, human resources and energy, and rearing coccinellids on artificial diets (5.2.10) has met with limited success. Therefore some authors have tried to use substitute insect prey that are easier to produce, mostly the **eggs of lepidopteran** stored product pests. Substitute prey often appear to be suitable. A recent review is by Evans (2009).

When *Cryptolaemus montrouzieri* larvae are reared on the eggs of *Sitotroga cerealella* neither survival during development nor the weight of emerging adults are reduced (Pilipjuk et al. 1982). The euryphagous *Har. axyridis* was reared more successfully on eggs of the pyralid moth *Ephestia kuehniella* than on *Acyrthosiphon pisum*. The pyralid eggs were UV-killed (Schanderl et al. 1988) (Table 5.22) or frozen (Berkvens et al. 2008). *E. kuehniella* eggs were, however, unsuitable for *Cer. undecimnotata* (Iperti & Trepanier-Blais 1972, Schanderl et al. 1988, Table 5.22) and *P. quatuordecimpunctata* (Bazzocchi et al. 2004), although this diet was reported as suitable for the oligophagous *C. septempunctata* (Sundby 1966) and *A. bipunctata* (de Clercq et al. 2005).

Upon being switched from a diet of aphids to an aqueous solution of sucrose, females of *C. tranversalis* ceased oviposition after 3 days and laid almost no eggs

Table 5.22 Eggs of *Ephestia kuehniella* as food for *Harmonia axyridis* and *Ceratomegilla undecimnotata* (Schanderl et al. 1988).

Coccinellid species	Generation*	Food†	Pre-imag. development mortality (%)	Pre-imag. development duration (days)	Adult weight (mg)	Reproduct. (%)	Oviposition rate (eggs/day)
Harmonia axyridis	control	aphid	11.4	14.8 ± 0.1	29.6 ± 0.9	80.0	22.7 ± 4.1
	1	eggs	2.6	14.1 ± 0.1	26.8 ± 0.9	85.0	38.6 ± 4.8
	2	eggs	11.7	16.0 ± 0.1	33.0 ± 1.1	80.0	40.9 ± 4.6
	3	eggs	4.7	15.9 ± 0.1	28.7 ± 1.5	72.2	34.2 ± 4.7
Ceratomegilla undecimnotata	control	aphid	6.0	12.3 ± 0.1	29.1 ± 0.7	100.0	20.4 ± 2.8
	1	eggs	16.8	15.1 ± 0.2	23.4 ± 0.8	55.0	†8.6 ± 3.7
	2	eggs	45.2	17.3 ± 0.2	23.6 ± 1.0	60.0	11.1 ± 4.0
	3	eggs	51.0	22.3 ± 0.7	19.7 ± 1.0	55.0	13.8 ± 3.4

*Both larvae and adults of all generations were fed on eggs of *E. kuehniella*, killed by x-rays.
†An essential aphid prey, *Acyrthosiphon pisum*, was used as control food.

on a diet of second instars of the moth *Helicoverpa armigera*. However, females laid eggs in small numbers (on average 2.7 eggs per day) when provided with a combination of both these alternative diets (Evans 2000; 5.2.5). Natural feeding by *Hip. variegata* on the eggs of *Helicoverpa armigera* in Australian cotton fields was demonstrated by ELISA (5.2.1; Mansfield et al. 2008).

Col. maculata preyed on eggs and larvae of three lepidopterans in the laboratory: *Plutella xylostella* was preyed upon more than *Pieris rapae* and *Trichoplusia ni*. *Col. maculata* adults preyed more on eggs, while the fourth instars preferred larvae (Roger et al. 2000; also 5.2.4.1). Roger et al. (2001) observed that *Col. maculata* larvae selected eggs of the noctuid *T. ni* according to their age: one day old eggs were preferred over three day old eggs, regardless of whether the eggs were parasitized by *Trichogramma evanescence* or not. In maize fields, *Col. maculata* is recorded as a very important predator of eggs of the noctuid *Helicoverpa zea*, contributing to about 45% of the observed predation (Pfannenstiel & Yeargan 2002).

It has even been recorded that the adults and third instars of *Har. axyridis* feed on the eggs and first instars of the monarch butterfly, *Danaus plexippus* (Koch et al. 2003).

The rearing of *Har. axyridis* for several years on eggs of *E. kuehniella* substantially decreased coccinellid **intensive searching behaviour** for aphid prey (5.4.1.2) compared to coccinellids continuously reared on aphids (Ettifouri & Ferran 1993). Any possible change in behaviour patterns, produced by mass-rearing coccinellids on a substitute diet should always be looked for, as it might hamper their efficiency in the biological control of natural prey.

Developmental stages of **Coleoptera** and other insect orders are also eaten by ladybirds. In the laboratory *Har. axyridis* and *C. septempunctata* consumed larvae of the **dipteran** cecidomyiid *Contarinia nasturtii*. *Har. axyridis* showed higher voracity than *C. septempunctata* and did not prefer *Myzus persicae* over larvae of *C. nasturtii*, but not on infested broccoli plants (Corlay et al. 2007).

Coleomegilla maculata fed on larvae of the **chrysomelids** *Xanthogaleruca luteola* (Weber & Holman 1976) and *Galerucella nymphaeae* (Schlacher & Cronin 2007). In spite of the reports of *Col. maculata* feeding on the eggs of *Leptinotarsa decemlineata* (5.2.4.1), these are not essential food for some ladybirds: larvae of four coccinellid species were not able to complete larval development on a diet solely of eggs of this chrysomelid (Snyder & Clevenger 2004). *Cleobora mellyi* and *Har. conformis* adults, however, mated and oviposited when supplied with eggs of another chrysomelid, *Chrysophtharta bimaculata* (Elliott & de Little 1980).

A series of studies on the curculionid *Hypera postica*, that is only an alternative prey for ladybirds in alfalfa fields, opens a new horizon in the field of coccinellid diets, stressing the importance of complementary food

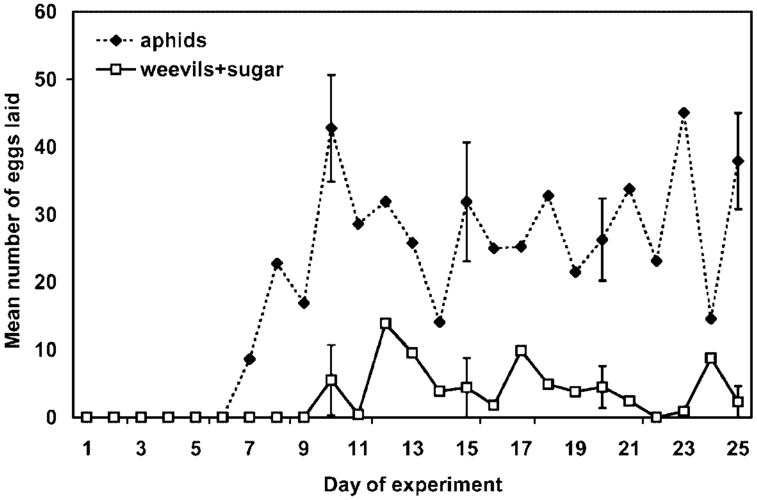

Figure 5.14 Effect of 25 days initial feeding by *Harmonia axyridis* females, on alternative foods (*Hypera postica* larvae, sugar water) versus aphids, on egg laying when pea aphids were provided ($n = 6$–8), the bars represent SE (from Evans & Gunther 2005).

(5.2.5). *H. postica* larvae feed on alfalfa together with aphids. In the laboratory only 5% of fourth instar *C. septempunctata* developed to adult when provided with live *H. postica* larvae. The proportion of successful development increased to 70% if the ladybirds received dead larvae. Observations revealed that *C. septempunctata* larvae were often deterred by the defensive wriggling of live *H. postica* larvae (Kalaskar & Evans 2001). Other predator–prey relations may quite often be affected by similar behavioural obstacles. Ladybirds are probably successful in preying on *H. postica* larvae when the latter moult.

The importance of alternative prey can be best assessed when it is an addition to a low amount of essential prey. The very low oviposition rate of *C. septempunctata* females with a limited supply of aphids is increased by addition of alfalfa weevil (*H. postica*) larvae, although this prey alone does not facilitate *C. septempunctata* egg laying. Consumption of coleopteran larvae apparently serves for self-maintenance of ladybird females; however, combined with essential nutrients from aphids it enables greater egg production (Evans et al. 2004). Also for the polyphagous *Har. axyridis*, larvae of *H. postica* are only alternative prey, as the females lay no eggs on this diet alone and larvae do not develop successfully (Kalaskar & Evans 2001). In the absence of aphids, this food facilitates survival and bodily maintenance of females, and speeds up oviposition after a switch to essential aphid food (Evans & Gunther 2005; Fig. 5.14). In alfalfa fields in Utah (USA), different coccinellid species respond differently to alternative prey: the native species *Hip. convergens* and *Hip. quinquesignata quinquesignata* respond by aggregating only when the essential prey *Acyrthosiphon pisum* is at high density. By contrast, the invasive species *C. septempunctata* also aggregates in response to high abundances of the alternative prey, *H. postica* larvae (Evans & Toler 2007; Fig. 5.15). The authors assume that this numerical response of *C. septempunctata* may partly account for the displacement of native ladybirds from alfalfa when aphid numbers decline.

In an experiment, both *C. septempunctata* adults and third instars preferred preying on **parasitized aphids**. *Aphis fabae* parasitized by *Lysiphlebus fabarum* were killed by adult ladybirds 3.5 times more often than non-parasitized aphids, and by ladybird larvae twice as often (Meyhöfer & Klug 2002). *Coccinella undecimpunctata* showed no preference for healthy *Myzus persicae* over those parasitized by *Aphidius colemani* (Bilu & Coll 2009). Fourth instars of *C. septempunctata* and *Hip. convergens* preyed upon fully formed mummies of

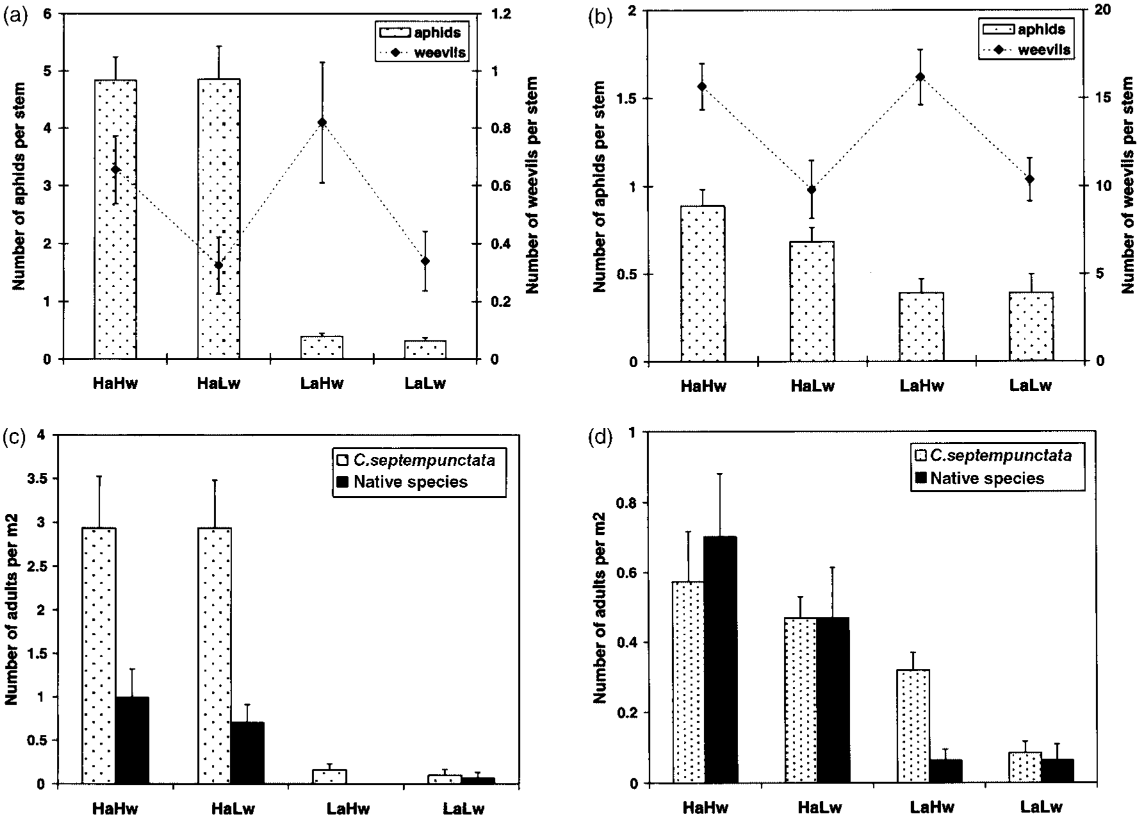

Figure 5.15 Role of alternative prey (larvae of *Hypera postica*) and essential prey (*Acyrthosiphon pisum*) shown in a field experiment where the populations of both types of prey on alfalfa plots were manipulated to produce four combinations: Ha and La, high and low numbers of aphids; Hw and Lw, high and low numbers of weevils. (a) and (b) mean number (± SE) per stem of aphids (columns) and weevils (points and lines) at the outset (24 May) and conclusion of experiment (31 May), respectively. (c) and (d) mean number (± SE) per m^2 of *Coccinella septempunctata* and several native ladybird species on 24 May and 31 May, respectively (from Evans & Toler 2007).

Schizaphis graminum, but a pure diet of mummies was unsuitable for the complete development to adults. A mixture of mummies and live aphids resulted in delayed development and smaller adults (Royer et al. 2008; Table 5.23).

Rodolia cardinalis avoided *Icerya purchasi* when the prey was **parasitized** by *Cryptochaetum iceryae*. The beetles would starve if only scales containing pupae of this parasitic fly were available (Quezada & de Bach 1973). *Delphastus pusillus*, a predator of all stages of whiteflies, exhibited a marked tendency to avoid fourth instar *Bemisia tabaci* containing third instar and pupal aphelinid endoparasitoids (Hoelmer et al. 1994).

Intraguild (IG) predation on heterospecific ladybird eggs and cannibalistic feeding on conspecific eggs is dealt with in 5.2.8 and Chapter 7. However, some recent findings are also discussed here. Eggs of *Col. maculata*, *Hip. convergens* and *Olla v-nigrum* as food (and also conspecific eggs) enable complete larval development of *Har. axyridis*. In contrast, the larvae of the former three species, native to North America, cannot develop to adult on eggs of *Har. axyridis* (Cottrell 2004, 2007; Fig. 5.16). Thus *Har. axyridis* appears to be a kind of generalist predator of ladybird eggs, but with certain limits: eggs of *A. bipunctata* are reported to be quite toxic to *Har. axyridis* (Sato & Dixon 2004,

Table 5.23 Consumption of *Schizaphis graminum* mummies parasitized by *Lysiphlebus testaceipes* by larvae of *Coccinella septempunctata* and *Hippodamia convergens* in a 24-hour no-choice test (after Royer et al. 2008).

		Mummies consumed (*n*)	
Stage	**Mummies provided (*n*)**	***Coccinella septempunctata***	***Hippodamia convergens***
1st instars (*n* = 5)	10	0	0
2nd instars (*n* = 5)	20	19*	17*
3rd instars (*n* = 5)	80	80	80
4th instars (*n* = 5)	150	150	150
Adults (*n* = 5)	150	150	150

*Feeding was attempted but mummies were only partially <50% consumed.

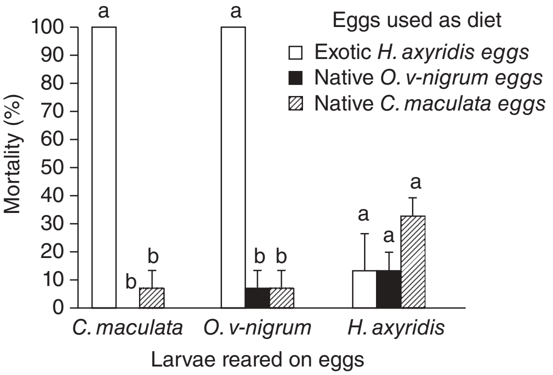

Figure 5.16 Mortality of larvae of *Coleomegilla maculata*, *Olla v-nigrum* or *Harmonia axyridis* reared from the first instar only on eggs of *Coleomegilla maculata*, *Olla v-nigrum* or *Harmonia axyridis*. Means separated by Tukey's HSD test and significant differences ($P < 0.05$) within groups of bars are indicated by different letters above individual bars (modified from Cottrell 2004).

Table 5.24 Suitability of different diets for growth and development in *Harmonia axyridis* and *Adalia bipunctata* (after Ware et al. 2009).

Parameter	***Harmonia axyridis***	***Adalia bipunctata***
Survival to adulthood	(A = C = D) > B	(A = C) > (B = D)
Larval development time	A > C > D > B	A > C > (B = D)
Maximum pronotal width	A > (C = D) > B	A > (C = B) > D

A, unlimited aphids; B, limited aphids; C, limited aphids plus conspecific eggs; D, limited aphids plus non-conspecific eggs. In this table '>' indicates a more suitable diet and '=' indicates two diets are of equal suitability. Suitability hierarchies are worked out on the basis of the significance of differences observed between diets.

but see Ware et al. 2009, also Sloggett et al. 2009a, Sloggett & Davis 2010). The latter study investigates the metabolic pathways of coccinellid alkaloids in the predator. The eggs of other species serve as suitable food also mutually for *Col. maculata*, *Hip. convergens* and *O. v-nigrum*, but not for *Cycloneda munda* (Cottrell 2007). The eggs of *Har. axyridis* were found harmful also for *A. bipunctata* in an experiment with mixed diets (Ware et al. 2009; Table 5.24).

In two species, *Har. axyridis* and *A. bipunctata*, laying single **trophic eggs**, which were eaten by the female immediately after oviposition, was reported in the absence of aphid prey (Santi & Maini 2007; 5.2.8.1). The laying of infertile eggs for the nutrition of sibling neonate larvae in the same clutch represents another adaptation, as they do not serve as food for the females (Perry & Roitberg 2005, 2006; 5.2.8.1).

For some insect females, the **spermatophore** is an important source of proteins. Thus the idea that this might also apply in ladybirds is quite plausible, because the females have been observed to eat

Table 5.25 Results of rearing aphidophagous coccinellids on drone honeybee powder[a] (Niijima et al. 1986).

Species	Larval development	Adult longevity	Fecundity	Generations reared
Adalia bipunctata	+	+	–	–
Anatis halonis	+	++	±	–
Calvia muiri	++	++	+	11
Coccinula crotchi	++	++	+	3
Coccinella explanata	+	++	+	2
C. septemp. brucki	+	++	+	4
Coelophora biplagiata	++	++	++	2
Harmonia axyridis	++	++	++	16
H. yedoensis	++	++	++	8
Hippodamia convergens	+	+	–	–
H. tredecimpunctata	++	+	+	2
Menochilus sexmaculatus	++	++	++	25
Propylea japonica	++	++	++	6
Scymnus hilaris	–	++	–	–
S. otohime	–	+	–	–

[a] ++, good; +, fair; ±, occasionally successful; –, unsuccessful.

spermatophores after copulation (Obata & Hidaka 1987). Omkar & Mishra (2005) assumed that *C. septempunctata* compensate costs for multiple mating by feeding on spermatophores. This assumption has recently been rejected by Perry & Rowe (2008). Neither spermatophore consumption, nor multiple matings (three and five times) influenced female longevity.

A powder from lyophilized **larvae of drone honey bees** proved a satisfactory substitute food for several aphidophagous coccinellid species. At first *Har. axyridis* was reared on non-modified larvae or pupae of males from *Apis mellifera* (Okada 1970). 'Drone powder' was used successfully with *Har. axyridis* (and *Har. yedoensis*), and later tried on other aphidophagous and coccidophagous coccinellids. The achievements of Okada's team were reviewed (Niijima et al. 1986) and the suitability of the drone powder for 15 coccinellid species compared (Table 5.25). For two oligophagous species of the genus *Coccinella* the drone powder was less suitable. *Adalia bipunctata* and *Hip. convergens* did not oviposit at all. A similarly negative result was received with another oligophagous species *Cer. undecimnotata* (Ferran et al. 1981).

Great stability is an advantage of the drone powder. It keeps its original quality at +5°C for several months and even at room temperature its nutritional value is the same after 3 months (Niijima et al. 1986). Drone powder appeared to be of about the same suitability as lyophilized aphids for *Har. axyridis*, but for the weight of the emerged adults it was much better than the powdered *Acyrthosiphon pisum*. Diets developed for *Chilocorus* spp. were also based on honey-bee brood. The most satisfactory diets contained royal jelly and other supplements (Hattingh & Samways 1993).

5.2.7.2 Non-aphid hemipterans

These have also been reported as coccinellid prey. Among 13 natural enemies species, *Har. axyridis* and *P. japonica* were predators of the **aleyrodid** *Bemisia tabaci* in cotton fields of northern China in 2003 through 2005 (Lin et al. 2008). In the laboratory, *C. septempunctata* adults preferred *Thrips tabaci* over the aleyrodid *Trialeurodes vaporariorum* on tomato. The aphid *Macrosiphum euphorbiae* was, however, preferred over both non-aphid prey (Deligeorgidis et al. 2005). **Psyllids**, which are also near relatives of aphids, both being Sternorrhyncha, unsurprisingly can be essential prey for ladybirds that are not specialists on psyllids. The invasive Asian citrus psyllid *Diaphorina citri* was found to be essential prey for four coccinellid species (*Olla v-nigrum*, *Exochomus childreni*, *Curinus coeruleus* and *Har. axyridis*); however, *Cycloneda sanguinea* females ceased egg laying after the second day on this prey. The performance of *C. sanguinea* larvae on *D. citri* was much lower than the other four coccinellid species (Michaud & Olsen 2004).

Adelgids, the nearest relatives of aphids, have not often been studied as coccinellid prey, but *Har. axyridis* was reported to be the most abundant predator (81%) of the hemlock woolly adelgid (*Adelges tsugae)* on two *Tsuga* species. *Har. axyridis* was moderately well synchronized with the adelgid life cycle; this may indicate that *A. tsugae* could be a suitable prey for this coccinellid (Wallace & Hain 2000), but it was reported that the larvae do not always complete development on this adelgid (Butin et al. 2004). Prey other than Hemiptera have also been recently reviewed by Evans (2009).

5.2.8 Cannibalism

As predators, ladybirds at times engage in cannibalism. Eggs, pupae and especially newly moulted individuals may serve as intraspecific prey. Cannibalism complicates mass production of ladybirds as biological control agents. It requires either isolation of vulnerable individuals, or the creation of sufficient physical complexity in rearing to reduce encounters between hungry, active individuals and vulnerable, inactive conspecifics (e.g. Shands et al. (1970) filled rearing cages with wood shavings). Cannibalism by ladybirds also often occurs in natural settings, raising questions about the adaptive significance and population consequences (Cushing 1992, Martini et al. 2009). Potential costs include risk of injury in attacking conspecifics, loss of inclusive fitness from consuming relatives, and transmission of disease from infected victims (Dixon 2000). However, the widespread nature of cannibalism among ladybirds suggests that there may often also be considerable benefits (Osawa 1992c). Two distinct kinds of cannibalism occur (Fox 1975). In **sibling cannibalism**, newly hatched first instars eat unhatched eggs in the same egg cluster. In **non-sibling cannibalism**, unrelated individuals (as larvae or adults) cannibalize eggs, larvae, pupae, or newly emerged adults. Aphidophagous species of ladybirds appear especially prone to cannibalism; coccidophagous coccinellids may encounter each other less frequently and be less aggressive. Also they are more likely to complete development before populations of their prey collapse (Dixon 2000).

Mills (1982b) and Osawa (1989, 1993, 2002) drew attention to egg cannibalism in natural populations, by determining the relative frequency of sibling and non-sibling cannibalism over the growing season. Sibling egg cannibalism may be much less frequent than non-sibling cannibalism of eggs (e.g. Mills 1982b), and it appears to occur without any influence of the availability of prey or the seasonal timing of oviposition (Osawa 1989). In contrast, the incidence of non-sibling cannibalism of eggs has been observed to increase over the growing season in studies of *Har. axyridis* on a peach tree (Osawa 1989) and artichoke (Osawa 1992a). (For feeding on heterospecific coccinellid eggs see 5.2.7.1 and Chapter 7.)

5.2.8.1 Sibling egg cannibalism

Often hatching asynchronously, young ladybird larvae remain at the egg cluster for approximately 8–36 hours before searching for food (e.g. Banks 1956, Dixon 1959, Brown 1972, Nakamura et al. 2006). Although early hatching larvae do not attack each other on the egg cluster (Brown 1972, Hodek 1996), they cannibalize late hatching and infertile eggs before dispersing (e.g. Kawai 1978, Osawa 1992c). In the laboratory, most (50–60%) eggs of *Cycloneda sanguinea*, *Har. axyridis* and *Olla v-nigrum*, hatched within 10 minutes. Of the remaining eggs, some hatched later but most were cannibalized (Michaud & Grant 2004; Fig. 5.17). Larvae remained at clusters until all unhatched eggs had been consumed and dispersal of

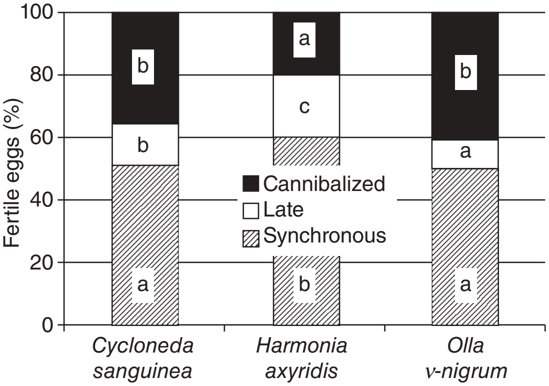

Figure 5.17 Percentages of fertile eggs of three coccinellid species that hatched synchronously (within 10 minutes of first hatch), late (>10 minutes after first hatch) or were cannibalized by siblings. Bars bearing the same letter were not significantly different among species within a category (test of proportions, P > 0.05) (from Michaud & Grant 2004).

larvae was delayed by several hours (see also Kawai 1978, Nakamura et al. 2006).

Sibling egg cannibalism by ladybirds may have considerable adaptive significance. Dispersing first instars risk starvation before finding and overcoming their first prey (Banks 1954, Dixon 1959, Kawai 1976, Wratten 1976). Initial consumption of sibling eggs may supply critical energy and nutrients, speeding development and increasing survival (Banks 1954, 1956, Kawai 1978, Roy et al. 2007). Osawa (1992c) recorded increasing larval survival to the second instar in *Har. axyridis* on citrus trees, at both low and high aphid density, due to having fed on up to three sibling eggs.

The two sexes may differ in how much they gain from sibling egg cannibalism. In a laboratory experiment, Osawa (2002) found that sibling consumption of a single egg (with aphid consumption thereafter) especially benefited males of *Har. axyridis*. Sibling egg cannibalism promoted both larger body size and weight (an advantage for mating success) and faster development time. Omkar et al. (2007) reported similar results for *P. dissecta* and *C. leonina transversalis*. Michaud and Grant (2004), however, reasoned that females are more resource-sensitive than males, and therefore would benefit most from sibling egg cannibalism. In support, they found that females of *Har. axyridis* and *O. v-nigrum* (but not of *C. sanguinea*) weighed more as adults, after engaging in sibling egg cannibalism and maturing on frozen eggs of *Ephestia kuehniella*. These authors noted that eggs of *E. kuehniella* were superior to *Aphis spiraecola* used by Osawa (2002). Thus, either males or females may benefit most from sibling egg cannibalism, depending on whether the diet subsequently is of low or high quality.

Sibling cannibalism may benefit females most when eggs are infected by bacteria that kill male embryos (Hurst & Majerus 1993, Majerus & Hurst 1997, Nakamura et al. 2006). Male-killing bacteria (including *Rickettsia, Wolbachia, Spiroplasma, Flavobacterium*, and gamma-proteobacteria) attack many species of ladybirds (Majerus 2006; Chapter 8). Because vertical transmission occurs only via egg cytoplasm, bacterial fitness is enhanced by killing males. Female-biased cannibalism (better termed scavenging) of male eggs killed by bacteria can further strengthen a strongly female-skewed, population sex ratio (e.g. Nomura & Niijima 1997). Nakamura et al. (2006), for example, report that the per capita consumption (sibling cannibalism) of unhatched eggs by female first instars of *Har. axyridis* was increased 4–14 times in egg clusters of a Japanese population highly infected with *Spiroplasma*. Cannibalism itself did not result in horizontal transmission of male-killing bacteria when uninfected larvae (fourth instar) of *Menochilus sexmaculatus* fed on infected conspecific eggs (or larvae and pupae) (Nomura & Niijima 1997).

Osawa (1992c) focussed on the critical issue of survival of first instars to moulting, and considered the inclusive fitness of three potential beneficiaries of sibling egg cannibalism: the cannibal, the victim, and the mother of the victim. Inclusive fitnesses were determined for cases in which the cannibal (*Har. axyridis*) consumed up to three sibling eggs. Survival to the second instar was measured in field releases of first instars on citrus trees with low or high densities of aphids (*Aphis spiraecola*). Osawa concluded that full sibling cannibalism may be adaptive for both cannibal and victim when aphid density is low, but not for the victim and only sometimes for the cannibal when prey density is high. The inclusive fitness of the mother did not vary with the degree of sibling cannibalism of her eggs when aphid density was low, but decreased with increasing cannibalism when prey density was high. Thus it appears that the evolution of sibling egg cannibalism is driven especially by the fitness gains of both cannibals and victims when prey (other than the victims) are scarce. This condition of prey scarcity may often hold for aphidophagous ladybirds that lay their eggs when aphids are abundant, with subsequent decline in aphid numbers as the larvae develop (e.g. Hemptinne et al. 1992).

Osawa (2003) further investigated the possibility of the mother influencing sibling egg cannibalism and concluded that the female may have little ability to manage sibling egg cannibalism in an adaptive fashion. Perry and Roitberg (2005) also explored whether female as well as offspring fitness may be promoted by laying infertile or late-hatching eggs. These authors placed reproductively active females of *Har. axyridis* in alternating low and high resource (prey) environments for 24 hours. Females laid 56% more infertile eggs in the low resource environment (Perry & Roitberg 2005; Fig. 5.18). The authors concluded that this was not a simple, direct result of resource limitation; the females were in good condition when introduced to low prey conditions, and were well able to tolerate such low food conditions for the following 24 hours. Instead, females

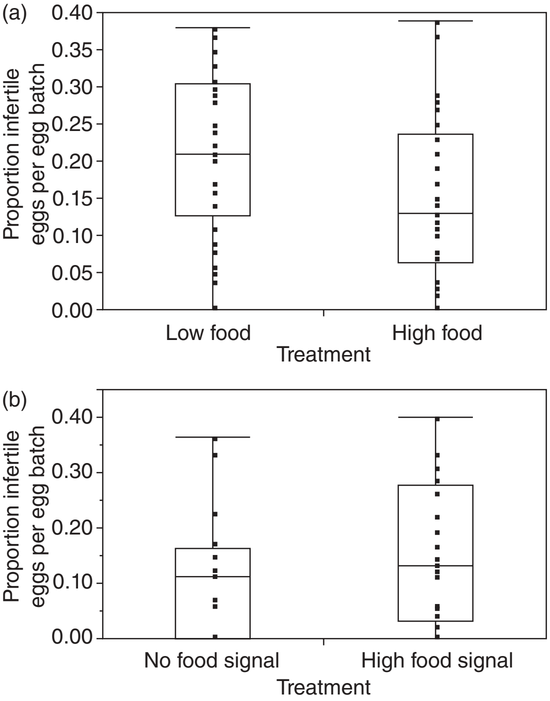

Figure 5.18 Proportion of trophic eggs produced when females of *Harmonia axyridis* were given information that there was low or high food availability through: (a) the internal cue of prey encounter and consumption or (b) the external cue of prey scent. Horizontal lines represent means, and whiskers indicate the range of observations. The proportion of trophic eggs was smaller under the low food treatment in the internal cue but not the external cue experiment (from Perry & Roitberg 2005).

may have withheld sperm to produce infertile eggs as an adaptive, maternal strategy to provide eggs as food for offspring when resource conditions were poor (Alexander 1974).

The conclusions of Osawa (1992c, 2003) and Perry and Roitberg (2005) differ strikingly as to whether (and how) sibling egg cannibalism may be controlled, at least in part, as an adaptive strategy of the ovipositing female (see also Osawa & Ohashi 2008). Another means of adaptive manipulation of sibling egg cannibalism was suggested by Michaud and Grant (2004), who found that eggs laid singly were less likely to be cannibalized by siblings than were eggs laid near each other. Roy et al. (2007) investigated whether hatching asynchrony (and therefore potential for sibling egg cannibalism) varied with dispersion pattern amongst eggs of *A. bipunctata* laid together, but found no difference between eggs laid linearly or as a cluster.

Trophic egg laying is another form of egg consumption by kin that is clearer in its benefits for ovipositing females. Thus Santi and Maini (2007) reported that when prey became scarce, starving (yet still gravid) females of *Har. axyridis* and *A. bipunctata* (but interestingly, not of *P. quatuordecimpunctata* and *Hip. variegata*) laid a single, inviable egg which they immediately consumed. If the experimenter removed the eggs, the female searched the local area intensively (seemingly searching for the egg). Laying of trophic eggs was repeated only when the egg was removed. When given prey, the same females laid eggs that hatched (60–70%).

5.2.8.2 Non-sibling egg cannibalism

Consumption of eggs

Dispersed ladybird larvae and adults often eat conspecific (and sometimes heterospecific) eggs, larvae and pupae (e.g. Wright & Laing 1982, Takahashi 1989, Yasuda & Shinya 1997). Eggs are highly vulnerable (5.4.1.3) when laid near or in aphid colonies; clusters of eggs are encountered frequently by foraging larvae and adults (e.g. Banks 1955, Osawa 1989). Species-specific oviposition site preferences can result in enhanced cannibalism over intraguild predation (e.g. Schellhorn & Andow 1999a). Mills (1982b) recorded cannibalism of *A. bipunctata* eggs on lime trees infested with *Eucallipterus tiliae*: adults (22%), first (19%), second (33%), and third instars (26%). Cannibalism was density dependent. The threat of egg cannibalism may underlie the tendency of aphidophagous ladybirds to oviposit at some distance from, rather than in an aphid colony (Osawa 1989, 1992b, 5.4.1.3). Dixon (2000) notes that eggs of aphidophagous ladybirds mature and hatch relatively quickly; he suggests that this too may reflect selection as imposed by cannibalism.

Non-sibling cannibalism may occur most when food is scarce (e.g. Takahashi 1989) and may be rare under less stressful conditions (e.g. Triltsch 1997). This has been confirmed in the laboratory (Agarwala & Dixon 1992, Cottrell 2005). In the field, egg cannibalism by *Col. maculata* (which is able to develop and reproduce on maize pollen alone; 5.2.9) occurred less frequently during anthesis in control plots (with abundant pollen) than in experimental plots of detasseled maize, i.e. without pollen (Cottrell & Yeargan 1998). Similarly among field populations of *Col. maculata*, *A. bipunctata* and *Hip. convergens* foraging on maize, Schellhorn & Andow (1999b) found that larval and pupal cannibalism occurred only when formerly abundant aphids disappeared. This study illustrates well why cannibalism is considered a 'life-boat strategy' (e.g. Cushing 1992).

Non-sibling cannibalism may be adaptive, both in providing critical energy and nutrients to the cannibal (especially when other food is scarce), and in eliminating a cannibal's potential competitors (Fox 1975, Polis 1981, Agarwala & Dixon 1992). Larvae of the coccidophagous ladybird *Exochomus flavipes* generally developed faster when fed on conspecific eggs than when fed on their usual prey, *Dactylopius opuntiae* (Geyer 1947). Similarly, *Col. maculata* larvae gained more weight by preying on conspecific eggs than on aphids (Gagné et al. 2002). Agarwala and Dixon (1992) found that conspecific eggs of *A. bipunctata* were superior to aphids as food for fourth instars; consumption of a greater biomass of aphids was required to support a given rate of growth. Furthermore, the first instars preferred conspecific eggs over aphids, and preferred aphids painted with egg extract over eggs painted with aphid extract. First instars were apparently attracted to eggs by chemical cues. Omkar et al. (2006b) obtained similar results when *C. tranversalis*, *P. dissecta*, and *Coelophora saucia* were presented with conspecific eggs and the essential prey, *Aphis gossypii*.

In some earlier reports conspecific eggs or other insect eggs were found inferior to aphids as food for coccinellid larvae. Larvae of *C. septempunctata* developed more slowly and attained smaller sizes on an exclusive diet of eggs than on aphids (Koide 1962), and even the first and second instars of *C. septempunctata brucki* moulted only to the next stage (Takahashi 1987). Larvae of *Col. maculata* took longer to develop when reared on conspecific eggs than on eggs of the fall webworm, *Hyphantria cunea* (Warren & Tadić 1967).

Egg cannibalism appears more common than intraguild egg predation in part because chemical defenses deter other ladybird species from attacking eggs (e.g. Agarwala & Dixon 1992, Hemptinne et al. 2000a, b). For example, adults of *Menochilus sexmaculatus* and *C. leonina transversalis* ate conspecific eggs much more readily than each other's eggs (Agarwala et al. 1998). Similarly, fourth instar and adult *Har. axyridis* consumed conspecific eggs more than eggs of *A. bipunctata*. Such feeding behaviour with a clear tendency towards cannibalism (i.e. stronger intraspecific than interspecific effect), may ultimately limit the adverse effects on the native species (*A. bipunctata*) of this exotic intraguild top predator (Burgio et al. 2002).

Consumption of larvae

The expression of cannibalistic larval behaviour towards other larvae, as influenced by prey availability, varies among genetic lines of *Har. axyridis* (Wagner et al. 1999) and also among species (e.g. Yasuda et al. 2001, Pervez et al. 2006). Pervez et al. (2006) reported stronger cannibalistic behaviour of larvae of *P. dissecta* than of *C. leonina transversalis*. The importance of any size disparity between attacking and attacked larvae was illustrated by Yasuda et al. (2001), who found that *C. septempunctata brucki* and *Har. axyridis* larvae generally escaped when attacked by conspecifics of the same age, but did so less frequently when attacked by an older larva. Omkar et al. (2006a) found similar results for escapes of *C. leonina transversalis* larvae from would-be cannibals, but interestingly also found that *P. dissecta* larvae generally escaped more often when attacked by older conspecific larvae than by larvae of the same age. Such studies on insects confined in limited space prevent emigration in response to declining prey density, a response that may be important in natural populations (Schellhorn & Andow 1999b, Sato et al. 2003). Osawa (1992a), for example, found that pupae of *Har. axyridis* fell victim to cannibalism less frequently when they pupated away from, rather than near an aphid colony.

Conspecific larvae often, but not always, may be relatively unsuitable (yet marginally adequate) for each other as food. Yasuda and Ohnuma (1999) found that fourth instar *C. septempunctata* gained significantly less weight on a diet of conspecific immobilized (i.e. the legs amputated) fourth instars than on *Aphis gossypii*. In contrast, fourth instars of the more polyphagous *Har. axyridis* (which were toxic as prey for *C. septempunctata*) developed just as well on a diet of conspecific fourth instars (or those of *C. septempunctata*) as on a diet of aphids. Interestingly, a diet of dead, conspecific larvae alone (i.e.without aphids in the diet) was unsuitable over the long term for *Har. axyridis* reared from hatching (Snyder et al. 2000). Survivorship and weight as adults were reduced and development time increased, when larvae of *Cycloneda sanguinea*, *Olla v-nigrum* and *Har. axyridis* were reared from hatching on a diet of frozen conspecific larvae versus a diet of frozen eggs of *Ephestia kuehniella* and bee pollen. Among all three species, the incidence of cannibalism increased with reduced provision of *E. kuehniella* eggs and with increased larval density (Michaud 2003). Pervez et al. (2006) compared conspecific eggs or first instar larvae with aphids (*Aphis gossypii*) as diets for larval *P. dissecta* and *C. leonina transversalis*. For both species, survivorship to the pupal stage and adult weight were reduced by feeding on conspecifics, especially on larvae. Larval performance was overall somewhat better on a diet of conspecific eggs than of larvae (both were inferior to aphid diet), perhaps because the less developed eggs are easier to digest. Nomura and Niijima (1997) also reported that fourth instars of *M. sexmaculatus* suffered from malnutrition and showed high mortality when reared on conspecific first and second instars and pupae, but not when reared on conspecific eggs.

Cannibalism on conspecific larvae is nonetheless important for ladybird development and survival, especially under low prey availability (Schellhorn & Andow 1999b, Wagner et al. 1999, Snyder et al. 2000). Wagner et al. (1999) reared larvae of *Har. axyridis* to the third instar under low or high aphid diets (*Myzus persicae*). When reared under low aphid availability, those third instars that cannibalized a single first instar developed significantly faster thereafter than controls, even though all individuals were provided with aphids *ad libitum* from the third instar onwards. Thus, cannibalism offset the adverse effects of earlier low aphid availability on larval growth rate that persisted even after aphids became highly available. Snyder et al. (2000) provided another example of cannibalism counteracting negative effects of a poor diet. Survival and rate of development increased in larvae of *Har. axyridis* feeding on aphids of relatively low nutritional quality (*Aphis fabae* and *Aphis nerii*), when the larvae cannibalized dead conspecific larvae every other day. The effect was intensified when the cannibalized larvae had fed on high quality food (pupae of *Apis mellifera*).

Kin recognition

A cost of cannibalism can lie in consuming kin, with subsequent reduction in inclusive fitness. But in at least some cases, ladybirds appear able to recognize and avoid cannibalizing their own kin. Agarwala and Dixon (1993) found that females of *A. bipunctata*, and their offspring (second instars), consumed fewer of their own eggs than eggs of other females when confined with equal numbers of both kinds of eggs. However, males ate as many of their own eggs as eggs sired by other males (perhaps because males invest much less energy in eggs and cannot safely distinguish them). Joseph et al. (1999) found that third instar *Har. axyridis* placed together were much less likely to cannibalize siblings than unrelated individuals. Michaud (2003) also found that larvae of *Har. axyridis*, but not of *Cycloneda sanguinea* and *Olla v-nigrum*, were less likely to cannibalize sibling than non-sibling larvae. Pervez et al. (2005) reported the same for third instars of *P. dissecta* and *C. leonina transversalis* but not for fourth instars, perhaps because of their greater voracity.

Population consequences

Cannibalism has intriguing potential consequences for population dynamics (e.g. Cushing 1992). Mills (1982b) and Osawa (1993) drew attention to the considerable potential of non-sibling egg cannibalism in regulating population size in ladybirds, perhaps often at levels below those necessary for effective biological control of target pests. As a strong intraspecific interaction limiting population size, cannibalism furthermore can reduce adverse interspecific effects on populations of other ladybird species, for example by **top intraguild predators** such as *Har. axyridis* (e.g. Burgio et al. 2002).

Cannibalism can limit population size through **disease transmission** as well as through victim mortality. Saito and Bjornson (2006) reported 100% horizontal transmission when first instars of *Hip. convergens* consumed conspecific eggs that were infected with an unidentified microsporidian (as noted above, however, Nomura and Niijima (1997) found that male-killing bacteria were not transmitted horizontally through egg cannibalism).

Egg cannibalism is also recorded in **phytophagous** ladybirds. Nakamura et al. (2004) assume that egg cannibalism causes the marked population cycle that occurs each generation in a lowland (but not a highland) population of *Epilachna vigintioctopunctata* in Indonesia.

5.2.9 Non-insect food (pollen, nectar, spores of fungi)

Among food of plant origin, **pollen** and **nectar** (both from flowers and from extrafloral nectaries), form an important food for even explicitly carnivorous coccinellids (see also 5.2.13, 5.2.14). This plant food allows the coccinellids to survive with a reduced mortality when insect food is scarce intermittently, or at the end of the season, when they accumulate reserves for diapause (5.2.5, Chapter 6).

Pollinivory was recorded very early in several coccinellid species (for refs see Hodek 1996 and Lundgren 2009). Pollinivory was found by dissections of the gut of ***P. quatuordecimpunctata*** (Hemptinne et al. 1988) and ***A. bipunctata*** (Hemptinne & Desprets 1986, Hemptinne & Naisse 1987) particularly in early spring. Polinivory of *A. bipunctata* has recently been studied by de Clercq and his team (de Clercq et al. 2005, Jalali et al. 2009a). Experimental feeding with pollen showed that for most entomophagous ladybirds, it represents alternative food which alone does not allow the oocytes to mature but may contribute to an earlier start of oviposition after aphids appear.

Adults of the introduced *Chilocorus kuwanae* were observed feeding on the nectar and pollen of two *Euonymus* spp. in North Carolina. The presence of this pollen in the gut of this species was documented through dissection (Nalepa et al. 1992). Non-aphid food was also documented in central Italy by gut analysis in *C. septempunctata* adults after their dispersal from matured crops (Ricci et al. 2005). The ladybirds fed on pollen of Asteraceae and Apiaceae, as well as on fungal spores of *Alternaria* spp. and *Cladosporium* spp. (Triltsch 1999, Ricci et al. 2005; Fig. 5.19).

Two years analysis of gut contents of *Cer. notata* brought the first details on the diet of this rare species. Both larvae and adults contained aphids, but in their

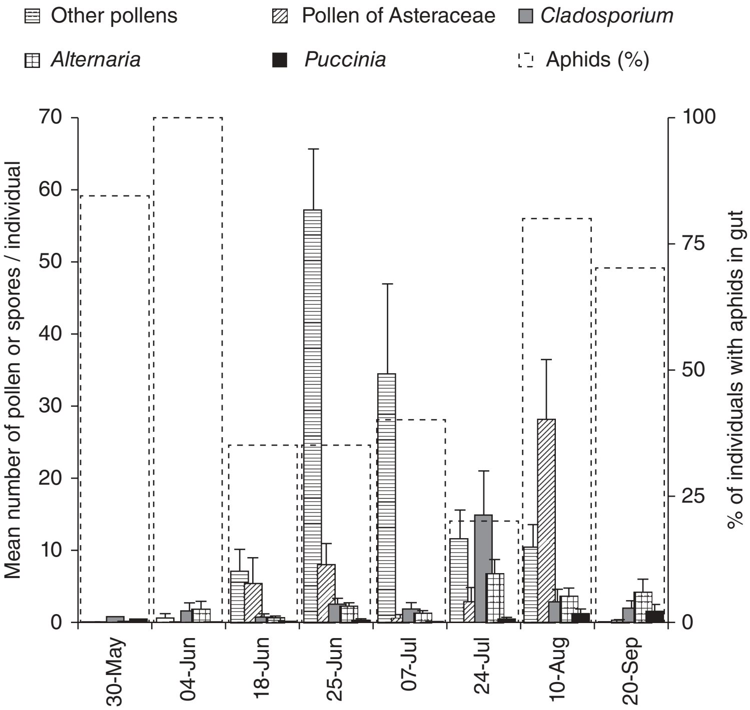

Figure 5.19 Number (±SE) of pollen grains and fungal spores found in the gut of an individual adult of *Coccinella septempunctata*, compared to the percentage of coccinellid adults with aphids in their gut (dotted bars) on different dates in 2002 in central Italy (from Ricci et al. 2005).

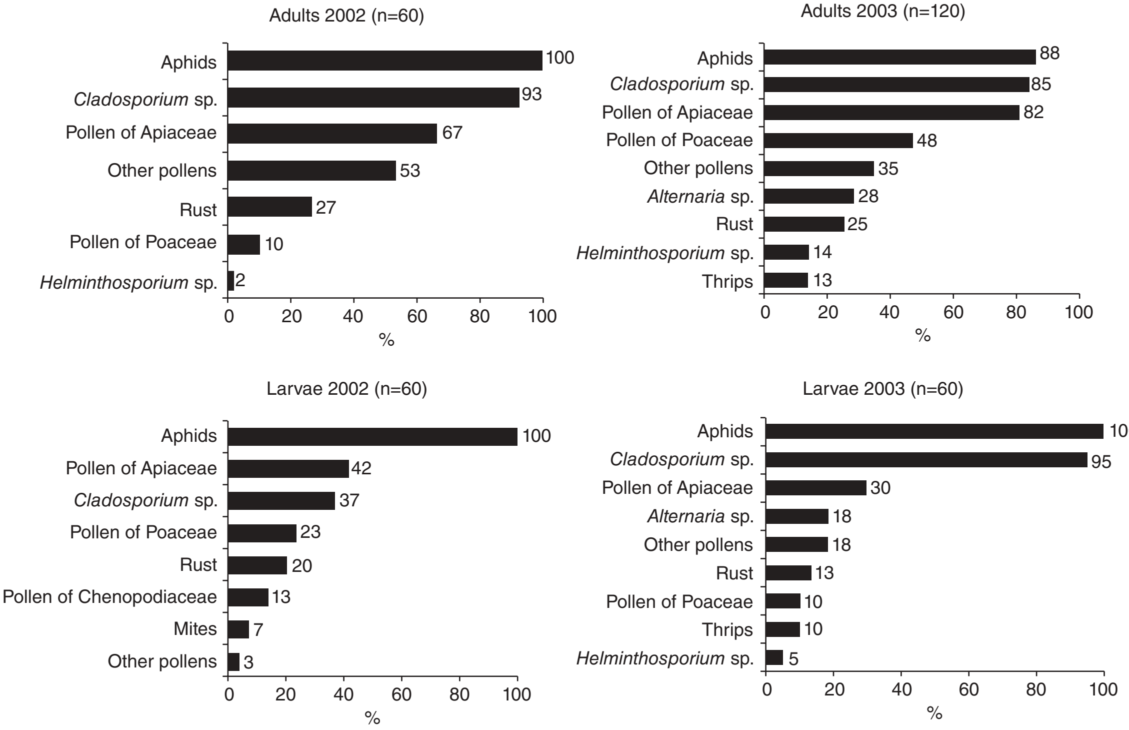

Figure 5.20 Food remains in the gut of *Ceratomegilla notata* adults and larvae in the northern Italian Alps (from Ricci & Ponti 2005).

absence the ladybirds consumed thrips. Also the incidence of pollen of Apiaceae and Poaceae, and fungal spores, mainly of *Cladosporium* spp., was very high (Ricci & Ponti 2005; Fig. 5.20).

Feeding on pollen can enable **reserves** to be accumulated to provide for long-term starvation during **dormancy** (Hagen 1962). An increase of reserves in the fat body, after feeding on maize pollen in the laboratory, was recorded in adult *C. septempunctata* collected during migration to hibernation sites (Ceryngier et al. 2004).

Pollens from different plants have different compositions (e.g. the pollen of *Pinus* contains much less protein than other pollens used in the study) and are not equally adequate as food for coccinellids (Smith 1960, 1961). Sunflower pollen proved fatal to both larvae and adults of *Col. maculata*; it adhered to the insect cuticle due to its surface structure (Michaud & Grant 2005). It was reported that pollen expressing the insecticidal Cry 3Bb1 protein for control of corn root worm had no measurable negative effect on the development to pupation of *Col. maculata* larvae nor on adult survival and reproduction (Duan et al. 2002).

For some coccinellid species, **pollen** may represent an **essential food**, and apparently the only essential food, so that they are in fact phytophagous. Particularly the high-altitude alpine coccinellid species, such as ***Coccinella reitteri*** or ***Ceratomegilla barovskii kiritschenkoi***, are adapted to feeding on pollen, often on edelweiss (*Leontopodium alpinum*), because their habitats often lack aphids (Savoiskaya 1970b). ***Bulaea lichatschovi*** is often mentioned as an example of pollinivory (e.g. Savoiskaya 1983), but detailed rearing experiments have not yet been undertaken to elucidate the physiological value of pollen in this species (5.2.13).

More is known about another pollen feeder, the polyphagous ***Coleomegilla maculata*** (5.2.4.1). It was found that *Col. maculata* may complete its full development on pollen of a number of plants (*Zea mays*, *Betula populifolia*, *Cannabis sativa*, *Carpinus caroliniana*) equally successfully as on aphids (Smith 1960). The species was reported to prefer pollen to aphids (Ewert & Chiang 1966), with its observed preference for the middle strata of crop plants considered as an indication of a predominant feeding on pollen. Preference for pollen was also recorded in maize in Kentucky where predation on *Helicoverpa zea* and cannibalism on conspecific eggs decreased in plots with abundant pollen (Cottrell & Yeargan 1998). **Maize pollen** was experimentally shown to be **essential food** for *Col. maculata* (Hodek et al. 1978). When fed exclusively with maize pollen (*Zea mays*), however, the adults have a doubled preoviposition period and a halved fecundity, compared with preying on aphids (Hodek et al. 1978; Fig. 5.21). It thus appears that pollinivory represents just one aspect of the wide polyphagy of this species, shown also by its acarophagy (5.2.4) and feeding on the eggs of Lepidoptera and Coleoptera (5.2.7).

In an Illinois cornfield, the density of *Col. maculata* eggs increased during anthesis and it was strongly correlated with the rate of pollen shed. Only a minority of *Col. maculata* larvae and adults preyed on aphids, although they were also abundant during anthesis. In contrast, the majority of larvae and adults of *Har. axyridis* preyed on aphids. This was also shown by dissection of guts of larvae and adults of both species (Lundgren and Wiedenmann 2004; Fig. 5.22). The organic content of corn pollen was strongly correlated with the survival of young adults of *Col. maculata*, suggesting that some critical micronutrient was present at suboptimal levels in some of the pollen. The efficiency with which *Col. maculata* larvae convert pollen into biomass increased as the larvae aged. The authors assume that there is a physiological change in late instar larvae which allows them to produce more biomass from the same amount of pollen. This is not the case with aphid prey (Lundgren et al. 2004).

Michaud and Grant (2005) compared the nutritive value of lepidopteran eggs with several pollens (maize, sorghum, bee-collected) for development of *Col. maculata*. When water was available, larval survival on pollen was 100%, as it was on frozen eggs of *E. kuehniella*. However, in a simulated drought treatment, larval survival on pollen was significantly reduced. The *Ephestia* egg diet facilitated a shorter development time and resulted in heavier adults. Thus not only aphids (Hodek et al. 1978), but also *Ephestia* eggs, are more suitable for *Col. maculata* then pollen (Michaud & Grant 2005). Also, for *Har. axyridis*, bee-collected pollen is a less suitable food than frozen eggs of *E. kuehniella*. A diet of pollen alone allowed 35–48% larvae to reach adulthood, but the development was 31–49% longer and the adults were 37–68% lighter. When provided exclusively with pollen both as larvae and adults, only

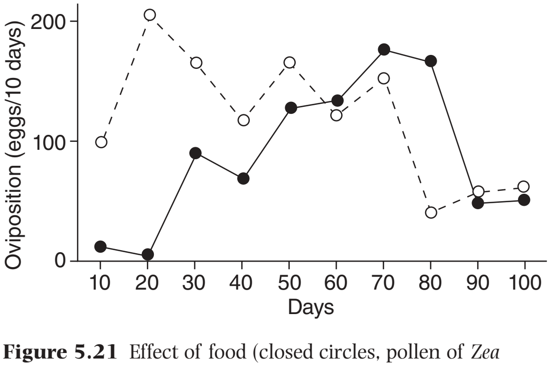

Figure 5.21 Effect of food (closed circles, pollen of *Zea mays*; open circles, *Acyrthosiphon pisum*) on the oviposition rate of *Coleomegilla maculata lengi* ($n = 20$) (modified from Hodek et al. 1978).

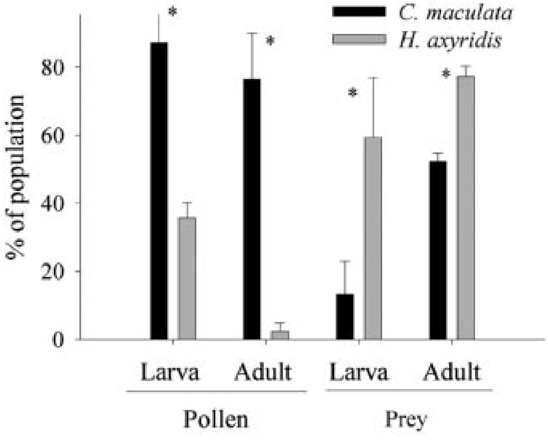

Figure 5.22 Percentage of *Harmonia axyridis* and *Coleomegilla maculata* adults that had pollen or prey in their digestive tracts. Only the individuals collected during anthesis were used. Error bars represent SEMs, and bars with asterisk above are significantly different (*t*-test, $\alpha = 0.05$) (from Lundgren et al. 2004).

about 40% of females were able to produce a small number of viable eggs (Berkvens et al. 2008).

Extrafloral nectaries were reported early as a source of substitution food by Watson and Thompson (1933) for *Leis conformis* (the plant was *Crotalaria striata*) and later, for example, by Putman (1955) for *Stethorus pusillus* (on young leaves of peach trees), by Ibrahim (1955b) for *C. undecimpunctata menetriesi* (nectaries on the midrib of cotton leaves) and by Anderson (1982) for *Apolinus lividigaster* (glands on the leaves of the euphorbiacean *Glochidion fernandii*). The importance of feeding on the extrafloral nectaries of cotton plants was documented by using nectariless varieties. The abundance of *Hip. convergens* was significantly reduced in the nectariless plots compared to plots with nectaried cotton (Schuster et al. 1976). In contrast, predation of *Har. axyridis* on *Aphis spiraecola* was reduced in the presence of extrafloral nectar (Spellman et al. 2006).

A long-standing question concerning the food relations of ***Tytthaspis sedecimpunctata*** was solved by Ricci (1982) in a detailed morpho-ethological study. The mandibles of the larvae in *T. sedecimpunctata* and *Coccinella nigrovittata* are equipped with 20–22 spine-like processes which form a kind of comb or rake. This structure enables the larvae to exploit their food sources: **pollen from *Lolium*** *perenne* and *L. multiflorum*, and spores of *Alternaria* sp. The larvae detach pollen and spores from their support by an upward movement of the head (Ricci 1982; Fig. 5.23, 5.4.3). The examination of adult gut contents after the mowing of meadows showed the pollen from Poaceae (most common was *L. perenne*), which is the preferred food, and **conidia and spores of fungi** (most often *Alternaria* sp. and *Cladosporium* sp.) (Fig. 5.24). Mites and thrips were also present (Ricci et al. 1983).

The **alternation** in feeding on grains of **pollen** and **spores** of fungi documented so precisely in *T. sedecimpunctata* by Ricci (1982, Ricci et al. 1983) is probably not exceptional. Other records indicate the same habit in *Illeis galbula* (conidia and hyphae of *Oidium*, pollen of *Ligustrum* spp. and *Acacia* spp., Anderson 1982) and in *Rhyzobius litura* (aphids, conidia of *Oidium*, *Alternaria* and *Cladosporium*, spores of *Puccinia*, pollen of Poaceae and *Mercurialis annua* (Ricci 1986b). Larvae of *R. litura* develop equally well on conidia of *Oidium monilioides* and on the aphid *Rhopalosiphum padi* (5.2.5).

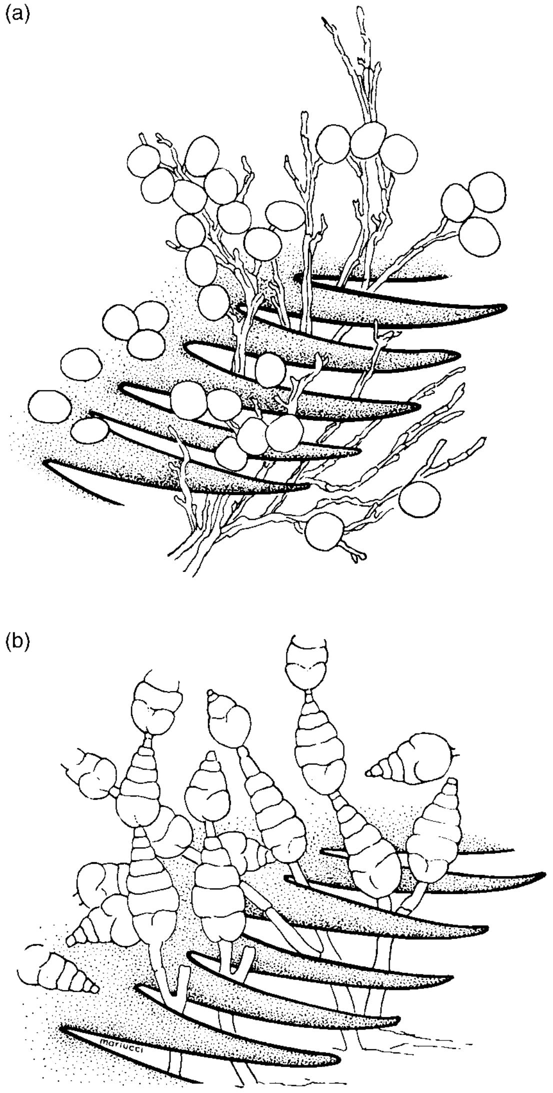

Figure 5.23 The use of the comb-like structure on the mandible of *Tytthaspis sedecimpunctata* for collecting pollen of *Lolium perenne* (a) and spores of *Alternaria* sp. (b) (from Ricci 1982).

Hukusima and Itoh (1976) attempted to rear four coccinellid species on pollen and powdery mildew. They failed with *C. septempunctata brucki* and *Menochilus sexmaculatus*. Meagre success was achieved in *P. japonica*; only 7% of individuals reached the adult stage on powdery mildew, while 10 and 16% reached adulthood on maize and rye pollen, respectively. In the notorious generalist *Har. axyridis*, the results were even

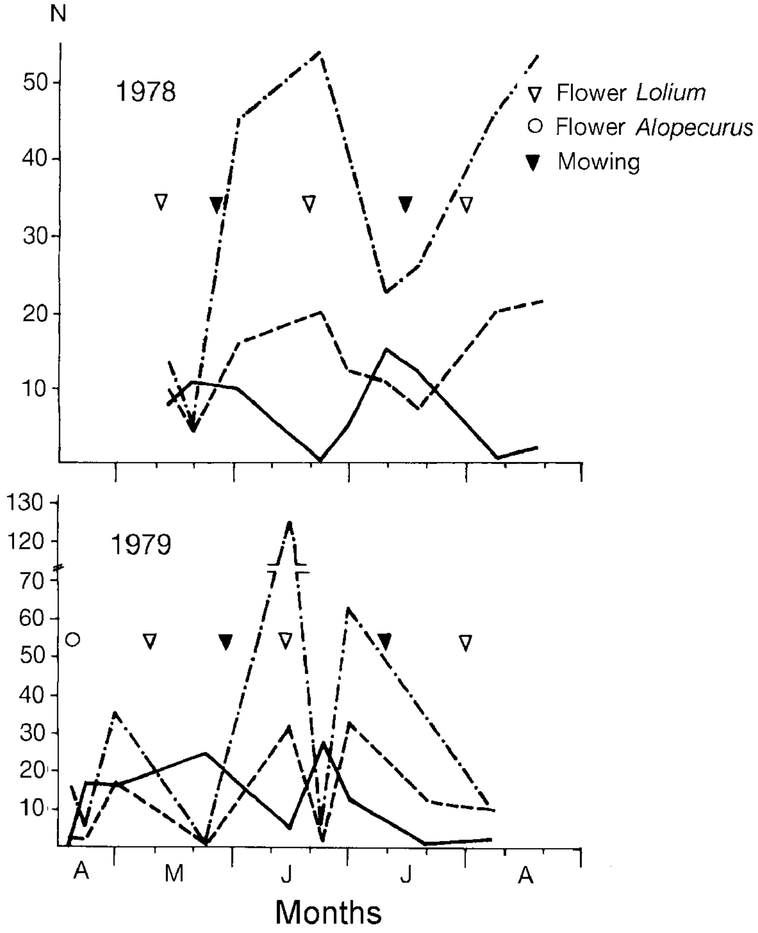

Figure 5.24 Number of grains of pollen and conidia of fungi in the gut contents of *Tytthaspis sedecimpunctata* adults in relation to flowering of *Lolium perenne* and *Alopecurus pratensis* and the hay harvest. Unbroken line, pollen; dot and dashed line, conidia of *Cladosporium* sp.; broken line, conidia of *Alternaria*; open triangles, flowering of grasses; closed triangles, hay harvest (from Ricci et al. 1983).

lower, 0, 10 and 7%, respectively. The authors quoted numerous early observations by Ninomiya of *C. s. brucki* feeding on powdery mildew on oak.

It should be noted that we still have few records of the food habits of ***Propylea*** *quatuordecimpunctata* and *P. japonica* and thus the polyphagy of this genus cannot be ruled out, although both species are usually considered to be specialized aphid feeders (e.g. Klausnitzer & Klausnitzer 1986 and Olszak 1988). However, Turian (1971) had already added *P. quatuordecimpunctata* to the list of micromycetophagous coccinellids, based on three observations of adults feeding on mildews (*Microsphaera alphitoides* on *Quercus*, *Sphaerotheca castagnei* on *Taraxacum*). In spite of the results above by Hukusima and Itoh (1976), pollen and mildew can only be considered a good alternative diet for *Propylea* spp.

Some coccinellids have been observed **consuming** small amounts of **leaf material**. The behaviour by *C. septempunctata* of scraping plant surfaces was considered unique by Legrand and Barbosa (2003), but observations on *C. septempunctata* feeding in spring on young leaves had already been mentioned by Hodek (1973). Feeding on leaf tissue by larvae of *Col.*

maculata and *Har. axyridis* has been recently reported (Moser et al. 2008, Moser & Obrycki 2009).

Koch et al. (2004) recorded that *H. axyridis* adults fed in autumn on damaged **ripening fruit**, such as apples, grapes, pumpkins and raspberries. Feeding by *A. bipunctata* adults on cherries and plums has also been observed recently (I. Hodek, unpublished). Coccinellids have even occasionally been reported **biting** fairly strongly **into human skin** (Klausnitzer 1989, Majerus & Kearns 1989), probably when drinking sweat.

5.2.10 Substitute diets and food supplements (sprays)

Aphids and coccids are available from the field for only part of the year, and can be demanding to rear in sufficient numbers to support large laboratory populations of ladybirds. Considerable effort therefore has been spent in developing substitute foods for ladybirds (see also 5.2.7). Dried or frozen aphids have been fed to ladybirds with mixed success. Using **dried aphids**, Smith (1965b) succeeded in rearing *Anatis mali*, *A. bipunctata*, *Hip. tredecimpuntata* and *Col. maculata*, but not *Coccinella* spp. In contrast, *C. septempunctata* was reared successfully with **quick-frozen aphids** (Shands et al. 1966), as was *Hip. convergens* (Hagen 1962).

Given the challenges of developing mixtures of solely chemically defined substances (i.e. **holidic diets**), most effort has been devoted to developing diets that include, in addition to such mixtures, natural substances (e.g. honey, yeast, royal jelly of bees, and vertebrate tissues) either in limited amount (**meridic diets**) or in sufficient amounts to provide most dietary requirements (**oligidic diets**; Racioppi et al. 1981). Smirnoff (1958) reported good results in rearing larvae and adults of multiple species of aphidophagous, coccidophagous, acarophagous, and mycophagous coccinellids, when the ladybirds were fed with diets including royal jelly, agar, cane sugar, honey, alfalfa flour, yeast and water, plus small quantities of their natural foods. Similarly, Chumakova (1962) reared *Cryptolaemus montrouzieri* on **small amounts of natural prey** mixed with a variety of substances. These successes could not be repeated by others, however (Tanaka & Maeta 1965, G. Iperti, unpublished).

To date, most success in developing a laboratory diet has been achieved for the polyphagous and pollinivorous ***Coleomegilla maculata*** (Hodek et al. 1978). Szumkowski (1952, 1961b) used liver, meat or fish mixed with vitamin C, honey or sugar, and found finally that a mixture of fresh yeast with glucose or sucrose solution was superior to the liver diet in promoting larval development. Szumkowski's diet of pig's liver with vitamins supported egg production of *Col. maculata* (Warren & Tadić 1967). However, these diets failed to support egg-laying and larval development of *Cycloneda sanguinea* and *Hip. convergens* (Szumkowski 1961a). Smith (1965b) succeeded in rearing *Col. maculata* larvae on a diet based on brewer's yeast and sucrose. When the yeast was replaced by liver, this diet also supported oviposition by adults. Other diets (including a banana diet) varied in their abilities to support oviposition in 13 species of coccinellids (Smith 1965a).

Based on analyses of aphids and calf liver, Atallah and Newsom (1966) formulated 16 diets for *Col. maculata*, six of which supported larval development and oviposition. The most successful diets included a high proportion of liver, and carotenoids and sterols extracted from cotton leaves. Addition of vitamin E stimulated copulation (see Hodek 1996, pp. 191–2). This diet was not satisfactory for *C. novemnotata*, *Cycloneda* spp., *Hip. convergens*, and *Olla v-nigrum*. Modifications, including adding carrot lipid, whole egg, beef liver and honey, made the diet suitable for rearing larvae of *A. bipunctata*. Although the resultant adults failed to oviposit when given the artificial diet, they did so when given aphids (Kariluoto et al. 1976). Adult emergence on this diet was promoted by adding antifungal agents (sorbic acid and methyl-p-hydroxybenzoate), not only with *A. bipunctata* but also with *C. septempunctata*, *C. transversoguttata*, *Hip. tredecimpunctata* and *P. quatuordecimpunctata* (Kariluoto 1978, 1980). Females of *A. bipunctata* (after a delay, compared to feeding on aphids), and *C. septempunctata* (to a lesser degree), produced eggs on this improved diet.

Another polyphagous species, ***Harmonia axyridis***, has over the years proved challenging to rear on artificial diet. Limited success with a mixture including agar, cellulose powder, yeast, saccharose, and amino acids was achieved by Hukusima and Takeda (1975). A powder from lyophilized larvae of honey-bee drones has proved a satisfactory (essential) food for *Har. axyridis, Har. yedoensis, Coelophora*

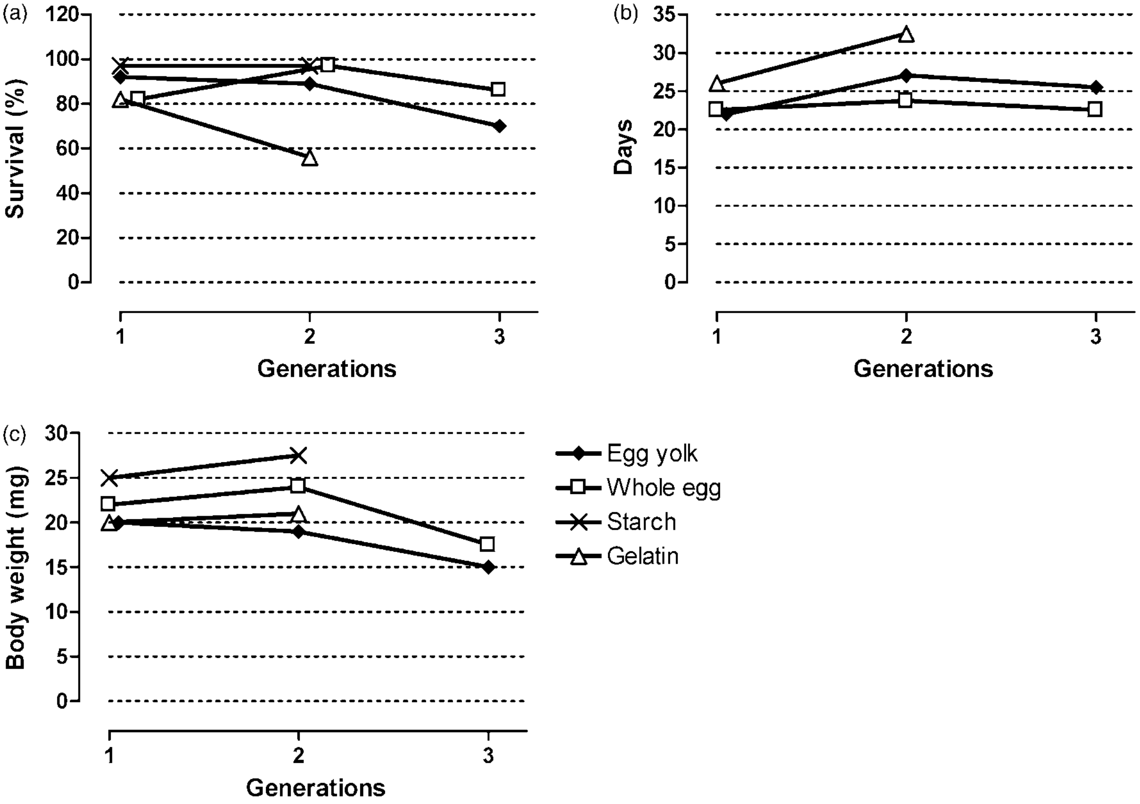

Figure 5.25 Survival rates (a), mean development times (b) and mean adult body weight (c) of *Harmonia axyridis* when maintained for successive generations on four artificial diets (from Dong et al. 2001).

biplagiata, *Menochilus sexmaculatus*, and *P. japonica* (e.g. Niijima et al. 1986; for more on 'drone powder' diet, see 5.2.7.1) Substitutive diets potentially producing multiple generations of *Har. axyridis* included chicken liver, brewer's yeast, sugars, salts, and vitamins, to which was added either whole egg or starch (most satisfactory), or egg yolk or gelatin (less satisfactory) (Dong et al. 2001; Fig. 5.25). Sighinolfi et al. (2008) used pork liver mixed with oils, sucrose, glycerine, yeast extract and vitamins, to rear *Har. axyridis* from egg to reproductive maturity, but immature development was delayed and adult emergence rate, weight, and fecundity reduced, compared to rearing on *Ephestia kuehniella* eggs.

Oviposition by ***Hippodamia convergens*** occurred on diets of banana, fresh liver, and casein + yeast + sugar (Smith 1965a). Racioppi et al. (1981) succeeded in rearing larvae of this species on a liver-based, oligidic diet, but the resultant adults did not oviposit unless also provided with aphids. With modifications of liver-based diets, Hussein and Hagen (1991) succeeded in rearing larvae of *Hip. convergens* (small resultant adults) and Bain et al. (1984) managed to rear the Australian coccinellid *Cleobora mellyi*.

Building on the work of Szumkowski (1952) and Smirnoff (1958), Chinese scientists developed diets for supporting both larval growth and oviposition of the oligophagous ***Coccinella septempunctata***. These liver-based diets included royal jelly, soybean oil or corn oil, and a juvenoid in olive oil (e.g. Chen et al. 1980, 1984, 1989, Chen & Qin 1982, Qin 1988).

A fruitful avenue for the development of artificial diets for coccinellids is the identification of key nutrient requirements (Silva et al. 2009, Pilorget et al. 2010). Atallah and Killebrew (1967), for example, identified specific amino acid requirements for *Col. maculata*, i.e. amino acids that must be ingested or derived from essential precursors in the food as opposed to those that the ladybird can synthesize itself. Svoboda & Robbins (1979) documented differences in saturated versus unsaturated sterols of the phytophagous *Epilachna varivestis* and the aphidophagous *C. septempunctata*. These differences reflect the sterols obtained from a plant versus insect diet, and can guide efforts to include sterols in artificial diets. Sighinolfi et al. (2008) characterized the amino acid and fatty acid content in *Har. axyridis* prepupae and adults and of their food, when the predators were reared on either a pork-based artificial diet (see above) or eggs of *E. kuehniella*. The analyses enabled Sighinolfi and colleagues to identify nutritional deficiencies in the artificial diet, and suggest possible improvements. A fuller discussion of artificial diets is provided by Hodek (1996) and recently by Bonte *et al*. (2010).

Sprays of food substitutes to crops to enhance numbers and activities of entomophagous insects (Hagen et al. 1971, Hagen 1986) have been explored. **Sugar** (usually sucrose, dissolved in water), when sprayed onto plant foliage as a substitute for floral nectar and honeydew, promotes local ladybird aggregation (e.g. Ewert & Chiang 1966, Schiefelbein & Chang 1966, Carlson & Chiang 1973, Mensah & Madden 1994, Evans & Richards 1997, van der Werf et al. 2000). Feeding on sugar (compared with only water) in the period of prey absence improved the reproduction of *Stethorus japonicus* in the subsequent period of ample prey: the pre-oviposition period was shortened from 2.25 to 1.44 days and only 203.7 *Tetranychus urticae* eggs were needed for oviposition to start, versus 368 eggs on water (Kishimoto & Adachi 2010).

Even stronger results are obtained from sprays that **mix protein supplements** (typically yeast-based) **with** the **sugar** (e.g. Hagen et al. 1971, 1976, Ben Saad & Bishop 1976b, Nichols & Neel 1977, Evans & Swallow 1993, Mensah 1997, 2002a, b, Mensah & Singleton 2003). The aggregating effect of food sprays appears to derive from arresting the ladybirds so that they linger longer in treated areas; cage experiments indicate that ladybird adults are not attracted by applications of protein supplement and sugar to alfalfa and cotton (Hagen et al. 1971, 1976, Nichols & Neel 1977). Ladybird adults (*Hippodamia* spp., *C. transversoguttata*, and *Scymnus postpinctus*) have been reported to be attracted, however, to potato plants sprayed with honey, molasses or tryptophan (Ben Saad & Bishop 1976a). The effects of a single food spray often dissipate within a week or so (e.g. Evans & Swallow 1993), but repeated applications can result in elevated ladybird densities over much of the growing season (e.g. Mensah 2002b, Mensah & Singleton 2003).

The goal of using food sprays is to build up large numbers of ladybirds and other natural enemies in crops early in the season while pest numbers are still low (e.g. Hagen et al. 1971, Ehler et al. 1997, Mensah & Singleton 2003). Other uses include concentrating the predators in protected areas prior to the application of an insecticide elsewhere (e.g. Evans & Richards 1997). While the results to date are intriguing, the mechanisms and benefits associated with responses of ladybirds and other natural enemies to field applications of food sprays are still little understood, and the implementation of this potential component of programmes in conservation biological control remains in its early stages (Wade et al. 2008).

5.2.11 Essential foods

The 'historical' and functional reasons for the introduction of the terms 'essential' and 'alternative' food/prey are explained in 5.2.2. The terms were defined more than 40 years ago (Hodek 1962); essential food supports successful immature development and adult reproduction, while alternative food merely maintains survival (Table 5.26, Fig. 5.1). Such a simple dichotomised definition is useful by focussing on the principal difference between the food classes and has been accepted by the scientific community (e.g. Mills 1981, Majerus 1994, Evans et al. 1999, Ware et al. 2008, Giorgi et al. 2009, Berkvens et al. 2010).

Naturally, there are **transitions** between both types. Thus essential foods show varying degrees of favourability, enabling different levels of developmental rate, fecundity and survival. Alternative foods may range from highly toxic (5.2.6.1) to quite suitable (5.2.6.3) for enabling survival in periods of scarcity of essential food by providing a supply of energy to compensate for metabolic losses or even to accumulate reserves for dormancy.

It may be considered a shortcoming that the two terms cannot be defined by numerical criteria. Decisions within the 'grey zone' of intermediate cases can only be subjective. One may hesitate as to whether 65% completion of larval development indicates somewhat

Table 5.26 List of essential foods.

Adalia bipunctata	*Adelges laricis* (L)	Mills 1981
	Acyrthosiphon pisum	Blackman 1965, 1967b, Hariri 1966a, b, Fye 1981
	A. pisum (dry powdered)	Smith 1965b
	Aphis fabae (L)	Mills 1981
	Aphis hederae (L)	Mills 1981
	Aphis pomi	Iperti 1965
	Aphis sambuci (L)	Mills 1981
	Aulacorthum solani (L)	Mills 1981
	Betulaphis quadrituberculata (L)	Mills 1981
	Brachycaudus helichrysi (L)	Mills 1981
	Brachycaudus persicae	Iperti 1965
	Brachycaudus tragopogonis	Iperti 1965
	Cavariella spp. (L)	Mills 1981
	Chaitophorus capreae (L)	Mills 1981
	Chaitophorus versicolor (L)	Mills 1981
	Chromaphis juglandicola (L)	Mills 1981
	Drepanosiphum platanoidis (L)	Mills 1981
	Eucallipterus tiliae	Wratten 1973
	E. tiliae (L)	Mills 1981
	Euceraphis punctipennis (L)	Mills 1981
	Hyalopterus pruni	Semyanov 1970
	H. pruni (L)	Mills 1981
	Macrosiphum rosae	Brun & Iperti 1978
	M. rosae (L)	Mills 1981
	Microlophium carnosum (L)	Mills 1981
	Microlophium carnosum	Blackman 1965, 1967b, Hariri 1966a, b
	Myzocallis boerneri (L)	Mills 1981
	Myzocallis carpini (L)	Mills 1981
	Myzocallis castanicola (L)	Mills 1981
	Myzocallis coryli (L)	Mills 1981
	Myzus cerasi	Iperti 1965, Ozder & Saglam 2003
	M. cerasi (L)	Mills 1981
	Myzus persicae	Blackman 1965, 1967b, Kariluoto 1980, Fye 1981
	Neomyzus circumflexus	Blackman 1965, 1967b
	Periphyllus lyropictus (L)	Mills 1981
	Phorodon humuli (L)	Mills 1981
	Phyllaphis fagi (L)	Mills 1981
	Pineus pini (L)	Mills 1981
	Pterocallis alni (L)	Mills 1981
	Rhopalosiphum maidis (dry) (slightly slower development)	Smith 1965b
	Rhopalosiphum padi (lower ovip.)	Semyanov 1970, Ozder & Saglam 2003
	Schizaphis graminum	Fye 1981
	Sitobion avenae	Ozder & Saglam 2003
	Tuberculatus annulatus (L)	Mills 1981
	Tuberolachnus salignus (L)	Mills 1981
	Uroleucon cirsii (L)	Mills 1981

Table 5.26 (*Continued*)

Adalia decempunctata	*Aphis pomi*	Iperti 1965
	Brachycaudus persicae	Iperti 1965
	Chaitophorus capreae (L)	Mills 1981
	Cinara palestinensis	Bodenheimer & Neumark 1955
	Drepanosiphum platanoidis (L)	Mills 1981
	Eucallipterus tiliae (L)	Mills 1981
	Euceraphis punctipennis (L)	Mills 1981
	Matsucoccus josephi	Bodenheimer & Neumark 1955[a]
	Myzocallis boerneri (L)	Mills 1981
	Myzocallis coryli (L)	Mills 1981
	Phyllaphis fagi (L)	Mills 1981
	Rhopalosiphum maidis	Iperti 1965
	Thelaxes dryophila (L)	Mills 1981
	Tuberculatus annulatus (L)	Mills 1981
Aiolocaria hexaspilota	*Chrysomela populi* (pre-imag.stages)	Savoiskaya 1983 (p. 155)
Anatis mali	*Acyrthosiphon pisum*	Smith 1965a
	Mindarus abietinus	Berthiaume et al. 2000
	Rhopalosiphum maidis	Smith 1965a
Anatis ocellata	*Euceraphis punctipennis* (L)	Mills 1981
	Myzus persicae (less suitable)	Kesten 1969
	Pineus pini (L)	Mills 1981
	Rhopalosiphum padi (less suitable)	Kesten 1969
	Schizolachnus pineti	Kesten 1969
	S. pineti (L)	Mills 1981
Aphidecta obliterata	*Adelges cooleyi*	Wylie 1958
	Adelges nusslini	Wylie 1958
	Elatobium abietinum (L)	Mills 1981, Day et al. 2006
	Pineus pini (L)	Mills 1981
	Rhopalosiphum padi	Oliver et al. 2006
Axinoscymnus cardilobus	*Bemisia tabaci*	Huang et al. 2006, 2008
Azya orbigera	*Coccus viridis*	Liere & Perfecto 2008
Brumoides suturalis	*Ferrisia virgata* (better for dev.)	Gautam 1990
	Planococcus minor (better for oviposition)	Gautam 1990
Calvia muiri	drone powder	Niijima 1979
Calvia quatuordecimguttata	*Acyrthosiphon pisum*	Ruzicka 2006
	Aphis pomi (L)	Mills 1981
	Eucallipterus tiliae (L)	Mills 1981
	Euceraphis punctipennis (L)	Mills 1981
	Apis mellifera – drone powder	Niijima 1979
	Psylla mali	Semyanov 1980
	Schizaphis graminum	Fye 1981
Calvia quindecimguttata	*Melasoma aenea* (pre-imag. stages)	Kanervo 1946
Ceratomegilla undecimnotata	*Aphis fabae*	Hodek 1960, Iperti 1965, Brun & Iperti 1978
	Acyrthosiphon pisum	Ruzicka 2006
	Myzus persicae	Brun & Iperti 1978
Cheilomenes lunata	*Aphis craccivora*	Ofuya & Akingbohungbe 1988
Cheilomenes propinqua vicina	*Aphis craccivora*	Mandour et al. 2006
Chilocorus bipustulatus	*Aspidiotus nerii*	Uygun & Elekcioglu 1998
	Chrysomphalus aonidum	Yinon 1969
Chilocorus circumdatus	*Aonidiella orientalis*	Elder & Bell 1998

(*Continued*)

Table 5.26 *(Continued)*

Chilocorus kuwanae	*Chionaspis salicis*	Kuznetsov & Pantyuchov 1988
	Chionaspis alnus	Kuznetsov & Pantyuchov 1988
	Chrysomphalus bifasciculatus	Tanaka 1981
	Unaspis euonymi	Ricci et al. 2006
	Unaspis yanonensis	Nohara 1962a, Tanaka 1981
Chilocorus malasiae	*Aonidiella orientalis*	Elder & Bell 1998
Chilocorus nigritus	*Abgrallaspis cyanophylli*	Ponsonby & Copland 1996, 1998, 2000, 2007b
	Acutaspis umbonifera	Ponsonby & Copland 2007a
	Aonidiella aurantii	Samways 1986
	A. aurantii (preferred by adults)	Samways & Tate 1986, Samways & Wilson 1988
	Aspidiotus nerii	Erichsen et al. 1991
	A. nerii (preferred by larvae)	Samways & Wilson 1988
	Coccus hesperidum	Ponsonby & Copland 2007a
	Pinnaspis buxi	Ponsonby & Copland 2007a
	Saissetia coffeae	Ponsonby & Copland 2007a
Chilocorus renipustulatus	*Chionaspis salicis* (L)	Mills 1981
Chilocorus rubidus	*Eulecanium caraganae* (eggs for larvae, eggs and larvae for adults)	Pantyukhov 1968
Chilocorus stigma (*bivulnerus*)	*Chrysomphalus aonidum*	Muma 1955
Clitostethus arcuatus	*Aleurodes proletella*	Bathon & Pietrzik 1986
	Aleurotuba jelinekii (L)	Mills 1981
	Siphoninus phillyreae	Bellows et al. 1992
Clitostethus oculatus	*Bemisia tabaci*	Liu et al. 1997, Liu & Stansly 1999, Ren et al. 2002
Coccinella hieroglyphica	*Galerucella sagittariae* (larvae)	Hippa et al. 1984
	Myzus persicae (less suitable than *G. sagittariae*)	Hippa et al. 1984
Coccinella magnifica	*Acyrthosiphon pisum*	Sloggett et al. 2002
	Aphis fabae	Sloggett et al. 2002
	Microlophium carnosum	Sloggett et al. 2002
Coccinella septempunctata	*Acyrthosiphon pisum*	Blackman 1965, 1967b, Schanderl et al. 1988, Obrycki and Orr 1990
	Aphis craccivora	Hodek 1960, Iperti 1965
	Aphis fabae	Hodek 1956, Blackman 1965, 1967a, Iperti 1965, Brun & Iperti 1978
	A. fabae (L)	Mills 1981
	Aphis glycines	Costamagna et al. 2008
	Aphis gossypii	Iperti 1965, Zhang 1992
	A. gossypii (G)	Agarwala et al. 1987
	Aphis jacobaeae (L)	Mills 1981
	Aphis nerii (on *Calotropis procera*)(G)	Agarwala et al. 1987
	Aphis urticata	Iperti 1965
	Brevicoryne brassicae (L)	Mills 1981
	Diuraphis noxia	Michels & Flanders 1992, Formusoh & Wilde 1993
	Hyalopterus pruni	Hodek 1960
	Hyperomyzus lactucae (L)	Mills 1981
	Lipaphis pseudobrassicae	Atwal & Sethi 1963, Sethi & Atwal 1964

Table 5.26 (*Continued*)

	L. pseudobrassicae (G)	Agarwala et al. 1987
	Longiunguis donacis	Iperti 1965
	Macrosiphoniella artemisiae	Iperti 1965
	Megoura viciae (slightly less suitable)	Blackman 1965, 1967b
	Metopolophium dirhodum (L)	Mills 1981
	Microlophium carnosum (L)	Mills 1981
	Myzus cerasi	Ozder & Saglam 2003
	Myzus persicae	Blackman 1965, 1967b, Brun & Iperti 1978, Kariluoto 1980
	M. persicae (L)	Mills 1981
	Myzus persicae nicotianae	Katsarou et al. 2005
	Rhopalosiphum maidis	Obrycki & Orr 1990
	Rhopalosiphum padi	Ozder & Saglam 2003
	Schizaphis graminum	Fye 1981, Michels & Behle 1991, Formusoh & Wilde 1993
	Sitobion avenae (L)	Mills 1981, Ozder & Saglam 2003
	Sitobion avenae	Ghanim et al. 1984
	Uroleucon aeneus	Hodek 1960
	Uroleucon cirsii (L)	Mills 1981
Coccinella septempunctata brucki	*C. s. brucki* (eggs) (development prolonged)	Koide 1962
	Myzus malisuctus	Hukusima & Sakurai 1964
	Myzus persicae	Hukusima & Sakurai 1964
	Neophyllaphis podocarpi	Maeta 1965
	Rhopalosiphum padi	Okamoto 1966
	Sitobion avenae	Hukusima & Sakurai 1964
	Vesiculaphis caricis	Takeda et al. 1964
Coccinella transversalis (*C. leonina transversalis*)	*Aphis craccivora*	Debaraj & Singh 1990, Agarwala & Yasuda 2001a
	A. craccivora (G)	Agarwala et al. 1987
	Aphis gossypii	Pervez et al. 2006
	Lipaphis pseudobrassicae (G)	Agarwala et al. 1987
Coccinella transversoguttata	*Myzus persicae*	Kariluoto 1980
	Phorodon humuli	Campbell & Cone 1999
	Schizaphis graminum	Fye 1981
Coccinella transversoguttata richardsoni	*Acyrthosiphon pisum* (dry)	Smith 1965b
Coccinella undecimpunctata	*Aleyrodes proletella*	Moura et al. 2006
	Aphis fabae	Moura et al. 2006, Soares & Serpa 2007
	Aphis pomi	Harpaz 1958
	Laingia psammae (L)	Mills 1981
	Metopolophium dirhodum (L)	Mills 1981
	Myzus persicae	Cabral et al. 2006
	Sitobion avenae (L)	Mills 1981
Coccinella undecimpunctata menetriesi	*Aphis gossypii*	Ibrahim 1955a, b
	Aphis laburni	Ibrahim 1955a, b
	Aphis nerii	Ibrahim 1955a, b
	Aphis punicae	Ibrahim 1955a, b
	Hyalopterus pruni	Ibrahim 1955a, b
	Lipaphis pseudobrassicae	Ibrahim 1955a, b
	Macrosiphoniella sanborni	Ibrahim 1955a, b
	Myzus persicae	Ibrahim 1955a, b

(*Continued*)

Table 5.26 *(Continued)*

Coelophora biplagiata	*Aphis gossypii*	Yu et al. 2005
Coelophora mulsanti	*Rhopalosiphum padi*	Sallée & Chazeau 1985
Coelophora quadrivittata	*Coccus viridis*	Chazeau 1981
Coelophora saucia	*Myzus persicae*	Omkar & Pathak 2006
Coleomegilla maculata (ssp. *lengi* incl.)	*Acyrthosiphon pisum* (also dry)	Smith 1965b
	Aphis glycines	Mignault et al. 2006
	C. maculata (eggs)	Warren & Tadić 1967
	Ephestia kuehniella (eggs)	Michaud & Grant 2005
	Hyphantria cunea (eggs)	Warren & Tadić 1967
	Leptinotarsa decemlineata (eggs) (less suitable than aphids or pollen)	Ferro & Hazzard 1991, Hazzard & Ferro 1991
	Myzus persicae	Ferro & Hazzard 1991, Hazzard & Ferro 1991
	Rhopalosiphum maidis (also dry) (slightly less suitable)	Smith 1965b
	corn pollen	Ferro & Hazzard 1991, Hazzard & Ferro 1991
	pollen (corn, sorghum)	Michaud & Grant 2005
Cryptognatha nodiceps	*Aspidiotus destructor*	Lopez et al. 2004
Cryptolaemus montrouzieri	*Maconellicoccus hirsutus*	Persad & Khan 2002
	Planococcus citri	Garcia & O'Neil 2000
	Pulvinaria psidii (eggs)	Mani & Krishnamoorthy 1990
Curinus coeruleus	*Diaphorina citri*	Michaud & Olsen 2004
	Heteropsylla cubana	Chazeau et al. 1992, da Silva et al. 1992
Cycloneda ancoralis	*Aphis gossypii*	Elliott et al. 1994
	Aphis helianthi	Elliott et al. 1994
	Diuraphis noxia	Elliott et al. 1994
	Lipaphis pseudobrassicae	Elliott et al. 1994
Cycloneda limbifer	*Aphis craccivora*	Zeleny 1969
Cycloneda munda	*Acyrthosiphon pisum*	Smith 1965b
Cycloneda sanguinea	*Aphis fabae*	Isikber & Copland 2002
	Aphis gossypii	Isikber & Copland 2001, 2002
	Myzus persicae	Isikber & Copland 2002
Delphastus catalinae	*Bemisia tabaci*	Pickett et al. 1999
		Simmons & Legaspi 2004, Zang & Liu 2007
Delphastus pusillus	*Bemisia tabaci*	Hoelmer et al. 1993, 1994, Guershon & Gerling 1999
Diomus austrinus	*Phenacoccus madeirensis*	Chong et al. 2005
	Planococcus citri	Chong et al. 2005
Exochomus childreni	*Diaphorina citri*	Michaud & Olsen 2004
Exochomus flavipes	*Dactylopius opuntiae*	Geyer 1947
	Matsucoccus josephi	Bodenheimer & Neumark 1955
Exochomus quadripustulatus	*Acyrthosiphon pisum*	Radwan & Lövei 1983
	Chionaspis salicis (L)	Mills 1981
	Dysaphis devecta	Radwan & Lövei 1983
	Dysaphis plantaginea	Radwan & Lövei 1983
	Planococcus citri	Katsoyannos & Laudeho 1977
	Pseudochermes fraxini (L)	Mills 1981
	Saissetia oleae	Katsoyannos & Laudeho 1977

Table 5.26 *(Continued)*

Harmonia axyridis	*Acyrthosiphon pisum*	Hukusima & Kamei 1970, Fye 1981, Schanderl et al. 1988
	Adelges tsugae	Wallace & Hain 2000, Flowers et al. 2005
	Aphis craccivora	Mogi 1969
	Aphis fabae	Soares et al. 2005
	Aphis glycines	Mignault et al. 2006, Costamagna et al. 2008
	Aphis pomi	Hukusima & Kamei 1970
	Apis mellifera-drone powder	Niijima 1979
	Brevicoryne brassicae (less suitable)	Hukusima & Kamei 1970
	Capitophorus elaeagni	Osawa 1992
	Diaphorina citri	Michaud & Olsen 2004
	Ephestia kuehniella (eggs)	Schanderl et al. 1988
	Hyalopterus pruni (less suitable)	Hukusima & Kamei 1970
	Hyperomyzus carduellinus	Hukusima & Kamei 1970
	Megoura viciae japonica	Hukusima & Kamei 1970
	Myzus persicae	Hukusima & Kamei 1970, Schanderl et al. 1985, Soares et al. 2005
	Nasonovia lactucae	Hukusima & Ohwaki 1972
	Neophyllaphis podocarpi	Maeta 1965
	Periphyllus californensis	Hukusima & Kamei 1970
	Rhopalosiphum padi	Okamoto 1966
	Schizaphis graminum	Fye 1981
	Sitobion ibarae	Hukusima & Kamei 1970
Harmonia conformis	*Acyrthosiphon pisum*	Fye 1981
	Aphis punicae	Moursi & Kamal 1946
	Macrosiphum rosae	Maelzer 1978
	Psylla jucunda	Hales 1979
	Schizaphis graminum	Fye 1981
Harmonia dimidiata	*Acyrthosiphon pisum*	Semyanov 1999, Ruzicka 2006
	Myzus persicae	Fye 1981, Semyanov 1999
	Eriosoma lanigerum	Chakrabarti et al. 1988
	Rhopalosiphum maidis	Semyanov 1999
	Sitotroga (eggs)	Semyanov 1999
Harmonia sedecimnotata	*Myzus persicae*	Semyanov 2000
Hippodamia convergens	*Diuraphis noxia*	Formusoh & Wilde 1993
	Phorodon humuli	Campbell & Cone 1999
	Rhopalosiphum padi	Phoofolo et al. 2007
	Schizaphis graminum	Michels & Behle 1991, Formusoh & Wilde 1993 Phoofolo et al. 2007
	Therioaphis maculata	Nielson & Currie 1960
Hippodamia parenthesis	*Acyrthosiphon pisum* (dry)	Smith 1965b
	A. pisum	Orr & Obrycki 1990
	Schizaphis graminum (less suitable than *A. pisum*)	Orr & Obrycki 1990
Hippodamia quinquesignata	*Acyrthosiphon pisum*	Kaddou 1960
Hippodamia sinuata	*Rhopalosiphum maidis*	Michels & Behle 1991
	Schizaphis graminum	Michels & Behle 1991
Hippodamia tredecimpunctata	*Acyrthosiphon pisum* (dry powdered)	Smith 1965b
	Diuraphis noxia (less suitable)	Michels & Flanders 1992
	Rhopalosiphum maidis (dry powdered) (slower development)	Smith 1965b
	Schizaphis graminum (more suitable)	Michels & Flanders 1992

(Continued)

Table 5.26 *(Continued)*

Hippodamia variegata	*Acyrthosiphon pisum*	Obrycki & Orr 1990
	Aphis craccivora	Iperti 1965
	Aphis fabae (on beans)	Brun & Iperti 1978
	Aphis glycines	Costamagna et al. 2008
	Aphis gossypii	El Habi et al. 2000
	Aphis nerii	Iperti 1965
	Aphis pomi (L)	Brun & Iperti 1978
	Diuraphis noxia (low fecundity)	Michels & Flanders 1992
	Dysaphis crataegi	Kontodimas & Stathas 2005
	Macrosiphoniella artemisiae	Iperti 1965
	Myzus persicae	Iperti 1965
	Rhopalosiphum maidis	Obrycki & Orr 1990
	Schizaphis graminum	Michels & Bateman 1986
	Schizaphis graminum (low larv. surv.)	Michels & Flanders 1992
Hyperaspis desertorum	*Orthezia urticae* (L)	Savoiskaya 1983 (p. 152)
Hyperaspis lateralis	*Pseudococcus aurilanatus*	McKenzie 1932
	Pseudococcus sequoiae (eggs, young larvae preferred prey)	McKenzie 1932
Hyperaspis notata	*Ferrisia virgata*	Staubli Dreyer et al. 1997b
	Phenacoccus madeirensis	Staubli Dreyer et al. 1997b
	Phenacoccus manihoti	Staubli Dreyer et al. 1997a
Hyperaspis pantherina	*Orthezia insignis*	Booth et al. 1995
Hyperaspis raynevali	*Phenacoccus herreni*	Kiyindou & Fabres 1987
Hyperaspis senegalensis hottentotta	*Phenacoccus manihoti*	Fabres & Kiyindou 1985
Lioadalia flavomaculata	*Schizaphis graminum*	Michels & Bateman 1986
Lindorus lophantae	*Aspidiotus nerii*	Honda & Luck 1995, Cividanes & Gutierrez 1996, Stathas 2000
	Phoenicococcus marlatti	Gomez 1999
Macroilleis hauseri	*Podosphaera leucotricha* (mildew)	Liu 1950
Megalocaria dilatata	*Pseudoregma bambucicola*	Puttarudriah & Channabasavanna 1952
Menochilus sexmaculatus	*Aphis craccivora*	Srikanth & Lakkundi 1990, Agarwala et al. 2001, Agarwala & Yasuda 2000, 2001a Omkar et al. 2005
	Aphis craccivora (G)	Agarwala et al. 1987
	Aphis gossypii	Agarwala & Yasuda 2000
	Aphis nerii (G)	Agarwala et al. 1987
	Aphis spiraecola	Agarwala & Yasuda 2000
	Aphis spiraecola (G)	Agarwala et al. 1987
	Lipaphis pseudobrassicae (G)	Agarwala et al. 1987
	Nasonovia lactucae	Hukusima & Komada 1972
	Schizaphis graminum	Fye 1981
	Sitobion ibarae	Hukusima & Komada 1974
Micraspis discolor	*Aphis craccivora* (G)	Agarwala et al. 1987
	Aphis spiraecola (G)	Agarwala et al. 1987
Myrrha octodecimguttata	*Pineus pini* (L)	Mills 1981
Nephus bilucernarius	*Dysmicoccus* spp.	Gonzáles-Hernández et al. 1999
Nephus bisignatus	*Planococcus citri*	Kontodimas et al. 2005
Nephus includens	*Planococcus citri*	Kontodimas et al. 2005

Table 5.26 (*Continued*)

Oenopia conglobata	*Aphis pomi*	Iperti 1965
	Brachycaudus persicae	Iperti 1965
	Cinara palestinensis	Bodenheimer & Neumark 1955
	Galerucella lineola (pre-imag.)	Kanervo 1946
	Matsucoccus josephi	Bodenheimer & Neumark 1955[a]
	Rhopalosiphum maidis	Iperti 1965
	Schizaphis graminum	Fye 1981
Oenopia conglobata contaminata	*Agonoscena pistaciae*	Mehrnejad & Jalali 2004
Olla v-nigrum	*Diaphorina citri*	Michaud & Olsen 2004
	Heteropsylla cubana	Chazeau et al. 1991
	Psylla uncatoides	Chazeau et al. 1991
	Trialeurodes vaporariorum	Chazeau et al. 1991
Paranaemia vittigera	*Diuraphis noxia*	Robinson 1992
Parastethorus nigripes	*Tetranychus urticae*	Bailey & Caon 1986
Pharoscymnus numidicus	*Parlatoria blanchardi*	Kehat 1968
	Prodenia litura (eggs)	Kehat 1968
Propylea dissecta	*Aphis craccivora*	Omkar & Mishra 2005
	Aphis gossypii	Omkar & Mishra 2005, Pervez et al. 2006
	Lipaphis pseudobrassicae	Omkar & Mishra 2005
	Rhopalosiphum maidis	Omkar & Mishra 2005
	Uroleucon compositae	Omkar & Mishra 2005
Propylea japonica	*Aphis gossypii*	Zhang 1992
	Ephestia kühniella (eggs, lower ovip.)	Hamasaki & Matsui 2006
	Nasonovia lactucae	Hukusima & Komada 1972
	Nilaparvata lugens	Bai et al. 2006
	Sitobion akabiae	Kawauchi 1979
	Sitobion ibarae	Hukusima & Komada 1972
	Uroleucon formosanum	Hukusima & Komada 1972
Propylea quatuordecimpunctata	*Acyrthosiphon pisum*	Obrycki & Orr 1990
	Aphis fabae (L)	Mills 1981
	Aphis glycines	Mignault et al. 2006
	Brachycaudus helichrysi (L)	Mills 1981
	Diuraphis noxia (low fecundity)	Michels & Flanders 1992
	Eucallipterus tiliae (L)	Mills 1981
	Metapolophium dirhodum (L)	Mills 1981
	Pterocallis alni (L)	Mills 1981
	Rhopalosiphum maidis	Brun & Iperti 1978, Obrycki & Orr 1990
	Schizaphis graminum	Fye 1981, Michels & Flanders 1992
	Sitobion avenae (L)	Mills 1981
	Uroleucon cirsii (L)	Mills 1981
	Uroleucon jaceae (L)	Mills 1981
Rhyzobius ventralis	*Eriococcus coriaceus*	Richards 1985
Rhyzobius litura	*Sitobion avenae* (L)	Mills 1981
	Uroleucon cirsii (L)	Mills 1981
	Uroleucon jaceae (L)	Mills 1981
Rodatus major	*Monophlebulus pilosior* (eggs)	Richards 1985
Sasajiscymnus tsugae	*Adelges tsugae*	Cheah & McClure 1998, Flowers et al. 2005
Scymnus auritus	*Phylloxera glabra*	Eastop & Pope 1966, 1969
Scymnus coccivora	*Maconellicoccus hirsutus*	Persad & Khan 2002
Scymnus frontalis	*Diuraphis noxia*	Naranjo et al. 1990, Farid et al. 1997
Scymnus levaillanti	*Aphis gossypii*	Isikber & Copland 2001
Scymnus marinus	*Saissetia oleae* (eggs)	Ba M'hamed & Chemseddine 2001

(*Continued*)

Table 5.26 *(Continued)*

Scymnus posticalis	*Aphis gossypii*	Agarwala & Yasuda 2001b
Scymnus sinuanodulus	*Adelges tsugae*	Lu & Montgomery 2001
Scymnus subvillosus	*Aphis sambuci*	Klausnitzer 1992
Serangium parcesetosum	*Bemisia tabaci*	Yigit 1992
	Dialeurodes citri	Yigit et al. 2003
	Coccus hesperidum	Yigit et al. 2003
Stethorus bifidus	*Tetranychus urticae*	Charles et al. 1985
Stethorus gilvifrons	*Panonychus ulmi*	Dosse 1967
	Tetranychus cinnabarinus (eggs)	Dosse 1967
	Tetranychus urticae (eggs)	Dosse 1967
Stethorus japonicus	*Tetranychus urticae*	Mori et al. 2005
	Tetranychus mcdanieli	Roy et al. 2003
	Tetranychus urticae	Rott & Ponsonby 2000
Stethorus punctum	*Panonychus ulmi*	Houck 1986
	Tetranychus urticae	Houck 1986, 1991
Stethorus pusillus	*Panonychus ulmi*	Putman 1955
	Tetranychus bimaculatus	Putman 1955
Stethorus tridens	*Tetranychus evansi*	Fiaboe et al. 2007
Synonycha grandis	*Paraoregma alexandri*	Shantibala et al. 1992
	Pseudoregma bambucicola	Puttarudriah & Channabasavanna 1952, Puttarudriah & Maheswariah 1966

(G) based on examination of gut content – 'common' food (Agarwala et al. 1987).

(L) based on observation of larvae of the coccinellid occurring together with the recorded prey (Mills 1981).

[a] Savoiskaya (1983, p. 142) doubts whether *M. josephi* is really an essential prey of *A. decempunctata* and *O. conglobata*. She is right mentioning that generally coccids are very unfavourable prey of Coccinellini.

less suitable essential prey or quite a good alternative prey.

An important refinement of the definitions was made by Michaud (2005), when he called attention to special cases where the relation to prey is not identical in predator larvae and adults. Michaud (2000) found, for example, that females of *Hip. convergens* had a good fecundity on *Toxoptera citricidus*, that this appears essential prey for females, while the larvae could not complete development on this prey. Michaud (2005) gave other examples of such **'non-symmetric' relations to essential food** and proposed to add the term '**complete food**' for prey that enables both larval development and female oviposition. Consequently we can recognize, for example, 'larval essential prey' of a coccinellid species, if it is not also recorded as essential for adults. To arrive at a numerical criterion for evaluating prey quality, Michaud (2005) suggests rearing ladybirds on conspecific eggs as a reference diet. However, Sloggett and Lorenz (2008) recorded nutritional differences of conspecific eggs in different species.

5.2.12 Tritrophic studies

The effect of the plant on a carnivorous insect via the herbivore is discussed in several sections of 5.2. The effect of plant **allelochemical substances** (secondary chemicals of Fraenkel 1959, 1969) was most probably the earliest topic studied in this respect. The observations on the toxic effect of allelochemicals from the elder *Sambucus* spp., acting through elder aphids (*Aphis sambuci* and *Aulacorthum magnoliae*) on *C. septempunctata* (Hodek 1956, Blackman 1965, Okamoto 1966) represented the very onset of studies of the wide field of prey specificity in coccinellids. Prey acquiring their toxicity from plants (5.2.6.1) are also included in this chapter.

Plants with a high **nutritional value** may have a positive effect, also transferred through the prey, on ladybirds. Compared with *Acyrthosiphon pisum* reared on *Vicia faba*, *A. pisum* reared on alfalfa stored significantly more fatty acids (particularly six times more myristic acid) which resulted in a 1.17-fold increase in available calories. Feeding on this more

Table 5.27 Survival of *Coccinella septempunctata* larvae, and ratio of female size at 24°C resulting from increasing daily levels of *Acythosiphon pisum* reared on either *M. sativa* or *V. faba* at 22°C (after Giles et al. 2002).

	***A. pisum* (mg/day)**							
	2.2	**2.2**	**4.3**	**4.3**	**8.2**	**8.2**	**16.4**	**16.4**
Variable	***M.s.*[*]**	***V.f.*[†]**	***M.s.***	***V.f.***	***M.s.***	***V.f.***	***M.s.***	***V.f.***
Larva	0.333	0.050[‡]	0.817	0.617	0.897	0.864	0.930	0.867
Female size[§]	0.167	0	0.158	0.174	0.540	0.325	0.780	0.432
n[**]	60	60	60	60	58	59	57	60

[*] Pea aphids reared on *Medicago sativa*.

[†] Pea aphids reared on *Vicia faba*.

[‡] Paired underlined values represent significant differences ($p < 0.05$) for 2×2 χ^2 tests between host-plants at each mg level.

[§] Elliptical body area was measured to estimate adult size (Obrycki et al. 1998).

[**] Number of *C. septempunctata* larvae at beginning of experiment.

nutritive prey increased larval survival, decreased development time and resulted in larger adults of *C. septempunctata* (Giles et al. 2002; Table 5.27). One of the tritrophic systems even occurs in a land-water ecotone: water lily–*Galerucella nymphaeae*–*Col. maculata* (Schlacher & Cronin 2007).

Another interesting tritrophic system consists of the willow, a leaf beetle (*Plagiodera versicolora*) and the predatory coccinellid *Aiolocaria hexaspilota* (see also 5.4.1.2 for this tritrophic relation). Cutting off willow trees leads to an **increase** in their **leaf nitrogen**. The relative growth rate of the chrysomelid increased when feeding on the nitrogen rich leaves, but nitrogen level did not increase in the body of the leaf beetle. Thus it is not clear why the relative growth rate also increased in the coccinellid larvae preying on the chrysomelid larvae feeding on N-rich leaves (Kagata & Ohgushi 2007; Table 5.28). Tritrophic studies based on pest-resistant plants are discussed in 5.2.6.3.

Elevated air CO_2 concentration significantly increased tannin and gossypol content and decreased N content in cotton. The survival of *Aphis gossypii* increased with higher CO_2 concentrations while their fatty acid content decreased. In contrast, the survival and fecundity of *P. japonica* was not significantly affected, but its development time was longer. As global CO_2 levels rise the authors speculated that *A. gossypii* may become a more serious pest due to its increased survival and the slower development of the ladybird (Gao et al. 2008).

Table 5.28 Qualitative traits of leaves, chrysomelids (*Plagiodera versicolora*) and ladybirds (*Aiolocaria hexaspilota*) on cut and uncut willows (modified after Kagata & Ohgushi 2007).

Willows	**Cut**	**Uncut (control)**
Leaves of host plant		
% Water (FM)	63.82 ± 0.51	62.12 ± 0.62
% Carbon (DM)	44.90 ± 0.75	45.23 ± 0.59
% Nitrogen (DM)	2.64 ± 0.11	2.31 ± 0.06
Chrysomelid prey		
Larval mass (mg FM)	5.20 ± 0.33	3.71 ± 0.19
% Water (FM)	76.29 ± 0.57	76.52 ± 0.42
% Carbon (DM)	48.73 ± 1.52	48.65 ± 1.31
% Nitrogen (DM)	8.43 ± 0.20	8.48 ± 0.16
Ladybird larva		
Larval mass (mg FM)	64.70 ± 4.10	50.81 ± 4.54
% Water (FM)	78.80 ± 0.51	78.93 ± 0.58
% Carbon (DM)	45.75 ± 1.96	42.47 ± 1.23
% Nitrogen (DM)	10.68 ± 0.50	9.23 ± 0.28

FM, fresh mass; DM, dry mass; Means ± SE.

Physiological condition (senescence) of the bean plant modified the incidence of adult diapause in coccinellids via the aphid prey (Rolley et al. 1974; Table 6.8, in Chapter 6).

A particular kind of tritrophic phenomenon is the so called 'crying for help' of **plants injured through herbivory**, i.e. the production of attractants for natural enemies of the herbivores (detected for the first time in predatory acari). Such attraction has already been observed in several coccinellid species, attracted for example by methylsalicylate produced at a higher level due to aphid infestation of plants (Zhu & Park 2005, Karban 2007; several cases are discussed in 5.4.1.2).

5.2.13 Food of phytophagous Coccinellidae

Phytophagous ladybirds of the subfamily Epilachninae feed especially (but not exclusively) on host plants of the families Solanaceae and Cucurbitaceae (Schaefer 1983). Some species have been studied intensively in relation to their feeding on economically important host plants. These include the Mexican bean beetle, *Epilachna varivestis*, a pest with a worldwide distribution (e.g. Fujiyama et al. 1998, Abe et al. 2000, Shirai & Yara 2001), and *H. vigintioctomaculata* (Fujiyama & Katakura 2002). Interestingly, a pest of cucurbits, *Henosepilachna elaterii* (=*Epilachna chrysomelina*) has been reported as also feeding on aphids (El Khidir 1969).

Closely related, **co-occurring species of *Henosepilachna (=Epilachna)*** differ in their abilities to feed on particular host plant species. In Japan, *H. vigintioctomaculata* preferred potato plants, and failed to develop on eggplant, whereas *H. vigintioctopunctata* fed and developed on both potatoes and eggplant (Iwao 1954). Similarly, among three closely related species of the *H. vigintioctomaculata* complex, the wild herb *Solanum japonense* was most suitable for development of *H. pustulosa*, less so for *H. niponica*, and least for *H. yasutomii* (Fujiyama & Katakura 2002).

The usual food of *H. pustulosa* is thistle (*Cirsium* spp.), but Iwao and Machida (1961) found that a varying proportion of individuals also accept potato plants, with a positive correlation between a female's acceptance of potato and her offspring's acceptance of this host plant. As a result of either pre-imaginal conditioning or negative selection (with high mortality on potatoes), a greater percentage of individuals that fed as larvae on potato versus thistles (74% vs. 31%) subsequently accepted potato as adults. Furthermore, individuals could also be conditioned during the first days of adult life to prefer either host plant thereafter (Iwao & Machida 1961). By contrast, Shirai and Morimoto (1999) found no difference between populations associated with potato and wild thistle in their abilities to feed on potato. Koji et al. (2004) compared feeding responses of two Japanese *H. niponica* populations, separated by 150 km and associated with different thistle species, to several geographically restricted populations of thistles. Although the two (Asiu and Yuwaku) populations were similar in many of their responses to the host plants (i.e. overall they shared a conserved hierarchy of feeding preferences and growth performance), they differed strikingly in their response to a host plant used naturally as a secondary food source by only the Yuwaku population. Asiu adults thus avoided *Cirsium kagamontanum*, and their offspring failed to develop on this host plant. Yuwaku adults, in contrast, preferred this thistle, and approximately 10% of their offspring developed on this host. Similarly, Fujiyama et al. (2005) found that adult preference and larval performance on an unusual host plant, the deciduous tree *Pterostyrax hispidus*, was higher for a population of *Henosepilachna yasutomii* that occurs on this tree than for other populations of this ladybird species naturally associated with other host plants (see also Kikuta et al. 2010, Kuwajima et al. 2010).

The **genetic basis** that may underlie such patterns of host use in *Epilachna* spp. has received considerable attention. The major host plants of *E. vigintioctopunctata* in Southeast Asia are solanaceous species (Shirai & Katakura 1999). Shirai and Katakura (2000) found natural populations of this ladybird using the legume *Centrosema pubescens* in Malaysia and Indonesia. When these legume-feeding strains were maintained for a number of generations on *Solanum nigrum*, however, they rapidly lost their ability to use the legume (Shirai & Katakura 2000; Fig 5.26). Interestingly, the authors were unable to select conversely for a shift in host use by rearing *Solanum*-feeding ladybird strains on the legume. Ueno et al. (1999) studied siblings of *H. vigintioctomaculata* collected from *Solanum tuberosum* on Honshu or from the novel host *Schizopepon bryoniaefolius* on Hokkaido. Since Ueno et al. (1999) did not find negative genetic correlations in established and novel host plant use, they suggested that the coccinellid expansion onto *S. bryoniaefolius* on Honshu is prevented by ecological and behavioural factors, rather than genetic constraints. A subsequent study (Ueno et al. 2001), using beetles associated with *S. bryoniaefolius* on Hokkaido, found lower heritabilities for growth performance when the beetles were reared on *S. bryoniaefolius* rather than on *S.*

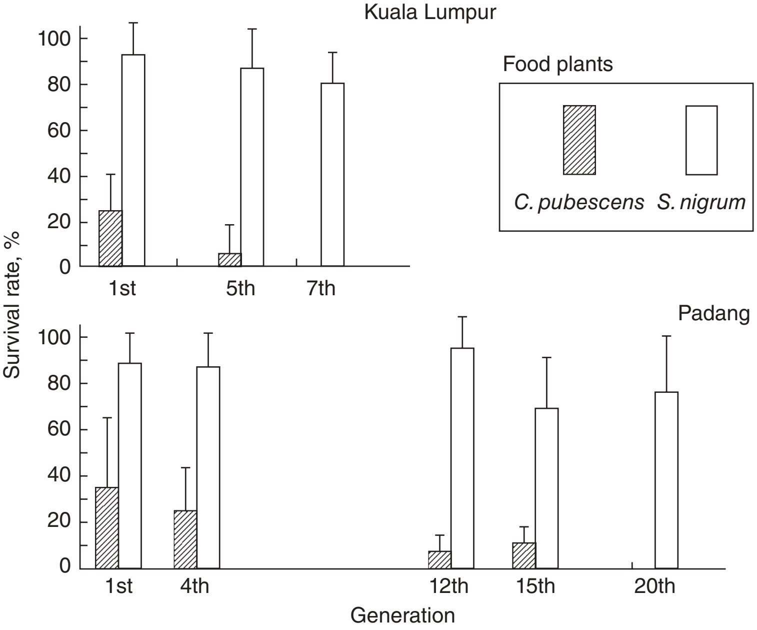

Figure 5.26 Survival rates (emergence rates from pupae) in successive laboratory-reared generations of *Henosepilachna vigintioctopunctata*, for two populations (top, from Kuala Lumpur; bottom, Padang in Indonesia) found feeding in the field on the legume *Centrosema pubescens*. Laboratory colonies were maintained on *Solanum nigrum*, with some individuals at each generation transferred as eggs to *C. pubescens* (from Shirai & Katakura 2000).

tuberosum, suggesting local adaptation in host plant use.

Intraspecific variation among plant genotypes of a given host species has been studied as well, for its influence on ladybird feeding and performance. In laboratory experiments, Fujiyama and Katakura (1997) examined responses of a population of *H. pustulosa* from Hokkaido to different clones of two host plants, thistle (*Cirsium kamtschaticum*) and blue cohosh (*Caulophyllum robustum*). Feeding rates of adult beetles differed significantly among clones for both of the host species, as did larval performance (measured by eclosion rate, duration of development and resultant adult size, when reared on a particular plant clone). When two thistle clones were transplanted to a common garden, the difference in their suitability for larvae narrowed, thus demonstrating also an environmental influence (Fujiyama & Katakura 2001). As further evidence of major environmental influence, eclosion rates increased significantly when larvae fed on shoots exposed to increasing light intensity, but adult female feeding preference was not affected. This suggested that females might respond primarily to host genotype, even when environmental conditions affect the suitability of that genotype for their offspring (Fujiyama & Katakura 2001). Examination of egg laying among clones by females in the field, however, affirmed the importance in host selection of environmental factors (clone size, soil moisture, and exposure to sunlight). As the growing season proceeded, females changed the distribution of eggs among clones from aggregated to more nearly random (Fujiyama et al. 2003).

Chemical and physical attributes of plants influencing host selection by phytophagous ladybirds have been explored in detail, especially among pest species (e.g. Napal et al. 2010). From analyses of potato leaf extracts, Endo et al. (2004) found that **methyl linolenate** acts synergistically with sugars (glucose and fructose) to stimulate feeding behaviour in *E. vigintioctomaculata*. **Luteolin 7-0-glucoside** in *Physalis alkekengi* stimulates *H. vigintioctopunctata* to feed on this host plant (Hori et al. 2005). Plant defences have been examined especially in plant resistance studies for the Mexican bean beetle, *E. varivestis* (Hammond & Coope 1999). For example, larval feeding on isolines of soybean with **trichomes** (versus a glabrous variety) resulted in increased mortality and reduced pupal mass (Gannon & Bach 1996). The 'Davis' soybean cultivar releases volatiles that attract females of *E. varivestis*, but this 'death-trap' cultivar is an unsuitable host: females that feed on it lay few eggs, and their offspring die by the third instar (Burden & Norris 1994). The importance of environmental factors on resistance expression was highlighted by Jenkins et al. (1997), who reported that resistance among varieties of soybean strengthened with decreasing soil moisture, since Mexican bean beetle larvae took longer to develop and suffered greater mortality. Induced resistance to the Mexican bean beetle was found when larvae fed on soybean plants that had been subjected to previous beetle feeding damage, or had been treated with jasmonic acid (Iverson et al. 2001). Underwood et al. (2000) found substantial variation among soybean genotypes in their constitutive and induced antifeedant resistance to *E. varivestis*, but the levels of these two forms of resistance were uncorrelated among varieties.

Non-pest as well as pest populations of *Epilachna* can reach high numbers and defoliate their host plants, with consequences for the number of beetles in future generations (e.g. Koji & Nakamura 2002). Food relationships therefore play a central role in the population dynamics of herbivorous ladybirds, especially among introduced populations that are subject to reduced pressure from natural enemies and that reach especially high abundance (Ohgushi & Sawada 1998). At such high abundance, there is strong intraspecific competition among larvae as they defoliate their host plants, leading to reduced overwintering survival with decreasing adult size (Ohgushi & Sawada 1995, Ohgushi 1996). Food relationships can also underlie major changes in population dynamics associated with the shift of *Epilachna* species from wild hosts to potatoes. Shirai and Morimoto (1997, 1999) documented key life history changes, including larger adult body size, higher fecundity, faster larval development and reduced life span, associated with such host shifts.

In contrast to the Epilachninae, which feed on vegetative parts of plants, the isolated **genus *Bulaea*** displays a more specialized form of phytophagy. Capra (1947) reported that *B. lichatschovi* and its close relatives were 'predominantly if not exclusively' pollinivorous both as larvae and adults, with a preference for Chenopodiaceae. Others (Dyadechko 1954, Bielawski 1959, Savoiskaya 1966,1970b) also consider *B. lichatschovi* as phytophagous. Savoiskaya (1966, 1970b) reported this species as pollinivorous on a variety of plants (*Euphorbia*, *Artemisia*, *Eurotia*, *Atriplex*, *Nitraria*, *Tamarix* and *Clematis*) in Kazakhstan. Savoiskaya (1970) further reported that, in central Asia, this species fed on pollen (of *Tamarix*, *Euphorbia*, *Artemisia*, *Eurotia ceratoides* and *Atriplex*), nectar (*Nitraria*, *Clematis*) and leaves of sugar beet and young apple trees. Goidanich (1943) reported pollinivory in another ladybird genus, *Micraspis*. (See also 5.2.9.)

5.2.14 Food of mycophagous Coccinellidae

Although Coccinellidae are taxonomically related to mostly mycophagous coleopteran families, ladybird mycophagy (together with phytophagy, aphidophagy, etc.) appears to be derived from an ancestral coccidophagous feeding behaviour (Giorgi et al. 2009). Sutherland and Parrella (2009) rightly divide mycophagy of coccinellids into facultative (5.2.9) and obligatory. The obligate mycophagous species of the genera ***Psyllobora* (=*Thea*)**, ***Vibidia***, ***Illeis*** and ***Halyzia*** belong to the tribe Halyziini, now Psylloborini (Vandenberg 2002). They feed on powdery mildew (Erisyphaceae). Species of these genera have often been mistakenly considered as carnivorous (see Hodek 1996). Their mycophagy is reflected in the distinctive shapes of their mandibles (Kovář 1996). Davidson (1921) checked in the laboratory that these fungi are their essential food: both larvae and adults of *Psyllobora vigintimaculata* died when offered arthropod food such as aphids, coccids and spider mites.

Strouhal (1926a, b) discussed the history of ecological and morphological differentiation among members of the tribe Halyziini and its consequences for taxonomy. Strouhal also compared adult and larval mouthparts among species in detail, and reviewed observations on mycophagy. Development of the mycophagous ***Illeis koebelei*** from egg to adult on drone powder (5.2.9) was possible, but the adults were small and did not oviposit (Niijima 1979). Fig. 5.27 shows the food relations of this species (Takeuchi et al. 2000).

Tytthaspis sedecimpunctata (tribe Coccinellini) has usually been reported as aphidophagous

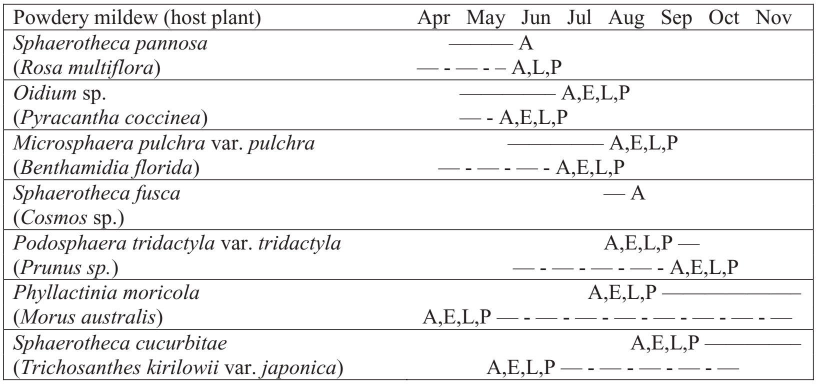

Figure 5.27 Seasonal occurrence of *Illeis koebelei* on different powdery mildews. Horizontal bars, observation period. A, adult; E, egg; L, larva; P, pupa. Full line, 1997; broken line, 1998 (modified from Takeuchi et al. 2000).

(Dyadechko 1954, Semyanov 1965, Klausnitzer 1966). Based on observations and preliminary experiments, Turian (1969) published the first precise information on its food, demonstrating that this species feeds on Erysiphaceae. Adults of *T. sedecimpunctata* seemingly show no specificity in ingesting various species of powdery mildew. Turian (1969) also observed *Psyllobora (=Thea) vigintiduopunctata* larvae and adults feeding on various Erysiphaceae, and proposed the term 'micromycetophagy' to describe feeding on lower fungi. For additional studies of ladybirds feeding on mildew (along with pollen and aphids) see 5.2.5.

5.3 QUANTITATIVE ASPECTS OF FOOD RELATIONS

The number or biomass of prey consumed by larval and adult ladybirds varies widely depending on specific circumstances (e.g. species of prey, rearing temperature). To complete their larval development, individuals may consume from 100 to well over 1000 aphids of various species; most food intake (typically 60–80%) occurs during the fourth instar (see Hodek 1996, and for coccinellids preying on scale insects part 2.3 in Hodek & Honěk 2009). Adult females, especially when ovipositing, feed more than males.

Methodological differences probably account for some of the variation in reported consumption rates of ladybirds. Baseline consumption may be estimated by comparing prey mortality in cages with and without predators (e.g. Hodek 1956), and by distinguishing predation mortality from other causes (e.g. Kaddou 1960). In some cases, the weight of prey consumed has been recorded (e.g. Blackman 1967, Ives 1981b, Ferran et al. 1984a, b); however, care must then be taken to consider changes in prey weight by dehydration. Isotope labelling (Ferran et al. 1981) and indirect measurement by faecal production (Honěk 1986) are useful additional methods. It is difficult to relate consumption rate to faecal production rate quantitatively without detailed information on digestion. The weight of faeces produced by *C. septempunctata* individuals following collection, however, provides an informative index of consumption rates of ladybirds in the field (Honěk 1986). Consumption rates can also be estimated from field observations (e.g. Latham & Mills 2009), or by assessing the hunger level of field-collected individuals. 'Hunger curves' were drawn from aphid consumption rates of *C. trifasciata* and *C. californica* after females or males were starved for 0–50 hours, and then field hunger levels were estimated by measuring their rates of aphid consumption in the laboratory (Frazer & Gilbert 1976, Frazer & Gill 1981; Fig. 5.28).

New molecular techniques, such as those using species-specific DNA sequences, can identify prey eaten and give quantitative estimates (e.g. Hoogendoorn & Heimpel 2001). Harwood and Obrycki (2005) have reviewed the diverse methods used with aphidophagous predators, which also include gut dissection, stable isotopes, protein analyses (by electrophoresis and use of antibodies) and chromatography to detect prey pigments (5.1; Chapter 10).

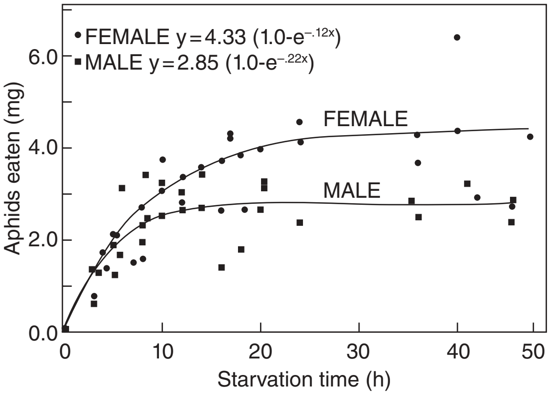

Figure 5.28 Hunger curves of male and female *Coccinella californica* (from Frazer & Gill 1981).

5.3.1 Effect of physical factors on consumption

5.3.1.1 Daily consumption rate

At temperatures favourable for growth and survival, the consumption rates of both larvae and adults generally increase with increasing temperature, and are correlated with the increase in developmental rate (Hodek 1996). Adults of *Delphastus catalinae* consumed increasing numbers per day of eggs and nymphs of the sweet potato whitefly *Bemisia tabaci* as ambient temperature increased from 14 to 35°C (Simmons & Legaspi 2004). Similar results were reported for larvae and adults of *Hip. convergens* attacking eggs of the cotton bollworm *Helicoverpa zea* (Parajulee et al. 2006) and for larvae of *Hip. convergens* and *C. septempunctata* consuming adult *Myzus persicae nicotianae* from tobacco (Katsarou et al. 2005). The number of prey (first and second instars of *Leptinotarsa decemlineata*) killed per day by larvae and adults of *Col. maculata* increased linearly with temperature (10–30°C) (Giroux et al. 1995).

At excessively high temperatures, ladybird foraging, development and survival are adversely affected (e.g. Alikhan & Yousef 1986, Huang et al. 2008, Taghizadeh et al. 2008). Consumption rates of fourth instars and adults of *Har. axyridis* were reduced at high temperature over the range of 10–30°C, especially for the darker morph *nigra*, and the thermal optimum (near 25°C) was 3.7°C lower for adults (but not larvae) of this morph (Soares et al. 2002, Fig. 5.29). Overall, the larger, darker (melanic) adults of the *nigra* morph appeared better adapted for cold regions, where this morph prevails in frequency over the *aulica* morph.

At temperatures below the development threshold, coccinellids cease to consume prey (e.g. at 7.5°C for *Col. maculata*, Giroux et al. 1995). Ricci et al. (2006) studied the foraging behaviour of adult *Chil. kuwanae* preying on overwintering females of the scale insect *Unaspis euonymi* on *Euonymus japonicus*. The ambient temperature was gradually reduced from 15 to 2°C (exposing the beetles to each, successively lower, temperature for 10 days), before the final increase to 15°C. With the lowering of temperature, the adults consumed scales at a gradually reduced rate and at 4 and 2°C they consumed almost no prey but continued, at reduced rates, to lift scale covers without consuming the scales; such scales then died.

5.3.1.2 Total food consumption

Hodek (1996, pp. 204–205) concluded from a review of the literature that, in general, the total food consumption during the entire larval development tends to remain relatively constant over a wide range of **constant temperatures**. Coccinellids appear similar to other insects in this respect (see Rubner 1908, cited in Allee et al. 1949). Katsarou et al. (2005) reported highest larval prey consumption both in *Hip. convergens* and *C. septempunctata* at 23°C versus at 14, 17 and 20°C. In *A. bipunctata* total larval food intake (mg wet weight) declined from 65 mg at 15°C to 52 mg at 25°C when larvae received an excess of *Sitobion avenae*. When the larvae were provided with a limited number of aphids, however, the intake was highest at intermediate temperature (28 mg at 20°C) (Schuder et al. 2004).

The consumption patterns of coccinellids have mostly been studied at constant temperatures. Hodek (1957a), however, found that total larval food consumption was doubled when larvae of *C. septempunctata* developed at **naturally fluctuating** summer **temperatures**. Sundby (1966) found no difference in the amount of food consumed by larvae of *C. septempunctata* under more limited alternation between only 16 and 21°C (the control was constant 16 or 21°C), but such alternating conditions nonetheless resulted in heavier pupae (R.A. Sundby unpublished,

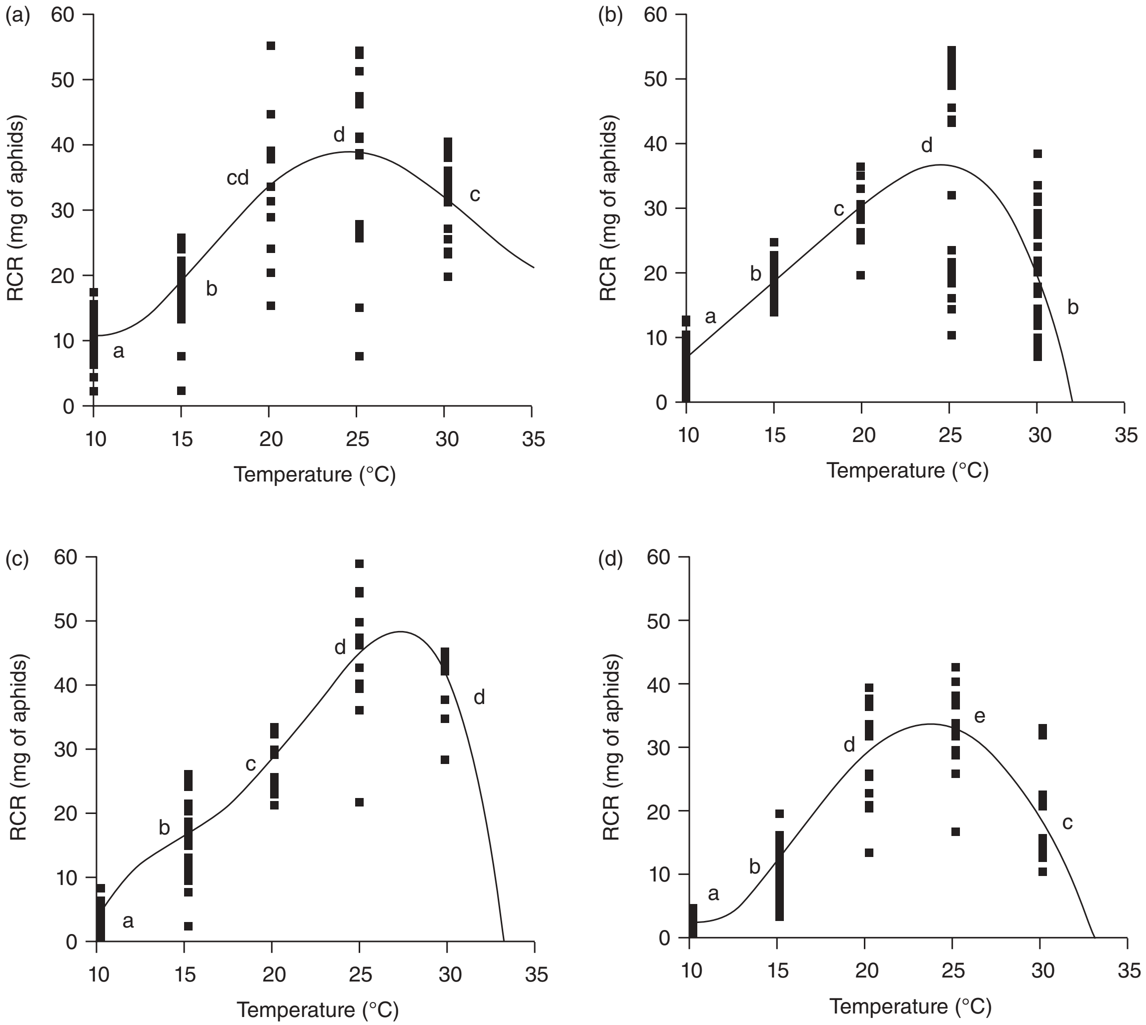

Figure 5.29 Relative consumption rate (RCR), at varying temperatures, of larval *Harmonia axyridis aulica* (A) and *nigra* (B), and adult *aulica* (C) and *nigra* (D) (after Soares et al. 2002).

in Ellingsen 1969). Temperatures fluctuating between 8 and 28°C resulted in an increase (10.6% more than at constant 18°C) in total food consumption by larvae of *A. bipunctata* (Ellingsen 1969). An important increase in food intake at alternating temperatures was also found in females of *Chil. nigritus* (Ponsonby & Copland 2000; Table 5.29).

Although little studied, **humidity** probably affects food consumption by ladybirds. Coccinellids may compensate for high evaporative water loss by consuming more prey with a high **water content**; Hodek et al. (1965) found indications of increased consumption of aphids in *C. septempuncata* at low relative humidities in the air. Foods with a low water content (e.g. pollen) may become unsuitable for ladybirds when free water is not available and humidity is low. There was no correlation, however, between initial water content of different foods and survivorship of larvae of *Col. maculata*,

Table 5.29 Significantly higher food intake at alternating temperatures: effect of temperature on number and weight of pre-ovipositing adult female *Abgrallaspis cyanophylli* eaten in a 24-hour period by adult *Chilocorus nigritus* 2 to 6 weeks after eclosion (modified after Ponsonby & Copland 2000).

Temperature (°C)	Predator	Mean number eaten (±SD)	Estimated weight eaten (mg)
15	Female	1.94 (2.89) a	0.394
	Male	1.28 (1.45) a	0.259
20	Female	3.94 (1.83) b	0.801
	Male	4.00 (1.45) b	0.812
26	Female	8.83 (4.11) c	1.793
	Male	5.17 (2.28) bd	1.049
30	Female	7.17 (3.31) c	1.455
	Male	6.94 (3.44) cd	1.409
14/30 (12 h/12 h)	Female	12.33 (4.92) e	2.504
	Male	7.22 (2.49) c	1.466

Means with the same letter within the column are not significantly different (LSD at 5% level = 1.9616).
n = 18 males and 18 females at each temperature level.

when reared under simulated drought conditions (Michaud & Grant 2005).

5.3.2 Effect of prey density on consumption: functional response

Pioneering ecologists distinguished key aspects of predation as it may influence prey population dynamics. Solomon (1949, 1964) defined the concept of a predator's **functional response** as the rate of prey consumption (i.e. number of prey consumed per unit time) as a function of prey density. Solomon also defined the **numerical response**, i.e. the change in numbers of predators occurring (through immigration or aggregation and reproduction) in response to a prey density. A crucially important development was Holling's (1959a, b, 1965) proposal of three basic types of functional response which reflect that the number of prey consumed by a predator as prey density increases may increase linearly (type I), in a decelerating fashion (type II) or in a sigmoidal fashion (type III).

In recent years, functional responses have been viewed broadly as the rate of prey consumption of an individual predator (Abrams & Ginzburg 2000) and often studied in coccinellids. The functional response can then be modelled as it varies not only with prey density, but also with other interacting factors (which may influence predator foraging) such as predator density (including in combination with dependence on the prey density to yield a ratio; e.g. Arditi & Ginzburg 1989, Mills & Lacan 2004, Schenk et al. 2005), densities of alternate prey (e.g. Tschanz et al. 2007), densities of the predator's natural enemies (e.g. Krivan & Sirot 2004), foraging substrate and abiotic conditions (e.g. temperature; Jalali et al. 2010, Khan & Khan 2010).

Most commonly ladybirds are studied foraging singly in simple laboratory arenas, or less commonly on caged host plants in the field, to estimate the number of prey consumed in response to experimentally varied densities of available prey. From these data, the functional response is then characterized to type.

The most common form for ladybirds is the type II functional response (Table 5.30). But simple extrapolation of laboratory estimates to field settings is questionable (e.g. O'Neil 1989, 1997). For example, *Col. maculata* larvae ate Colorado potato beetle eggs on caged potato plants in the field at only about half the rate as they did on excised potato leaves in the laboratory; in both settings, however, a type II response was observed (Munyaneza & Obrycki 1997).

In some instances, ladybirds have shown type III responses (e.g. Sarmento et al. 2007) that may arise from predator learning (e.g. as in **prey-switching**; 5.2.5), and such a response has the potential to stabilize predator–prey interactions (Hassell 1978). In a laboratory experiment, Murdoch and Marks (1973) tested for prey-switching in *C. septempunctata* when presented with varying ratios of two prey

Table 5.30 Examples of experimental studies of functional responses, illustrating both the settings and foraging substrates, and the prey attacked by the predators. Results are characterized by basic response type, as concluded by the authors. 'Petri dish' or 'Cage' indicates an absence of plant material.

Coccinellid species	Prey species	Setting	Response type	Reference
Adalia bipunctata	*Myzus persicae*	Petri dish	II	Jalali et al. (2010)
Aphidecta obliterata (adults)	*Elatobium abietinum*	Petri dish (lab)	II	Day et al. (2006)
Aphidecta obliterata (4th instars and adults)	*Elatobium abietinum*	Spruce section	II	Timms et al. (2008)
Coccinella septempunctata (adults)	*Macrosiphum euphorbiae*	Rose leaves (lab)	II	Deligeorgidis et al. (2005)
Coccinella undecimpunctata (4th instars and adults)	*Myzus persicae*	Cage (lab)	II	Cabral et al. (2009)
Coleomegilla maculata (4th instars)	*Leptinotarsa decemlineata* eggs	Petri dish (lab) Potato plants (greenhouse, field)	II	Munyaneza and Obrycki (1997)
Delphastus pusillus (female)	*Bemisia tabaci* nymphs	Cotton leaves (lab)	II	Guershon and Gerling (1999)
Eriopis connexa (female)	*Macrosiphum euphorbiae*	Cage (lab)	III	Sarmento et al. (2007a)
	Tetranychus evansi	Cage (lab)	II	
Harmonia axyridis (larvae and adults)	*Aphis gossypii*	Cucumber leaves (lab)	II	Lee and Kang (2004)
Harmonia axyridis (larvae and adults)	*Danaus plexippus* eggs and larvae	Petri dish (lab) larvae eating eggs and larvae, adults eating eggs	II I	Koch et al. (2003)
Harmonia conformis (adults and larvae)	*Eriosoma lanigerum*	Petri dish (lab)	II	Asante (1995)
Harmonia dimidiata (females)	*Cervaphis quercus*	Cage (lab)	II	Agarwala et al. (2009)
Orcus australasiae (adults)	*Eriosoma lanigerum*	Petri dish (lab)	II	Asante (1995)
Propylea dissecta (larvae and adults)	*Aphis gossypii*	Leaves of *Lagenaria vulgaris* (lab)	II	Omkar and Pervez (2004)
Propylea quatuordecimpunctata (adults)	*Diuraphis noxia*	Petri dish (lab) Indian rice grass (lab) Crested wheatgrass (lab)	II II III	Messina and Hanks (1998)
Scymnus creperus (larvae and adults)	*Aphis gossypii*	Cotton leaves (lab)	II	Wells et al. (2001)
Stethorus tridens (females)	*Tetranychus evansi*	*Solanum* leaves	II	Britto et al. (2009)

(*Acyrthosiphon pisum* and *Aphis fabae*) which occur in different microhabitats. That these authors failed to find evidence for prey-switching re-inforced the consensus that the functional responses of ladybirds are most likely to be type II.

The behavioral mechanisms underlying a given functional response are sometimes examined explicitly, but more often are simply inferred by extracting estimates from a standard model applied to experimental data. Type II responses are typically fitted (most often following polynomial regression) using Holling's (1966) **disc equation**, or Rogers' (1972) variant for the disc equation when consumed prey are not replaced (e.g. see Parajulee et al. 2006). Attack coefficients and handling time are then estimated as assumed constants across the range of prey densities studied. However, the mechanistic basis of a type II (or III) functional response is often far from clear (e.g. Holling 1966, Mills 1982a, van Rijn et al. 2005), despite widespread use of such assumed constants. Models incorporating these assumptions therefore may serve better for simulating population dynamics than for understanding the foraging behaviour of predators that in fact underlies these dynamics.

Foraging ladybirds in fact may **spend less time handling and processing** individual prey as prey density increases, either because the predator processes prey more quickly or because it consumes less of each prey. Particularly in the latter case, this can increase the 'killing power' of the predator. The handling time of adults of the mite-feeding *Stethorus bifidus*, for example, decreases at increased densities of *Tetranychus lintearius* as the predator extracts less of the killed prey contents (Peterson et al. 2000; Fig. 5.30). Because this promotes an increase in the proportion of the prey killed as prey density increases, the predator may contribute to the regulation of prey numbers.

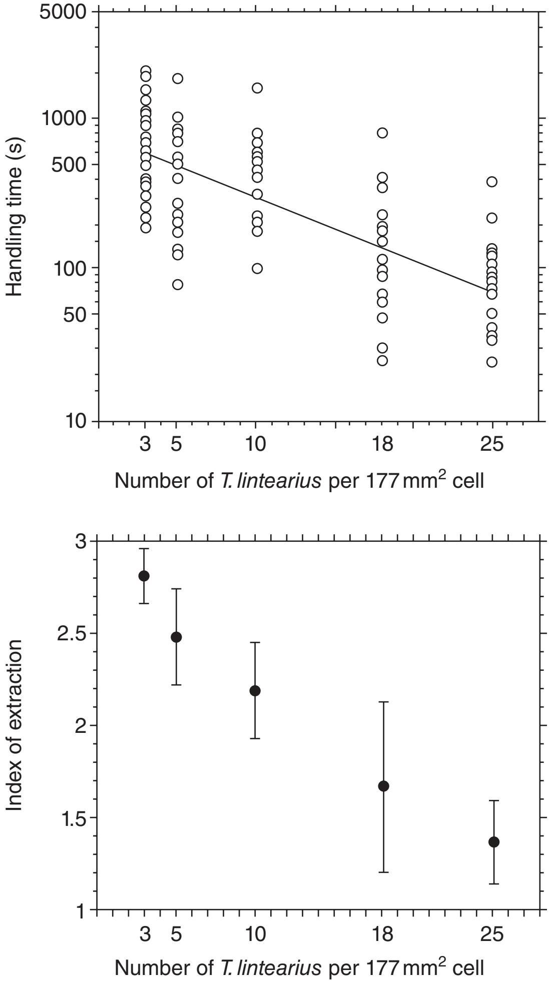

Figure 5.30 The handling time (top) and (bottom) the index of extraction (reflecting the proportion of body contents removed from an individual prey) of *Stethorus bifidus* adults foraging at different densities of the mite *Tetranychus lintearius* (from Peterson et al. 2000).

The nature of the host plant as a **substrate for foraging** may interact with prey density to influence a ladybird's functional response (Guershon & Gerling 1999, Siddiqui et al. 1999; 5.4.1.1). Larvae of *Hip. convergens* foraging for *Acyrthosiphon pisum* on normal or reduced-wax bloom pea varieties had different type II responses as the instantaneous search rate was higher on reduced-wax bloom plants (Rutledge & Eigenbrode 2003). Most probably the predator was better able to attach to plants with reduced-wax bloom, and its search rate was elevated. Handling time of prey, however, did not differ between pea plants with reduced wax and normal wax bloom.

The foraging substrate can even shift the basic nature of the functional response. Messina and Hanks (1998) found that, in attacking the Russian wheat aphid *Diuraphis noxia*, *P. quatuordecimpunctata* followed a type II response on Indian ricegrass (*Oryzopsis* *hymenoides*), but type III on crested wheatgrass (*Agropyron desertorum*). As prey density increased on the wheatgrass, a decreasing proportion of the aphids apparently occurred in locations (e.g. within rolled leaves) where they escaped the predators.

Through their effects on prey quality, **host plants** may additionally influence the functional responses of predators. In Petri dish pairings of larvae of *C. septempunctata* with varying densities of aphid nymphs of *Lipaphis pseudobrassicae*, Kumar et al. (1999) recorded differences in the rate with which percentage prey consumption decreased with an increase in prey density for prey reared on *Brassica campestris*, *B. oleracea* or *Rhaphanus sativus*. For each of these three prey, however, the predator's functional response was type II.

The **activity of other predators** may also influence a predator's functional response, as formalized in the concept of **mutual interference** (Hassell 1978). The searching efficiency of *C. septempunctata* females decreased linearly with an increase in density of conspecifics (Siddiqui et al. 1999). A similar effect was recorded for *P. dissecta* (Omkar & Pervez 2004).

The availability of **co-occurring prey** may further influence a predator's functional response through **prey selection**. Typically, the predator consumes fewer alternative prey when an essential prey is also available (5.2.7). Hazzard and Ferro (1991) found in the laboratory, and Mallampalli et al. (2005) in field cages, that *Col. maculata* consumed fewer Colorado potato beetle eggs (its alternative prey; Snyder & Clevenger 2004) when essential prey, *Myzus persicae* was present. *Coleomegilla maculata* and *Har. axyridis* attacked fewer eggs of *Ostrinia nubilalis* when *Rhopalosiphum maidis* were present (Musser & Shelton 2003). Additional examples are provided by Lucas et al. (2004) and Koch et al. (2005), as discussed further by Evans (2008).

Prey activity may influence the relative amounts of co-occurring prey consumed. *Har. axyridis* selected *Tetranychus urticae* and not the cicadellid *Hyaliodes vitripennis* that could defend itself, but selected the latter as the better prey when it had been immobilized (Provost et al. 2006).

5.3.3 Effects of consumption on growth and reproduction

5.3.3.1 Larval development

Predaceous ladybirds often have to cope with prey scarcity, including its intermittent absence. In particular, aphidophagous species have a pronounced ability to adjust to this. Larval development can be completed even when rates of prey consumption are very low; larvae of *C. septempunctata* allowed to consume only 33–40% of the number of aphids consumed when provided in excess still completed their development (Hodek 1957, Sundby 1966). Nonetheless, **reduced rates of prey consumption** result in slower development and greater mortality (both of larvae and adults) (Phoofolo et al. 2008; Table 5.31) as well as lower weights and smaller sizes of pupae and adults (for earlier papers see Hodek 1996). The number of ovarioles may also vary among adult ladybird females as a function of larval food consumption (Rhamhalinghan 1985, Dixon & Guo 1993).

Variable **prey quality** similarly affects larval growth and development (e.g. Smith 1965a, b, Obrycki & Orr

Table 5.31 Effect of food deprivation in the fourth instars on the completion of development to adults in three ladybird species (modified after Phoofolo et al. 2008).

Food deprivation period (days)	***Coleomegilla maculata***		***Harmonia axyridis***		***Hippodamia convergens***	
	n	**% female**	***n***	**% female**	***n***	**% female**
0	20	50.0	15	71.4	10	50.0
1	19	42.1	16	50.0	12	50.0
2	20	55.0	16	62.5	12	50.0
3	11	18.2	10	10.0	13	30.8

Number of consecutive days of the fourth instar during which lady beetle larvae were deprived of food until they either pupated or died.

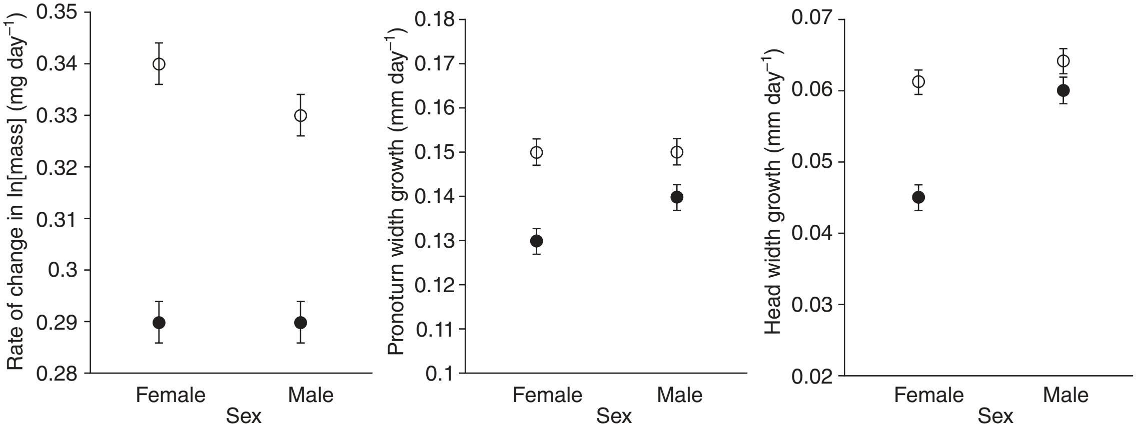

Figure 5.31 Mean growth rates of weight, pronotum width and head width of *Harmonia axyridis* larvae provisioned with high food availability, following an initial six-day period (upon egg hatch) of low (open circles) or high (filled circles) food availability. Growth rates were based on measurements made at the end of the initial period and at eclosion (from Dmitriew & Rowe 2007).

1990, Giles et al. 2002, Omkar & James 2004; 5.2). The quality and quantity of prey consumed may have interactive effects. Phoofolo et al. (2007) reared larvae of *Hip. convergens* on *ad libitum* versus limited (4 mg per day) quantities of *Schizaphis graminum* and *Rhopalosiphum padi*, both aphids from winter wheat. The larvae grew at the same rates on *ad libitum* diets of the two aphids, but the development of fourth instars was slowed significantly more on limited diets of *R. padi* than of *S. graminum*.

Different species of ladybirds differ in their developmental responses to increasing availability of a given prey species (e.g., Phoofolo et al. 2008, 2009). When provided variable quantities of *Acyrthosiphon pisum*, larvae of *Anatis mali* were more flexible than larvae of *Col. maculata* in **adjusting their rates of developmen**t and their adult weight. Thus, with reduced prey consumption, larvae of *A. mali*, but not of *Col. maculata*, were able to convert a greater percentage of food consumed into body weight (Smith 1965b).

Smith's (1965a) study illustrates the considerable flexibility in developmental responses that ladybirds show to varying prey quantity and quality. Furthermore, as shown by a split-brood full-sib experiment with families of *Har. axyridis* larvae that were provided with aphids or an artificial diet, such phenotypic plasticity in developmental time, adult size, and other characters, can have a strong underlying genetic basis (Grill et al. 1997), and thus quite plausibly can be shaped by natural selection. Dmitriew and Rowe (2007; Fig. 5.31) investigated the lifetime consequences for *Har. axyridis*, and the **compensatory ability** of older larvae, in response to temporary food shortage early in development. First and second instars received abundant prey (*A. pisum*) but only on alternate days. As third instars, they were fed continuously. Then following diet restriction, the larvae grew more slowly and achieved smaller weights and sizes than did continuously fed larvae. But when ample food was restored, the diet-restricted individuals fully compensated for lost growth, and achieved the same weight and size at adult eclosion as the control. Compensation arose both through extended time until pupation and accelerated larval growth rates. Thus, temporary food shortage and compensatory larval responses thereafter resulted in a small lifetime fitness cost in terms of a prolonged larval period, greater larval mortality and more rapid death when food was removed 100 days after experimental subjects reached adulthood. Longevity, lifetime female fecundity and male mating success of adults that had been subjected to diet restriction as larvae were unaffected.

5.3.3.2 Adult performance

The foods consumed by adult lady beetles can vary greatly in quality (5.2) as reflected both in how much they promote longevity (e.g. Omkar & James 2004), and in how well they support **reproduction** (e.g. Omkar & James 2004, Michaud & Qureshi 2005). Effects of the foods depend on the physical conditions (e.g. temperature or humidity; e.g. Michaud & Grant 2004) and on their consumption as either sole diet or as part of a mixed diet (e.g. Evans et al. 1999, Soares et al. 2004; 5.2.5). Furthermore, the suitability of a particular food for reproduction versus larval development may be quite different (Michaud 2005), and its suitability for reproduction may vary, depending on the diet experienced previously during the larval stages (Michaud & Jyoti 2008).

Egg laying depends on the quantity of consumed food of a given type (review of earlier evidence in Hodek 1996). Ives (1981a, b) found that females of *C. trifasciata* and *C. californica* did not produce eggs at very low rates of aphid consumption. Above a threshold (presumably set by the need for self-maintenance), egg production increased linearly with increasing aphid consumption (see also Ibrahim 1955 and Ferran et al. 1984b). Decreased egg laying and increased incidence of oosorption was studied in relation to temporary food restriction in *Harmonia axyridis* (Osawa 2005, see also Kajita & Evans 2009; Fig. 5.32).

When self-maintenance needs in *C. septempunctata* were met by alternative prey (weevil larvae), the females produced more eggs with lower aphid consumption than in the absence of the alternative prey (Evans et al. 2004). Such a complementary pattern of egg production at very low levels of essential food may enable mobile, widely searching ladybird females to oviposit quickly upon discovery of local patches with favourable prey conditions for their offspring (Evans 2003).

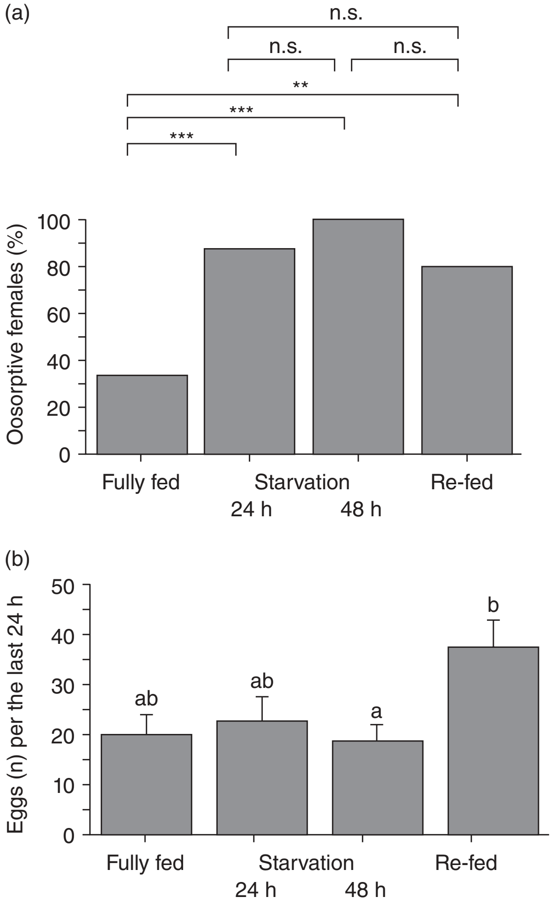

Figure 5.32 Effect of temporary (24- and 48-hour) starvation and resumed 24-hour feeding (after 24-hour starvation) on (a) incidence of oosorptive individuals, and (b) egg laying; for (a), statistical differences at $P = 0.01$, $P = 0.001$, $P = 0.0001$ and $P > 0.05$ in a χ^2- test on the number of individuals indicated by horizontal bars with signs above; for (b) vertical lines indicate SE, and different letters indicate statistical differences at $P = 0.05$ using Scheffe's range test (modified from Osawa 2005).

5.3.4 Conversion and utilization of consumed food

Larvae of *Har. axyridis* compensated for earlier food shortages by accelerating their growth rates when given the same amount of food as well fed controls throughout larval development (Dmitriew & Rowe 2007; 5.3.3.1). Thus it appears that the food conversion rate, or ECI (efficiency of conversion of ingested material (Waldbauer 1968); i.e. percentage of consumed prey biomass converted into predator biomass) varied with food conditions, so as to reduce the adverse effects of food shortage (see also Smith 1965). Food conversion rates of *A. bipunctata* larvae consuming *Sitobion avenae* increased to 34–40% from 22–29% (wet weight) when the predators received a reduced number of aphids, only 25% of what larvae ate when they were offered aphids *ad libitum* (Schuder et al. 2004). Similar increased rates of ECI at low levels of food consumption were found in aphidophagous mirids and chrysopids (Glen 1973, Zheng et al. 1993). Aphidophages thus apparently feed with less than full efficiency of conversion at high prey levels, although the fitness benefits of so doing are not yet clear (Dmitriew & Rowe 2007).

Food conversion rates of ladybirds can also vary for a given prey depending on the age of the predator, the morph of the prey, and the host plant on which the prey feeds. Fourth instars of *Scymnus levaillanti* and *Cycloneda sanguinea* that fed on *Aphis gossypii* had lower ECIs (approximately 50% and 20%, respectively, of dry weight) at several temperatures than did earlier instars. This may reflect the metabolic costs of preparation for pupation (Isikber & Copland 2001). Wipperfuerth et al. (1987) reported higher egg production by *Hip. convergens* feeding on apterous virginoparous nymphs of *Myzus persicae* than on the same weight of alatiform gynoparous ones. Shannag and Obeidat (2006) found a higher ECI (19% dry weight basis) throughout the larval period of *C. septempunctata* when feeding on *Aphis fabae* from susceptible *Vicia faba*, when compared with an ECI of 14% on aphids from a resistant cultivar.

ECIs differ between ladybird species in their **nature of feeding** and **type of prey**. The higher ECIs of larvae of *S. levaillanti* than of *C. sanguinea* when both species fed on cotton aphids reflects greater pre-oral digestion in *S. levaillanti* (Isikber & Copland 2001; see also Cohen 1989 and 5.4.3). Specty et al. (2003) reported a much higher ECI of eggs of *E. kuehniella* (with high protein and lipid content) than of pea aphids (with high carbohydrate but similar water content) by fourth instar *Har. axyridis*. Mills (1982a) hypothesized that better assimilation of nutrients in coccidophagous versus aphidophagous ladybirds might contribute to the success of coccidophages in biological control. Based on a literature survey of conversion efficiencies that did not differ between aphidophages and coccidophages (varying between 0.10 and 0.30) Dixon (2000, table on p. 206) opposed Mills' (1982b) hypothesis.

In general, ECIs depend both on the predator's ability to **digest** and **assimilate consumed food** (e.g. Mills 1982b, Bilde & Toft 1999, Bilde et al. 2000, Jalali et al. 2009a, b, Lundgren 2009, Lundgren & Weber 2010) and on the **allocation** of assimilated nutrients towards maintenance, growth (biomass accumulation) and activities such as foraging and reproduction (e.g. O'Neil & Wiedenmann 1987, Nakashima & Hirose 1999, Dixon & Agarwala 2002, Agarwala et al. 2008, Kajita et al. 2009). When maintained on a diet of *Hypera postica* larvae compared with a diet of pea aphids, adult females of *Har. axyridis* not only had lower rates of consumption, but also lower rates of assimilation of consumed prey, and they allocated more of the assimilated nutrients and energy to searching (Evans & Gunther 2005). Both rate of consumption and assimilation efficiency (as measured by the weight ratio of faeces produced to weight of aphids consumed) decreased (along with egg production) in females of *Menochilus sexmaculatus*, *C. transversalis* and *Har. axyridis* (Dixon & Agarwala 2002). The improved ability of ladybirds to grow and reproduce given a selection of different prey (Rana et al. 2002) is likely to include increased assimilation as well as consumption of prey.

The predator's utilization of consumed food will also reflect its ability to balance its nutritional needs against the nutritional properties of its prey. Specty et al. (2003) compared the body composition of prey and adults of the polyphagous *Har. axyridis* when reared on eggs of *E. kuehniella* with feeding on nymphs and adults of pea aphids. The biochemical profiles of the ladybird adults reflected those of the prey: adults reared on eggs had higher protein and lipid content than adults reared on aphids, but the difference in body composition was less marked between the two groups of predators than between the two types of prey.

In an interesting test of how the biochemical composition of prey and predator may influence consumption patterns of ladybirds, Kagata and Katayama (2006) examined nutritional aspects of intraguild predation by *Har. axyridis* and *C. septempunctata* (Chapter 7). The authors addressed the hypothesis that intraguild predation is an adaptive response to **nitrogen limitation in the diet** (Denno & Fagan 2003). These two ladybird species prey on each other in a strongly asymmetric fashion, with *Har. axyridis* acting as the intraguild predator far more frequently than *C. septempunctata* (e.g. Yasuda et al. 2001, 2004). Kagata and Katayama tested predictions that *Har. axyridis* has higher nitrogen content than *C. septempunctata* when both feed on aphids, and that *Har. axyridis* has lower nitrogen-use efficiency than *C. septempunctata*. Both considerations might favour greater intraguild predation by *Har. axyridis*, such that the predator could capitalize by consuming the relatively nitrogen-rich tissues of the intraguild prey (versus nitrogen-poor tissues of aphids); however, neither prediction was supported. Hence, it does not appear that nitrogen shortage promotes the strong tendency of *Har. axyridis* to engage in intraguild predation.

5.3.5 Aggregative numerical response

5.3.5.1 Temporal and spatial patterns

The collective outcome of individual ladybirds searching for prey can be evaluated by examining the degree to which the predators concentrate in areas of high prey density. This population-level phenomenon is the aggregative component of the predators' numerical response to varying prey density (Solomon 1949, 1964). After finding a prey, an individual ladybird increases the thoroughness of searching. Its movement becomes slower, often with turning after only a short distance. This change from extensive to intensive searching (5.4.1.2) has generally been assumed to be the basis (or at least one of the important mechanisms) of the aggregative numerical response.

Having highly mobile adults which range widely across landscapes, ladybirds are well known to aggregate (and reproduce) in response to **local prey density**. Thus, large numbers of adults often occur near colonies of prey such as aphids (e.g. Banks 1956), mites (e.g. Hull et al. 1976) and chrysomelid beetles (e.g. Matsura 1976). Numbers of aphidophagous ladybirds (and their offspring) generally rise and fall in parallel with changes in aphid population size, although the temporal matching is often less than perfect (e.g. Radcliffe et al. 1976, Wright & Laing 1980, Frazer & Raworth 1985, Hemptinne et al. 1992, Agarwala & Bardhanroy 1999, Osawa 2000, Rana 2006, Kajita & Evans 2010).

Prey density varies widely over time and space at varying scales. Ladybirds frequently aggregate most strongly in areas **within a habitat** (e.g., within an agricultural field) where prey are most abundant (Frazer et al. 1981, Sakuratani et al. 1983, Cappuccino 1988, Turchin & Kareiva 1989, Obata & Johki 1990, Giles et al. 1994, Elliott & Kieckhefer 2000, Osawa 2000, Evans & Toler 2007). The degree of predator–prey **spatial matching** within a habitat can vary widely over the growing season. Park and Obrycki (2004) mapped spatial correlations over the season between the local abundance of *Rhopalosiphum maidis* and adults and larvae of *Har. axyridis*, *Col. maculata* and *C. septempunctata*). Coccinellids aggregated at sites of local aphid abundance during the peak population period (Park & Obrycki 2004; Fig 5.33).

Ladybirds also aggregate at locally high concentrations of their prey at the **landscape scale**, as for example shown in differences among crop fields (Honěk 1982, Evans & Youssef 1992, Elliott et al. 2002a, b, Brown 2004, Evans 2004). Ives et al. (1993) found that individual adults of *C. septempunctata* and *Hip. variegata* responded very weakly to aphid density on individual stems of fireweed (*Chamerion angustifolium*), but responded from moderately to very strongly to aphid density among populations of fireweed stems. Similarly, Schellhorn and Andow (2005) found that, whereas adults of *A. bipunctata* and *Hip. tredecimpunctata* responded to variation in aphid abundance on individual corn plants within 10 m × 10 m plots, *Col. maculata* adults were sensitive to spatial variation in aphid abundance at a larger scale, and responded to differences in aphid numbers between 10 m × 10 m plots. A fourth species (*Hip. convergens*) responded to variation in aphid abundance at both spatial scales. The authors noted that such differing responses among the four ladybird species were complementary, and together might lead to greater aphid suppression.

5.3.5.2 Modeling of aggregative responses

Kareiva and Odell (1987) parameterized quantitative models of ladybird movements within habitats by using field observations of foraging individuals of *C. septempunctata* (e.g. the rate with which the beetles reversed their direction, taken as a function of hunger level, when moving along linear arrays of host plants). From these models of individual beetle behaviour, the authors demonstrated how observed aggregations of the predator population can develop at local patches of high prey density. In addressing a larger spatial scale, Krivan (2008) tested alternate models of emigration and immigration behaviour to account for the observed increase in numbers of adults of *C. septempunctata* in different alfalfa fields with increasing aphid density, as reported by Honěk (1982). The model best accounting for the field data was one in which the emigration rate was assumed to increase with decreasing local prey density (as discussed above), and the immigration rate was assumed to be independent of local prey density.

5.3.5.3 Factors other than focal prey density

The presence of other vegetation in the vicinity of host plants can influence the numerical response of

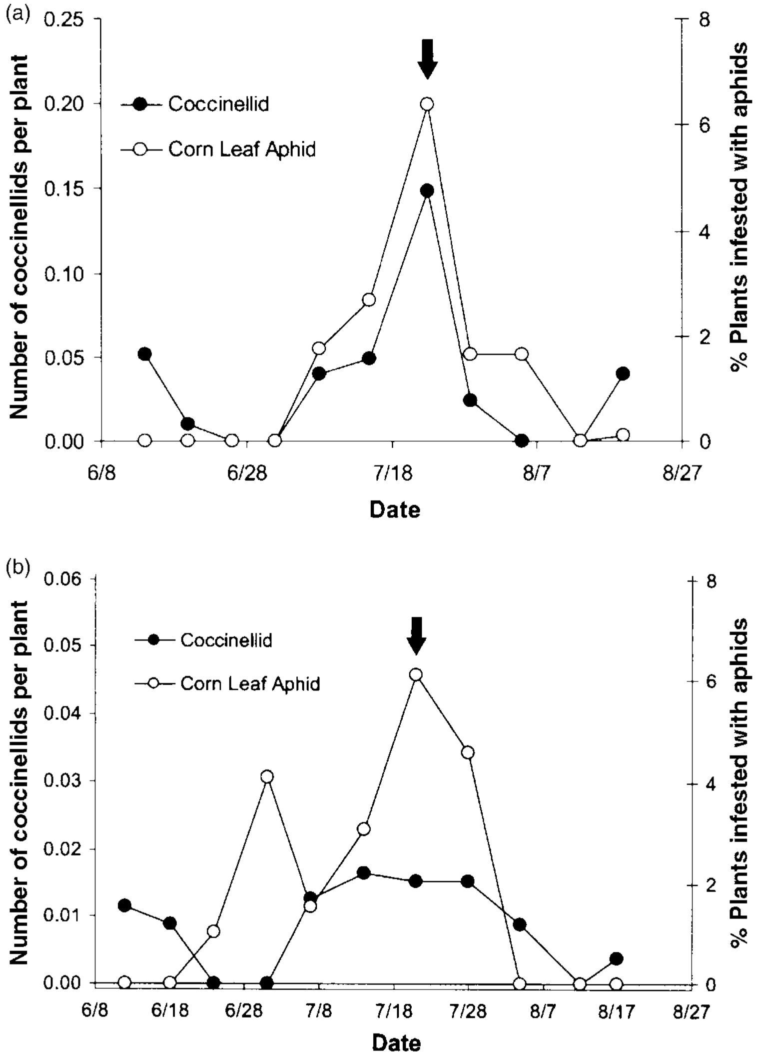

Figure 5.33 Population dynamics of corn leaf aphids (*Rhopalosiphum maidis*) and ladybirds (*Harmonia axyridis*, *Coleomegilla maculata*, *Coccinella septempunctata*) in June, July and August. Arrow, the week of peak corn anthesis. (a) large-scale study (970 samples in a 8-ha cornfield). (b) small-scale study (196 samples in a 50 m × 50 m cornfield) (from Park & Obrycki 2004).

ladybirds. Within alfalfa fields, Harmon et al. (2000) found that adults of *Col. maculata* aggregated in patches with high densities of dandelions (yielding pollen for this pollinivorous species; 5.2.9). These patches supported only low densities of pea aphids, apparently because of the local build-up in ladybird numbers. Similarly, Sengonca et al. (2002) found that *C. septempunctata*, *A. bipunctata* and *P. quatuordecimpunctata* occurred in greater numbers in plots of lettuce that included weeds (wormwood, tansy or stinging nettle), and aphid (especially *M. persicae*) populations were correspondingly reduced. The authors suggested that the weeds attracted predators by **plant volatiles** as well as providing shelter and additional prey.

The potential importance of **additional prey** for the aggregative response of ladybirds was established by placing potted nettles with *Microlophium carnosum*, adjacent to grass plots infested by *Rhopalosiphum padi* (Müller & Godfray 1997). Coccinellids accumulated in large numbers in the highly infested grass and rapidly drove numbers of *R. padi* to low levels. The predators, many now swollen with eggs, then shifted to the nearby potted nettles where they laid their eggs, and where they and their offspring fed on *Microlophium carnosum*.

At least some aphidophagous ladybirds may also be responsive to the availability of **non-aphid prey** within a habitat. This possibility has been most explored in alfalfa (e.g. Evans & Youssef 1992, Giles et al. 1994), but probably occurs in a variety of settings. The introduced *C. septempunctata* has become the most common aphidophagous ladybird in alfalfa fields of the inter-mountain west of North America. In contrast to native coccinellids, this generalist predator colonizes and persists in alfalfa even when aphid densities are low, and shows a positive numerical response to an alternative non-aphid prey, the abundant larvae of the alfalfa weevil (Evans & Toler 2007). Significant numbers of *C. septempunctata* early in the growing season may now be a key factor in restricting pea aphid population growth, with a consequence that native coccinellids have recently largely abandoned alfalfa fields in the absence of sufficient numbers of aphids to retain them (Evans 2004).

A numerical response of coccinellids to one prey can lead to a subsequent numerical response later in the season to **another prey in the same habitat** or nearby. The presence of the non-damaging *Rhopalosiphum maidis* on grain sorghum early in the season elicits an aggregative numerical response by *Hippodamia* spp., followed by a strong reproductive response by colonizing adults. This leads to heavy ladybird predation on *Sitobion graminum* that appear on sorghum later in the season (Michels & Burd 2007). Rand and Louda (2006) recorded the dispersal of adult coccinellids from prey on agricultural crops into adjacent grassland where they heavily attacked an aphid species (*Bipersona* sp.) on a native thistle.

The **importance of alternate prey** for aggregative numerical responses of ladybirds may be one reason that this response is very much influenced by **vegetation diversity** within fields and by increasing patchiness of non-cultivated land surrounding a field. This aspect has been explored in a variety of agricultural settings (Elliott et al. 1998, 2002a). For example, Elliott et al. (2002b) found that factors associated with the landscape matrix in which individual fields of alfalfa occur (e.g. percentage of the surrounding landscape that is wetlands, woodlands or crops) can sometimes overshadow the direct numerical response of ladybirds (*Hip. convergens*, *Hip. parenthesis* and *C. septempunctata*) to the aphid populations within these fields.

5.4 FOOD-RELATED BEHAVIOUR

5.4.1 Foraging behaviour

In studies of ladybird behaviour, a number of paradoxical features are manifest. Ladybirds, particularly adults, move in a seemingly chaotic way which appears maladaptive. For example, they sometimes walk over suitable aphids without attacking them. Their behaviour appears so 'aimless' in contrast to that of parasitoids that Murdie (1971) once called them 'blundering idiots'. In fact many aspects of ladybird foraging behaviour are rather sophisticated, e.g. the oviposition deterrent cues (5.4.1.3) and the attraction of ladybirds to volatiles from injured plants (5.4.1.2).

Armed with the axiom of optimality, i.e. that females should produce an optimal number of progeny, we might be astonished at the sight of huge numbers of ladybirds at the seashore that are victims of 'non-economic' overproduction of offspring (5.4.1.5). However, is it truly a waste? The production of very numerous offspring under diverse environmental conditions potentially ensure wide genetic variance and thus increase the probability of overwintering survival and also successful dispersal to new areas.

The reductionist approach suggests limiting the number of species studied and attempting to generalize for the whole family, or at least for one of its food guilds. However, as stressed by Sloggett (2005), coccinellids exhibit considerable diversity in their ecology and ethology. More specifically Harmon et al. (1998), in their analysis of the role of vision in foraging in four species, say the same: 'while the historical trend has been to generalize behavioural traits found in one species to all coccinellids, our study demonstrates the wide variation in the use of foraging cues'. Such interspecific comparisons can lead to understanding why individual species may co-exist in one ecosystem or why they become invasive.

The field of predator foraging behaviour is an area of behavioural ecology marked by two isolated methodological approaches: while empirical data continue to be collected and analyzed, optimality models are constructed by computing fitness components. As long ago as 1988 it was proposed that: 'The next twenty years in insect behavioural ecology will be dominated by the **empirical testing of hypotheses**.' (Burk 1988); this empirical testing still needs to be carried out today. Although there are stimulating concepts and models, we need data as 'specific quantitative tests of particular hypotheses and focussed on individuals and their phenotypic variation. With such data, we will be in a position to decide whether acceptable models have been devised' (Burk 1988). For the research of spatial relations in predator–prey interactions, Inchausti and Ballesteros (2008) invite the 'experimental and field biologists to investigate carefully, how the tendency to switch patches relates to foraging success' of predators. Roitberg (1993) warned that testable hypotheses cannot be built on oversimplified assumptions. Currently, a wide gap seemingly remains between the two above-mentioned approaches as far as coccinellids are concerned, while some studies on insect parasitoids have achieved a much higher standard of research (Wajnberg et al. 2008).

Observations must be performed (and subsequently verified) under experimental conditions as similar as possible to those in nature. Although this prerequisite seems obvious, many experiments have been undertaken under unnatural conditions, which are likely to have introduced **artefacts**. Danks (1983) and Okuyama (2008) provide another important warning: not to work with only 'central measures' such as averages of behaviour parameters. **Variation** is typically treated as a nuisance in many behavioural studies. However, this variation can provide important ecological perspectives: behavioural variation, because it is very large, can cause a substantial change in community dynamics (Okuyama 2008). It is important to test **multiple working hypotheses** and alternatives to optimal models for predator foraging (Ward 1992, 1993, Nonacs & Dill 1993). Lederberg's (1992) conviction that 'the most revolutionary discoveries have arisen out of observation that did not fit prevailing scientific doctrine, and required a **re-examination of the fundamental concepts**' is of great importance. One of the research lines showing hopeful progress in this much needed direction is the prey size–density study (Sloggett 2008b; 5.2.3).

General information on optimal foraging theory and related topics is provided by e.g. Krebs & McCleery (1984), Bell (1985, 1990), Waage & Greathead (1986), Ward (1992, 1993), Nonacs & Dill (1993), Godfray (1994), Jervis (2005), Inchausti and Ballesteros (2008) and Raubenheimer et al. (2009). Foraging behaviour of coccinellid larvae has been reviewed by Ferran and Dixon (1993) and of ovipositing females by Seagraves (2009).

The location of prey by ladybirds may be divided into three steps (Vinson 1977, Hodek 1993): (i) finding a habitat, (ii) finding the prey within the habitat and (iii) accepting the prey. Both the prey and the host plant, particularly when damaged by herbivores, emit attractive volatiles (5.4.1.2). In this chapter we prefer not to use the classification of semiochemicals into pheromones, allomones, kairomones and synomones (see e.g. Hatano et al. 2008), as the terms are often used ambiguously or arbitrarily.

We broadly follow a sequence of prey-related behavioural steps. The first aim of adults is to find food (5.4.1.1 and 5.4.1.2) and mate, and then find a suitable place for oviposition (5.4.1.3). Finding a suitable prey-bearing **habitat**, while ranging across the landscape, remains a rather mysterious process: how, for example, does a ladybird discover a crop field with initially scarce, small aphid colonies? One explantion might be that ladybirds orient to prey using plumes of volatile semiochemicals (5.4.1.5).

Rather more evidence is available on phase (ii). Foraging on the **host plants** is guided partly indirectly, by taxes and the structure and surface of host plants (5.4.1.1). Studies on this have evolved from an earlier assumption of fully random foraging to the idea that foraging is partly guided by visual and olfactory cues (5.4.1.2). A very important moment is the first **encounter** with prey, an encounter that strikingly changes behaviour from extensive to intensive searching (5.4.1.2).

Well-fed and mated females look for **oviposition sites** (5.4.1.3). Prey suitable for larvae is usually also used by females, although not always (5.2).

First instar larvae can increase their vitality by feeding on sibling eggs (5.2.8), which can be either unfertilized or otherwise non-viable or even trophic eggs (5.2.7). After dispersal from egg clutches, larval behaviour is similar to that of adults, though they are probably equipped with less complex sensory capabilities (5.4.1.2, 5.4.1.4). Aphidophagous coccinellids, due to the inherently intermittent occurrence of aphids, often face prey shortage and resort to cannibalism (5.2.8) and/or feeding on alternative foods (5.2.9).

Table 5.32 Time budget of adult *Coccinella septempunctata* behaviour in the experiments (after Minoretti & Weisser 2000).

Behaviour	Aphid-free plant (*n* = 13)	Aphid-infested plant 10-aphid colony (*n* = 10)	 30-aphid colony (*n* = 9)
Searching	67.0 ± 4.9	63.7 ± 6.8	40.3 ± 6.1
Grooming	4.0 ± 1.7	9.9 ± 3.1	14.6 ± 3.6
Resting	12.3 ± 5.0	8.9 ± 3.9	8.6 ± 4.3
Handling prey	0	16.9 ± 2.7	24.0 ± 3.4
Feeding on plant tissue	5.4 ± 2.5	1.0 ± 0.8	0.5 ± 0.5
Feeding on nectar	5.4 ± 3.8	2.2 ± 1.3	11.1 ± 4.9

Values are percentages of the total time spent on a plant (mean percentage ± SE).

5.4.1.1 Indirect factors in foraging

Indirect factors in foraging include taxes, plant structure, plant surface, diurnal periodicity. Coccinellids spend most of their time searching for prey (Table 5.32). On a plant, the encounter of predator and prey is made more probable by certain regular behaviours such as taxes, and features of the structure and surface of plants.

Taxes

Encounters are made more likely, at least between aphidophagous and acarophagous species and their prey, by similar tactic responses. Coccinellids, like mites and aphids, exhibit positive phototaxis and negative geotaxis (Fleschner 1950, Dixon 1959, Kaddou 1960, Baensch 1964, 1966, Kesten 1969). However, satiated larvae of *Menochilus sexmaculatus* were observed to be negatively phototactic (Ng 1986).

Plant structure

To study the movements of predator **larvae** on the stem and twigs of plants, Baensch (1964, 1966) used a 50 cm high model tree. When moving upwards on the stem, coccinellids stop at bifurcations, but soon continue walking upwards to follow the main axis. After an unsuccessful search on the top the larvae return down the stem and search upwards at bifurcations. If unsuccessful on a twig, they return to the main stem and move to the top again. So, on the model tree, the larvae were more or less 'trapped' between the apex and the tops of branches (Fig. 5.34). If the **larvae** eventually reach the ground, they do not move upwards until they have covered a certain sideways distance. The **adults** soon fly away after an unsuccessful search. Kareiva (1990) compared the effect of plant structure on the movement of *C. septempunctata* adults. There was strong aggregation on goldenrod (*Solidago* sp.), weak aggregation on beans (*Vicia* sp.) and no aggregation on pea (Fig. 5.35). The importance of plant morphology was shown in a comparison of 'normal' peas and a 'leafless' variety. *C. septempunctata* beetles fall off less frequently from the latter plants and moved faster. One day after release they were aggregated on aphid-infested leafless plants, but still randomly distributed on 'normal' peas (Kareiva 1990).

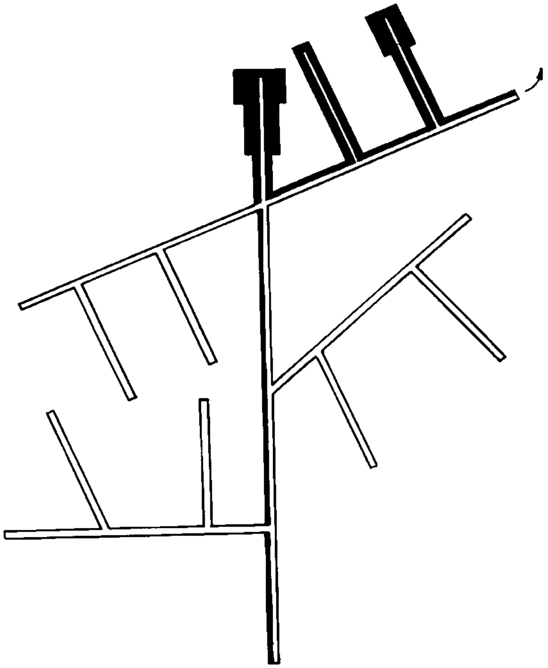

Figure 5.34 Search pattern of one *Adalia bipunctata* adult on a model tree until flying away (arrow) after 23 minutes. The thickness of the line indicates the searching frequency of the predator (modified from Baensch 1964).

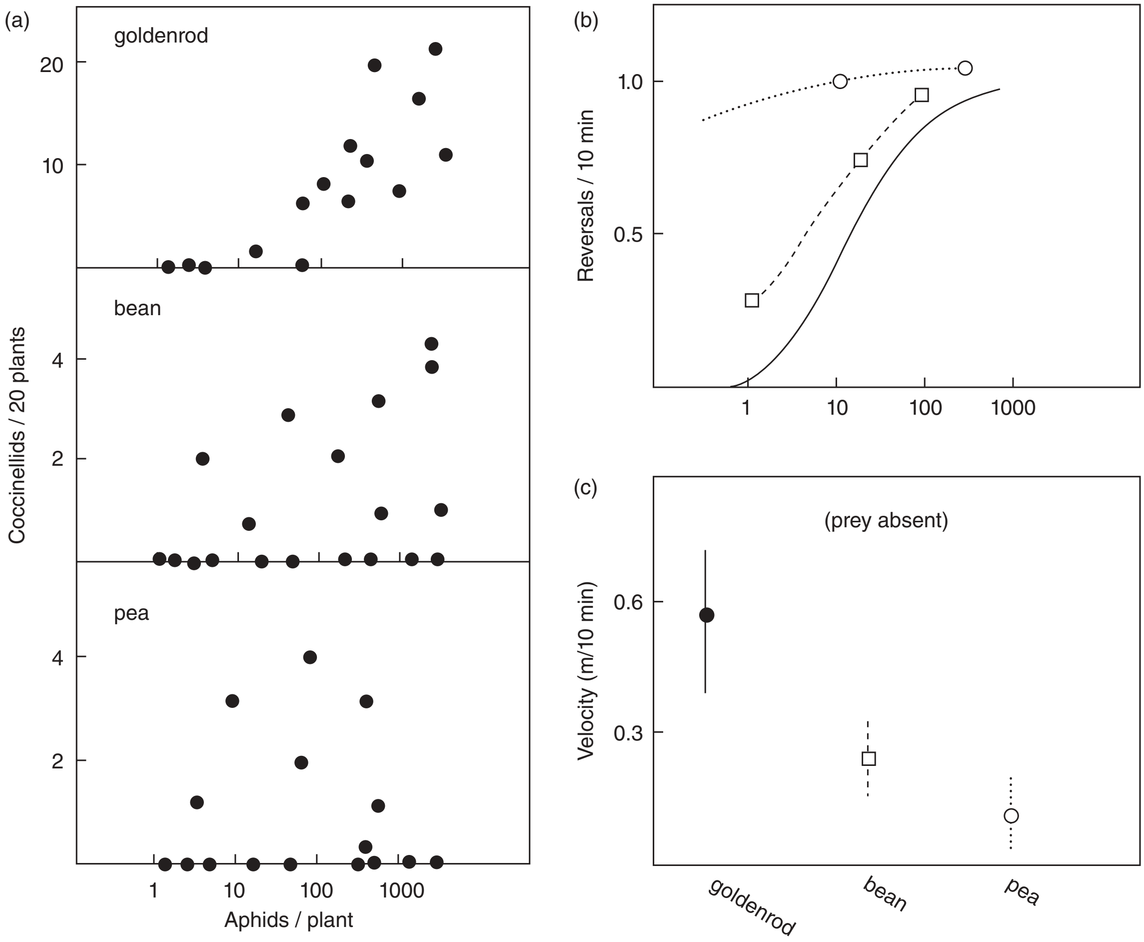

Figure 5.35 Left, aggregations of *Coccinella septempunctata* beetles two days after their release in fields of goldenrod (*Solidago* sp.), bean (*Vicia* sp.) and pea (*Pisum* sp.). A positive association between the number of beetles per 20 plants (sampled in 1 m^2 plots) and the density of aphids on the plants indicates aggregation; slopes can be used as a measure of the rate of aggregation. (a) Movement of *Coccinella septempunctata*, starved for 12 hours, on rows of three plant species; closed circle and unbroken line, goldenrod; open squares, bean; open circles, pea. (b) Number of reversals per 10 minutes. (c) Velocity (m/10 min) (from Kareiva 1990).

The different structure of two host plants of *Uroleucon* aphids affected the searching efficiency of *C. septempunctata* fourth instars. They spent most of the time on the shoots of *Carduus crispus*, yet only detected 55% of first instar aphids; in contrast, 90% of first instar aphids were detected by larvae on *Centaurea jacea*, even though the larvae searched on shoots only one third of the time (Table 5.33). The explanation was that first instar aphids were hidden on the structurally complex stem of *C. crispus*, which are covered with small leaves, spines and hairs, whereas they were exposed on *C. jacea* (Stadler 1991).

Foraging efficiency may be increased by the tendency of coccinellids to crawl along an edge or a raised surface. Thus **on leaves**, **veins** influence the direction of movement, and it is near veins that colonies of aphids most often occur (Banks 1957, Dixon 1959, Baensch 1964, 1966, Marks 1977, Shah 1982). There are, of course, modifications of this general scheme. While prominent veins of sycamore and lime leaves were successfully searched by *A. bipunctata* (Dixon 1970, Wratten 1973), the larvae of *C. septempunctata* searched mainly the **edge of leaves** and the **stem** on pea and bean plants, where the veins of leaves are not

Table 5.33 Proportion of *Uroleucon* spp. colonies encountered (A) and aphids eaten (B) by 4th instar larvae of *Coccinella septempunctata* on five host plants (Stadler 1991).

Host plant	***Centaurea jacea***	***Centaurea scabiosa***	***Cirsium arvense***	***Carduus crispus***	***Cichorium intybus***
Aphid	***Uroleucon (Uromelan) jaceae***	***Uroleucon jaceae ssp.henrichi***	***Uroleucon (Uromelan) cirsii***	***Uroleucon (Uromelan) aeneus***	***Uroleucon (Uromelan) cichorii***
First instar (A)	90	80	60	55	100
Adult aphid (A)	100	100	70	80	100
First instar (B)	90	90	80	70	90
Adult aphid (B)	20	15	15	25	10

prominent. Their searching was thus not very successful on pea and bean, as the aphids occurred mostly around the veins (Carter et al. 1984). Similar observations were made on wheat leaves: when the last instar larva of *C. septempunctata* searches for *Sitobion avenae* it walks along the leaf edge, so that the central area is not searched and aphids there are not found (Ferran & Deconchat 1992). The aphid *Rhopalosiphum padi* may often be found in the space between the stem and the ear of wheat which cannot be entered by third and fourth instar larvae of *C. septempunctata* (Ferran & Dixon 1993).

Plant surface

Banks (1957) observed how important the plant surface is for the foraging of coccinellid larvae (Table 5.34). **Glandular trichomes** on tobacco plants impeded foraging of larvae in *Col. maculata* (Elsey 1974) and *Hip. convergens* (Belcher & Thurston 1982). In a study of *A. bipunctata* larvae, no feeding was observed on tomato and tobacco plants covered with long, dense, upright trichomes and glandular hairs, or on bush beans with hook-shaped hairs. Leaves of another six plants without these characteristics were suitable (Shah 1982). Foraging for nymphs of *Heteropsylla cubana* by *Curinus coeruleus* adults was significantly affected by the leaf surface of different species of *Leucaena* host plant (Da Silva et al. 1992).

Crop plants selected for herbivore-resistant pubescence are also unsuitable for entomophagous insects (but see 5.4.1.3, egg protection). On the richly glandular pubescent leaves of aphid-resistant potato, newly hatched larvae of *C. transversoguttata*, *C. septempunctata*, *Col. maculata* and *Hip. convergens* accumulated trichome exudates on their appendages and bodies and moved only c. 5 mm from the egg within 48 hours. By contrast, on the normal potato plants, ladybird larvae walked over 100 mm (Obrycki & Tauber 1984). The movement of 2 day old larvae of *P. quatuordecimpunctata* was impeded on the hairy leaves of egg-plant (speed 6.3–8.8 cm/minute), while the glabrous leaves of pepper (22.6 cm/minute) and particularly the lower surface of maize leaves (30.0 cm/min) were suitable. The larvae usually followed the veins of the maize leaves (Quilici & Iperti 1986).

Table 5.34 Mean rates of movements of first instar larvae of *Propylea quatuordecimpunctata* on various surfaces (Banks 1957).

	Paper	**Clean bean leaf**	**Honey-dewed bean**	**Hairy potato leaf**
mm/min	151	154	104	54
m/1–1.5 day		225–300	150–200	75–100

For the acarophagous larvae of *Stethorus pusillus*, the surface of plant leaves is also important. Leaves of tomato and pepper plants facilitate the highest consumption of *Tetranychus urticae* by ladybird larvae (0.68 and 0.55 prey eaten/10 minutes), respectively, while aubergine (0.26 prey/10 minutes) was intermediate and cucumber plants (0.19 prey/10 minutes) the least favourable; the responsible factor was not specified (Rott & Ponsonby 2000; Table 5.35). **Surface waxes** may also significantly affect the suitability of host plants for coccinellids. They captured fewer aphids on the leaves of *Brassica oleracea* than on other comparable plant species, because of the thick, slippery wax layer (Shah 1982). Although *A. pisum* densities

Table 5.35 Effect of plant surface on behaviour of *Stethorus pusillus* observed on leaf discs with *Tetranychus urticae* as prey (modified after Rott & Ponsonby 2000).

	Distance (mm) moved in 10 min	Time moving (%)	Prey encountered	Prey eaten
Tomato	23.4 ± 2.73 a	11 ± 1.0 a	1.44 ± 0.11 a	0.68 ± 0.05 a
Pepper	24.7 ± 2.50 a	8 ± 0.8 a	0.85 ± 0.07 b	0.55 ± 0.04 a
Aubergine	10.9 ± 0.76 b	4 ± 0.4 b	0.30 ± 0.04 c	0.26 ± 0.04 b
Cucumber	15.7 ± 1.20 b	5 ± 0.4 b	0.24 ± 0.04 c	0.19 ± 0.03 b

Mean ± SE within a treatment followed by the same letter are not significantly different at $P = 0.05$ (Tukey's Test).

were significantly lower on peas with reduced surface wax, numbers of predatory coccinellids did not differ consistently between reduced-wax and normal-wax peas. This failed to support a hypothesis that higher predator numbers on reduced-wax peas contribute to lower aphid density there (White & Eigenbrode 2000). On normal-wax peas *Hip. convergens* larvae exhibited higher rates of falling and lower search rate than on reduced-wax peas (Rutledge & Eigenbrode 2003). A strong reduction of surface wax bloom in mutated peas appeared to eliminate the avoidance response by fourth instar *Hip. convergens* larvae to leaves exposed to conspecifics of the same instar (Rutledge et al. 2008; 5.4.1.3). Predation efficacy of *C. septempunctata* on *Acyrthosiphon pisum* was found to be affected differentially on three types of pea plants that differed in surface waxes and content of allelochemicals (Legrand & Barbosa 2003).

Larvae of individual ladybird species vary in their ability to adhere to plant surfaces. When comparing the **attachment ability** of larvae of five species to pea plants with crystalline epicuticular waxes, Eigenbrode et al. (2008) recorded high ability for *A. bipunctata* larvae. These authors also measured the attachment force on clean glass and found much higher values in the primarily arboreal species *Har. axyridis* (11.4 mN) and *A. bipunctata* (6.3 mN) than in the eurytopic, primarily field species *C. septempunctata*, *C. transversoguttata* and *Hip. convergens* (2.6–2.8 mN). A morphological study of the attachment system in *Cryptolaemus montrouzieri* was combined with measurements of attachment forces generated by beetles on the plant surface (Gorb et al. 2008).

Diurnal periodicity of foraging

C. septempunctata brucki adults locate their prey visually from a very short distance, but only in light (5.4.1.2). In complete darkness they can only capture prey after contact (Nakamuta 1984, 1985). This may be why, under 16L:8D, their searching activity is highest between 09.00 and 16.00 hours (with lights on at 04.00) (Nakamuta 1987). The periodicity of *C. septempunctata* is similar to that of *Har. axyridis* (Miura & Nishimura 1980) and, perhaps, also to that of other species which are mostly found foraging in the field from 09.00 to 17.00 (*Hip. convergens*, *C. transversoguttata* and *Col. maculata*; Mack & Smilowitz 1978). Just over half (53%, $n = 36$) of unspecified ladybird larvae foraged from 15.00 to 21.00 on sugar beet in August (Meyhöfer 2001). Larvae and both sexes of adult *Stethorus punctum* cease their feeding activity at dusk and resume it at dawn (Hull et al. 1977). Under constant light the rhythm persists (i.e. it is endogenous), but the endogenous period is shorter than 24 hours, as in other diurnal animals (Nakamuta 1987). *Col. maculata* lay eggs mostly in the early afternoon (Fig. 5.36; Staley & Yeargan 2005).

When *C. septempunctata brucki* adults are starved, their activity increases for several hours and then it decreases with continuing **starvation**, so that it is highest on the first day (Nakamuta 1987). Similarly, the activity of starving larvae of *P. quatuordecimpunctata* increases during the first day, remains high until the middle of the second day and then decreases (Quilici & Iperti 1986).

5.4.1.2 The role of senses in foraging

Recent findings suggest that, at least for coccinellid adults and in case of short distance perception, Thompson (1951) was right when he maintained that Coccinellidae have 'sense organs and there is no doubt that they can perceive their hosts at a distance. Certainly there seems no reason to think . . . that their behaviour can be described in any sense as random action'.

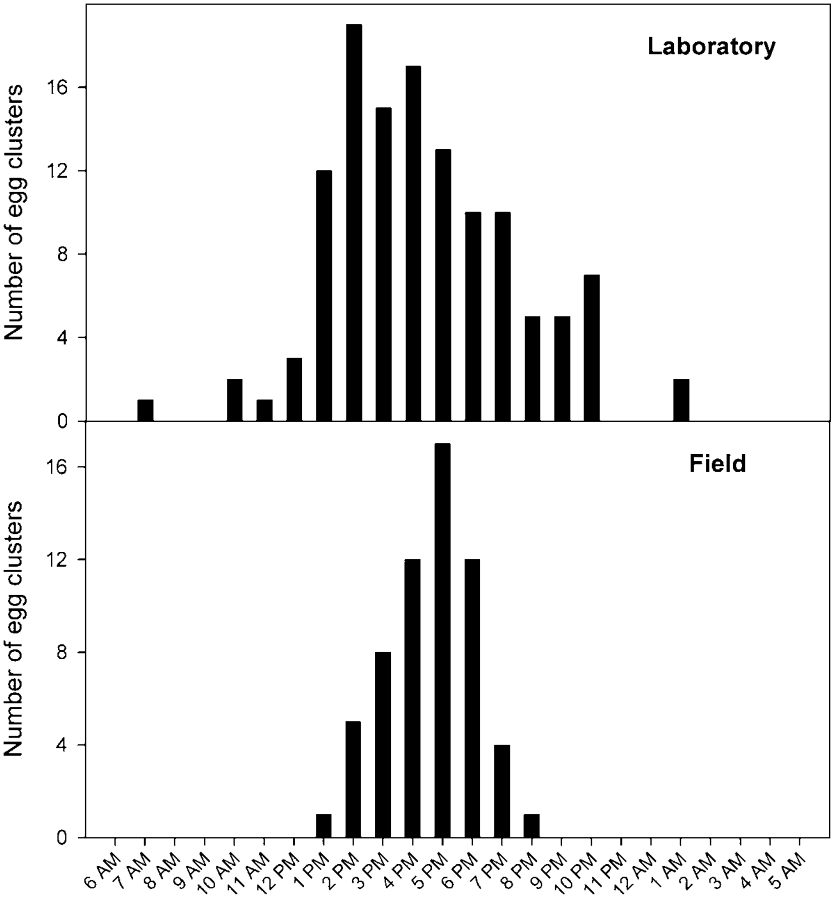

Figure 5.36 Diel periodicity of *Coleomegilla maculata* oviposition in the laboratory and in the field. Bars represent number of egg clusters laid during the hour that ended at the time shown on the *x*-axis (from Staley & Yeargan 2005).

There is a contrast between this statement and Murdie's (1971) assumption that coccinellids are just 'blundering idiots'. Many other specialists have also believed in such **'non-sensory'** behaviour of ladybirds (see Hodek 1996 for early references, and Liu & Stansly 1999 for the case of the psyllophagous *Delphastus catalinae* and *Clitostethus oculatus*). It was thought for a long time that prey are not detected by a coccinellid until actual contact occurs and reports were that prey may not be detected even when only a few millimeters away (Banks 1957), and even when the wind carries the smell of the prey to the coccinellid (Baensch 1964, 1966, experiments on larvae). Some individuals indeed do not react to prey until they touch it and often it is observed both in the laboratory and in the field that 'coccinellids walk right over aphids without eating them' (McAllister & Roitberg 1987). This may be because the coccinellid is at that moment in another phase of its behaviour, i.e. a satiated adult, a male searching for a mate, or a female looking for a place to oviposit (Hodek 1993).

One reason why ladybirds' crawling was frequently believed to be **random**, was the observation that they **revisit** places already searched while neglecting other areas. For example, a first instar larva of *P. quatuordecimpunctata*, moving for 3 hours on a clump of 14 bean stems, spent 52% of the time searching on leaves visited more than once and only 12% on leaves visited only once, the remaining time being spent on stems or stationary (Banks 1957). Marks (1977) suggested there might be adaptive value in behaviour that leads the coccinellid to re-cross its former track. After disturbance, many aphids such as *Acyrthosiphon pisum* or *Aphis fabae* withdraw their stylets and move away from where they were feeding. These aphids can then be captured by coccinellid larvae the next time they traverse their original search path.

Effect of encounter

After feeding, the predator increases the thoroughness of subsequent searching by slower, winding movements in the immediate vicinity, often turning frequently after only short distances (Banks 1957, for later reports see Hodek 1996). This behavioural change is generally considered to enhance the efficiency of searching for aggregated resource items (Curio 1976). Thus, for example, the larvae of *C. septempunctata* which have found aphid colonies remain close to them for long periods (e.g. 18 hours; Banks 1957; Fig. 5.37). In fact, this behaviour is recorded also in non-entomophagous insects (for examples see Bell 1985, Nakamuta 1985b).

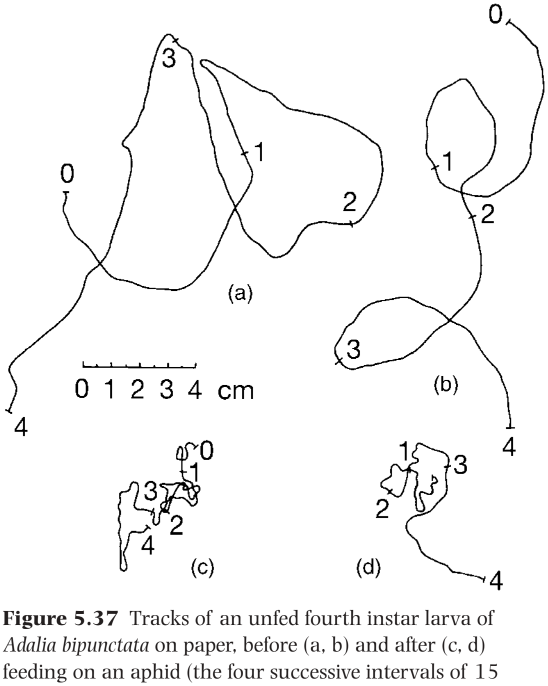

Figure 5.37 Tracks of an unfed fourth instar larva of *Adalia bipunctata* on paper, before (a, b) and after (c, d) feeding on an aphid (the four successive intervals of 15 seconds are marked by numbers along the tracks) (from Banks 1957).

Following the early reports by Fleschner (1950) and Banks (1957), this phenomenon has been variously termed as 'area-concentrated' (Curio 1976, Nakamuta 1985a, b), 'success motivated' (Vinson 1977) or 'area-restricted' searching (Carter & Dixon 1982). It seems best to speak about a '**switchover from extensive to intensive search behaviour**'. However, the analysis of the mechanism and its variability did not make much progress until experiments by Nakamuta and Ferran in the 1980s and 1990s (see below), and our understanding is still far from complete.

Switching to intensive search seems to be **learned**; it is not shown by newly hatched adults and only develops after some experience of prey capture (Ettifouri & Ferran 1992). Nakamuta (1985a, b) discriminated in experiments between contact with an aphid (*Myzus persicae*), biting an aphid and consumption of an aphid; he suggested that **contact with a prey**, rather than its consumption, is the cue that elicits the switchover. This may be an adaptation to situations where the contacted aphid escapes capture (5.4.2). Ferran and Dixon (1993) suggested, however, that the **ingestion** is the cue eliciting the switch. The **duration** of intensive search in *C. septempunctata* adults depends on the quality of the signal (Nakamuta 1985a, b; Table 5.36). Consumption of an aphid produced the longest response. The parameters of the intensive search in fourth instar *C. septempunctata* are affected by the duration of fasting before the encounter with prey (Carter & Dixon 1982). In *C. septempunctata* larvae, the change to intensive search may also be induced by the presence of honeydew (Carter & Dixon 1984). Intraspecific variability in searching behaviour, neglected in the optimal foraging approach (5.4.1; Bell 1990), has been reported in *Cer. undecimnotata*. The larvae show a highly variable response to prey capture, 'adopting intensive search immediately, later or never' (Ferran & Dixon 1993).

In two coccidophagous species, *Chil. bipustulatus* and *Chil. kuwanae*, the same change from extensive to intensive search was observed on encountering prey (Podoler & Henen 1986; Table 5.37). The phenomenon has also been observed in acarophagous coccinellids (Houck 1991; Table 5.38).

Earlier observations on sensorial perception

The 'early' observations (before and in the 1980s) on prey perception are mostly indirect, and a combination of olfactory and visual cues has mostly just been assumed. Not all early workers rejected the possibility of sensory orientation by coccinellids towards their prey. Fleschner (1950) reported distant perception of prey by *Stethorus punctum picipes*, but only from about 0.5 mm. In *Har. axyridis*, the perception of olfactory (together with visual) cues was reported in adults, when they were attracted to gauze and polyethylene bags contaning aphid-infested leaves (Obata 1986, 1997).

Two early observations on two **large coccinellids** preying on coleopteran and lepidopteran larvae indicated prey-orientation behaviour. Older instars of *Aiolocaria hexaspilota*, a predator of chrysomelid larvae, actively pursue their prey (Savoiskaya 1970a). Similar behaviour was reported for the adults of *Anatis ocellata* preying on larvae of the tortricid *Choristoneura pinus*. Foraging beetles stopped within a distance of 13–19 mm from the prey before moving forward and quickly snatching a caterpillar in their mandibles (Allen et al. 1970).

Two other early reports suggest that coccinellids are guided by **olfactory cues**. Coccinellid adults were observed to follow the **trails of** *Formica polyctena* **ants** (Bhatkar 1982) that tolerated them, and in this way arrive at aphid colonies. In the laboratory, the coccinellids followed such a trail 150 mm long, previously used by 20 ants and apparently chemically marked by them.

Table 5.36 Duration of area-concentrated search of 24-hour starved ladybird beetles, *Coccinella septempunctata brucki*, exposed to different feeding stimuli (Nakamuta 1985a, b).

Types of feeding stimuli	Duration (s)
No stimulation	2.1 ± 0.7a
Contact with an aphid	5.3 ± 2.0b
Biting an aphid	12.9 ± 6.3c
Consumption of an aphid	19.8 ± 9.6d
Contact with an agar block	5.4 ± 2.1b
Consumption of an agar block coated with aphid body fluid	16.7 ± 7.3e

Values are means ± SD of 10 different individuals. Means followed by different letters are significantly different at 0.05 level by Cochran-Cox's *t*-test.

Table 5.38 Proportion of time *Stethorus punctum* females and 3rd instar larvae spent searching, feeding and resting, when they encountered an abundance of all instars of *Tetranychus urticae* (Houck 1991).

	Proportion of time (%) spent		
	searching	feeding	resting
Satiated females	45.1	14.4	40.5
Starved females*	24.4	43.3	32.3
Satiated larvae	78.4	21.6	0
Starved larvae*	47.1	52.9	0

*The increased feeding time was due to a more complete removal of prey contents.

Table 5.37 Response (within 10 seconds) of *Chilocorus bipustulatus* to the contact with prey, a diaspidid scale (modified after Podoler & Henen 1986).

Predator stage	Prey instar	Mean speed (cm/sec)	Mean change in angle (degrees/cm)	Mean number of turns
Adult	Control	0.80a	26.00a	6.80a
	1st	0.37b	116.57b	7.93a
	2nd	0.43b	70.43c	7.97a
	3rd	0.48b	61.43c	7.43a
Larva	Control	0.52a	34.43a	3.00a
	1st	0.30b	80.28b	5.60b
	2nd	0.35b	59.71c	5.47b
	3rd	0.36b	52.43ac	5.43b

Within columns and species groups, numbers followed by different letters are significantly different at $P < 0.05$ (Duncan's Multiple Range Test).

Marks (1977) observed that fourth instar *C. septempunctata* searched much longer (for 215 seconds) the first time than in repeat searches (5–40 seconds) and supposed that the larva leaves a **chemical marker** when it dabs the surface with the anal disc. As the larvae never ignored plants previously visited by other larvae, the author assumed that there was an individual-specific means of marking a surface. Moving larvae held their maxillary palps (bearing fine distal setae) close to the surface, apparently to perceive the trail. Marking of the surface by larvae was later confirmed in studies on oviposition deterrence of adult females (Ruzicka 1997; 5.4.1.3). Furthermore, after 30 years, Marks' finding on the ability of ladybird larvae to perceive trails of conspecific larvae, and avoid searching the marked surfaces, finally appears to have been confirmed (Reynolds 2007, Rutledge et al. 2008; 5.4.1.3). Thus not only adult females, but **also larvae** seem to **perceive sensory cues** left by larvae.

Heidari and Copland (1992) reported that the fourth instar *Cryptolaemus montrouzieri* perceive prey only by physical contact, while adults were able to detect their mealybug (Pseudococcidae) prey by **sensory stimuli**. The distance at which the adults stop and then 'jump' towards the prey was reported to be 14 mm, slightly greater than the **perception distance** experimentally established for two subspecies of *C. septempunctata*. Nakamuta (1984b) and Nakamuta and Saito (1985) found that adults of *C. s. brucki* orientated themselves towards aphid prey from a distance of about 7 mm in light, while they were unable to locate it in darkness. Thus, these results suggest that adult coccinellids may perceive the prey also visually at close proximity. In adults of *C. s. septempunctata*, **visual** perception of aphids was reported to be up to 10 mm, while for **olfactory** perception by fourth instars this distance was 7 mm (Stubbs 1980). The experiments with larvae used an aphid crushed onto filter paper: an intact aphid might elicit a different, perhaps less intense olfactory stimulus. Nakamuta's results (1984a) further suggest that the aphid body fluid is the final cue to prey recognition. Many **later findings** also support **sensory orientation** (see Vision, olfaction). The reason why visual and olfactory perception was overlooked may be that the distances involved are very small (Stubbs 1980).

Honeydew, sucrose

With **honeydew**, acting either as an arrestant for *C. septempunctata* larvae (Carter & Dixon 1984) or an oviposition stimulant (Evans & Dixon 1986), olfaction is clearly involved. Honeydew has a similar effect to that of prey. Larvae do not discriminate between different amounts of honeydew, although *C. septempunctata* larvae do discriminate between differences in the density of aphid honeydew droplets. They climbed more often over a surface contaminated with honeydew of the ant-tended *Aphis craccivora* (but here deprived of ants) than over a similar surface with the less dense honeydew droplets of the non-ant-tended *Acyrthosiphon pisum* (Ide et al. 2007).

The role of prey traces (honeydew, exuviae) in eliciting responses from coccinellids was later documented using a Y-tube olfactometer. More *Har. axyridis* beetles preferred the odour of leaves of buckthorn naturally infested with *Aphis glycines* to that of artificially infested or uninfested buckthorn (Bahlai et al. 2008; Table 5.39). Similar observations with prey traces have been made on coccidophages. Wax and honeydew of mealybugs (*Phenacoccus manihoti*, *Planococcus citri*) arrested *Exochomus flaviventris* and *Diomus* sp., which are predators of *P. manihoti*, the cassava mealybug (van den Meiracker et al. 1990).

The **sex pheromones of coccids** attract coccidophagous ladybirds. *Rhyzobius* sp. responded to sex pheromones of two matsucoccids, *Matsucoccus feytaudi* and *M. matsumurae* (Branco et al. 2006).

The **arrestant effect** of honeydew has been used **in augmentative biological control**, in which honeydew being replaced by sucrose. **Sucrose** dissolved in water (150 g/l) applied to alfalfa arrested *C. septempunctata* and *C. transversoguttata richardsoni*:, within 24–48 hours ladybird densities increased 2–13 times in the centre of the treated plots, whereas in the surrounding fields densities of ladybirds decreased to less than two-thirds of their former density. 'Artificial honeydew' might be used not only to bring ladybirds to fields with still only few aphids, but also – by spraying an adjacent crop – push the coccinellids away from fields scheduled for insecticide treatment (Evans & Richards 1997). In a study of dispersal using mark–release–recapture, the residence time of beetles was 20–30% longer in sugar-sprayed plots and the density of unmarked beetles rose by a factor of 10–20 in sugar-sprayed plots during the first 4–6 hours following early morning spraying. Such a **fast aggregation** seems difficult to explain by random arrival. Because sugar is not volatile, the authors hypothesized that later arriving ladybirds were attracted by earlier arrivals (Van der Werf et al. 2000; Chapter 9.4).

Table 5.39 Preferences of collected adult *Harmonia axyridis* recorded in a Y-type tube olfactometer for cues derived from a hedgerow ecosystem (modified after Bahlai et al. 2008).

Comparison				**% Choice**	
T1	**T2**	***n***	**% Response**	**T1**	**T2**
R. cathartica[*]	Blank	30	75.0	70.0	30.0[‡]
R. cathartica	*M. domestica* odor[†]	31	77.5	32.3	67.7[‡]
R. cathartica	Artificially aphid infested *R. cathartica* odor	32	80.0	53.1	46.9
R. cathartica	Naturally aphid infested *R. cathartica* odor	38	95.0	31.6	68.4[‡]

[*] *Rhamnus cathartica* (buckthorn), winter host of *Aphis glycines*, frequent in agricultural hedgerows.

[†] *Malus domestica*, apple.

[‡] Significant, nonrandom responses.

Sensory receptors

The spectral sensitivity and structure of the compound eyes of *C. septempunctata* adults have been studied (Agee et al. 1990, Lin & Wu 1992, Lin et al. 1992) and photoreceptors for three electromagnetic wavelength ranges have been documented: UV, green and a third between UV and green. Storch (1976) found visual perception to be of little importance to fourth instar *C. transversoguttata*; however, the **prolegs** were important in the detection of prey as they bear sensillae which detect prey at a distance. Kesten (1969) thought that the **maxillary palps** are perhaps the most important sensory organs through which both adults and larvae of *Anatis ocellata* recognize prey. Yan et al. (1982) assumed that chemoreception is situated in the sensillae on the terminal segment of the **labial palp** of *C. septempunctata* adults. According to Nakamuta (1985), prey contact by maxillary palps or maxillae elicits capture behaviour. Da Silva et al. (1992) observed that *Curinus coeruleus* adults seemed unaware of their prey (*Heteropsylla cubana*) until contact was made, usually with the maxillary palps. The number of sensory receptors on the maxillary palps was compared across coccinellid adults with different food specializations. The aphidophagous polyphage *C. septempunctata* has 1800 chemoreceptors on each palp, the aphidophagous oligophage *Cer. undecimnotata* has 1100 receptors and a coccidophagous *Chilocorus* sp. has 830 receptors. In all three cases **olfactory** receptors are more numerous than gustatory ones. The **phytophagous** *Epilachna* '*chrysomelina*', however, has more gustatory than olfactory receptors, in total only 480 (Barbier et al. 1996). The importance of the maxillary palps for discriminating between clean surfaces and those with deterrent larval tracks (5.4.1.3) was proved by maxillary palp amputation in experiments with *Cycloneda limbifer* and *Cer. undecimnotata* (Ruzicka 2003). Sensilla on antennae of *Har. axyridis* were described in detail by Chi et al. (2009).

Vision

A strong positive response to yellow (chosen from seven colours) sticky panels was exhibited by *C. septempunctata* adults, while *Hip. parenthesis* did not show visual orientation to any particular colour (Maredia et al. 1992). Lorenzetti et al. (1997) reported a significantly greater abundance of coccinellids on stressed and therefore yellow maize plants, while chrysopids preferred greener control plants. Laboratory experiments also examined the role of vision in close-proximity foraging behaviour in three of four species, but **colour vision** in only two species (Harmon et al. 1998). It is not clear how pollinivory in *Col. maculata* is related to the finding in this study that this species appears not to use colour or any other type of visual cue. When responding to red or green morphs of *Acyrthosiphon pisum* on green or red backgrounds, *C. septempunctata* could distinguish between red and green morphs and used colour contrast with the background in foraging. *Har. axyridis*, however, consumed more red than green morphs regardless of background. *Hip. convergens* did not respond to colour, but its foraging was decreased in the dark (Harmon et al. 1998).

In an arena, *Har. axyridis* adults, particularly females, strongly preferred yellow paper pillars over green ones. This has recently been confirmed by Adedipe and Park (2010). No female visited the green pillars (Mondor & Warren 2000). These authors also found a clear **effect of conditioning** once the females had located the food on top of the green pillars over a 3-week period; they then spent more time searching green than yellow pillars in a subsequent trial. These interesting findings, however, do not seem to prove that *Har. axyridis* adults 'effectively locate prey over large distances' as interpreted by Rutledge et al. (2004). These important results relate to the question posed recently by Pasteels (2007): 'To what degree are ladybird responses to various cues innate or learned?' Also coccinellid larvae can learn: rejection of lower quality prey (parasitized old versus non-parasitized young lepidopteran eggs) by fourth instars of *Col. maculata* gradually increased at subsequent encounters (Boivin et al. 2010). This learned behaviour was partly forgotten after 48 hours.

In visual bioassays in a tube arena, *Har. axyridis* significantly chose **silhouettes** over blank spaces (Bahlai et al. 2008). As with a study on *Chil. nigritus* (Hattingh & Samways 1995), the authors interpret the finding as indicating long-range visual orientation for location of prey habitats. Another tenable explanation might be that the response to silhouettes was related to the hypsotactic orientation to hibernation sites (Chapter 6.3.1).

Olfaction

A full understanding of the olfactory response of coccinellids to their prey, particularly Sternorrhyncha, has to be based on complex studies of the chemoecological properties, not only of the phytophagous prey but also of their host plants. Chemical cues from both damaged and intact plants, and sex pheromones and alarm pheromones of the prey have to be included in research. Recent general reviews may be found in Pickett and Glinwood (2007), Hatano et al. (2008) and Pettersson et al. (2008) (also Chapter 9). In the response to combined signals there may be a high degree of **mutual synergism**, e.g. to prey plus prey waste (Bahlai et al. 2008; Table 5.39) or inhibition (e.g. inhibition of response to (*E*)-β-farnesene by the alarm pheromone inhibitor (–)-β-caryophyllene; Al Abassi et al. 2000). Thus it is not surprising that there are inconsistencies across experimental results, particularly when individual olfactory cues are studied in isolation.

Olfactory responses were detected many times in coccinellids in the late 1990s and 2000s. when **olfactometers and electroantennograms (EAG)** began to be used. However, already in the 1960s, Colburn and Asquith (1970) had found that *Stethorus punctum* adults were attracted to their prey by smell in an olfactory cage. Sengonca and Liu (1994) demonstrated in an eight-arm olfactometer that adults of *C. septempunctata* were attracted to odours of two aphid species, while the odour of a non-prey insect, *Epilachna varivestis*, was not attractive. In contrast, in a Y-tube olfactometer and a choice arena, Schaller and Nentwig (2000) did not find a positive response of *C. septempunctata* to its essential prey *Acyrthosiphon pisum* or its honeydew, while they found positive orientation to plant stimuli and of males to females. A strong odour of aphids (1000 *Myzus persicae*) stimulated female *Har. sedecimnotata*, that had been deprived of aphid prey for 30 days, to lay eggs rapidly (Semyanov & Vaghina 2001). The females of *Cycloneda sanguinea* reacted more intensively to a superior prey, *Macrosiphum euphorbiae*, than to an inferior prey, *Tetranychus evansi*, while they responded negatively to plants hosting another coccinellid *Eriopis connexa* (Sarmento et al. 2007).

In several experiments coccinellids have been found to respond to the cues emanating from **intact plants without prey**. In *Col. maculata*, the greatest EAG responses were to a plant cue, the maize volatiles alpha-terpineol and 2-phenylethanol, and to the aphid sex pheromone (4aS, 7S, 7aR)-nepetalactone (Zhu et al. 1999). The response of *Col. maculata* to maize volatiles may be related to the feeding of this species on maize pollen (J.J. Sloggett, unpublished). *Coccinella septempunctata* also responded positively in a four-arm olfactometer to the single plant volatile (Z)-jasmone. However, the response of *C. septempunctata* to a combination of cues from barley and two weeds, *Cirsium arvense* and *Elytrigia repens* was higher than to barley alone, both in the field and in an olfactometer (Birkett et al. 2000). In contrast, neither *Myzus persicae* alone, nor cabbage alone (also when dammaged mechanically) were attractive for larvae and adults of *Har.*

Table 5.40 Response of aphid predators choosing tea shoot-aphid complexes (*Toxoptera aurantii*) or blank control in a Y-tube olfactometer (modified after Han & Chen 2002).

Number of aphids/100		2	4	6	8	12	20	28	36
Number of aphid-damaged shoots		4	10	15	20	30	50	70	90
Number of natural enemies choosing odor or control									
Chrysopa sinica	Odor	10	11	12	13	13	15*	17**	19**
	Control	10	9	8	7	7	5	3	1
Coccinella septempunctata	Odor	10	12	13	14	15*	17**	18**	19**
	Control	10	8	7	6	5	3	2	1

χ^2 test is used to determine the difference between number of natural enemies choosing odor and number of choosing control.

* and ** indicate statistical significance at $P < 0.05$ and $P < 0.01$, respectively.

axyridis. Only cabbages with 60 aphids were attractive (Yoon et al. 2010).

A. bipunctata adults responded to a **combined stimulus of host plant** (*Vicia faba*) **and aphid** (*Aphis fabae*) and not to the control odour source which was the plant alone (Raymond et al. 2000). *Coccinella septempunctata* adults responded to several sources of semiochemicals related to tea aphids, *Toxoptera aurantii* (rinses of aphid cuticle, honeydew and volatiles emitted from aphid-damaged tea shoots). An increase in dose of any of the above cues decreased the EAG responses of *C. septempunctata* (Han & Chen 2002; Table 5.40).

Larvae and adults of *A. bipunctata* were attracted by crushed *A. pisum* and *M. persicae*, but not *Brevicoryne brassicae*. (*E*)-β-farnesene (EBF), the **aphid alarm pheromone**, was proved by bioassay with the pure compound to be the effective semiochemical involved in the attraction. Plant leaves alone (*V. faba*, *Brassica napus*, *Sinapis alba*) or leaves with intact aphids did not attract ladybirds. The volatile sesquiterpene EBF attracted both male and female *Har. axyridis* and elicited EAG responses (Verheggen et al. 2007). **Volatilization** of EBF was **quantified** for 60 minutes: after the initial burst it declined exponentially, but detectable amounts were still present after 30 minutes (Schwartzberg et al. 2008). The absence of attraction by *B. brassicae* has been assumed to be due to **inhibition** of the aphid **alarm pheromone** by isothiocyanates that are emitted from this aphid (Francis et al. 2004). Similar inhibition of the attractiveness of EBF, this time by (–)-β-caryophyllene, was demonstrated by Al Abassi et al. (2000). Such inhibition might explain why *B. brassicae* siphuncle droplets (containing EBF) were not attractive to *Har. axyridis* in contrast to those from *A. pisum* (Mondor & Roitberg 2000).

The phenomenon that **plants damaged** by herbivores produce **volatiles attracting their natural enemies**, originally discovered in phytophagous and predaceous acari (Dicke et al. 1990) as well as in caterpillars and their parasitoids (Turlings et al. 1990), has also been studied in ladybirds (Ninkovic et al. 2001). Significantly more methylsalicylate was released from aphid-infested than from uninfested soybean plants. In addition, (*D*)-limonene and (*E*,*E*)-α-farnesene were released. Studies coupling gas chromatography to EAG with volatile extracts from soybean plants showed that **methylsalicylate** elicited significant electrophysiological responses in *C. septempunctata*. In field tests, traps baited with methylsalicylate were highly attractive to *C. septempunctata* adults, but not to *Har. axyridis* (Zhu & Park 2005). Attraction by volatiles from a damaged host plant (sagebrush, *Artemisia tridentata*) has also been demonstrated for two further coccinellid species, *Hip. convergens* and *Brumoides septentrionis* (Karban 2007). *Aiolocaria hexaspilota*, a predator of chrysomelid larvae, also responds to volatiles (E-β-ocimene is the most abundant) from willows damaged by the larvae but not the adults of the chrysomelid (Yoneya et al. 2009). The production of volatiles depends on the severity of plant damage. Thus *Rhopalosiphum maidis*, which uses intercellular stylet penetration, does not damage plant cells of maize and this is probably why emissions of volatiles were not recorded by Turlings et al. (1998).

Volatiles can be **destroyed** by air pollutants. Common herbivore-induced plant volatiles, such as inducible terpenes and green-leaf volatiles, are completely degraded by exposure to moderately enhanced atmospheric ozone (O_3) levels (60 and 120 nl/l). However, orientation of natural enemies was not disrupted in assays of either of two tritrophic systems involving parasitoids and acarophagous acari, and a similar situation in coccinellids may be assumed. Other herbivore induced volatiles, such as a nitrile and methyl-salicylate, were not reduced by elevated O_3 and might thus replace the above less stable volatiles as attractants (Pinto et al. 2007).

General remarks on sensory orientation

After a long period in which sensory orientation of ladybirds was considered unimportant (with exceptions such as Fleschner 1950, Allen et al. 1970, Marks 1977, Obata 1986 and in the case of large ladybirds), there now seems to be a general consensus in favour of **non-contact sensory orientation**, both visual and olfactory, to conspecifics and prey, and also olfactory orientation to volatiles from prey-damaged plants (Zhu & Park 2005, Karban 2007) or even intact plants (Zhu et al. 1999, Birkett et al. 2000). An important novel observation appears to open new directions of research: this is that the **learned response** to colours recorded by Mondor & Warren 2000) may not be limited just to colours. The olfactory responses to volatiles indicate that they involve complex synergistic relations between the cues emanating from host plants and prey, but also by antagonistic relations such as between allelochemicals from plants and aphid alarm pheromone.

Agrawal (2011) considers jasmonic acid a master regulator of plant defensive responses.

An irony of research history lies with Marks' (1977) two findings and interpretations. These were not believed at the time by experienced authors, but rediscovered much later in the deposition of a chemical marker by the larval anal disc (Laubertie et al. 2006) and **perception** of the cue **by the maxillary palps** in adults (Ruzicka 2003) and larvae (Reynolds 2007, Rutledge et al. 2008).

Attempts to understand perception and processing of olfactory signals from food (and conspecifics) by coccinellids are still in their infancy. **In the field**, the volatile semiochemicals are mixed and diluted, creating a **dynamic olfactory environment**. To interpret the complex natural situation, researchers should not content themselves with only studying coccinellid literature. Studies on this topic in parasitoids are more advanced; general reviews, such as e.g. Vet and Dicke (1992), De Bruyne and Baker (2008), van Emden et al. (2008), Lei and Vickers (2008) and Riffell et al. (2008) can provide important insights for coccinellid researchers.

The notorious temporary absence of aphid prey and the frequent need to feed on alternative prey evidently worked against the evolution of the **gustatory senses** in aphidophagous and other predaceous ladybirds. This is indicated both by their inability to discriminate between suitable and toxic prey (5.2.6.1) and the low number of gustatory sensors on the palps compared to much larger number in the Epilachninae (p. 223).

5.4.1.3 Finding an oviposition site

Females foraging for prey search mostly in parallel with their search for suitable oviposition sites. Thus much of the evidence dealing with sensory orientation (5.4.1.2) is equally important when considering oviposition. The most important cue would seem to be the **amount and quality of prey** available; thus ensuring that the hatching larvae do not have to travel too far before finding aphids. Honěk (1980) ascertained the aphid density necessary for the induction of egg laying by *C. septempunctata* on several crops. However, this is not the only important factor; here there is 'a **trade-off** between two opposing risk factors: potential progeny starvation if eggs are laid **too far** from the food supply, and their potential loss to cannibalism or predation if they are laid in **too close** proximity' (Michaud & Jyoti 2007). This paper reports how *Hip. convergens* females solve that dilemma on sorghum plants infested by *Rhopalosiphum maidis* in Kansas fields. The egg clusters are typically placed on the undersides of lower, non-infested leaves and stems, some 30–50 cm distant from the aphid colonies that are higher up on the plants, in the whorl. Osawa also (1989, 2003) stressed that *Har. axyridis* females oviposit a metre distant from the nearest aphid colonies on *Prunus persica* trees. This behaviour apparently evolved under the pressure of intense predation on ladybirds near aphid colonies. Eggs of *C. magnifica*

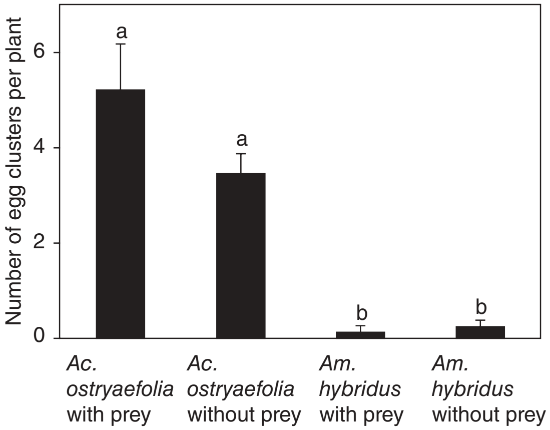

Figure 5.38 Number (±SE) of *Coleomegilla maculata* egg clusters oviposited over an 8-day period on *Acalypha ostryaefolia* and *Amaranthus hybridus* plants with and without prey (200 *Heliothis zea* eggs) added every other day. Means sharing the same letter are not significantly different (P > 0.05, Fisher protected LSD test) (from Griffin & Yeargan 2002).

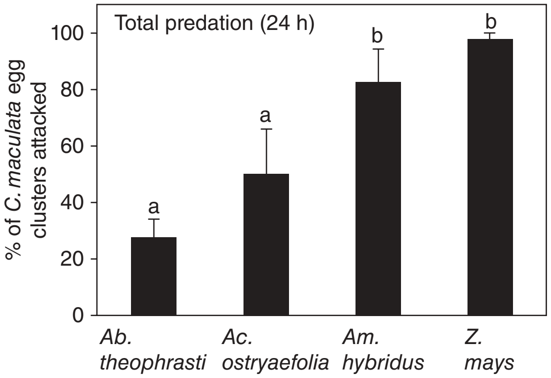

Figure 5.39 Percentage (±SE) of *Coleomegilla maculata* egg clusters attacked by predators on selected plants over a 24 hour period. Plants: *Abutilon theophrasti, Acalypha ostryaefolia, Amaranthus hybridus, Zea mays*. Means sharing the same letter are not significantly different (P > 0.05, Fisher protected LSD test) (from Griffin & Yeargan 2002).

were, however, laid as close as <10 cm from aphids (Sloggett & Majerus 2000).

Another **egg protection behaviour** reported in two tritrophic systems is the occurrence of a large number of eggs of coccinellids on **highly pubescent plants**. Higher egg predation on plants with less or no pubescence has probably selected for this oviposition preference. Although the presence of trichomes on leaves of aphid-resistant potato hinders the movement of coccinellid larvae (*C. septempunctata, C. leonina transversalis, Col. maculata, Hip. convergens*), particularly of first instars, such potato plants often harbour many eggs. Highly pubescent plants had the highest percentage of coccinellid eggs, while plants with the lowest densities of trichomes had the highest percentage of beetles. The difference was not caused by a difference in the abundance of aphids. It is possible that the eggs were more readily removed by **cannibalism on the low-pubescence plants** (Obrycki & Tauber 1984, 1985). *Coleomegilla maculata* females also prefer to lay eggs on plants with glandular trichomes of velvet leaf (*Abutilon theophrasti*) or *Acalypha ostryaefolia*, although they spent more time on smooth pigweed plants (*Amaranthus hybridus*) (Griffin & Yeargan 2002, Staley & Yeargan 2005, Seagraves & Yeargan 2006; Figs 5.38, 5.39). Almost 10 times more *Col. maculata* eggs were found on the pubescent tomato companion crop than on less pubescent maize and the eggs on tomato had 2.6–5.9 times higher survival.

Aggregation

Localized aphid densities are usually variable within fields and the predators' aggregation to patches of high aphid density has often been observed. The aggregation results during intensive search from slowed movement adopted after finding prey (5.4.1.2), and has been termed the 'aggregated numerical response' (5.3.5). This spatial dimension in predator–prey interactions has been emphasized by Kareiva and Odell (1987) and Kareiva (1990) (5.4.1.1 for details).

Age of prey colony

The adaptive significance of reduced attractiveness to predators of very old colonies seems obvious. But it is not easy to define the cues used by the ladybirds to determine colony age. On 200 *Pittosporum tobira* trees in the open, Johki et al. (1988) observed that adults of several coccinellid species were less attracted to aphid colonies which were so old that the trees were sticky with honeydew. The number of coccinellid adults increased with **increasing prey density** only until

Table 5.41 Abundance of coccinellids (mean number per tree) in relation to aphid infestation (*Toxoptera odinae*, *Aphis spiraecola*) on trees of *Pittosporum tobira* (Johki et al. 1988).

	Infestation grade*				
	0	**I**	**II**	**III**	**IV**
Harmonia axyridis	0	0.87	1.41	1.60	0.32
Coccinella septempunctata	0	0.25	0.27	0.36	0.32
Menochilus sexmaculatus	0	0.31	0.64	0.57	0.26
Propylea japonica	0	0.21	0.29	0.42	0.21
Scymnus posticalis	0	0.28	0.25	0.47	0.05
Number of trees	8	61	59	53	19

*I–III, each colony consists of a fundatrix and few young nymphs (I), of 10–20 nymphs (II), of 21–50 nymphs (III); IV,colonies extend from leaf to stem (honeydew makes the tree sticky). Kyoto, Japan, 20 May.

the colonies contained 50 nymphs (Table 5.41). It is a pity that the number of eggs laid is not given. The negative effect of the excessively high aphid infestation was strong for the small *Scymnus posticalis* and negligible for *C. septempunctata*.

In the laboratory, a significantly lower number of *Chilocorus nigritus* adults were found on *Cucurbita* fruits with high infestations of *Aspidiotus nerii* (>60 scales per cm^2) than on less heavily infested fruits (24 scales per cm^2) (Erichsen et al. 1991). Based also on earlier findings (Samways 1986) the authors assumed that the coccids become less suitable prey at such a high density. This is one of rare reports on this topic in coccidophagous ladybirds, where the decision on oviposition site is less critical due to the coccid population being much more stable in time than aphids.

Females of *C. septempunctata* laid significantly more eggs in a 4-hour period on previously uninfested 3-week old bean plants infested with immature aphids than on previously infested 2-month old plants with adult aphids (Hemptinne et al. 1993). The authors related the decrease in oviposition with the combination of older plants and older aphids (the 'old combination' of the paper) to the presence of adult aphids indicating a greater age for the aphid colony. However, the presence of adult aphids as an indication of 'risky' old colonies was not accepted by Hodek (1996, p. 214) and later the hypothesis was withdrawn (Dixon 2000, p. 128): 'aphidophagous ladybirds do not appear to use cues associated with the age structure of the aphid colony or phenological age of the plant, but respond positively to high aphid abundance'. Majerus (1994, p. 315) reported coccinellids ovipositing at old aphid colonies on nettles. In the above observations by Johki et al. (1988) and Hemptinne et al. (1993), the negative cue was probably the **excessive presence of honeydew** that can impede movement of coccinellids, particularly of small species. An adequate level of honeydew, however, does act as an arrestant (Carter & Dixon 1984; 5.4.1.2).

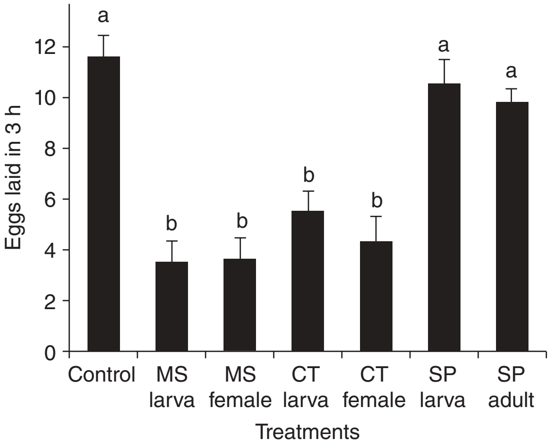

Figure 5.40 The effect of mutual sizes on deterrence. Number (±SE) of eggs laid in 3 hours (vertical axis) by *Menochilus sexmaculatus* (MS) females in interaction with larvae or adults of conspecific or heterospecific predators (horizontal axis). Same letters above bars indicate no difference between the treatments (Scheffé multiple range test, $P > 0.05$). CT, *Coccinella leonina transversalis*; SP, *Scymnus pyrocheilus* – small size (modified from Agarwala et al. 2003a, b).

Oviposition deterrence

The observation that *A. bipunctata* females did not oviposit in patches where they encountered conspecific larvae led at first to the erroneous assumption that it is **physical contact** that produces the inhibition (Hemptinne et al. 1992), although Marks (1977) had already suggested much earlier that coccinellid larvae sign the surface with chemical markers from their anal disc. Action of volatile semiochemicals was dismissed: 'Larval odour had no significant effect on ladybird oviposition' (Hemptinne et al. 1992, p. 241). More recently, Agarwala et al. (2003b; Fig. 5.40) again

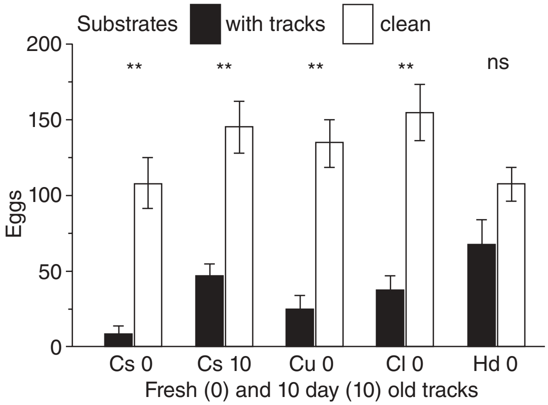

Figure 5.41 Number (±SE) of eggs laid by 10 *Menochilus sexmaculatus* females on substrates with and without larval tracks in choice tests with tracks of first instar larvae of: Cs, conspecifics; Cu, *Ceratomegilla undecimnotata*; Cl, *Cycloneda limbifer*; Hd, *Harmonia dimidiata*. (Wilcoxon paired-sample test: **, $P < 0.01$; ns, not significant) (modified from Ruzicka 2006).

experimented with **direct encounters**. *Menochilus sexmaculatus* females reduced their oviposition when exposed to immobilized conspecifics or *C. leonina transversalis* individuals, but not larvae or adults of *Scymnus pyrocheilus*; this small ladybird apparently does not represent a great risk of being an intraguild predator (Chapter 7).

The above interpretations pre-date an important discovery: crawling larvae of aphidophagous predators deposit **oviposition-deterring semiochemicals** (ODS) that **inhibit conspecific females from ovipositing**. This discovery was made both with chrysopids (Ruzicka 1994, 1996) and coccinellids (Ruzicka 1997, Doumbia et al. 1998). The lasting deterrence, based on persistent semiochemicals left in the trail, is obviously more efficient than direct encounters. The probability of inhibition is also spatially increased. The distribution of offspring among numerous prey patches certainly reduces intraspecific competition and cannibalism (Fig. 5.41).

Although, after only about 10 years of research, robust comparisons are not yet possible, the deterrence of conspecific larval tracks seems **stronger with smaller coccinellid species** (Ruzicka 2001). While also operating in *C. septempunctata*, this deterrent mechanism is weaker than in other species, e.g. *Cer. undecimnotata* (Ruzicka 2001; Table 5.42). The ODS left by coccinellid larvae also vary among species in their degree of **environmental persistence**. Whereas the residues of *Cycloneda limbifer* lasted >30 days (Ruzicka 2002), 10 days in *A. bipunctata* (Hemptinne et al. 2001), 5 days in *Cer. undecimnotata* and only 1 day in *C. septempunctata* (Ruzicka 2002). In the predator of adelgids and the green spruce aphid, *Aphidecta obliterata*, the inhibition effect of larval track density was studied simultaneously with the stimulatory effect of prey density (Oliver et al. 2006; Fig. 5.42). Oviposition deterrence depends on the physiological condition of the ovipositing female. Old females of *A. bipunctata* were less reluctant than young females to lay eggs in patches with ODS. Oviposition deterrence similarly diminishes due to continuous exposure for 15 days to an ODS contaminated paper (Frechette et al. 2004; Fig. 5.43). Intraspecific oviposition deterrence was also recorded in *Har. axyridis* females of a flightless strain on cucumbers infested with *A. gossypii*: the females moved to the control half of the greenhouse free from conspecific larvae (Gil et al. 2004).

The overall less intensive response of *C. septempunctata* females is shown by their low sensitivity to **tracks of heterospecific larvae**, for example, of *Cycloneda limbifer* (Ruzicka 2001). This may indicate that the large *C. septempunctata* is less sensitive to the risk of intraguild predation compared to smaller native coccinellids. Intraspecific oviposition deterrence was confirmed in the aggressive intraguild predator *Har. axyridis* (Chapter 7), but this species, not surprisingly, exhibited no significant response to larval tracks of *C. septempunctata* (Yasuda et al. 2000). The authors plausibly assumed that this low oviposition-deterring response reflected a low risk of predation on *Har. axyridis* eggs by *C. septempunctata*, as they observed in the field that *C. septempunctata* avoided eating *Har. axyridis* eggs.

Michaud & Jyoti (2007) studied the intensity of heterospecific oviposition deterrence in relation to **niche overlap**. On sorghum plants *Hip. convergens* responded intensively to conspecific oviposition-deterring cues. Heterospecific oviposition deterrence of *Hip. convergens* females to *Col. maculata* larval trails was weaker, evidently due to a substantial niche overlap between the two species (Figs. 5.44, 5.45). Magro et al. (2007) arrived at a contrasting conclusion on the effect of niche overlap when they recorded a strong oviposition-deterring response to heterospecific tracks in two *Adalia* species, while *C. septempunctata* females were not deterred by the tracks of both *Adalia* species. Magro

Table 5.42 Egg laying by females of *Ceratomegilla undecimnotata*, *Harmonia dimidiata*, *Cycloneda limbifer*, *Coccinella septempunctata* on clean substrates with tracks of first instar larvae in choice test (modified after Ruzicka 2001).

	Coccinellid larvae tested							
	C. limbifer		***C. undecimnotata***		***C. septempunctata***		***H. dimidiata***	
Females tested	**clean**	**tracks**	**clean**	**tracks**	**clean**	**tracks**	**clean**	**tracks**
C. limbifer								
eggs	200 (21)**	33 (13)	276 (20)**	38 (12)	174 (39) ns	151 (32)	230 (35)**	91 (33)
% eggs	86	14	88	12	56	43	73	27
C. undecimnotata								
eggs	149 (25) ns	59 (18)	180 (27)**	49 (20)	150 (21) ns	85 (17)	212 (24)**	16 (14)
% eggs	70	30	80	20	63	37	93	7
C. septempunctata								
eggs	196 (27) ns	191 (23)	167 (15) ns	205 (33)	367 (30)*	208 (32)	236 (23) ns	185 (39)
% eggs	50	50	47	53	64	36	59	41
H. dimidiata								
eggs	151 (26) ns	154 (21)	137 (22) ns	93 (26)	128 (22) ns	147 (19)	173 (22) ns	109 (27)
% eggs	49	51	61	39	46	54	63	37

Mean number per replicate (SE in brackets) and mean percentage. Ten females of each species were tested in 10 replicates. Numbers of eggs on substrates were compared with Wilcoxon paired sample test, *, $P < 0.05$; **, $P < 0.01$; ns, not significantly different ($P \geq 0.05$).

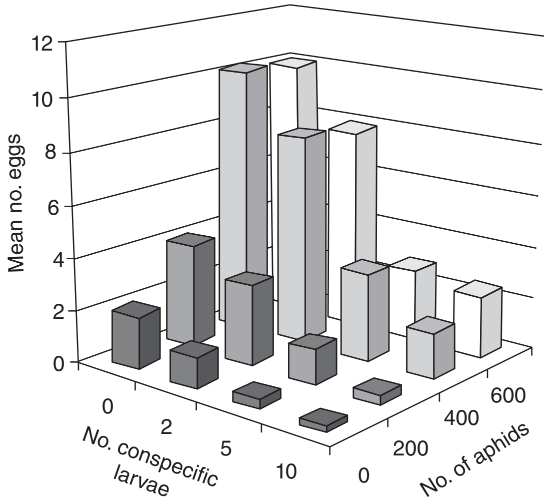

Figure 5.42 Mean number of eggs laid by *Aphidecta obliterata* females over 24 hours on filter paper substrates differentially contaminated with conspecific larval tracks made by different numbers of larvae across a range of prey densities (from Oliver et al. 2006).

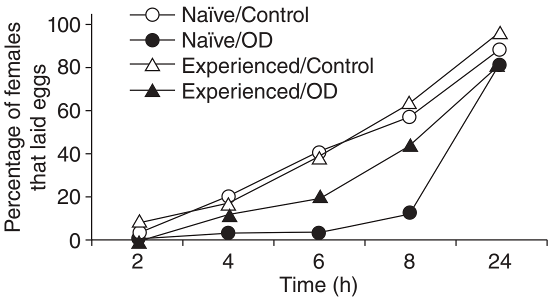

Figure 5.43 The percentage of experienced (triangles) and naïve (circles) females of *Adalia bipunctata* that laid eggs in oviposition-deterrence (OD) (black lines) and control treatments (grey lines) after 2, 4, 6, 8, and 24 hours (modified from Frechette et al. 2004).

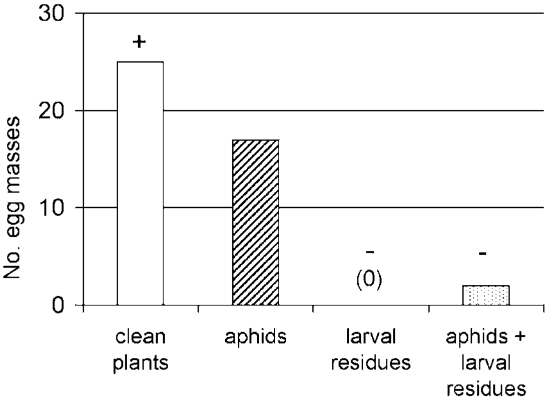

Figure 5.44 Number of egg masses laid by 38 *Hippodamia convergens* females on four types of three-leaf sorghum plants when tested individually in experimental arenas for 24–48 hours. Plant treatments: no additional stimulus (clean plants); a colony of *Schizaphis graminum*; residues of conspecific larvae (larval residues); a colony of *S. graminum* and conspecific larval residues. Plus and minus plant types, respectively, receiving significantly more or fewer egg masses than would be expected by chance if no plant type were preferred over any other (χ^2 goodness-of-fit test, $P < 0.05$) (from Michaud & Jyoti 2007).

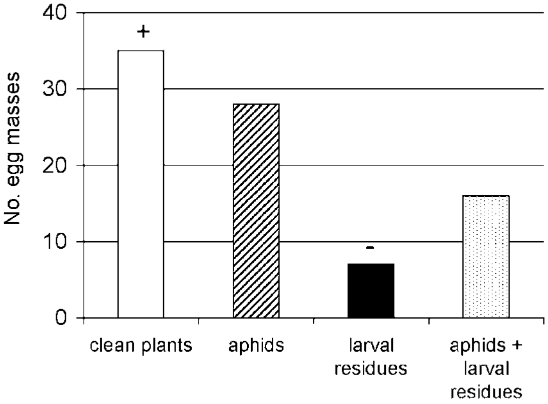

Figure 5.45 Numbers of egg masses laid by 56 *Hippodamia convergens* females on four types of three-leaf sorghum plants when tested individually in experimental arenas for 24–48 hours. Plant treatments: no additional stimulus (clean plants); a colony of *Schizaphis graminum* (aphids); residues of *Coleomegilla maculata* larvae (larval residues); a colony of *S. graminum* and *C. maculata* larval residues (aphids + larval residues). For other explanations see Fig. 5.44 (from Michaud & Jyoti 2007).

et al. (2007) assume that the three studied species do have overlapping habitats but, in fact, *A. decempunctata* and *C. septempunctata* only exceptionally share the same habitat (Majerus 1994, p. 142, Honěk 1985; also Table 5.12 and Fig. 5.16 in Hodek & Honěk 1996).

With *Menochilus sexmaculatus*, the behavioural function of the first **chemically defined ODS** was finally proved in coccinellids. A cuticular alkene, (Z)-pentacos-12-ene, was found in the chloroform extracts of first instars. It was then synthesized and its oviposition-deterring activity **proved by bioassay** (Klewer et al. 2007; Table 5.43). Several semiochemical substances were also found in *A. bipunctata* (Hemptinne et al. 2001), *A. decempunctata* and *C. septempunctata* (Magro et al. 2007), but their deterrent activity was not checked by bioassays.

Data on the **movement of females** (Ruzicka & Zemek 2003) **seemingly conflict** with Ruzicka's earlier findings (1997, 2001, 2002). However, the parameters measured here were different: not the number of eggs laid, but the **time spent on the substrates** and the distance walked on them. Females of *Cycloneda limbifer* stayed longer on a surface with conspecific tracks than on a clean surface. In contrast, they stayed less time where there were heterospecific tracks left by *Cer. undecimnotata* (Ruzicka & Zemek 2003). *Cer. undecimnotata* also spent longer on clean substrates than on those with conspecific tracks; that is, it behaved in a way similar to the oviposition-deterrence response. When number of eggs is recorded (Ruzicka 2003), *C. limbifer* shows the usual oviposition-deterrence response.

Ruzicka and Zemek (2008; Fig. 5.46) have recently documented with an automatic video tracking system that **larvae** (fourth instars of *C. limbifer*) also respond to the tracks of conspecific first instars. Inhibition of larval origin by conspecific larvae was found in *Hip. convergens* (Rutledge et al. 2008). These larval responses to larval tracks recall the old findings by Marks (1977).

Faeces of coccinellids appear to have a **similar function** as the larval tracks. Females of *Har. axyridis* and *P. japonica* reduce feeding and oviposition when exposed to conspecific larval and adult faeces or a faecal water extract. This mechanism might prevent repeated foraging on the same areas. *P. japonica* also responded to the faeces of *Har. axyridis* with the response being even stronger than that to conspecific faeces. As *P. japonica* is a potential IG prey while *Har.*

Table 5.43 Number of eggs laid by *Menochilus sexmaculatus* females on filter paper treated with a chloroform extract of conspecific first-instar larvae (*) and with different amounts of (Z)-pentacos-12-ene (+) versus solvent controls (after Klewer et al. 2007).

Concentration $\mu g/cm^2$ or larval equivalent/cm^2 (*)	Treatment	Control	Wilcoxon test
0.25*	46 ± 6.7	81.5 ± 4.7	$P = 0.002$
1.25(+)	121.5 ± 12.4	207.5 ± 10.9	$P = 0.004$
0.125(+)	105.0 ± 16.3	166.7 ± 11.0	$P = 0.006$
0.0125(+)	148.7 ± 10.4	135.9 ± 10.4	$P = 0.625$

Mean number of eggs laid in dual-choice tests with 10 replicates of 10 females. Altogether 100 individuals were tested in 10 replicates in one test. Wilcoxon paired sample test.

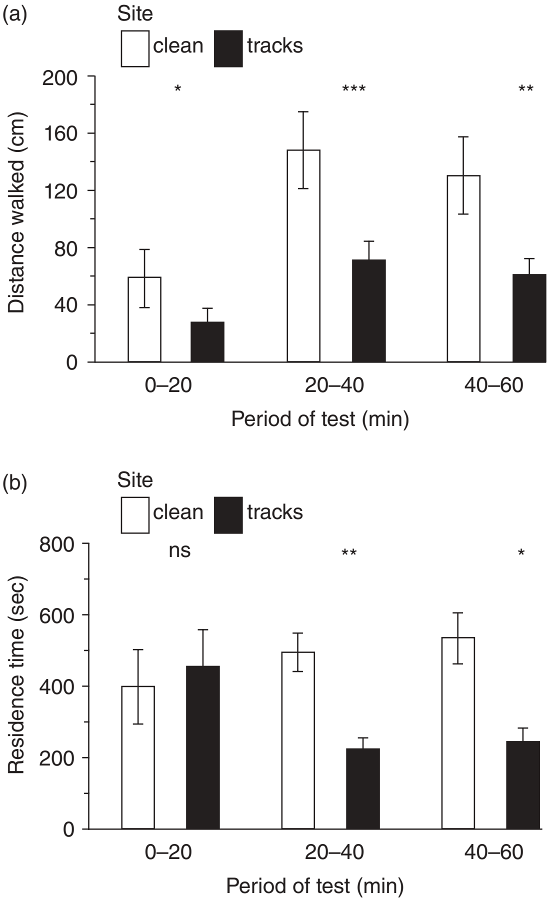

Figure 5.46 Effects of conspecific tracks of first instar *Cycloneda limbifer* on (a) the distance walked and (b) residence time of fourth instars (modified from Ruzicka & Zemek 2008).

Table 5.44 Effect of water extract of larval and adult feces of conspecifics and heterospecifics on oviposition by *Propylea japonica* and *Harmonia axyridis*; cues of the small species do not affect oviposition of *H. axyridis* (after Agarwala et al. 2003a).

Treatment by water extract of	Eggs laid after 24 hr by female (mean ± SE)	
	P. japonica	*H. axyridis*
P. japonica feces		
Adults	7.8 ± 0.95 (a)	40.5 ± 2.58 (a)
Larvae	7.3 ± 0.53 (a)	37.5 ± 2.31 (a)
H. axyridis feces		
Adults	3.7 ± 0.81 (b)	23.3 ± 2.57 (b)
Larvae	3.1 ± 0.67 (b)	21.8 ± 1.73 (b)
Water only (control)	14.8 ± 1.14 (b)	38.9 ± 2.00 (a)

Different letters in a column indicate significant difference at $P < 0.05$; Scheffé's multiple range test ($n = 10$).

axyridis a strong IG predator, the response may help *P. japonica* to avoid dangerous encounters (Agarwala et al. 2003a; Table 5.44).

Coccinellid tracks are even avoided by **parasitoids**. *Aphidius ervi* avoided the trails of *C. septempunctata* adults or fourth instars (Nakashima & Senoo 2003). The signal lost its function rather quickly, after about 18–24 hours. An OD response to **eggs**, but not larval tracks, was found in a **phytophagous** coccinellid *Henosepilachna niponica*, a specialized herbivore on *Cirsium kagamontanum* (Ohgushi & Sawada 1985).

The discovery of OD caused by conspecific larval tracks (Ruzicka 1994, 1997) makes the scenario likely that an aphid patch becomes – after a certain delay of time – unsuitable for ovipositing females due to a **critical density of larval tracks** from an earlier oviposition.

In a hypothetical concept Kindlmann and Dixon (1993) expressed a general assumption that 'the coccinellids should lay a few eggs early in the development of an aphid colony'. The authors rightly mention that their model is relevant only for isolated aphid patches, escape from which might br dangerous for the larvae because of long distance to alternative patches, (i.e. 'when no other aphid colonies are available', in Kindlmann and Dixon 1993, p. 448). In most situations, however, the larvae can reach another food resource; even just emerged first instar larvae may walk without prey for 1.0–1.5 days (Banks 1957). Ruzicka's (1994) discovery of oviposition deterrence was incorporated into the concept that closing of the period suitable for oviposition ends due to 'the adults' response to the tracks left by conspecific larvae' (Dixon 2000, p. 106).

Coccinellid species often have specific preferences for certain microhabitats or **vegetation strata** and this affects their choice of oviposition sites. Thus *Col. maculata*, which prefers more shaded and more humid environments and feeds on maize pollen that has fallen onto the lower leaf axils (Ewert & Chiang 1966, Foott 1973), deposits all its eggs on lower leaves of the maize, while *C. septempunctata* and *Hip. tredecimpunctata* lay about one-third of their eggs on upper leaves (Coderre & Tourneur 1986). The location of the egg batches may also be affected by **temperature preferences**; thus in early spring *C. septempunctata* prefer the warm lower parts of wheat plants (Honěk 1979, 1983). Sometimes the eggs are laid in unexpected places. Females sometimes avoid the growing parts of the plants, which are usually the most aphid-infested, and instead oviposit in places unsuitable for the hatching larvae, e.g. on the **soil or stones** (Ferran et al. 1989). In the mild winter of central Honshu, pupae and/or eggs of *C. s. brucki* were found in directly insolated but unusual microhabitats such as metal cans or paper and wooden material on sites exposed to solar radiation (Ohashi et al. 2005).

5.4.1.4 Foraging of first instars

It has been suggested that egg size is constrained by the need to assure energetic reserves for the neonate larvae (Stewart et al. 1991). Osawa (2003) questions this premise with the alternative suggestion that newly hatched larvae get energy by eating conspecific eggs. Sloggett and Lorenz (2008) suggested that **egg nutrient content** rather than egg size is the most important means of parental provision of energetic reserves. They compared three ladybird species (*A. bipunctata*, *A. decempunctata*, *Anisosticta novemdecimpunctata*) that exhibited a decrease in egg mass as food specialisation increased. As the more specialised ladybirds can persist at lower aphid densities than generalists (Sloggett & Majerus 2000, Sloggett 2008b), it would appear that the more specialized ladybirds in this comparison are not provisioned adequately for foraging at low prey density. However, analysis of the eggs showed that the smaller eggs of *A. novemdecimpunctata* contained relatively more **lipid and glycogen**, and are thus actually the richer in energy (Sloggett & Lorenz 2008). A part of the lipid remains in the larva as an energy source.

Before moving on to the following section on the stresses of neonate larvae, we draw the reader's attention to sections 5.2.8 and 8.4.5.2.

Newly hatched first instars risk heavy mortality when searching for prey when it is at a very low prey density. The first instar larvae of aphidophagous ladybirds spend some time on the empty eggshells (Banks, 1957, reported 12–24 hours for *P. quatuordecimpunctata*) and eventually indulge in cannibalism. Then they can maintain their active search for prey for 25–35 hours before becoming inactive due to exhaustion. Therefore, they need to find food within 1.0–1.5 days (Table 5.34, p. 217). Ng (1988) reported similar evidence, quoting a survival range of 15–32 hours for several species.

Sibling cannibalism on eggs of the same clutch usually prolongs survival (5.2.8) and the searching capacity of newly hatched larvae. The consumption of just a single egg nearly doubled the survival of the first instars (Banks 1954, species not given). Significantly increased survival of first instar larvae after feeding on sibling eggs that hatch late, are unfertilized or killed by microorganisms (Chapter 8.4), was also later recorded in other species (see Hodek 1996). Hurst and Majerus (1993) reported not only an increased survival (by 75%), but also an increased speed of movement in neonate larvae of *A. bipunctata* after eating an egg. First instar *Cheilomenes lunata* moulted to the second instar after eating only two eggs (Brown 1972). This was achieved in *A. bipunctata* (Banks 1956), and in *Har. axyridis* (Osawa 1992b) after eating three eggs.

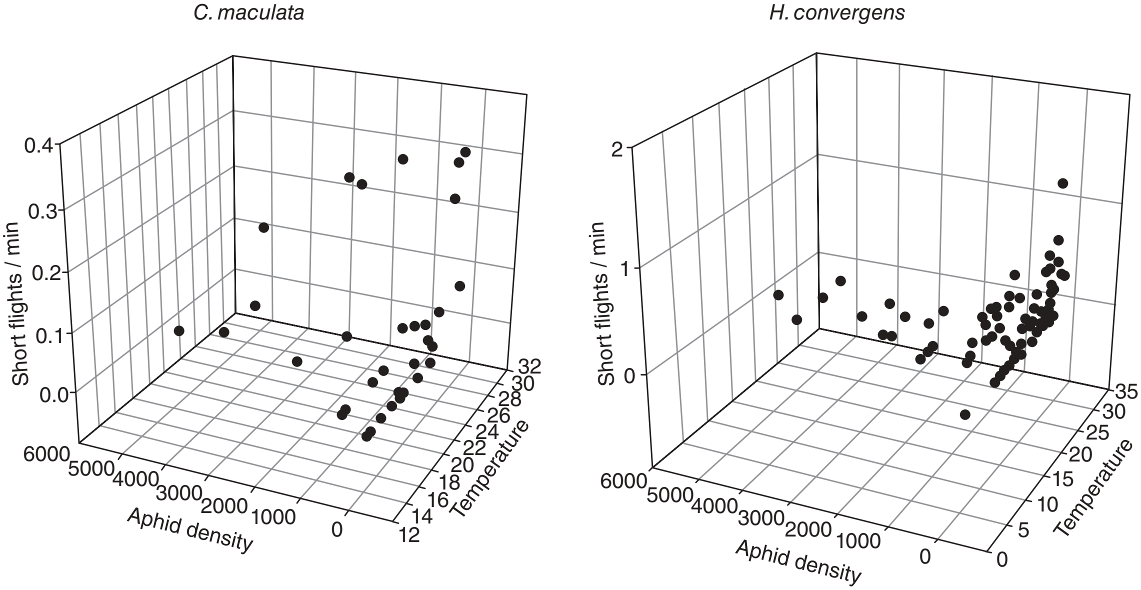

Figure 5.47 The frequency of short (<2 m) flights (number of flights/min.) by *Coleomegilla maculata* and *Hippodamia convergens* in relation to ambient temperature (°C) and cereal aphid density. Note differences in scales of the vertical axes (modified from Elliott et al. 2000).

5.4.1.5 Movement among habitats/patches in the landscape

After small scale foraging (e.g. at the level of the individual plant) discussed above, we now discuss **larger scale foraging**. Highly mobile coccinellid generalists range widely and feed and reproduce in many habitats. When a prey patch becomes unsuitable for oviposition, the females search for other favourable patches; their offspring are thus widely scattered. Dispersion is aided by the deterrent effect on oviposition of larval tracks (5.4.1.3), preventing clumping of pre-imaginal stages in the richest patches of prey and reducing intraspecific competition.

Interspecific differences in vagility were noted by Elliott et al. (1998, 2000; Fig. 5.47), who observed that the more vagile *C. septempunctata* and *Hip. convergens* were more affected by broader scale variation in landscape structure than the less vagile *Col. maculata* and *Hip. parenthesis* (see also Brewer & Elliott 2004). Evans (2004) reported that, in alfalfa fields, *C. septempunctata* females are more abundant when *Acyrthosiphon pisum* populations are low than are native ladybird species. Snyder et al. (2004) suggested that such an early arrival of *C. septempunctata* to developing aphid colonies, and their earlier oviposition there, gave larvae a size advantage over the later-developing offspring of native species.

Habitat features (Chapter 4) can reduce the success of ladybirds in locating incipient outbreaks of prey. Kareiva (1987), for example, found that **habitat fragmentation** impaired the searching ability of *C. septempunctata* adults foraging in experimental arrays of goldenrod, with isolated aphid populations. The ability of ladybirds to discover localized prey populations reflects effective resource tracking, brought about by constant movement of individuals between host plants as shown for *Har. axyridis* (Osawa 2000). Building on Kareiva's (1987) results, With et al. (2002) found that adults of *Har. axyridis* tracked aphid population dynamics more effectively than did adults of *Col. maculata* within and across experimentally fragmented landscapes with 10–80% cover of red clover planted in clumped or fragmented fashion. Grez et al. (2005, 2008) assessed and distinguished between the effects of habitat loss and habitat fragmentation on population levels of ladybirds and aphids in differently fragmented plots of alfalfa.

The **use of alternative habitats** by *C. septempunctata* was followed in detail over two seasons in Michigan, USA, by Maredia et al. (1992). A diverse agroecosystem, composed of a mosaic of habitats, supported *C. septempunctata* from late April till late August, with the coccinellid feeding on various aphid species on annual and perennial crops (wheat, maize, soybean and alfalfa), poplar and weeds. The ability of ladybirds to track prey populations through space and time can lead to rapid large-scale changes in resource use by a species, as in the colonization of orchards by *Olla v-nigrum* following the invasion of the citrus psyllid in Florida (Michaud 2001). In northern Italy, Burgio et al. (2006) observed seasonal movements of *Hip. variegata, C. septempunctata* and *P. quatuordecimpunctata* among arable crops, fallow, vegetable crops and weedy field margins.

Immigration/emigration

A heterogeneous landscape presents a mosaic of potential patches within which highly mobile coccinellid adults can select those that are suitable. The **initial discovery** by predators of local prey populations of low density is intriguing. When such responses are rapid and strong, ladybirds may be effective in preventing large-scale outbreaks of their prey (Frazer et al. 1981). Field experiments reveal that small, highly localized populations of mites and aphids can be quickly discovered and reduced in size by ladybirds (Frazer et al. 1981, Congdon et al. 1993, Evans 2004). Evidence is still lacking with respect to the sensory cues employed by **flying** coccinellid **adults** to **locate profitable patches**. There are records of adult olfactory responses to aphids at short distances, but these cues have not yet been checked as long-distance attractants (5.4.1.2). Visual cues (e.g. host discolouration from aphid damage) might act over longer distances (e.g. Lorenzetti et al. 1997). Generally, long-distance searching behaviour of ladybirds needs further intensive investigation.

Many workers have suggested that immigration rates of ladybirds are independent of local prey density (Ives et al. 1993, Osawa 2000, van der Werf et al. 2000, Cardinale et al. 2006). In the study by Cardinale et al. (2006), immigration rates of adult *C. septempunctata, Col. maculata* and *Har. axyridis* were independent of aphid density in adjacent 1 m^2 plots. Flying adults arrive in patches at random and then make decisions to stay or leave based on the presence or abundance of prey, as well as signals left by conspecific larvae (5.4.1.3). Frazer (1988) estimated that as many as 50% of ladybirds emigrate from a patch every day only to be replaced by immigrants. Thus the abundance of adult coccinellids in a patch reflects the net balance between rates of immigration and emigration. Empirical evidence indicates that there is greater **emigration** from patches of lower quality than from patches of higher quality (Kareiva 1990). When placed on individual potted plants in the laboratory, adults of *C. septempunctata* varied in how long they remained before leaving, depending on the number of aphids present (Minoretti & Weisser 2000). In a diversified garden, Osawa (2000) found that marked adults of *Har. axyridis* tended to stay longer at sites with greater numbers of aphids. The rate of emigration from an alfalfa field was particularly high in one of three mark–recapture experiments in which the resident aphid density was especially low (van der Werf et al. 2000). On a smaller spatial scale, Cardinale et al. (2006) used visual censuses to measure emigration rates of adults from patches of alfalfa with one of three aphid densities. Emigration rates of *C. septempunctata* and *Col. maculata* (but not *Har. axyridis*) increased with decreasing aphid density among patches. In a **model**, based on empirical data on dispersal of aphidophagous coccinellids, the best fit for three scenarios was the one including unconditional immigration rates (Krivan 2008; 5.3.5). Detailed studies on the emigration of ladybirds are warranted and should focus on the levels of adult satiation, as suggested by Evans (2003).

Foraging over landscape in swarms

In spite of behavioural traits predicted by the optimal foraging theory (5.4.1), in order to keep the abundance of progeny within the limits of optimal fitness, coccinellids can exhibit population explosions resulting in travelling swarms of young 'hungry' beetles. The 'swarming' beetles may ultimately get into lakes or sea, are then washed up and form aggregations on beaches (Klausnitzer 1989, Isard et al. 2001, Denemark & Losey 2010). Although the ladybird 'swarming' is not yet fully understood, it has been recorded many times and described in reviews and books (e.g. Hagen 1962, Hodek 1973, p. 82, Hodek et al. 1993, Majerus 1994, p. 186, Majerus & Majerus 1996, Nalepa et al. 1998, Turnock & Wise 2004). The species often described as behaving in this manner is *C. septempunctata*. In Surrey, UK, Majerus (1994) recorded densities of over 1000 pupae of *C. septempunctata* per square metre in a nettle patch. There were 126 individuals on a single nettle stem. For *Hip. convergens,* Dickson et al. (1955) estimated 54,000 individuals per 0.4 ha of alfalfa. In some years, when coccinellids emerge from their pupae, aphids are scarce, having already been consumed by them as larvae or by other aphidophaga. The deteriorating physiological state of host plants, emigration of aphids and their infestation by fungi also play a role in the disappearance of aphids.

This phenomenon has rarely been reported in other than aphidophagous coccinellids. The tendency towards the 'risky' overproduction of progeny, particularly in *C. septempunctata*, has not been out-selected, although it seems to work against the constraints and models of an 'optimal' strategy. The idea that overpopulation is a 'suboptimal behaviour' leading to 'low numbers the following year' (Kindlmann & Dixon 1993) is not in concert with observations. There is no evidence that fewer adults enter dormancy in years of population explosion.

Maximum reproductive potential is realized in spite of the risk that a great proportion of the offspring is lost. This might be a result of the evolutionary trade-off between such loss and the fact that individual parents thereby increase the probability of random survival of their offspring. Evidently enough individuals originating from a population explosion survive to reproduce the next spring and perpetuate this life-history trait. Perhaps this feature is one reason why *C. septempunctata* has proved to be an exceptionally successful competitor during the rapid expansion of its distribution area in the Nearctic region (Krafsur et al. 2005, Snyder & Evans 2006, Frank & McCoy 2007, Harmon et al. 2007) from the Atlantic to the Pacific coast.

5.4.1.6 Ladybird foraging and ants

Many species of ants attend honeydew-producing Sternorrhyncha (see also Chapter 8.1.4). Early observations and experiments showing that attendant ants are hostile to enemies (including Coccinellidae) of Sternorrhyncha are summarized by Nixon (1951) and particularly by Way (1963). Nixon supposed that the ants do not protect the honeydew producers actively as a source of food, but merely incidentally. Way (1963) suggested that the ants are **aggressive towards intruders** on their food sources, but that intruders are tolerated away from the food source. From a study of a colony of *Aphis fabae* on *Cirsium arvense* tended by *Myrmica ruginodis*, Jiggins et al. (1993) also concluded that the ants vigorously **defend the aphid colony** against coccinellids that are in the colony or nearby. *Lasius niger* workers are not hostile to coccinellid adults that they meet away from attended aphids (Bhatkar 1982). Thus, the protection given by ants to Sternorrhyncha is related to their value as a food source.

Defence provided by attendant **ants** can **nullify the effectiveness** of aphid predators (Powell & Silverman 2010). In laboratory experiments, *Aphis gossypii* was tended by the red imported fire ant, *Solenopsis invicta*, which was killing both adults and larvae of *Hip. convergens*, and also larval chrysopids and syrphids (Vinson & Scarborough 1989). A project of inundative biological control of aphids (*Brachycaudus persicae, B. prunicola, Hyalopterus pruni, Myzus persicae*) in peach orchards by *Adalia bipunctata* larvae was impaired by ants (*Lasius niger, Formica rufibarbis*) until the latter were excluded from the trees by glue bands (Kreiter & Iperti 1986). Ants may kill both adult and larval coccinellids (Sloggett et al. 1999). Even the wax-producing larvae of *Cryptognatha nodiceps, Pseudoazya trinitatis* and *Zagloba aeneipennis* were eaten by several species of ant attending the coccid *Aspidiotus destructor* in the New Hebrides (Cochereau 1969). However, the specific wax with ultraviolet reflectiveness (unique in Coccinellidae) does protect pupae of *Apolinus lividigaster* (Richards 1980). *Scymnus* larvae with experimentally removed wax cover were more vulnerable to the attacks by carabids and ants, while the wax cover did not influence cannibalism or interspecific coccinellid predation (Voelkl & Vohland 1996).

Larvae of *C. septempunctata* had a higher predation rate on *Aphis craccivora* than on *Acyrthosiphon pisum* when neither was guarded by ants. *A. pisum* is a non-tended aphid, while *A. craccivora* is facultatively ant-tended. The difference in foraging efficiency of ladybirds on these two aphids can be explained by aphid behaviour (Table 5.45). In the non-protected *A. pisum* dropping off from plants has evolved as a response to alarm pheromone. This predator-avoidance behaviour decreases the efficiency of foraging coccinellid larvae. When *A. craccivora* was guarded by ants, the predation by *C. septempunctata* larvae was much lower than in absence of the ants (Suzuki & Ide 2008). An increase in coccinellid populations (mainly *A. decempunctata* and *Scymnus interruptus*) was observed in citrus trees infested by *Aphis spiraecola* (Piñol et al. 2009).

Table 5.45 Behaviour of *Coccinella septempunctata* larvae and two species of aphids on *Vicia faba* as affected by ants (*Lasius japonicus*) (modified after Suzuki & Ide 2008).

	In the absence of ants				In the presence of ants		
	Aphis craccivora		*Acyrthosiphon pisum*		*Aphis craccivora*		
Parameters of behaviour	***n***	**Mean**	***n***	**Mean**	***n***	**Mean**	***P****
Aphids attacked (*n* per hr)	20	14.09 a	20	14.97 a	100	5.70 b	<0.0001
Predation success rate	20	0.98 a	20	0.74 b	81	0.81 ab	0.0001
Aphids eaten (*n* per hr)	20	13.74 a	20	10.98 b	100	4.22 c	<0.0001
Aphids escaped by dropping (*n* per hr)	20	9.36 a	20	59.05 b	100	6.50 a	<0.0001
Aphids escaped by walking (*n* per hr)	20	12.86 a	20	2.26 b	100	4.18 c	<0.0001
Resident time on plant (s)	20	7942.80 a	20	3500.60 b	100	1438.20 c	<0.0001

*Kruskal-Wallis test.

Values followed by different letters indicate significant differences (Mann-Whitney U-test with Bonferroni adjustments for multiple tests, $P < 0.0167$), (values of SE omitted).

The predation rate of the myrmecophilous coccinellid *Azya orbigera*, an important predator of the green coffee scale *Coccus viridis*, is not decreased in the presence of the mutualistic ant *Azteca instabilis*. Furthermore, the ant showed aggressive behaviour toward *A. orbigera*'s parasitoids and its presence effectively decreased the parasitisation (Liere & Perfecto 2008). Similar behaviour was observed in *Platynaspis luteorubra* (Voelkl 1995).

It is generally assumed that the Argentine ant, *Linepithema humile*, tends honeydew-excreting scale insects and its presence impacts negatively on natural enemies. This was analysed by exclusion experiments in Californian vineyards infested by the mealybugs *Pseudococcus maritimus* and *Pseudococcus viburni*. Argentine ants, however, increased the density of the ladybird *Cryptolaemus montrouzieri* (Table 5.46). The ants also increased the population density of mealybugs, but not by disrupting the activity of natural enemies. The effect was rather due to the removal of honeydew; when ants did not remove the honeydew, mealybug crawlers became trapped in it. The larvae of *C. montrouzieri*, which resemble mealybugs by also being covered with wax, successfully mimic mealybugs to avoid detection by ants (Daane et al. 2007).

Ant protection of trophobionts may be ineffective against specialized predators (including coccinellids) that circumvent attack by trophobiont-tending ants. The profiles of three aphid predators' cuticular hydrocarbons (CHCs) are strikingly convergent to those of ant-attended aphids, while the CHC profiles of ants are different. Chemically mimicking the CHCs of prey allows the predators to avoid detection both by the aphids and by tending ants (Lohman et al. 2006). Larvae of *Platynaspis luteorubra* also mimic the CHCs of prey aphids (cited by Majerus et al. 2007).

When tending the soybean aphid *Aphis glycines*, the ant *Monomorium minimum* was observed harassing or killing *Har. axyridis* and an anthocorid. Ant-attendance resulted in reduced predation and increased

Table 5.46 Density per vine per sample of Argentine ants, obscure mealybugs (MB), and mealybug destroyer on vines in ant-exclusion and ant-tended treatments in two vineyards in the Californian Central Coast wine grape region (modified after Daane et al. 2007).

Vineyard	**Insect**	**Ant-tended**	**Ant-excluded**
A	Argentine ant*	33.8 ± 7.4	0
	Obscure MB†	303.2 ± 45.8	11.8 ± 4.1
	MB destroyer‡	0.31 ± 0.09	0.07 ± 0.04
B	Argentine ant	38.6 ± 7.0	0.4 ± 0.3
	Obscure MB	129.2 ± 20.5	59.2 ± 11.7
	MB destroyer	0.29 ± 0.09	0.09 ± 0.05

**Linepithema humile.*

†*Pseudococcus viburni.*

‡*Cryptolaemus montrouzieri.*

aphid numbers up to 10-fold. Coccinellid adults were attacked by ants immediately, while the larvae were not attacked until direct physical contact had occurred (Herbert & Horn 2008). Small colonies of *Aphis craccivora* were less preyed upon by *C. septempunctata* when the host plant had extrafloral nectaries that attracted the aphid-attending ants (Katayama & Suzuki 2010).

5.4.2 Prey capture

When an encounter betwen a coccinellid and a prey occurs, the coccinellid may fail to capture and feed on the latter. This aspect of predator–prey relationships may be of paramount importance for the impact of the predator (Varley & Gradwell 1970), but has not yet attracted enough attention.

Although **aphids** are generally considered to be completely 'helpless' (Imms 1947), their **defensive and escape behaviour** may actually be quite efficient. Several authors have studied such responses of aphids towards two *Adalia* spp., both larvae and adults of *A. decempunctata* (Dixon 1958, 1959), and larvae of *A. bipunctata* (Klingauf 1967, Wratten 1976). Stadler (1991) compared such behaviour within the genus *Uroleucon* (Fig. 5.48). The **aphids** show various **defence** responses, e.g. kicking movements, movements of the body, pulling free the appendage seized by the coccinellid and 'waxing' the coccinellid with an oily liquid appearing on the tip of the siphunculi. Moreover, the aphids may **escape** by walking away or dropping off the plant (Prasad & Snyder 2010). The intensity of the aphid response varies with the stage of the predator; thus *A. decempunctata* adults induce escape rather than defence in *Microlophium carnosum* (Dixon 1959). The success or failure of a predator to **capture the prey** depends on their relative sizes. Older larvae of *A. bipunctata* (9 mm long) succeed in capturing 90–100% of first instar and about 60–70% of adult *Myzus persicae* or *Neomyzus circumflexus*, but only 0–50% of the much larger *Acyrthosiphon pisum* (Klingauf 1967). Aphids with long appendages are more difficult for *Hip. quinquesignata* larvae to capture than are more compact aphids with short appendages (Kaddou 1960).

The suitability of an aphid species as prey for *A. bipunctata* was strongly determined by capture efficiency (Mills 1979). The latter amounted to 58% for the most suitable prey, *Eucallipterus tiliae*, but only to 21% for the least suitable *Drepanosiphum platanoidis*. The level of predation by *A. bipunctata* larvae on three birch aphid species was also dependent upon aphid behaviour (Hajek & Dahlsten 1987). The long-legged *Euceraphis betulae*, the most successful escapee, was highly mobile and frequently walked

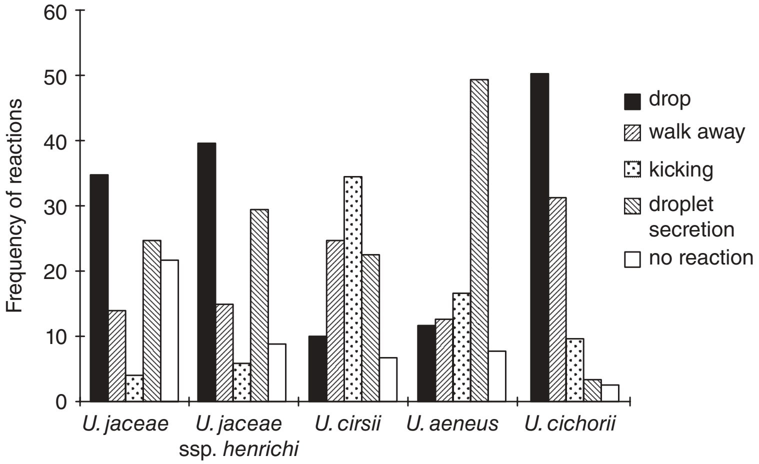

Figure 5.48 Relative frequency of defence and escape reactions of different *Uroleucon* species to attacks by *Coccinella septempunctata* larvae. Reactions are arranged according to the defence value for the aphids (drop > walk away > kicking > droplet secretion > no reaction) (from Stadler 1991).

Table 5.47 Results of encounters between three species of birch aphids, *Betulaphis brevipilosa*, *Callipterinella calliptera*, *Euceraphis betulae* and larvae of *Adalia bipunctata* (Hajek & Dahlsten 1987).

	Aphid species	Total encounters	% captures	% active escapes	% passive escapes	% aphid winning over coccinellid
			L1 *Adalia bipunctata*			
L1	*B. brevipilosa*	33	60.6	0.0	39.4	0.0
L4	*B. brevipilosa*	56	35.7	8.9	55.4	0.0
L1	*C. calliptera*	51	39.2	41.2	19.6	0.0
L4	*C. calliptera*	214*	8.4	71.5	20.1	0.0
L1	*E. betulae*	216*	6.9	75.5	0.0	17.6
L4	*E. betulae*	260*	0.0	71.5	0.0	28.5[†]
			L4 *Adalia bipunctata*			
L1	*B. brevipilosa*	65	30.8	1.5	67.7	0.0
L4	*B. brevipilosa*	38	52.6	0.0	47.4	0.0
L1	*C. calliptera*	33	60.6	9.1	30.3	0.0
L4	*C. calliptera*	66*	30.3	60.6	9.1	0.0
L1	*E. betulae*	104*	19.2	78.8	1.0	1.0
L4	*E. betulae*	375*	1.9	82.6	0.0	15.5

*The numbers of encounters were increased for these mobile aphids.

[†] A leg or rostrum of L4 *E. betulae* was often grasped by L1 *A. bipunctata*. The coccinellid did not hold the prey long before the aphid simply pulled away with no evidence of impairment.

away from the predator. In contrast *Betulaphis brevipilosa*, a flat and sessile species, was the least successful active escapee, but often passively escaped detection (Table 5.47).

Wratten (1976) stressed the importance of the direction of the predator's approach to the prey, *Eucallipterus tiliae*. The larvae of *A. bipunctata* achieved the highest contact rate when they approached fourth instars from the rear, suggesting that aphid vision is important in predator avoidance. Earlier, it was supposed that the escape response of aphids resulted from their **visual ability**. According to Klingauf (1967), *A. pisum* perceives the predator at a distance of 4–10 mm, while some predators perceive the prey only by contact. This time advantage for the prey can be used for escape. However, the ability to perceive the prey at a short distance (7–10 mm) has now been found in several aphidophagous coccinellid species (5.4.1.2) and consequently the above explanation of successful escape by aphids has partly lost its plausibility. An aphid may gain time when a small coccinellid larva at first shows a fright response and only attacks the prey after a delay (Baensch 1964). The intensity of the fright response depends on the size of the prey and is suppressed by learning once several prey have been captured (Baensch 1964, Klingauf 1967).

Another efficient escape/defence mechanism is the secretion of **alarm pheromone** (5.4.1.2) by attacked aphids (early numerous references in Hodek 1996). Most authors worked with the aphid *A. pisum*, which easily drops off plants when disturbed. *A. bipunctata* adults forage more vigorously at higher temperatures and this producei greater vibrations and a high rate of aphid dropping behaviour. Pea aphids react to vibrations which enhance their responsiveness to later alarm pheromone stimuli (Clegg & Barlow 1982, Brodsky & Barlow 1986).

Of the aphid species tested for an alarm pheromone response, *Schizaphis graminum* has been the most sensitive. In field tests on sorghum plants, *S. graminum* adults and larvae were dislodged five and four times more often, respectively, than they were consumed by *C. septempunctata* adults (McConnell & Kring 1990; Table 5.48). The ratio between disturbed and consumed aphids is species-specific. In *A. pisum*, this ratio is 30:1, while in *Aphis gossypii* it is only 1:14. The level of disturbance is also coccinellid-specific. Thus *A. bipunctata* causes little disturbance and so the

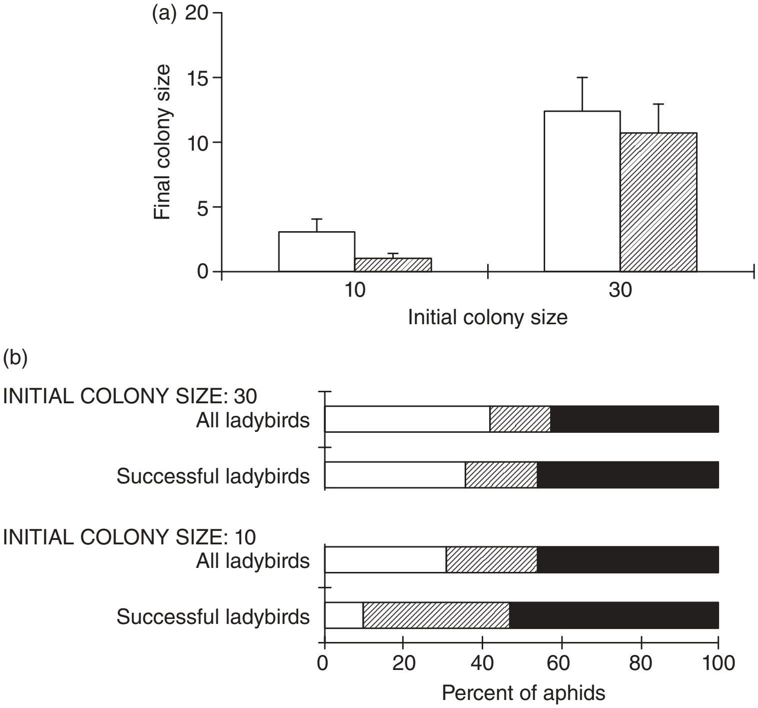

Figure 5.49 Fate of *Acyrthosiphon pisum* on bean plants after visit of a single *Coccinella septempunctata* adult, as affected by initial size of the aphid colony ($n = 9$–11). (a) Number of aphids remaining on the plants at the end of the experiments; open bars, all replicates; hatched bars, only replicates in which ladybirds killed at least one aphid. (b) Aphids eaten (hatched); emigrated from the host plant, i.e. dislodged (black); remaining on the plant (open) (from Minoretti & Weisser 2000).

Table 5.48 Number of aphids consumed and dislodged by *Coccinella septempunctata* in laboratory and field tests (mean ± SEM) (McConnell & Kring 1990).

Aphid stage	Consumed	Dislodged
Laboratory		
Adults	6.7 ± 0.4	12.0 ± 1.0
Nymphs	26.9 ± 2.2	34.8 ± 2.9
Field		
Adults	6.7 ± 0.4	33.7 ± 2.6
Nymphs	8.9 ± 0.6	35.6 ± 2.6

percentage of prey consumed is high (28:72 and 19:81) whereas in *C. septempunctata* the proportion of disturbed aphids dominates (94:6 for *A. pisum* and 82:18 for *Schizaphis graminum*) (Nelson & Rosenheim 2006). The ratio of aphids disturbed to aphids consumed also depends on the size of their colonies (Minoretti & Weisser 2000; Fig. 5.49).

Predation by *Har. axyridis* on *A. pisum* was reduced by approximately 40% by aphids dropping (Francke et al. 2008). The ratio between aphid dropping and aphid consumption is correlated with the predator's stage of development and its rate of movement. *Har. axyridis* daubed with aphid pheromone droplets cause a greater proportion of aphids to drop off a plant (Mondor & Roitberg 2004).

Dispersal of dropping pea aphids, caused by adult coccinellids (*C. californica*), may have a negative effect on crops by spreading plant viruses (Roitberg & Myers 1978, Roitberg et al. 1979).

When the host plants of aphids are infected by **endophytic fungi** the production of winged aphids, as a response to predator (*A. bipunctata* larvae) threat, is decreased (Zuest et al. 2008).

Some aphids, e.g. *Ceratovacuna* and *Pseudoregma* spp., produce sterile **soldiers** that **attack aphid predators** (Aoki et al. 1981, Arakaki 1992b, c; also Chapter 8.1.5). *Sasajiscymnus kurohime* is a specialized predator of such aphids, successfully attacking the sugar cane woolly aphid, *Ceratovacuna lanigera*, in spite of its soldier-like first instars that defend the colony. This is because the coccinellid larvae can move among the woolly aphids without eliciting an escape response from them. Only 7.5–12.9% of the aphids secreted alarm pheromone when attacked by larvae of *S. kurohime*, while the figure was 82.5% for attack by adults. It is assumed that the coccinellid larva is protected by its waxy covering, similar to that of the aphid (Arakaki 1992b, c). However, chemical mimicry may be more likely (J.J. Sloggett, unpublished), similar to the case described by Daane et al. (2007; 5.4.1.6).

In addition to defensive movements the aphids use also **chemo-mechanical defences**. Early on, Palmer (1914) reported that large aphids of the genus *Macrosiphum* smear the mouthparts of *Hip. convergens* with a glue excreted from the siphunculi and thus cause starvation of the coccinellid. This defence seems successful only at low temperatures; at higher temperatures the coccinellids can ingest the glue. A similar defence mechanism was reported in *Hyalopterus pruni* against *A. bipunctata* (Hawkes 1920). The monophagous aphid, *Aulacorthum nipponicum*, feeding exclusively on *Paederia foetida*, is seldom attacked by coccinellids. Biting into the aphid is immediately followed by dropping the prey, salivating and by a persistent grooming of mouthparts. The droplets on the tip of the siphunculi contain a potent **deterrent**, an iridoid glycoside **paederoside**, originating from the host plant (Nishida & Fukami 1989).

5.4.3 Food intake

The epilachnine **phyllophagous** coccinellids scrape the parenchyma off the leaves and suck it out, imbibing only fluid. The sucked-out parenchyma remains on the leaf, leaving a characteristic feeding pattern (Butt 1951, Klausnitzer 1965). The **pollinivorous** and **mycophagous** larva of *Tytthaspis sedecimpunctata* uses a comb-like mandible to collect pollen and spores (Ricci 1982; Fig. 5.42, 5.2.9).

The food of **aphidophagous** coccinellids mostly consists not only of the sucked body fluid of aphids, but also frequently solid parts of the aphid body, such as legs, antennae, etc. (Butt 1951, Triltsch 1999). The type of feeding depends on the comparative size of prey and predator. When the prey is too large, it is merely sucked out and the skin with appendages is discarded (Butt 1951, Harpaz 1958, Hagen 1962, Kesten 1969). This type of feeding behaviour is normal in younger larvae (first and second instar). Older larvae and adults may consume smaller prey completely (Butt 1951, Hagen 1962, Kesten 1969, Triltsch 1999).

Most coccinellids, particularly when larvae, show **extra-intestinal digestion** (extra-oral digestion of Richards & Goletsos 1991); they periodically regurgitate fluid from the gut into the chewed prey and suck back the pre-digested food. Some coccinellid larvae even perform extra-intestinal digestion through their **sucking mandibles**, as do the larvae of *Dytiscus*, *Chrysopa*, etc. (Wigglesworth 1953). This type of predigestion has been observed in larvae of *Stethorus* spp. (Blattny & Osvald 1949, Fleschner 1950, Putman 1955, Hagen 1962) and in the unusually shaped larvae of *Platynaspis luteorubra*. These larvae have repeatedly been observed sucking aphids hollow merely via one of the aphid's legs; during this process the body of the aphid is alternately deflated and inflated (I. Hodek unpublished). Ricci (1979) gives a detailed description of extra-intestinal digestion in *P. luteorubra*.

Feeding can easily be observed, especially with pale-coloured aphids, for the internal and surrounding tissues of the part seized by the larva's mandibles become darker during the injection process and return to their natural colour a few seconds later during reimbibition (for details see Hodek 1996). The extra-intestinal (extra-oral) feeding of the larvae of *Apolinus lividigaster* (Richards & Goletsos 1991) is similar to that of *P. luteorubra*. The adults of *A. lividigaster* have bifid mandibles and chew their prey, while the sickle-shaped unidentate mandibles of the larvae pierce and then hold prey during the repeated sucking. In the larvae of *Scymnus* s. str., *Scymnus subvillosus* and perhaps also *Nephus includens* it appears that feeding is similar (Ricci 1979).

A special type of feeding behaviour was observed by Richards (1980, 1985). *Rhyzobius ventralis* larvae sometimes attack the vulnerable females of the coccid *Eriococcus coriaceus* through a large opening in the latter's sac, through which the tip of its abdomen protrudes and crawlers escape. The coccinellid larva usually makes a hole in the lower part of the sac, curls itself around it and remains there feeding until the prey is empty. Larvae and adults of the large Australian coccidophagous species *Rodatus major* (originally described as *Rhizobius*) are specialized on the eggs of *Monophlebulus pilosior* (Margarodidae), and the fourth instar feeds on the eggs as they are laid 'lying with its mouth close to the margarodid's genital opening' (Richards 1985). A similar behaviour has been recorded in first instar *Sasajiscymnus kurohime*, attacking the larvae of the 'soldier' producing aphid *Ceratovacuna lanigera* at the moment when they are born (Arakaki 1992a; 5.4.2).

5.5 CONCLUSIONS

The analysis of coccinellid food relations is not only very interesting and important from a theoretical point of view, but also for its practical consequences – for **predicting** ladybird **activity** in the field and for **improving** their **impact** in the contexts of conservation and augmentative biological control.

It is worth **comparing** the progress achieved in **individual** food-related **fields**. A very great qualitative step forwards has been made in **ethological research** (5.4) and thus partially matches the earlier greater progress with parasitoids. Fifteen years ago, it was still an enigma as to whether ladybirds find their prey by random movements – in spite of a few observations of non-random behaviour. In addition to indirect clues on matters such as taxes or characteristics of host plants (5.4.1.1), the only mechanism definitely known in foraging was the **role of encounter** that switches ladybird movement to a concentrated search (5.4.1.2). In contrast, there is now a wealth of evidence on cues that guide coccinellid behaviour. At least four types should be mentioned: **volatiles of plants** and/or **of prey**, aphid alarm pheromones (all in 5.4.1.2) and oviposition-deterrent chemicals in **larval tracks** (5.4.1.3). Study of ladybird orientation to volatiles has not progressed beyond laboratory tests, with field assays remaining to be completed. In searching for an oviposition site, there is a trade-off for coccinellids between two factors: whether to lay eggs near to prey, so that the first instars find prey early, or whether to reduce attacks by conspecific or heterospecific ladybirds on offspring by ovipositing further away (5.4.1.3).

Although the research discussed in 5.2 and 5.3 has not stagnated in the course of the last 15 years, not so many breakthroughs have been made in these fields. Since about 50 years ago, when **prey specificity** in coccinellids was discovered and the principal definition of essential v. alternative food established (5.2.2, 5.2.11), further evidence has accumulated, and new **allelochemicals** recorded (5.2.6.1) – on which the trophic specificity is mostly based. However, recently prey specificity has begun to be discussed also from a novel angle: **size relations** appear to be more important in predator–prey relations, particularly in evolutionary terms, than the chemical composition of the prey (5.2.3). Support for this view is based on records that ladybirds do not refuse unsuitable/toxic prey and it is not avoided even when when offered in a mixture with suitable prey. This is perhaps due to a less developed **gustatory sense** of coccinellids. However, high (or total) larval mortality and inhibition of egg laying (5.2.2) on non-essential prey/food certainly plays an important role for a coccinellid species in the predator–prey relationship (and eventually also in the impact on the prey).

Thus the **adequacy of prey** can only be safely estalbihsed by experimentally recorded levels of life-history parameters, such as successful completion of larval development and high reproductive performance. While earlier research has worked with single prey/foods, some recent studies have revealed the importance of **mixed food** (5.2.5). Although modern serological and molecular methods were developed for the detection of prey consumed by predators (5.2.1; also Chapter 10), the classical microscopical analysis of food remnants from the gut can also yield precise evidence.

While the food resources of phytophagous (but also coccidophagous) ladybirds are rather stable, **specialized adaptive characteristics** have evolved **in aphidophagous** species under the pressure exerted by the inherently ephemeral occurrence of their prey. This constraint has led to the evolution of a number of adaptive life-history traits, such as, for example, fast development (Chapter 3), high adult mobility, high speed of larval movement and reversible oosorption (Chapter 6).

(See also the general comments in 5.1 and 5.4.1 and partial conclusions in 5.4.1.2.)

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REFERENCES

Abe, Y., T. Nakamura and H. Inoue. 2000. Exploitation of Fabaceae plants by the Mexican bean beetle *Epilachna varivestis* (Coleoptera: Coccinellidae) in Japan. *Appl. Entomol. Zool.* 35: 81–85.

Ables, J. R., S. L. Jones and D. W. McCommas Jr. 1978. Response of selected predator species to different densities of *Aphis gossypii* and *Heliothis virescens* eggs. *Environ. Entomol.* 7: 402–404.

Abrams, P. A. and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* 15: 337–341.

Adedipe, F. and Y.-L. Park. 2010. Visual and olfactory preference of *Harmonia axyridis* (Coleoptera: Coccinellidae) adults to various companion plants. *J. Asia Pac. Entomol.* 13: 319–323.

Agarwala, B. K. and P. Bardhanroy. 1999. Numerical response of ladybird beetles (Col., Coccinellidae) to aphid prey (Hom., Aphididae) in a field bean in north-east India. *J. Appl. Entomol.* 123: 401–405.

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. Why do ladybirds lay eggs in clusters? *Funct. Ecol.* 7: 541–548.

Agarwala, B. K. and A. K. Ghosh. 1988. Prey records of aphidophagous Coccinellidae in India. A review and bibliography. *Trop. Pest Manag.* 34: 1–14.

Agarwala, B. K. and H. Yasuda. 2000. Competitive ability of ladybird predators of aphids: a review of *Cheilomenes sexmaculata* (Fabr.) (Coleoptera: Coccinellidae) with a worldwide checklist of preys. *J. Aphidol.* 14: 1–20.

Agarwala, B. K. and H. Yasuda. 2001a. Larval interactions in aphidophagous predators: effectiveness of wax cover as defence shield of *Scymnus* larvae against predation from syrphids. *Entomol. Exp. Appl.* 100: 101–107.

Agarwala, B. K. and H. Yasuda. 2001b. 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., S. Das and A. K. Bhaumik. 1987. Natural food range and feeding habits of aphidophagous insects in north east India. *J. Aphidol.* 1: 18–22.

Agarwala, B. K., H. Yasuda and Y. Kajita. 2003a. 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.

Agarwala, B. K., H. Yasuda and S. Sato. 2008. Life history response of a predatory ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), to food stress. *Appl. Entomol. Zool.* 43: 183–189.

Agarwala, B. K., P. Bardhanroy, H. Yasuda and T. Takizawa. 2001. Prey consumption and oviposition of the aphidophagous predator *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) in relation to prey density and adult size. *Environ. Entomol.* 30: 1182–1187.

Agarwala, B. K., P. Bardhanroy, H. Yasuda and T. Takizawa. 2003b. Effects of conspecific and heterospecific competitors on feeding and oviposition of a predatory ladybird: a laboratory study. *Entomol. Exp. Appl.* 106: 219–226.

Agarwala, B. K., T. K. Singh, R. K. Lokeshwari and M. Sharmila. 2009. Functional response and reproductive attributes of the aphidophagous ladybird beetle, *Harmonia dimidiata* (F.) in oak trees of sericultural importance. *J. Asia Pac. Entomol.* 12: 179–182.

Agee, H. R., E. R. Mitchell and R. V. Flanders. 1990. Spectral sensitivity of the compound eye of *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* 83: 817–819.

Agrawal, A. A. 2011. Current trends in the evolutionary ecology of plant defence. *Func. Ecol.* 25: 420–432.

Al Abassi, S., M. A. Birkett, J. Pettersson et al. 2000. Response of the seven-spot ladybird to an aphid alarm pheromone and an alarm pheromone inhibitor is mediated by paired olfactory cells. *J. Chem. Ecol.* 26: 1765–1771.

Alexander, R. D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5: 325–383.

Alhmedi, A., E. Haubruge and F. Francis. 2008. Role of prey–host plant associations on *Harmonia axyridis* and *Episyrphus balteatus* reproduction and predatory efficiency. *Entomol. Exp. Appl.* 128: 49–56.

Alikhan, M. A. and M. Yousef. 1986. Temperature and food requirements of *Chilomenes sexmaculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 15: 800–802.

Allee, W. C., A. E. Emerson, K. P. Schmidt, O. Park and T. Park. 1949. *The Principles of Animal Ecology*. Saunders, Philadelphia. 837 pp.

Allen, D. C., F. B. Knight and J. L. Foltz. 1970. Invertebrate predators of the jack-pine budworm, *Choristoneura pinus*, in Michigan. *Ann. Entomol. Soc. Am.* 63: 59–64.

Anderson, J. M. E. 1982. Seasonal habitat utilization and food of the ladybirds *Scymnodes lividigaster* (Mulsant) and *Leptothea galbula* (Mulsant) (Coleoptera: Coccinellidae). *Aust. J. Zool.* 30: 59–70.

Aoki, S., S. Akimoto and S. Yamane. 1981. Observations on *Pseudoregma alexanderi* (Homoptera, Pemphigidae), an aphid species producing pseudoscorpion-like soldiers on bamboos. *Kontyû* 49: 355–366.

Arakaki, N. 1992a. Feeding behaviour of the ladybird *Pseudoscymnus kurohime*. *J. Ethol.* 10: 7–13.

Arakaki, N. 1992b. Feeding by soldiers of the bamboo aphid *Pseudoregma koshunensis* (Homoptera: Aphididae). *J. Ethol.* 10: 147–148.

Arakaki, N. 1992c. Shortened longevity of soldiers of the bamboo aphid *Pseudoregma koshunensis* (Takahashi) (Homoptera: Aphididae) due to attack behaviour. *J. Ethol.* 10: 149–151.

Arditi, R. and L. R. Ginzburg. 1989. Coupling in predator–prey dynamics: ratio dependence. *J. Theor. Biol.* 139: 311–326.

Asante, S. K. 1995. Functional responses of the European earwig and 2 species of coccinellids to densities of *Eriosoma lanigerum* (Hausmann) (Hemiptera, Aphididae). *J. Aust. Entomol. Soc.* 34: 105–109.

Atallah, Y. H. and R. Killebrew. 1967. Ecological and nutritional studies on *Coleomegilla maculata* (Coleoptera: Coccinellidae). Amino acid requirements of the adult determined by the use of C^{14}-labeled acetate. *Ann. Entomol. Soc. Am.* 60: 186–188.

Atallah, Y. H. and L. D. Newsom. 1966. Ecological and nutritional studies on *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae). I. The development of an artificial diet and a laboratory rearing technique. *J. Econ. Entomol.* 59: 1173–1179.

Atlıhan, R. and M. B. Kaydan. 2002. Development, survival and reproduction of three coccinellids feeding on *Hyalopterus pruni* (Geoffr.) (Homoptera: Aphididae). *Turk. J. Agric. For.* 26: 119–124.

Atlıhan, R. and M. S. Ozgokce. 2002. Development, fecundity and prey consumption of *Exochomus nigromaculatus* feeding on *Hyalopterus pruni*. *Phytoparasitica* 30: 443–450.

Atwal, A. S. and S. L. Sethi. 1963. Biochemical basis for the food preference of a predator beetle. *Curr. Sci.* 32: 511–512.

Azam, K. M. and M. H. Ali. 1970. A study of factors affecting the dissemination of the predatory beetle, *Coccinella septempunctata* L. *Final. Techn. Rep.* (F6-IN-249, A7-ENT-40) Dept. Entomol. Andhra Pradesh Agr. Univ., Rajendranagar, Hyderabad, India.

Baensch, R. 1964. Vergleichende Untersuchungen zur Biologie und zum Beutefangverhalten aphidovorer Coccinelliden, Chrysopiden und Syrphiden. *Zool. Jb. Syst.* 91: 271–340.

Baensch, R. 1966. On prey-seeking behaviour of aphidophagous insects. *In* I. Hodek (ed.). *Ecology of Aphidophagous Insects*. Academia, Prague and W. Junk, The Hague. pp. 123–128.

Ba M'Hamed, T. and M. Chemseddine. 2001. Assessment of temperature effects on the development and fecundity of *Pullus mediterraneus* (Col., Coccinellidae) and consumption of *Saissetia oleae egg*s (Hom., Coccoida). *J. Appl. Ent.* 125: 527–531.

Bahlai, C. A., J. A. Welsman, E. C. MacLeod et al. 2008. Role of visual and olfactory cues from agricultural hedgerows in the orientation behavior of multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environ. Entomol.* 37: 973–979.

Bai, Y. Y., M. X. Jiang, J. A. Cheng and D. Wang. 2006. Effects of Cry1Ab toxin on *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae) through its prey, *Nilaparvata lugens* Stal (Homoptera: Delphacidae), feeding on transgenic *Bt* rice. *Environ. Entomol.* 35: 1130–1136.

Bailey, P. and G. Caon. 1986. Predation of twospotted mite, *Tetranychus urticae* Koch (Acarina: Tetranychidae) by *Haplothrips victoriensis* Bagnall (Thysanoptera: Phlaeothripidae) and *Stethorus nigripes* Kapur (Coleoptera: Coccinellidae) on seed lucerne crops in South Australia. *Aust. J. Zool.* 34: 515–525.

Bain, J., P. Singh, M. D. Ashby and R. J. van Boven. 1984. Laboratory rearing of the predatory coccinellid *Cleobora mellyi* (Col.: Coccinellidae) for biological control of *Paropsis charybdis* (Col.: Chrysomelidae) in New Zealand. *Entomophaga* 29: 237–244.

Balachowsky, A. 1930. L'extension de la cochenille australienne (*Icerya purchasi* Mask.) en France et de son prédateur *Novius cardinalis* Muls. *Annls Epiphyt.* 16: 1–24.

Balduf, W. V. 1935. *The Bionomics of Entomophagous Coleoptera*. (13. Coccinellidae lady-beetles). John S. Swift, Chicago, New York. 220 pp.

Banks, C. J. 1954. The searching behaviour of coccinellid larvae. *Br. J. Anim. Behav.* 2: 37–38.

Banks, C. J. 1955. An ecological study of Coccinellidae (Col.) associated with *Aphis fabae* Scop. on *Vicia faba*. *Bull. Entomol. Res.* 46: 561–587.

Banks, C. J. 1956. Observations on the behaviour and mortality in Coccinellidae before dispersal from the egg shells. *Proc. R. Entomol. Soc. Lond. (A)* 31: 56–60.

Banks C. J. 1957. The behaviour of individual Coccinellid larvae on plants. *Br. J. Anim Behav.* 5: 12–24.

Barbier, R., J. Le Lannic and J. Brun. 1996. Récepteurs sensoriels des palpes maxillaires de coccinellidae adultes aphidiphages, coccidiphages et phytophages. *Bull. Soc. Zool. Fr.* 121: 255–268.

Bathon, H. and J. Pietrzik. 1986. Zur Nahrungsaufnahme des Bogen-Marienkäfers, *Clitostethus arcuatus* (Rossi) (Col., Coccinellidae), einem Vertilger der Kohlmottenlaus, *Aleurodes proletella* Linné (Hom., Aleurodidae). *J. Appl. Entomol.* 102: 321–326.

Bazzocchi, G. G., A. Lanzoni, G. Accinelli and G. Burgio. 2004. Overwintering, phenology and fecundity of *Harmonia axyridis* in comparison with native coccinellid species in Italy. *BioControl* 49: 245–260.

Behmer, S. T., S. J. Simpson and D. Raubenheimer. 2002. Herbivore foraging in chemically heterogeneous environments: nutrients and secondary metabolites. *Ecology* 83: 2489–2501.

Belcher, D. W. and R. Thurston. 1982. Inhibition of movement of larvae of the convergent lady beetle by leaf trichomes of tobacco. *Environ. Entomol.* 11: 91–94.

Bell, W. J. 1985. Sources of information controlling motor patterns in arthropod local search orientation. *J. Insect Physiol.* 31: 837–847.

Bell, W. J. 1990. Searching behavior patterns in insects. *Annu. Rev. Entomol.* 35: 447–467.

Bellows, T. S., T. D. Paine and D. Gerling. 1992. Development, survival, longevity, and fecundity of *Clitostethus arcuatus* (Coleoptera: Coccinellidae) on *Siphoninus phillyreae* (Homoptera: Aleyrodidae) in the laboratory. *Environ. Entomol.* 21: 659–663.

Ben Saad, A. A. and G. W. Bishop. 1976a. Attraction of insects to potato plants through use of artificial honeydews and aphid juice. *Entomophaga* 21: 49–57.

Ben Saad, A. A. and G. W. Bishop. 1976b. Effect of artificial honeydews on insect communities in potato fields. *Environ. Entomol.* 5: 453–457.

Benham, B. R. and J. Muggleton. 1970. Studies on the ecology of *Coccinella undecimpunctata* Linn. (Col. Coccinellidae). *Entomologist* 103: 153–170.

Berkvens, N., J. Bonte, D. Berkvens et al. 2008. Pollen as an alternative food for *Harmonia axyridis*. *BioControl* 53: 201–210.

Berkvens, N., C. Landuyt, K. Deforce et al. 2010. Alternative foods for the multicoloured Asian ladybeetle *Harmonia axyridis* (Coleoptera, Coccinellidae). *Eur. J. Entomol* 107: 189–195.

Berthiaume, R., C. Herbert and C. Cloutier. 2000. Predation on *Mindarus abietinus* infesting balsam fir grown as Christmas trees: the impact of coccinellid larval predation with emphasis on *Anatis mali*. *BioControl* 45: 425–438.

Bhatkar, A. P. 1982. Orientation and defense of ladybeetles (Col., Coccinellidae), following ant trail in search of aphids. *Folia Entomol. Mexic.* 53: 75–85.

Biddinger, D. J., D. C. Weber and L. A. Hull. 2009. Coccinellidae as predators of mites: Stethorini in biological control. *Biol. Contr.* 51: 268–283.

Bielawski, R. 1959. *Biedronki-Coccinellidae. Klucze do oznaczania owadów Polski*. Part 19, Tom 76. Panstw. wyd. nauk. Warszawa. 92 pp. (In Polish.)

Bilde, T. and S. Toft. 1999. Prey consumption and fecundity of the carabid beetle *Calathus melanocephalus* on diets of three cereal aphids: high consumption rates of low-quality prey. *Pedobiologia* 43: 422–429.

Bilde, T., J. A. Axelsen and S. Toft. 2000. The value of Collembola from agricultural soils as food for a generalist predator. *J. Appl. Ecol.* 37: 672–683.

Bilu, E. and M. Coll. 2009. Parasitized aphids are inferior prey for a coccinellid predator: implications for intraguild predation. *Environ. Entomol.* 38: 153–158.

Birkett, M. A., C. A. M. Campbell, K. Chamberlain et al. 2000. New roles for cis-jasmone as an insect semiochemical and in plant defense. *Proc. Nat. Acad. Sci. USA* 97: 9329–9334.

Blackman, R. L. 1965. Studies on specificity in Coccinellidae. *Ann. Appl. Biol.* 56: 336–338.

Blackman, R. L. 1967a. Selection of aphid prey by *Adalia bipunctata* L. and *Coccinella 7-punctata L. Ann. Appl. Biol.* 59: 331–338.

Blackman, R. L. 1967b. The effects of different aphid foods on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. *Ann. Appl. Biol.* 59: 207–219.

Blattny, C. and C. V. Osvald. 1949. Contribution à la connaisance des signes géneriques et de la biologie du *Stethorus punctillum* Weise. *Věst. Čs. spol. zool.* 13: 30–40. (In Czech with English summary.)

Bodenheimer, F. S. and S. Neumark. 1955. *The Israel Pine Matsucoccus (*Matsucoccus josephi *n. sp.)*. Kiryath Sepher, Jerusalem. 122 pp.

Boivin, G., C. Roger, D. Coderre and E. Wajnberg. 2010. Learning affects prey selection in larvae of a generalist coccinellid predator. *Entomol. Exp. Appl.* 135: 48–55.

Bonte M., M. A. Samih, P. De Clercq. 2010. Development and reproduction of *Adalia bipunctata* on factitious and artificial foods. *BioControl* 55: 485–491.

Booth, R. G., A. E. Cross, S. V. Fowler and R. H. Shaw. 1995. The biology and taxonomy of *Hyperaspis pantherina* (Coleoptera: Coccinellidae) and the classical biological control of its prey, *Orthezia insignis* (Homoptera: Ortheziidae). *Bull. Entomol. Res.* 85: 307–314.

Branco, M., J. C. Franco, E. Dunkelblum et al. 2006a. A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). *Bull. Entomol. Res.* 96: 179–185.

Branco, M., M. Lettere, J. C. Franco, A. Binazzi and H. Jactel. 2006b. Kairomonal response of predators to three pine bast scale sex pheromones. *J. Chem. Ecol.* 32: 1577–1586.

Brewer, M. J. and N. C. Elliott. 2004. Biological control of cereal aphids in North America and mediating effects of host plant and habitat manipulation. *Annu. Rev. Entomol.* 49: 219–242.

Bristow, C. M. 1991. Are ant–aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. *Oecologia* 87: 514–521.

Britto, E. P. J., M. G. C. Gondim, J. B. Torres et al. 2009. Predation and reproductive output of the ladybird beetle *Stethorus tridens* preying on tomato red spider mite *Tetranychus evansi*. *BioControl* 54: 363–368.

Brodsky, L. M. and C. A. Barlow. 1986. Escape responses of the pea aphid, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae): influence of predator type and temperature. *Can. J. Zool.* 64: 937–939.

Brown, H. D. 1972. The behaviour of newly hatched coccinellid larvae (Coleoptera: Coccinellidae). *J. Entomol. Soc. south. Africa* 35: 149–157.

Brown, M. W. 2004. Role of aphid predator guild in controlling spirea aphid populations on apple in West Virginia, USA. *Biol. Contr.* 29: 189–198.

Brun, J. and G. Iperti. 1978. Influence de l'alimentation sur la fécondité des Coccinelles aphidiphages. *Ann. Zool.-Ecol. Anim.* 10: 449–452.

de Bruyne, M. and T. C. Baker. 2008. Odor detection in insects: volatile codes. *J. Chem. Ecol.* 34: 882–897.

Burden, B. J. and D. M. Norris. 1994. Ovarian failure induced in *Epilachna varivestis* by a 'death-trap' 'Davis' variety of *Glycine max*. *Entomol. Exp. Appl.* 73: 183–186.

Burgio, G., F. Santi and S. Maini. 2002. On intra-guild predation and cannibalism in *Harmonia axyridis* (Pallas) and *Adalia bipunctata* L. (Coleoptera: Coccinellidae). *Biol. Contr.* 24: 110–116.

Burgio, G., R. Ferrari, L. Boriani, M. Pozzati and J. Van Lenteren. 2006. The role of ecological infrastructures on Coccinellidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems. *Bull. Insectol.* 59: 59–67.

Burk, T. 1988. Insect behavioral ecology: Some future paths. *Annu. Rev. Entomol.* 33: 319–335.

Butin, E. E., N. P. Havill, J. S. Elkinton and M. E. Montgomery. 2004. Feeding preference of three lady beetle predators of the hemlock woolly adelgid (Homoptera: Adelgidae). *J. Econ. Entomol.* 97: 1635–1641.

Butt, F. H. 1951. Feeding habitats and mechanism of the Mexican bean beetle. *Cornell Univ. Agr. Exp. Sta., Mem.* 306, 32 pp.

Cabral, S., A. O. Soares, R. Moura and P. Garcia. 2006. Suitability of *Aphis fabae*, *Myzus persicae* (Homoptera: Aphididae) and *Aleyrodes proletella* (Homoptera: Aleyrodidae) as prey for *Coccinella undecimpunctata* (Coleoptera: Coccinellidae). *Biol. Contr.* 39: 434–440.

Cabral, S., A. O. Soares and P. Garcia. 2009. Predation by *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae) on *Myzus persicae* Sulzer (Homoptera: Aphididae): Effect of prey density. *Biol. Contr.* 50: 25–29.

Camargo, F. 1937. Notas taxonomicas e biologicas sobre alguns Coccinellideos do genera *Psyllobora* Chevrolat (Col. Coccinellidae). *Revta Entomol. Rio de J.* 7: 362–377.

Campbell, C. A. M. and W. W. Cone. 1999. Consumption of damson-hop aphids (*Phorodon humuli*) by larvae of *Coccinella transversoguttata* and *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biocontr. Sci. Technol.* 9: 75–78.

Canard, M. 1977. Diminution du taux de survie du prédateur *Chrysopa perla* (L.) (Neuroptera, Chrysopidae) en relation avec le comportement du puceron *Aphis nerii* B. de F. (Homoptera, Aphididae). *In* J. Médioni and E. Boesiger (eds). *Mécanismes Ethologiques de l'Evolution*. Masson, Paris. pp. 49–51.

Cappuccino, N. 1988. Spatial patterns of goldenrod aphids and the response of enemies to patch density. *Oecologia* 76: 607–610.

Capra, F. 1947. Note sui Coccinellidi (Col.) III. La larva ed il regime pollinivoro di *Bulaea lichatschovi* Hummel. *Mem. Soc. Entomol. Ital.*, Suppl. 26: 80–86.

Cardinale, B. J., J. J. Weis, A. E. Forbes, K. J. Tilmon and I. R. Ives. 2006. Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator–prey system. *J. Anim. Ecol.* 75: 497–505.

Carlson, R. E. and H. C. Chiang. 1973. Reduction of an *Ostrinia nubilalis* population by predatory insects attracted by sucrose sprays. *Entomophaga* 18: 204–211.

Carter, M. C. and A. F. G. Dixon. 1982. Habitat quality and the foraging behaviour of coccinellid larvae. *J. Anim. Ecol.* 51: 865–878.

Carter, M. C. and A. F. G. Dixon. 1984. Honeydew: an arrestant stimulus for coccinellids. *Ecol. Entomol.* 9: 383–387.

Carter, M. C., D. Sutherland and A. F. G. Dixon. 1984. Plant structure and the searching efficiency of coccinellid larvae. *Oecologia* 63: 394–397.

Causton, C. E., M. P. Lincango and T. G. A. Poulsom. 2004. Feeding range studies of *Rodolia cardinalis* (Mulsant), a candidate biological control agent of *Icerya purchasi* Maskell in the Galapagos islands. *Biol. Contr.* 29: 315–325.

Ceryngier, P., J. Havelka and I. Hodek. 2004. Mating and activity of gonads in pre-dormant and dormant ladybirds (Coleoptera: Coccinellidae). *Invert. Repr. Dev.* 45: 127–135.

Chakrabarti, S., D. Ghosh and N. Debnath. 1988. Developmental rate and larval voracity in *Harmonia* (*Leis*) *dimidiata* (Col., Coccinellidae), a predator of *Eriosoma lanigerum* (Hom., Aphididae) in western Himalaya. *Acta Entomol. Bohemoslov.* 85: 335–339.

Charles, J. G., E. Collyer and V. White. 1985. Integrated control of *Tetranychus urticae* with *Phytoseiulus persimilis* and *Stethorus bifidus* in commercial raspberry gardens. *N. Zealand J. Exp. Agr.* 13: 385–393.

Chazeau, J. 1981. Données sur la biologie de *Coelophora quadrivittata* (Col.: Coccinellidae), prédateur de *Coccus viridis* (Hom.: Coccidae) en Nouvelle-Calédonie. *Entomophaga* 26: 301–312.

Chazeau, J., E. Bouye and L. B. Delarbogne. 1991. Development and life table of *Olla v-nigrum* (Col., Coccinellidae), a natural enemy of *Heteropsylla cubana* (Hom., Psyllidae) introduced in New Caledonia. *Entomophaga* 36: 275–285.

Chazeau, J., I. Capart and L. Bonnet de Larbogne. 1992. Biological control of the Leucaena psyllid in New Caledonia: the introduction of *Curinus coeruleus* (Coccinellidae). *Leucaena Res. Reports* 13: 59–61.

Cheah, C. A. S. J. and M. S. McClure. 1998. Life history and development of *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae), a new predator of the hemlock wooly adelgid (Homoptera: Adelgidae). *Environ. Entomol.* 27: 1531–1536.

Chen, Z.-H. and J. Qin. 1982. The nutritional role of water content in the artificial diet of *Coccinella septempunctata*. *Acta Entomol. Sinica* 25: 141–146. (In Chinese with English summary.)

Chen, Z.-H., E.-Y. Chen and F.-S. Yan. 1980. Effects of diets on the feeding and reproduction of *Coccinella septempunctata* L. *Acta Entomol. Sinica* 23: 141–148. (In Chinese with English summary.)

Chen, Z.-H., J.-D. Qin and C.-L. Shen. 1989. Effects of altering composition of artificial diets on the larval growth and development of *Coccinella septempunctata*. *Acta Entomol. Sinica* 32: 385–392.

Chen, Z.-H., J.-D. Qin, X.-M. Fan and X.-L. Li. 1984. Effects of adding lipids and juvenoid into the artificial diet on feeding and reproduction of *Coccinella septempunctata* L. *Acta Entomol. Sinica* 27: 136–146. (In Chinese with English summary.)

Chi, D. F., G. L. Wang, J. W. Liu, Q. Y. Wu and Y. P. Zhu. 2009. Antennal morphology and sensilla of Asian multicolored ladybird beetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Entomol. News* 120: 139–152.

Chong, J. H., R. D. Oetting and L. S. Osborne. 2005. Development of *Diomus austrinus* Gordon (Coleoptera: Coccinellidae) on two mealybug prey species at five constant temperatures. *Biol. Contr.* 33: 39–48.

Chumakova, B. M. 1962. Experiments in rearing of predatory beetle *Cryptolaemus montrouzieri* Muls. on an artificial diet. *Zesz. Probl. Postep Nauk Roln.* 35: 195–200.

Cividanes, F. J. and A. P. Gutierrez. 1996. Modeling the age-specific per capita growth and reproduction of *Rhizobius lophanthae* (Col.: Coccinellidae). *Entomophaga* 41: 257–266.

Clegg, J. M. and C. A. Barlow. 1982. Escape behaviour of the pea aphid *Acyrthosiphon pisum* (Harris) in response to alarm pheromone and vibration. *Can. J. Zool.* 60: 2245–2252.

Cochereau, P. 1969. Controle biologique d'*Aspidiotus destructor* Signoret (Homoptera, Diaspinae) dans l'Ile Vaté (Nouvelles Hébrides) au moyen de *Rhizobius pulchellus* Montrouzier (Coleoptera, Coccinellidae). *Cahiers O.R.S.T.O.M.* 8: 57–100.

Coderre, D. and J. C. Tourneur. 1986. Vertical distribution of aphids and aphidophagous insects on maize. *In* I. Hodek (ed). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht. pp. 291–296.

Cohen, A. C. 1989. Ingestion efficiency and protein consumption by a heteropteran predator. *Ann. Entomol. Soc. Am.* 82: 495–499.

Cohen, A. C. and D. L. Brummett. 1997. The non-abundant nutrient (NAN) concept as a determinant of predator–prey fitness. *Entomophaga* 42: 85–91.

Colburn, R. and D. Asquith. 1970. A cage used to study the finding of a host by the ladybird beetle, *Stethorus punctum*. *J. Econ. Entomol.* 63: 1376–1377.

Congdon, B. D., C. H. Shanks and A. L. Antonelli. 1993. Population interaction between *Stethorus punctum picipes* (Coleoptera, Coccinellidae) and *Tetranychus urticae* (Acari, Tetranychidae) in red raspberries at low predator and prey densities. *Environ. Entomol.* 22: 1302–1307.

Corlay, F., G. Boivin and G. Belair. 2007. Efficiency of natural enemies against the swede midge *Contarinia nasturtii* (Diptera: Cecidomyiidae), a new invasive species in North America. *Biol. Contr.* 43: 195–201.

Costamagna, A. C., D. A. Landis and M. J. Brewer. 2008. The role of natural enemy guilds in *Aphis glycines* suppression. *Biol. Contr.* 45: 368–379.

Cottrell, T. E. 2004. Suitability of exotic and native lady beetle eggs (Coleoptera: Coccinellidae) for development of lady beetle larvae. *Biol. Contr.* 31: 362–371.

Cottrell, T. E. 2005. Predation and cannibalism of lady beetle eggs by adult lady beetles. *Biol. Contr.* 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 K. V. Yeargan. 1998. Effect of pollen on *Coleomegilla maculata* (Coleoptera: Coccinellidae) population density, predation and cannibalism in sweet corn. *Environ. Entomol.* 27: 1402–1410.

Crook, N. E. and K. D. Sunderland. 1984. Detection of aphid remains in predatory insects and spiders by ELISA. *Ann. Appl. Biol.* 105: 413–422.

Curio, E. 1976. *The Ethology of Predation*. Springer, Berlin. 250 pp.

Cushing, J. M. 1992. A size-structured model for cannibalism. *Theor. Popul. Biol.* 42: 347–361.

Daane, K. M., K. R. Sime, J. Fallon and M. L. Cooper. 2007. Impacts of Argentine ants on mealybugs and their natural enemies in California's coastal vineyards. *Ecol. Entomol.* 32: 583–596.

Danks, H. V. 1983. Extreme individuals in natural populations. *Bull. Entomol. Soc. Am.* 29(1): 41–46.

Dauguet, P. 1949. *Les Coccinellini de France*. Paris. 46 pp.

Davidson, L. N. and E. W. Evans. 2010. Frass analysis of diets of aphidophagous lady beetles (Coleoptera: Coccinellidae) in Utah alfalfa fields. *Environ. Entomol.* 39: 576–582.

Davidson, W. M. 1921. Observations on *Psyllobora taedata* LeConte, a coccinellid attacking mildews. *Entomol. News* 32: 83–89.

Day, K. R., M. Docherty, S. R. Leather and N. A. C. Kidd. 2006. The role of generalist insect predators and pathogens in suppressing green spruce aphid populations through direct mortality and mediation of aphid dropping behavior. *Biol. Contr.* 38: 233–246.

Debaraj, Y. and T. K. Singh. 1990. Biology of an aphidophagous coccinellid predator, *Coccinella transversalis* Fab. *J. Biol. Control* 4: 93–95.

De Clercq, P., M. Bonte, K. Van Speybroeck, K. Bolckmans and K. Deforce. 2005. Development and reproduction of *Adalia bipunctata* (Coleoptera: Coccinellidae) on eggs of *Ephestia kuehniella* (Lepidoptera: Phycitidae) and pollen. *Pest Manage. Sci.* 61: 1129–1132.

Deligeorgidis, P. N., C. G. Ipsilandis, G. Kaltsoudas and G. Sidiropoulos. 2005. An index model on predatory effect of female adults of *Coccinella septempunctata* L. on *Macrosiphum euphorbiae* Thomas. *J. Appl. Entomol.* 129: 1–5.

Deligeorgidis, P. N., C. G. Ipsilandis, M. Vaiopoulou, G. Kaltsoudas and G. Sidiropoulos. 2005. Predatory effect of *Coccinella septempunctata* on *Thrips tabaci* and *Trialeurodes vaporariorum*. *J. Appl. Entomol.* 129: 246–249.

Denemark, E. and J. E. Losey. 2010. Causes and consequences of ladybug washups in the Finger Lakes Region of New York State (Coleoptera: Coccinellidae). *Entomol. Am.* 116: 78–88.

Denno, R. F. and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? *Ecology* 84: 2522–2531.

Dicke, M., M. W. Sabelis, J. Takabayashi, J. Bruin and M. A. Posthumus. 1990. Plant strategies of manipulating predator–prey interactions through allelochemicals: prospects for application in pest control. *J. Chem. Ecol.* 16: 3091–3118.

Dickson, R. C., E. F. Laird and C. R. Pesho. 1955. The spotted alfalfa aphid (*Therioaphis maculata*).(Predator relationship: Hemiptera, Coccinellidae, Syrphidae, Neuroptera). *Hilgardia* 24: 93–118.

Dixon, A. F. G. 1958. The escape response shown by certain aphids to the presence of the coccinelid *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. 1970. Factors limiting the effectiveness of the coccinellid beetle, as a predator of the sycamore aphid, *Drepanosiphum platanoides* (Schr.). *J. Anim. Ecol.* 39: 739–751.

Dixon, A. F. G. 2000. *Insect Predator–Prey Dynamics. 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 B. K. Agarwala. 2002. Triangular fecundity function and ageing in ladybird beetles. *Ecol. Entomol.* 27: 433–440.

Dixon, A. F. G. and Y. Guo. 1993. Egg and cluster size in ladybird beetles (Coleoptera: Coccinellidae): The direct and indirect effects of aphid abundance. *Eur. J. Entomol.* 90: 457–463.

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., M. Martin-Smith and G. Subramanian. 1965. Constituents of *Megoura viciae* Buckton. *J. Chem. Soc.* 1965: 1562–1564.

Dixon, A. F. G. and L. A. Stewart. 1991. Size and foraging in ladybird beetles. *In* L. Polgar, R. J. Chambers, A. F. G. Dixon and I. Hodek (eds). *Behaviour and Impact of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 123–132.

Dmitriew, C. and L. Rowe. 2007. Effects of early resource limitation and compensatory growth on lifetime fitness in the ladybird beetle (*Harmonia axyridis*). *J. Evol. Biol.* 20: 1298–1310.

Dong, H., J. J. Ellington and M. D. Remmenga. 2001. An artificial diet for the lady beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Southw. Entomol.* 26: 205–213.

Dosse, G. 1967. Schadmilben des Libanons und ihre Prädatoren. *Z. Angew. Entomol.* 59: 16–48.

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.

Duan, J. J., G. Head, M. J. McKee et al. 2002. Evaluation of dietary effects of transgenic corn pollen expressing Cry3Bb1 protein on a non-target ladybird beetle, *Coleomegilla maculata*. *Entomol. Exp. Appl.* 104: 271–280.

Dyadechko, N. P. 1954. *Coccinellids of the Ukrainian SSR*. Kiev. 156 pp. (In Russian.)

Eastop, V. F. and R. D. Pope. 1966. Notes on the ecology and phenology of some British Coccinellidae. *Entomologist* 99: 287–289.

Eastop, V. F. and R. D. Pope. 1969. Notes on the biology of some British Coccinellidae. *Entomologist* 102: 162–164.

Ehler, L. E., R. F. Long, M. G. Kensey and S. K. Kelley. 1997. Potential for augmentative biological control of black bean aphid in California sugarbeet. *Entomophaga* 42: 241–256.

Eigenbrode, S. D., J. E. Andreas, M. G. Cripps et al. 2008. Induced chemical defenses in invasive plants: a case study with *Cynoglossum officinale* L. *Biol. Invasions* 10: 1373–1379.

El Habi, M., A. Sekkat, L. El Jadd and A. Boumezzough. 2000. Biology of *Hippodamia variegata* Goeze (Col., Coccinellidae) and its suitability against *Aphis gossypii* Glov (Hom., Aphididae) on cucumber under greenhouse conditions. *J. Appl. Entomol* 124: 365–374.

El Khidir, E. 1969. A contribution to the biology of *Epilachna chrysomelina* F., the melon lady-bird beetle in the Sudan (Col., Coccinellidae). *Sudan Agric. J.* 4: 32–37.

Elder, R. J. and K. L. Bell. 1998. Establishment of *Chilocorus* spp. (Coleoptera: Coccinellidae) in a *Carica papaya* L. orchard infested by *Aonidiella orientalis* (Newstead) (Hemiptera: Diaspididae). *Aust. J. Entomol.* 37: 362–365.

Elliot, H. J. and D. W. De Little. 1980. Laboratory studies on predation of *Chrysopharta bimaculata* (Olivier) (Col.: Chrysomelidae) eggs by the coccinellids *Cleobora mellyi* Mulsant and *Harmonia conformis* (Boisduval). *Gen. Appl. Entomol.* 12: 33–36.

Elliott, N. C. and R. W. Kieckhefer. 2000. Response by coccinellids to spatial variation in cereal aphid density. *Popul. Ecol.* 42: 81–90.

Elliott, N. C., R. W. Kieckhefer and D. A. Beck. 2000. Adult coccinellid activity and predation on aphids in spring cereals. *Biol. Contr.* 17: 218–226.

Elliott, N. C., R. W. Kieckhefer and D. A. Beck. 2002a. Effect of aphids and the surrounding landscape on the abundance of Coccinellidae in cornfields. *Biol. Contr.* 24: 214–220.

Elliott, N. C., B. W. French, G. J. Michels and D. K. Reed. 1994. Influence of four aphid prey species on development, survival, and adult size of *Cycloneda ancoralis*. *Southwest. Entomol.* 19: 57–61.

Elliott, N. C., R. W. Kieckhefer, J.-H. Lee and B. W. French. 1998. Influence of within-field and landscape factors on aphid predator populations in wheat. *Landscape Ecol.* 14: 239–252.

Elliott, N. C., R. W. Kieckhefer, G. J. Michels Jr. and K. L. Giles. 2002b. Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. *Environ. Entomol.* 31: 253–260.

Ellingsen, J.-L. 1969. Effect of constant and varying temperature on development, feeding, and survival of *Adalia bipunctata* L. (Col., Coccinellidae). *Norsk Entomol. Tidsskr.* 16: 121–125.

Elsey, K. D. 1974. Influence of plant host on searching speed of two predators. *Entomophaga* 19: 3–6.

van Emden, H. F., A. P. Storeck, S. Douloumapaka et al. 2008. Plant chemistry and aphid parasitoids (Hymenoptera: Braconidae): Imprinting and memory. *Eur. J. Entomol.* 105: 477–483.

Emrich, B. H. 1991. Erworbene Toxizität bei der Lupinenblattlaus *Macrosiphum albifrons* und ihr Einfluß auf die aphidophagen Prädatoren *Coccinella septempunctata*, *Episyrphus balteatus* und *Chrysoperla carnea*. *J. Plant Diseases Prot.* 98: 398–404.

Endo, N., M. Abe, T. Sekine and K. Matsuda. 2004. Feeding stimulants of Solanaceae-feeding lady beetle, *Epilachna vigintioctomaculata* (Coleoptera: Coccinellidae) from potato leaves. *Appl. Entomol. Zool.* 39: 411–416.

Erichsen, C., M. J. Samways and V. Hattingh. 1991. Reaction of the ladybird *Chilocorus nigritus* (F.) (Col., Coccinellidae) to a doomed food resource. *J. Appl. Entomol.* 112: 493–498.

Ettifouri, M. and A. Ferran. 1992. Influence d'une alimentation prealable et du jeune sur l'apparition de la recherche intensive des proies chez *Semiadalia undecimnotata*. *Entomol. Exp. Appl.* 65: 101–111.

Ettifouri, M. and A. Ferran. 1993. Influence of larval rearing diet on the intensive searching behaviour of *Harmonia axyridis* (Col.: Coccinellidae) larvae. *Entomophaga* 38: 51–59.

Evans, E. W. 2000. Egg production in response to combined alternative foods by the predator *Coccinella transversalis*. *Entomol. Exp. Appl.* 94: 141–147.

Evans, E. W. 2003. Searching and reproductive behaviour of female aphidophagous ladybirds (Coleoptera: Coccinellidae): a review. *Eur. J. Entomol.* 100: 1–10.

Evans, E. W. 2004. Habitat displacement of North American ladybirds by an introduced species. *Ecology* 85: 637–647.

Evans, E. W. 2008. Multitrophic interactions among plants, aphids, alternate prey and shared natural enemies: a review. *Eur. J. Entomol.* 105: 369–380.

Evans, E. W. 2009. Lady beetles as predators of insects other than Hemiptera. *Biol. Contr.* 51: 255–267.

Evans, E. W. and A. F. G. Dixon. 1986. Cues for oviposition by ladybird beetles (Coccinellidae): response to aphids. *J. Anim. Ecol.* 55: 1027–1034.

Evans, E. W. and D. I. Gunther. 2005. The link between food and reproduction in aphidophagous predators: a case study with *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 102: 423–430.

Evans, E. W. and D. R. Richards. 1997. Managing the dispersal of ladybird beetles (Col.: Coccinellidae): use of artificial honeydew to manipulate spatial distributions. *Entomophaga* 42: 93–102.

Evans, E. W. and J. G. Swallow. 1993. Numerical responses of natural enemies to artificial honeydew in Utah alfalfa. *Environ. Entomol.* 22: 1392–1401.

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.

Evans, E. W. and N. N. Youssef. 1992. Numerical responses of aphid predators to varying prey density among Utah alfalfa fields. *J. Kans. Entomol. Soc.* 65: 30–38.

Evans, E. W., D. R. Richards and A. Kalaskar. 2004. Using food for different purposes: female responses to prey in the predator *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Ecol. Entomol.* 29: 27–34.

Evans, E. W., A. T. Stevenson and D. R. Richards. 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. *Oecologia* 121: 107–112.

Ewert, M. A. and H. C. Chiang. 1966a. Dispersal of three species of coccinellids in corn fields. *Can. Entomol.* 98: 999–1003.

Ewert, M. A. and H. C. Chiang. 1966b. Effects of some environmental factors on the distribution of three species of Coccinellidae in their microhabitat. *In* I. Hodek (ed.). *Ecology of Aphidophagous Insects*. Academia, Prague and W. Junk, The Hague. pp. 195–219.

Fabres, G. and A. Kiyindou. 1985. Comparaison du potentiel biotique de deux coccinelles (*Exochomus flaviventris* et *Hyperaspis senegalensis hottentotta*, Col. Coccinellidae) predatrices de *Phenacoccus manihoti* (Hom. Pseudococcidae) au Congo. *Acta Œcol.* 6: 339–348.

Farid, A., J. B. Johnson and S. S. Quisenberry. 1997. Compatibility of a coccinellid predator with a Russian wheat aphid resistant wheat. *J. Kansas Entomol. Soc.* 70, 114–119.

Ferran, A. and M. Deconchat. 1992. Exploration of wheat leaves by *Coccinella septempunctata* L. (Coleoptera, Coccinellidae) larvae. *J. Insect Behav.* 5: 147–159.

Ferran, A. and A. F. G. Dixon. 1993. Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 90: 383–402.

Ferran, A., L. A. Buscarlet and M. M. Larroque. 1981. Utilization de $HT^{18}O$ pour mesurer la consommation alimentaire chez les larves agées de *Semiadalia 11notata* (Col.: Coccinellidae). *Entomophaga* 26: 71–77.

Ferran, A., M. O. Cruz de Boelpaepe, H. Schanderl and M. M. Larroque. 1984a. Les aptitudes trophiques et reproductrices des femelles de *Semiadalia undecimnotata* (Col.: Coccinellidae). *Entomophaga* 29: 157–170.

Ferran, A., M. O. Cruz de Boelpaepe, L. A. Buscarlet, M. M. Larroque and H. Schanderl. 1984b. Les relations trophiques entre les larves de la coccinelle *Semiadalia undecimnotata* Schn. et le puceron *Myzus persicae* Sulz.: generalization à d'autres couples 'proieprédateur' et influence des conditions d'élevage de l'auxiliaire. *Acta Oecol.* 5: 85–97.

Ferran, A., P. Gubanti, G. Iperti, A. Migeon and J. Onillon. 1989. La répartition spatiale des différents stades de *Coccinella septempunctata* dans un champ de blé: variation au cours de la saison. *Entomol. Exper. Appl.* 53: 229–236.

Fiaboe, K. K. M., M. G. C. Gondim, G. J. De Moraes, C. K. P. O. Ogol and M. Knapp. 2007. Bionomics of the acarophagous ladybird beetle *Stethorus tridens* fed *Tetranychus evansi*. *J. Appl. Entomol.* 131: 355–361.

Fleschner, C. A. 1950. Studies on the searching capacity of the larvae of three predators of the Citrus red mite (*Paratetranychus citri*) (*Stethorus picipes*, *Conwentzia hageni*, *Chrysopa californica*). *Hilgardia* 20: 233–265.

Flowers, R. W., S. M. Salom and L. T. Kok. 2005. Competitive interactions among two specialist predators and a generalist predator of hemlock wooly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in the laboratory. *Environ. Entomol.* 34: 664–675.

Foott, W. H. 1973. Observations on Coccinellidae in corn fields in Essex county, Ontario. *Proc. Entomol. Soc. Ontario* 104: 16–21.

Formusoh, E. S. and G. E. Wilde. 1993. Preference and development of two species of predatory coccinellids on the Russian wheat aphid and greenbug biotype E (Homoptera: Aphididae). *J. Agr. Entomol.* 10: 65–70.

Fox, L. R. 1975. Cannibalism in natural populations. *Annu. Rev. Ecol. Syst.* 6: 87–106.

Fraenkel, G. 1959. The raison d'être of secondary plant substances. *Science* 129: 1466–1470.

Fraenkel, G. 1969. Evaluation of our thoughts on secondary plant substances. *Entomol. Exp. Appl.* 12: 473–486.

Francis, F., E. Haubruge and C. Gaspar. 2000. Influence of host plants on specialist/generalist aphids and on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 97: 481–485.

Francis, F., G. Lognay and E. Haubruge. 2004. Olfactory responses to aphid and host plant volatile releases: (E)-β-farnesene an effective kairomone for the predator *Adalia bipunctata*. *J. Chem. Ecol.* 30: 741–755.

Francis, F., G. Lognay, J. P. Wathelet and E. Haubruge. 2001. Effects of allelochemicals from first (Brassicaceae) and second (*Myzus persicae* and *Brevicoryne brassicae*) trophic levels on *Adalia bipunctata*. *J. Chem. Ecol.* 27: 243–256.

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.

Frank, J. H. and E. D. McCoy. 2007. The risk of classical biological control in Florida. *Biol. Contr.* 41: 151–174.

Frazer, B. D. 1988. Coccinellidae. *In* A. K. Minks and P. Harrewijn (eds). *Aphids: Their Biology, Natural Enemies and Control*. Volume 2B. Elsevier, Amsterdam. pp. 231–247.

Frazer, B. D. and N. Gilbert. 1976. Coccinellids and aphids: a quantitative sudy of the impact of adult lady-birds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *J. Entomol. Soc. Br. Columbia* 73: 33–56.

Frazer, B. D. and B. Gill. 1981. Hunger, movement, and predation of *Coccinella californica* on pea aphids in the laboratory and in the field. *Can. Entomol.* 113: 1025–1033.

Frazer, B. D. and D. A. Raworth. 1985. Sampling for adult coccinellids and their numerical response to strawberry aphids (Coleoptera: Coccinellidae; Homoptera: Aphididae). *Can. Entomol.* 117: 153–161.

Frazer, B. D., N. Gilbert, V. Nealis and D. A. Raworth. 1981. Control of aphid density by a complex of predators. *Can. Entomol.* 113: 1035–1041.

Frechette, B., A. F. G. Dixon, C. Alauzet and J. L. Hemptinne. 2004. Age and experience influence patch assessment for oviposition by an insect predator. *Ecol. Entomol.* 29: 578–583.

Frechette, B., A. F. G. Dixon, C. Alauzet, N. Boughenou and J. L. Hemptinne. 2006. Should aphidophagous ladybirds be reluctant to lay eggs in the presence of unsuitable prey? *Entomol. Exp. Appl.* 118: 121–127.

Freeland, W. J. and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. *Am. Nat.* 108: 269–289.

Fujiyama, N. and H. Katakura. 1997. Individual variation in two host plants of the ladybird beetle, *Epilachna pustulosa* (Coleoptera: Coccinellidae). *Ecol. Res.* 12: 257–264.

Fujiyama, N. and H. Katakura. 2001. Variable correspondence of female host preference and larval performance in a phytophagous ladybird beetle *Epilachna pustulosa* (Coleoptera: Coccinellidae). *Ecol. Res.* 16: 405–414.

Fujiyama, N. and H. Katakura. 2002. Host plant suitability of *Solanum japonense* (Solanaceae) as an alternative larval food for three closely related *Epilachna* ladybird beetles (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 37: 551–557.

Fujiyama, N., H. Katakura and Y. Shirai. 1998. Report of the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae) in Japan. *Appl. Entomol. Zool.* 33: 327–331.

Fujiyama, N., T. Koizumi and H. Katakura. 2003. Conspecific thistle plant selection by a herbivorous ladybird beetle, *Epilachna pustulosa*. *Entomol. Exp. Appl.* 108: 33–42.

Fujiyama, N., K. Matsumoto, N. Kobayashi, Y. Ohta and H. Katakura. 2005. Differentiation in the ability to utilize *Pterostyrax hispida* (Ebenales: Styracaceae) among four local populations of the phytophagous ladybird beetle *Henosepilachna yasutomii* (Coleoptera: Coccinellidae). *Popul. Ecol.* 47: 91–98.

Fukunaga, Y. and S.-I. Akimoto. 2007. Toxicity of the aphid *Aulacorthum magnoliae* to the predator *Harmonia axyridis* (Coleoptera: Coccinellidae) and genetic variance in the assimilation of the toxic aphids in *H. axyridis* larvae. *Entomol. Sci.* 10: 45–53.

Gagné, 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.

Fye, R. E. 1981. Rearing and release of coccinellids for potential control of pear psylla. *Adv. Agric. Technol.*, US Dept. Agric. West. Ser. 20: 1–9.

Gagné, 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.

Gannon, A. J. and C. E. Bach. 1996. Effects of soybean trichome density on Mexican Bean Beetle (Coleoptera: Coccinellidae) development and feeding preference. *Environ. Entomol.* 25: 1077–1082.

Gao, F., S.-R. Zhu, Y. C. Sun et al. 2008. Interactive effects of elevated CO_2 and cotton cultivar on tritrophic interaction of *Gossypium hirsutum*, *Aphis gossypii* and *Propylea japonica*. *Environ. Entomol.* 37: 29–37.

Garcia, J. F. and R. J. O'Neil. 2000. Effect of *Coleus* size and variegation on attack rates, searching strategy, and selected life history characteristics of *Cryptolaemus montrouzieri* (Coleoptera: Coccinellidae). *Biol. Contr.* 18: 225–234.

Gautam, R. D. 1990. Mass-multiplication technique of coccinellid predator, ladybird beetle (*Brumoides suturalis*). *Indian J. Agr. Sci.* 60: 747–750.

George, K. S. 1957. Preliminary investigations on the biology and ecology of the parasites and predators of *Brevicoryne brassicae* (L.). *Bull. Entomol. Res.* 48: 619–629.

Geyer, J. W. C. 1947. A study of the biology and ecology of *Exochomus flavipes* Thunb. (Coccinellidae, Coleoptera). Part 1. 2. *J. Entomol. Soc. South. Africa* 9: 219–234; 10: 64–109.

Ghanim, A. E.-B., B. Freier and T. Wetzel. 1984. Zur Nahrungsaufnahme und Eiablage von *Coccinella septempunctata* L. bei unterschiedlichem Angebot von Aphiden der Arten *Macrosiphum avenae* (Fabr.) und *Rhopalosiphum padi* (L.). *Arch. Phytopathol. PflSch.* 20: 117–125.

Gil, L., A. Ferran, J. Gambier et al. 2004. Dispersion of flightless adults of the Asian lady beetle, *Harmonia axyridis*, in greenhouses containing cucumbers infested with the aphid *Aphis gossypii*: effect of the presence of conspecific larvae. *Entomol. Exp. Appl.* 112: 1–6.

Giles, K. L., J. J. Obrycki and T. A. DeGooyer. 1994. Prevalence of predators associated with *Acyrthosiphum pisum* (Homoptera: Aphididae) and *Hypera postica* Gyllenhal (Coleoptera: Curculionidae) during growth of the first crop of alfalfa. *Biol. Contr.* 4: 170–177.

Giles, K. L., R. D. Madden, R. Stockland, M. E. Payton and J. W. Dillwith. 2002. Host plants affect predator fitness via the nutritional value of herbivore prey: Investigation of a plant–aphid–ladybeetle system. *BioControl* 47: 1–21.

Giorgi, J. A., N. J. Vandenberg, J. V. McHugh et al. 2009. The evolution of food preferences in Coccinellidae. *Biol. Contr.* 51: 215–231.

Giroux, S., R. M. Duchesne and D. Coderre. 1995. Predation of *Leptinotarsa decemlineata* (Coleoptera, Chrysomelidae) by *Coleomegilla maculata* (Coleoptera, Coccinellidae) – comparative effectiveness of predator developmental stages and effect of temperature. *Environ. Entomol.* 24: 748–754.

Glen, D. M. 1973. The food requirements of *Blepharidopterus angulatus* (Heteroptera: Miridae) as a predator of the lime aphid, *Eucallipterus tiliae*. *Entomol. Exp. Appl.* 16: 255–267.

Godfray, H. C. J. 1994. *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey. 488 pp.

Goidanich, A. 1943. Due Coccinelle igrofile e pollinivore sul riso (*Hippodamia 13-punctata* L., *Anisosticta 19-punctata* L.) *Risicoltura* 33: 145–156, 169–177.

Gomez Vives, S. 1999. Biology of *Lindorus lophantae* Blaisdell (Col.: Coccinellidae), a candidate biocontrol agent of *Phoenicococcus marlatti* (Hom.: Phoenicococcidae) in the date-palm grove of Elche, Spain. *In* M. Canard and Beyssat-Arnaouty (eds). *Proceedings of the 1st Regional Symposium for Applied Biological Control in Mediterranean Countries*, Cairo, Egypt, 1998. Toulouse, France.

Gonzáles-Hernández, H., N. J. Reimer and M. W. Johnson. 1999. Survey of the natural enemies of *Dysmicoccus* mealybugs on pineapple in Hawai. *BioControl* 44: 47–58.

Gorb, E., D. Voigt, S. D. Eigenbrode and S. Gorb. 2008. Attachment force of the beetle *Cryptolaemus montrouzieri* (Coleoptera, Coccinellidae) on leaflet surfaces of mutants of the pea *Pisum sativum* (Fabaceae) with regular and reduced wax coverage. *Arthropod–Plant Interact.* 2: 247–259.

Greenstone, M. H. and S. C. Trowell. 1994. Arthropod predation: a simplified immunodot format for predator gut analysis. *Ann. Entomol. Soc. Am.* 87: 214–217.

Greenstone, M. H., D. L. Rowley, D. C. Weber, M. E. Payton and D. J. Hawthorne. 2007. Feeding mode and prey detectability half-lives in molecular gut-content analysis: an example with two predators of the Colorado potato beetle. *Bull. Entomol. Res.* 97: 201–209.

Grez, A. A., T. Zaviezo and M. Rios. 2005. Ladybird (Coleoptera: Coccinellidae) dispersal in fragmented alfalfa landscapes. *Eur. J. Entomol.* 102: 209–216.

Grez, A. A., T. Zaviezo, S. Diaz, B. Comousseight and G. Cortes. 2008. Effects of habitat loss and fragmentation on the abundance and species richness of aphidophagous beetles and aphids in experimental alfalfa landscapes. *Eur. J. Entomol.* 105: 411–420.

Griffin, M. L. and K. V. Yeargan. 2002. Factors potentially affecting oviposition site selection by the lady beetle *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 31: 112–119.

Grill, C. P., A. J. Moore and E. D. Brodie III. 1997. The genetics of phenotypic plasticity in a colonizing population of the ladybird beetle, *Harmonia axyridis*. *Heredity* 78: 261–269.

Gruppe, A. and P. Roemer. 1988. The lupin aphid (*Macrosiphum albifrons* Essing, 1911. (Hom., Aphididae) in West Germany: its occurrence, host plants and natural enemies. *Z. Angew. Entomol.* 106: 135–143.

Guershon, M. and D. Gerling. 1999. Predatory behavior of *Delphastus pusillus* in relation to the phenotypic plasticity of *Bemisia tabaci* nymphs. *Entomol. Exp. Appl.* 92: 239–248.

Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. *Annu. Rev. Entomol.* 7: 289–326.

Hagen, K. S. 1986. Ecosystem analysis: plant cultivars (HPR), entomophagous species and food supplements. *In* D. J. Boethel and R. D. Eikenbary (eds). *Interactions of Plant Resistance and Parasitoids and Predators of Insects*. Wiley, New York. pp. 151–197.

Hagen, K. S., P. Greany, E. F. Sawall Jr. and R. L. Tassan. 1976. Tryptophan in artificial honeydews as a source of an attractant for adult *Chrysopa carnea*. *Environ. Entomol.* 5: 458–468.

Hagen, K. S., E. F. Sawall Jr. and R. L. Tassan. 1971. The use of food sprays to increase effectiveness of entomophagous insects. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 2: 59–81.

Hagley, E. A. C. and W. R. Allen. 1990. The green apple aphid, *Aphis pomi* DeGeer (Homoptera: Aphididae), as prey of polyphagous arthropod predators in Ontario. *Can. Entomol.* 122: 1221–1228.

Hajek, A. E. and D. L. Dahlsten. 1987. Behavioral interactions between three birch aphid species and *Adalia bipunctata* larvae. *Entomol. Exper. Appl.* 45: 81–87.

Hales, D. 1979. Population dynamics of *Harmonia conformis* (Boisd.) (Coleoptera: Coccinellidae) on acacia. *Gen. Appl. Entomol.* 11: 3–8.

Hamasaki, K. and M. Matsui. 2006. Development and reproduction of an aphidophagous coccinellid, *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae), reared on an alternative diet, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. *Appl. Entomol. Zool.* 41: 233–237.

Hammond, R. B. and R. L. Coope. 1999. Antibiosis of released soybean germplasm to Mexican bean beetle (Coleoptera: Coccinellidae). *J. Entomol. Sci.* 34: 183–190.

Han, B. and Z. M. Chen. 2002. Behavioral and electrophysiological responses of natural enemies to synomones from tea shoots and kairomones from tea aphids, *Toxoptera aurantii*. *J. Chem. Ecol.* 28: 2203–2219.

Hariri, G. 1966a. Laboratory studies on the reproduction of *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae). *Entomol. Exp. Appl.* 9: 200–204.

Hariri, G. 1966b. Changes in metabolic reserves of three species of aphidophagous Coccinellidae (Coleoptera) during metamorphosis. *Entomol. Exp. Appl.* 9: 349–358.

Harmon, J. P., A. R. Ives, J. E. Losey, A. C. Olson and K. S. Rauwald. 2000. *Coleomegilla maculata* (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions. *Oecologia* 125: 543–548.

Harmon, J. P., J. E. Losey and A. R. Ives. 1998. The role of vision and color in the close proximity foraging behavior of four coccinellid species. *Oecologia* 115: 287–292.

Harmon, J. P., E. Stephens and J. Losey. 2007. The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. *J. Insect Conserv.* 11: 85–94.

Harpaz, I. 1958. Bionomics of the 11-spotted ladybird beetle, *Coccinella undecimpunctata* L., in a subtropical climate. *Proc. 10th Int. Congr. Entomol.* Montreal 1956, 2: 657–659.

Harwood, J. D. and J. J. Obrycki. 2005. Quantifying aphid predation rates of generalist predators in the field. *Eur. J. Entomol.* 102: 335–350.

Harwood, J. D., S. W. Phillips, J. Lello et al. 2009. Invertebrate biodiversity affects predator fitness and hence potential to control pests in crops. *Biol. Contr.* 51: 499–506.

Hassell, M. P. 1978. *The Dynamics of Arthropod Predator–Prey Systems*. Monographs in Population Biology 13. Princeton Univ. Press, Princeton. 237 pp.

Hatano, E., G. Kunert, J. P. Michaud and W. W. Weisser. 2008. Chemical cues mediating aphid location by natural enemies. *Eur. J. Entomol.* 105: 797–806.

Hattingh, V. and M. J. Samways. 1991. A forced change in prey type during field introductions of coccidophagous biocontrol agents *Chilocorus* species (Coleoptera: Coccinellidae): is it an important consideration in achieving establishment? *In* L. Polgár, R. J. Chambers, A. F. G. Dixon and I. Hodek (eds). *Behaviour and Impact of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 143–148.

Hattingh, V. and M. J. Samways. 1993. Evaluation of artificial diets and two species of natural prey as laboratory food for *Chilocorus* spp. *Entomol. Exp. Appl.* 69: 13–20.

Hattingh, V. and M. J. Samways. 1995. Visual and olfactory location of biotopes, prey patches, and individual prey by the ladybeetle *Chilocorus nigritus*. *Entomol. Exp. Appl.* 75: 87–98.

Hauge, M. S., F. H. Nielsen and S. Toft. 1998. The influence of three cereal aphid species and mixed diet on larval survival, development and adult weight of *Coccinella septempunctata*. *Entomol. Exp. Appl.* 89: 319–323.

Hawkes, O. A. M. 1920. Observations on the life-history, biology, and genetics of the lady-bird, *Adalia bipunctata* (Mulsant). *Proc. Zool. Soc. Lond.* 33: 475–490.

Hawkes, O. A. M. and T. F. Marriner. 1927. A preliminary account of the life-history of *Coccinella 11–punctata* (L.). *Trans. R. Entomol. Soc. Lond.* 75: 47–52.

Hazzard, R. V. and D. N. Ferro. 1991. Feeding responses of adult *Coleomegilla maculata* (Coleoptera: Coccinellidae) to eggs of the Colorado potato beetle (Coleoptera: Chrysomelidae) and green peach aphids (Homoptera: Aphididae). *Environ. Entomol.* 20: 644–651.

Heidari, M. and M. J. W. Copland. 1992. Host finding by *Cryptolaemus montrouzieri* (Col., Coccinellidae) a predator of mealybugs (Hom., Pseudococcidae). *Entomophaga* 37: 621–625.

Hemptinne, J.-L. and A. Desprets. 1986. Pollen as a spring food for *Adalia bipunctata*. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht. pp. 29–35.

Hemptinne, J.-L. and J. Naisse. 1987. Ecophysiology of the reproductive activity of *Adalia bipunctata* L. (Col., Coccinellidae). *Med. Fac. Landbouww. Rijksuniv. Gent* 52: 225–233.

Hemptinne, J.-L., A. F. G. Dixon and J. Coffin. 1992. Attack strategy of ladybird beetles (Coccinellidae): factors shaping their numerical response. *Oecologia* 90: 238–245.

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., J. Naisse and S. Os. 1988. Glimps of the life history of *Propylea quatuordecimpunctata* (L.) (Coleoptera: Coccinellidae). *Med. Fac. Landbouww. Rijksuniv. Gent* 53: 1175–1182.

Hemptinne, J.-L., A. F. G. Dixon, J. L. Doucet and J. E. Petersen. 1993. Optimal foraging by hoverflies (Diptera: Syrphidae) and ladybirds (Coleoptera: Coccinellidae): mechanisms. *Eur. J. Entomol.* 90: 451–455.

Hemptinne, J.-L., G. Lognay, M. Doumbia and A. F. G. Dixon. 2001. Chemical nature and persistence of the oviposition deterring pheromone in the tracks of the larvae of the two spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Chemoecology* 11: 43–47.

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 *Glycines macumura* (Hemiptera: Aphididae). *Envir. Entomol.* 37: 1258–1263.

Hilbeck, A., C. Eckel and G. G. Kennedy. 1997. Predation on Colorado potato beetle eggs by generalist predators in research and commercial potato plantings. *Biol. Control* 8: 191–196.

Hippa, H., S. Koponen and R. Roine. 1984. Larval growth of *Coccinella hieroglyphica* (Col., Coccinellidae) fed on aphids and preimaginal stages of *Galerucella sagittariae* (Col., Chrysomelidae). *Rep. Kevo Subarctic Res. Stat.* 19: 67–70.

Hodek I. 1956. The influence of *Aphis sambuci* L. as prey of the ladybird beetle *Coccinella septempunctata* L. *Věst. Čs. Spol. Zool.* 20: 62–74. (In Czech, Engl. summ.).

Hodek, I. 1957a. The influence of *Aphis sambuci* L. as food for *Coccinella 7-punctata* L. II. *Čas. Čs. Spol. Entomol.* 54: 10–17. (In Czech, Engl. summ.).

Hodek, I. 1957b. The larval food consumption of *Coccinella 7-punctata* L. *Zool. Listy (Folia Zoologica)* 6: 3–11. (In Czech with English summary.)

Hodek, I. 1959. Ecology of aphidophagous Coccinellidae. *In Proc. Int. Conf. Insect Path. Biol. Control*, Academia, Prague, 1958: 543–547.

Hodek, I. 1960. The influence of various aphid species as food for two lady-birds *Coccinella 7-punctata* L. and *Adalia bipunctata* L. *In The Ontogeny of Insects*. (Proc. Symp. Praha 1959). Academia, Prague. pp. 314–316.

Hodek, I. 1962. Essential and alternative food in insects. *Proc. 11th Int. Congr. Entomol.* Vienna 1960, 2: 696–697.

Hodek, I. 1967. Bionomics and ecology of predaceous Coccinellidae. *Annu. Rev. Entomol.* 12: 79–104.

Hodek, I. 1973. *Biology of Coccinellidae*. Academia, Prague and W. Junk, The Hague. 260 pp.

Hodek. I. 1993. Habitat and food specificity in aphidophagous predators. *Biocont. Sci. Tech.* 3: 91–100.

Hodek, I. 1996. Food relationships. *In* I. Hodek and A. Honěk (eds). *Ecology of Coccinellidae*. Kluwer, Dordrecht. pp. 143–238.

Hodek, I. and A. Honěk, eds. 1996. *Ecology of Coccinellidae*. Kluwer, Dordrecht. 464 pp.

Hodek, I. and A. Honěk. 2009. Scale insects, mealybugs, whiteflies and psyllids (Hemiptera, Sternorrhyncha) as prey of ladybirds. *Biol. Contr.* 51: 232–243.

Hodek, I. and J. P. Michaud. 2008. Why is *Coccinella septempunctata* so successful? (A point-of-view). *Eur. J. Entomol.* 105: 1–12.

Hodek, I., G. Iperti and M. Hodková. 1993. Long-distance flights in Coccinellidae (Coleoptera). *Eur. J. Entomol.* 90: 403–414.

Hodek, I., Z. Ruzicka and M. Hodková. 1978. Pollinivorie et aphidiphagie chez *Coleomegilla maculata*. *Ann. Zool.-Ecol. Anim.* 10: 453–459.

Hodek, I., K. Novák, V. Skuhravý and J. Holman. 1965. The predation of *Coccinella septempunctata* L. on *Aphis fabae* Scop. on sugar beet. *Acta Entomol. Bohemoslov.* 62: 241–253.

Hoelmer, K. A., L. S. Osborne and R. K. Yokomi. 1993. Reproduction and feeding behaviour of *Delphastus pusillus* (Coleoptera: Coccinellidae), a predator of *Bemisia tabaci* (Homoptera: Aleyrodidae). *J. Econ. Entomol.* 86: 322–329.

Hoelmer, K. A., L. S. Osborne and R. K. Yokomi. 1994. Interactions of the whitefly predator *Delphastus pusillus* (Coleoptera: Coccinellidae) with parasitized sweetpotato whitefly (Homoptera: Aleyrodidae). *Environ. Entomol.* 23: 136–139.

Holling C. S. 1959a. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385–398.

Holling, C. S. 1959b. The components of predation as revealed by a study of small mammal predation of the European sawfly. *Can. Entomol.* 91: 293–320.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* 45: 3–60.

Holling, C. S. 1966. Functional response of invertebrate predators to prey density. *Mem. Entomol. Soc. Can.* 48: 1–87.

Honda, J. Y. and R. F. Luck. 1995. Scale morphology effects on feeding behaviour and biological control potential of *Rhyzobius lophantae* (Coleoptera: Coccinellidae). *Ann. Entomol. Soc. Am.* 88: 441–450.

Honěk, A. 1979. Plant density and occurrence of *Coccinella septempunctata* and *Propylea quatuordecimpunctata* (Coleoptera, Coccinellidae) in cereals. *Acta Entomol. Bohemoslov.* 76: 308–312.

Honěk, A. 1980. Population density of aphids at the time of settling and ovariole maturation in *Coccinella septempunctata* (Col.: Coccinellidae). *Entomophaga* 25: 427–430.

Honěk, A. 1982. Factors which determine the composition of field communities of adult aphidophagous Coccinellidae (Coleoptera). *Z. Angew. Entomol.* 94: 157–168.

Honěk, A. 1983. Factors affecting the distribution of larvae of aphid predators (Col., Coccinellidae and Dipt., Syrphidae) in cereal stands. *Z. Angew. Entomol.* 95: 336–343.

Honěk, A. 1985. Habitat preferences of aphidophagous coccinellids (Coleoptera). *Entomophaga* 30: 253–264.

Honěk, A. 1986. Production of faeces in natural populations of aphidophagous coccinellids (Col.) and estimation of predation rates. *J. Appl. Entomol.* 102: 467–476.

Honěk, A., A. F. G. Dixon and Z. Martinkova. 2008a. Body size, reproductive allocation, and maximum reproductive rate of two species of aphidophagous Coccinellidae exploiting the same resource. *Entomol. Exp. Appl.* 127: 1–9.

Honěk, A., A. F. G. Dixon and Z. Martinkova. 2008b. Body size and the temporal sequence in the reproductive activity of two species of aphidophagous coccinellids exploiting the same resource. *Eur. J. Entomol.* 105: 421–425.

Hoogendoorn, M. and G. E. Heimpel. 2001. PCR-based gut content analysis of insect predators: using ribosomal ITS-1 fragments from prey to estimate predation frequency. *Mol. Ecol.* 10: 2059–2068.

Hori, M., Y. Araki, W. Sugeno, Y. Usui and K. Matsuda. 2005. Luteolin 7-O-glucoside in hozuki leaves, *Physalis alkekengi*, is involved in feeding stimulation in *Epilachna vigintioctopunctata*. *Jpn. J. Appl. Entomol. Zool.* 49: 251–254.

Hosseini, R., O. Schmidt and M. A. Keller. 2008. Factors affecting detectability of prey DNA in the gut contents of invertebrate predators: a polymerase chain reaction-based method. *Entomol. Exp. Appl.* 126: 194–202.

Houck, M. A. 1986. Prey preference in *Stethorus punctum* (Coleoptera: Coccinellidae). *Environ. Entomol.* 15: 967–970.

Houck, M. A. 1991. Time and resource partitioning in *Stethorus punctum* (Coleoptera: Coccinellidae). *Environ. Entomol.* 20: 494–497.

House, H. L. 1974. Digestion. *In* M. Rockstein (ed.). *The Physiology of Insects*. Academic Press, New York. pp. 63–120.

Huang, Z., S.-X. Ren and P. D. Musa. 2008. Effects of temperature on development, survival, longevity, and fecundity of the *Bemisia tabaci* Gennadius (Homoptera: Aleyrodidae) predator, *Axinoscymnus cardilobus* (Coleoptera: Coccinellidae). *Biol. Contr.* 46: 209–215.

Huang, Z., S.-X. Ren and S.-L. Yao. 2006. Life history of *Axinoscymnus cardilobus* (Col., Coccinellidae), a predator of *Bemisia tabaci* (Hom., Aleyrodidae). *J. Appl. Entomol.* 130: 437–441.

Huffaker, C. B. and R. L. Doutt. 1965. Establishment of the coccinellid, *Chilocorus bipustulatus* Linneus, in California olive groves. *Pan-Pacif. Entomol.* 44: 61–63.

Hukusima, S. and K. Itoh. 1976. Pollen and fungus as food for some coccinellid beetles. *Res. Bull. Fac. Agr. Gifu Univ.* 39: 31–38.

Hukusima, S. and M. Kamei. 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Res. Bull. Fac. Agric. Gifu Univ.* 29: 53–66.

Hukusima, S. and N. Komada. 1972. Effects of several species of aphids as food on development and nutrition of *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae). *Proc. Kansai Plant Prot. Soc.* 14: 7–13. (In Japanese with English summary.)

Hukusima, S. and S. Kouyama. 1974. Life histories and food habits of *Menochilus sexmaculatus* Fabricius (Coleoptera: Coccinellidae). *Res. Bull. Fac. Agric. Gifu Univ.* 36: 19–29.

Hukusima, S. and T. Ohwaki. 1972. Further notes on feeding biology of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Res. Bull. Fac. Agric. Gifu Univ.* 33: 75–82.

Hukusima, S. and H. Sakurai. 1964. Aphid consumption by adult *Coccinella septempunctata bruckii* Mulsant in relation to temperature (Coleoptera: Coccinellidae). *Annu. Rev. Plant Protection North Japan* 15: 126–128. (In Japanese.)

Hukusima, S. and S. Takeda. 1975. Artificial diets for larvae of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), an insect predator of aphids and scale insects. *Res. Bull. Fac. Agr. Gifu Univ.* 38: 49–53.

Hull, L. A., D. Asquith and P. D. Mowery. 1976. Distribution of *Stethorus punctum* in relation to densities of the European red mite. *Environ. Entomol.* 5: 337–342.

Hull, L. A., D. Asquith and P. D. Mowery. 1977a. The functional responses of *Stethorus punctum* to densities of the European red mite. *Environ. Entomol.* 6: 85–90.

Hull, L. A., D. Asquith and P. D. Mowery. 1977b. The mite searching ability of *Stethorus punctum* within an apple orchard. *Environ. Entomol.* 6: 684–688.

Hurst, G. D. D. and M. E. N. Majerus. 1993. Why do maternally inherited microorganisms kill males? *Heredity* 71: 81–95.

Hussein, M. Y. and K. S. Hagen. 1991. Rearing of *Hippodamia convergens* on artificial diet of chicken liver, yeast and sucrose. *Entomol. Exp. Appl.* 59: 197–199.

Ibrahim, M. M. 1955a. Studies on *Coccinella undecimpunctata aegyptiaca* Reiche. 1. Preliminary notes and morphology of the early stages. *Bull. Soc. Entomol. Egypte* 39: 251–274.

Ibrahim, M. M. 1955b. Studies on *Coccinella undecimpunctata aegyptiaca* Reiche. 2. Biology and life-history. *Bull. Soc. Entomol. Egypte* 39: 395–423.

Ide, T., N. Suzuki and N. Katayama. 2007. The use of honeydew in foraging for aphids by larvae of the ladybird beetle, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Ecol. Entomol.* 32: 455–460.

Imms, A. D. 1947. *Insect Natural History*. London.

Inchausti, P. and S. Ballesteros. 2008. Intuition, functional responses and the formulation of predator–prey models when there is a large disparity in the spatial domains of the interacting species. *J. Anim. Ecol.* 77: 891–897.

Iperti, G. 1965. Contribution a l'étude de la specificité chez les principales Coccinelles aphidiphages des Alpes-Maritimes et des Basses-Alpes. *Entomophaga* 10: 159–178.

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.

Iperti, G. and N. Trepanier-Blais. 1972. Valeur alimentaire des oeufs d'*Anagasta kuehniella* Z. (Lep., Pyralidae) pour une coccinelle aphidiphage: *Adonia undecimnotata* Schn. (Col., Coccinellidae). *Entomophaga* 17: 437–441.

Isard, S. A., D. A. R. Kristovich, S. H. Gage, C. J. Jones and N. F. Laird. 2001. Atmospheric motion systems that influence the redistribution and accumulation of insects on the beaches of the Great Lakes in North America. *Aerobiologia* 17: 275–291.

Isikber, A. A. and M. J. W. Copland. 2001. Food consumption and utilization by larvae of two coccinellid predators, *Scymnus levaillanti* and *Cycloneda sanguinea*, on cotton aphid, *Aphis gossypii*. *BioControl* 46: 455–467.

Isikber, A. A. and M. J. W. Copland. 2002. Effects of various aphid foods on *Cycloneda sanguinea*. *Entomol. Exp. Appl.* 102: 93–97.

Iverson, A. L., R. B. Hammond and L. R. Iverson. 2001. Induction of soybean resistance to the Mexican Bean Beetle (Coleoptera: Coccinellidae). *J. Kans. Entomol. Soc.* 74: 185–191.

Ives, A. R., P. Kareiva and R. Perry. 1993. Response of a predator to variation in prey density at three hierarchical scales: lady beetles feeding on aphids. *Ecology* 74: 1929–1938.

Ives, P. M. 1981a. Estimation of coccinellid numbers and movement in the field. *Can. Entomol.* 113: 981–997.

Ives, P. M. 1981b. Feeding and egg production of two species of coccinellids in the laboratory. *Can. Entomol.* 113: 999–1005.

Iwao, S. 1954. On the distributions of *Epilachna sparsa orientalis* Dieki and *E. vigintioctomaculata* Motschulsky and the boundary of their geographical distributions (I). *Oyo-Kontyû* 9: 135–141. (In Japanese with English summary.)

Iwao, S. and A. Machida. 1961. Further experiments on the host-plant preference in a phytophagous ladybeetle, *Epilachna pustulosa* Kono. *Insect Ecol.* 9: 9–16. (In Japanese with English summary.)

Iwata, K. 1932. On the biology of two large lady-birds in Japan. *Trans. Kansai Entomol. Soc.* 3: 13–26.

Iwata, K. 1965. Supplement on the biology of two large ladybirds in Japan. *Acta Coleopter.* 2: 57–68.

Jalali, M. A., L. Tirry and P. De Clercq. 2009a. Effects of food and temperature on development, fecundity and life-table parameters of *Adalia bipunctata* (Coleoptera: Coccinellidae). *J. Appl. Entomol.* 113: 615–625.

Jalali, M. A., L. Tirry and P. De Clercq. 2009b. Food consumption and immature growth of *Adalia bipunctata* (Coleoptera: Coccinellidae) on a natural prey and a factitious food. *Eur. J. Entomol.* 106: 193–198.

Jalali, M. A., L. Tirry and P. De Clercq. 2010. Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*. *BioControl* 55: 261–269.

Jenkins, E. B., R. B. Hammond, S. K. St. Martin and R. L. Cooper. 1997. Effect of soil moisture and soybean growth stage on resistance to Mexican bean beetle (Coleoptera: Coccinellidae). *J. Econ. Entomol.* 90: 697–703.

Jervis, M. A., ed. 2005. *Insects as Natural Enemies: A Practical Perspective*. Kluwer, Dordrecht, The Netherlands. 764 pp.

Jiggins, C., M. Majerus and U. Gough. 1993. Ant defence of colonies of *Aphis fabae* Scopoli (Hemiptera: Aphididae). against predation by ladybirds. *Br. J. Ent. Nat. Hist.* 6: 129–137.

Johki, Y., S. Obata and M. Matsui. 1988. Distribution and behaviour of five species of aphidophagous ladybirds (Coleoptera) around aphid colonies. *In* E. Niemczyk and A. F. G.

Dixon (eds). *Ecology and Effectiveness of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 35–38.

Jöhnssen, A. 1930. Beiträge zur Entwicklungs- und Ernährungsbiologie einheimischer Coccinelliden unter besonderer Berücksichtigung von *Coccinella septempunctata* L. *Z. Angew. Entomol.* 16: 87–158.

Joseph, S. B., W. E. Snyder and A. J. Moore. 1999. Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. *J. Evol. Biol.* 12: 792–797.

Kaddou, I. K. 1960. The feeding behavior of *Hippodamia quinquesignata* (Kirby) larvae. *Univ. Calif. Publ. Entomol.* 16: 181–230.

Kagata, H. and N. Katayama. 2006. Does nitrogen limitation promote intraguild predation in an aphidophagous ladybird? *Entomol. Exp. Appl.* 119: 239–246.

Kagata, H. and T. Ohgushi. 2007. Carbon–nitrogen stoichiometry in the tritrophic food chain: willow, leaf beetle, and predatory ladybird beetle. *Ecol. Res.* 22: 671–677.

Kajita, Y. and E. W. Evans. 2009. Ovarian dynamics and oosorption in two species of predatory lady beetles (Coleoptera: Coccinellidae). *Physiol. Entomol.* 34: 185–194.

Kajita, Y. and E. W. Evans. 2010. Alfalfa fields promote high reproductive rate of an invasive predatory lady beetle. *Biol. Invasions* 12: 2293–2302.

Kajita, Y., E. W. Evans and H. Yasuda. 2009. Reproductive responses of invasive and native predatory lady beetles (Coleoptera: Coccinellidae) to varying prey availability. *Environ. Entomol.* 38: 1283–1292.

Kalaskar, A. and E. W. Evans. 2001. Larval responses of aphidophagous lady beetles (Coleoptera: Coccinellidae) to weevil larvae versus aphids as prey. *Ann. Entomol. Soc. Am.* 94: 76–81.

Kalushkov, P. 1998. Ten aphid species (Sternorrhyncha: Aphididae) as prey for *Adalia bipunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 95: 343–349.

Kalushkov, P. and I. Hodek. 2001. New essential aphid prey for *Anatis ocellata* and *Calvia quatuordecimguttata* (Coleoptera: Coccinellidae). *Biocontr. Sci. Technol.* 11: 35–39.

Kalushkov, P. and I. Hodek. 2004. The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. *BioControl* 49: 21–32.

Kalushkov, P. and I. Hodek. 2005. The effects of six species of aphids on some life history parameters of the ladybird *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol* 102: 449–452.

Kanervo, V. 1940. Beobachtungen und Versuche zur Ermittlung der Nahrung einiger Coccinelliden. *Ann. Entomol. Fenn.* 6: 89–110.

Kanervo, V. 1946. Studien über die natürlichen Feinde des Erlenblattkäfers, *Melasoma aenea* L. (Col., Chrysomelidae). *Ann. Zool. Soc. Vanamo* 12: 206. (In Finish with German summary.)

Karban, R. 2007. Damage to sagebrush attracts predators but this does not reduce herbivory. *Entomol. Exp. Appl.* 125: 71–80.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* 326: 388–390.

Kareiva, P. 1990. The spatial dimension in pest–enemy interactions. *In* M. Mackauer, L. E. Ehler and J. Roland (eds). *Critical Issues in Biological Control*. Intercept Andover, Hants. pp. 213–227.

Kareiva, P. and G. Odell. 1987. Swarms of predators exhibit 'preytaxis' if individual predators use area-restricted search. *Am. Nat.* 130: 233–270.

Kariluoto, K. T. 1978. Optimum levels of sorbic acid and methyl-p-hydroxybenzoate in an artificial diet for *Adalia bipunctata* L. (Coleoptera, Coccinellidae) larvae. *Ann. Entomol. Fenn.* 44: 94–97.

Kariluoto, K. T. 1980. Survival and fecundity of *Adalia bipunctata* (Coleoptera, Coccinellidae) and some other predatory insect species on an artificial diet and a natural prey. *Ann. Entomol. Fenn.* 46: 101–106.

Kariluoto, K. T., E. Junnikkala and M. Markkula. 1976. Attempts at rearing *Adalia bipunctata* L. (Col., Coccinellidae) on different artificial diets. *Ann. Entomol. Fenn.* 92: 91–97.

Katayama, N. and N. Suzuki. 2010. Extrafloral nectaries indirectly protect small aphid colonies via ant-mediated interactions. *Appl. Entomol. Zool.* 45: 505–511.

Katsarou, I., J. T. Margaritopoulos, J. A. Tsitsipis, D. Ch. Perdikis and K. D. Zarpas. 2005. Effect of temperature on development, growth and feeding of *Coccinella septempunctata* and *Hippodamia convergens* reared on the tobacco aphid, *Myzus persicae nicotianae*. *BioControl* 50: 565–588.

Katsoyannos, P. and Y. Laudeho. 1977. Contribution a la mise au point de l' elevage d' *Exochomus quadripustulatus* L. (Col., Coccinellidae). *Biologia Gallo-Hellenica* 6: 251–258.

Kawai, A. 1976. Analysis of the aggregation behavior in the larvae of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) to prey colony. *Res. Popul. Ecol.* 18: 123–134.

Kawai, A. 1978. Sibling cannibalism in the first instar larvae of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Kontyû* 46: 14–19.

Kawauchi, S. 1979. Effects of prey density on the rate of prey consumption, development and survival of *Propylea japonica* Thunberg (Coleoptera: Coccinellidae). *Kontyû* 47: 204–212.

Kehat, M. 1968. The feeding behaviour of *Pharoscymnus numidicus* (Coccinellidae), predator of the date palm scale *Parlatoria blanchardi*. *Entomol. Exp. Appl.* 11: 30–42.

Kesten, U. 1969. Zur Morphologie und Biologie von *Anatis ocellata* (L.) (Coleoptera, Coccinellidae). *Z. Ang. Entomol.* 63: 412–455.

Khan, M. R. and M. R. Khan. 2010. The relationship between temperature and the functional response of *Coccinella sep-*

tempunctata (L.) (Coleoptera: Coccinellidae). *Pakistan J. Zool.* 42: 461–466.

Kikuta, S., N. Fujiyama and H. Katakura. 2010. Local variation in the thistle species *Cirsium grayanum* affects its utilization by the herbivorous ladybird beetle *Henosepilachna niponica*. *Entomol. Exp. Appl.* 136: 262–270.

Kindlmann, P. and A. F. G. Dixon. 1993. Optimal foraging in ladybird beetles (Coleoptera: Coccinellidae) and its consequences for their use in biological control. *Eur. J. Entomol.* 90: 443–450.

Kishimoto, H. and I. Adachi. 2010. Effects of sucrose on survival and oviposition of the predacious insects *Stethorus japonicus* (Coleoptera: Coccinellidae), *Oligota kashmirica benefica* (Coleoptera: Staphylinidae), and *Scolothrips takahashii* (Thysanoptera: Thripidae). *Appl. Entomol. Zool.* 45: 621–626.

Kiyindou, A. and G. Fabres. 1987. Etude de la capacite d'accroisement chez *Hyperaspis raynevali*, predateur introduit au Congo pour la regulation des populations de *Phenacoccus manihoti* (Hom.: Pseudococcidae). *Entomophaga* 32: 181–189.

Klausnitzer, B. 1965. Zur Biologie der *Epilachna argus* Geoffr. (Col. Coccinellidae). *Entomol. Nachr.* 9: 87–89.

Klausnitzer, B. 1966. Übersicht über die Nahrung der einheimischen Coccinellidae (Col.). *Entomol. Ber.* 1966: 91–102.

Klausnitzer, B. 1989. Marienkäferansammlungen am Ostseestrand. *Entomol. Nachr. Ber.* 33: 189–194.

Klausnitzer, B. 1992. Coccinelliden als Prädatoren der Holunderblattlaus (*Aphis sambuci* L.) im Wärmefrühjahr 1992. *Entomol. Nachr. Ber.* 36: 185–190.

Klausnitzer, B. and H. Klausnitzer. 1986. *Marienkäfer (Coccinellidae)*. (3rd ed.). A. Ziemsen Verlag, Wittenberg-Lutherstadt. 104 pp.

Klausnitzer, B. and H. Klausnitzer. 1997. *Marienkäfer – Coccinellidae* (4th ed.). Westarp Wissenschaften, Magdeburg. 175 pp.

Klewer, N., Z. Ruzicka and S. Schulz. 2007. (Z)-pentacos-12-ene, an oviposition-deterring pheromone of *Cheilomenes sexmaculata*. *J. Chem. Ecol.* 33: 2167–2170.

Klingauf, F. 1967. Abwehr- und Meideraktionen von Blattläusen (Aphididae) bei Bedrohung durch Räubern und Parasiten. *Z. Angew. Entomol.* 60: 269–317.

Koch, R. L., E. C. Burkness, S. J. W. Burkness and W. D. Hutchison. 2004. Phytophagous preferences of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) for autumn-ripening fruit. *J. Econ. Entomol.* 97: 539–544.

Koch, R. L., W. D. Hutchison, R. C. Venette and G. E. Heimpel. 2003. Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biol. Contr.* 28: 265–270.

Koch, R. L., R. C. Venette and W. D. Hutchison. 2005. Influence of alternate prey on predation of monarch butterfly (Lepidoptera: Nymphalidae) larvae by the multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environ. Entomol.* 34: 410–416.

Koide, T. 1962. Observations on the feeding habit of the larva of *Coccinella septempunctata bruckii* Mulsant. The feeding behaviour and number of prey fed under different temperatures. *Kontyû* 30: 236–241. (In Japanese with English summary.)

Koji, S. and K. Nakamura. 2002. Population dynamics of a thistle-feeding lady beetle *Epilachna niponica* (Coccinellidae: Epilachninae) in Kanazawa, Japan. 1. Adult demographic traits and population stability. *Popul. Ecol.* 44: 103–112.

Koji, S., K. Nakamura and M. Yamashita. 2004. Adaptive change and conservatism in host specificity in two local populations of the thistle-feeding ladybird beetle *Epilachna niponica*. *Entomol. Exp. Appl.* 112: 145–153.

Kontodimas, D. C. and G. J. Stathas. 2005. Phenology, fecundity and life table parameters of the predator *Hippodamia variegata* reared on *Dysaphis crataegi*. *BioControl* 50: 223–233.

Kontodimas, D. C., P. A. Eliopoulos, G. J. Stathas and L. P. Economou. 2004. Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): Evaluation of a linear and various nonlinear models using specific criteria. *Envir. Entomol.* 33: 1–11.

Kovář, I. 1996. Morphology and anatomy. *In* I. Hodek and A. Honěk (eds). *Ecology of Coccinellidae*. Kluwer, Dordrecht. pp. 1–18.

Krafsur, E. S., J. J. Obrycki and J. D. Harwood. 2005. Comparative genetic studies of native and introduced Coccinellidae in North America. *Eur. J. Entomol.* 102: 469–474.

Krebs, J. R. and R. H. McCleery. 1984. Optimization in behavioural ecology. *In* J. R. Krebs and N. B. Davies (eds). *Behavioural Ecology: An Evolutionary Approach* (2nd edn). Blackwell Sci. Publ., Oxford. pp. 91–121.

Kreiter, S. and G. Iperti. 1986. Effectiveness of *Adalia bipunctata* against aphids in a peach orchard with special reference to ant/aphid relationships. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht. pp. 537–543.

Krivan, V. 2008. Dispersal dynamics: distribution of lady beetles (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 105: 405–409.

Krivan, V. and E. Sirot. 2004. Do short-term behavioural responses of consumers in tri-trophic food chains persist at the population time-scale? *Evol. Ecol. Res.* 6: 1063–1081.

Kumar, A., N. Kumar, A. Siddiqui and C. P. M. Tripathi. 1999. Prey–predator relationship between *Lipaphis erysimi* Kalt. (Hom., Aphididae) and *Coccinella septempunctata* L. (Col., Coccinellidae). II. Effect of host plants on the functional response of the predator. *J. Appl. Entomol.* 123: 591–596.

Kuwajima, M., N. Kobayashi, T. Katoh and H. Katakura. 2010. Detection of ecological hybrid inviability in a pair of sympatric phytophagous ladybird beetles (*Henosepilachna* spp.). *Entomol. Exp. Appl.* 134: 280–286.

Kuznetsov, N. Ya. 1948. *Principles of Insect Physiology*. Vol. I. Izd. Akad. Nauk SSSR. 380 pp. (In Russian.)

Kuznetsov, V. N. 1975. Fauna and ecology of coccinellids (Coleoptera, Coccinellidae) in Primorye region. *Tr. Biol.-pochv. Inst.* 28: 3–24. (In Russian.)

Kuznetsov, V. N. 1993. *Coccinellids (Coleoptera, Coccinellidae) of the Russian Far East*. Dalnauka, Vladivostok. 334 pp. (In Russian.)

Kuznetsov, V. N. and G. A. Pantyuchov. 1988. Ecology of *Chilocorus kuwanae* Silv. (Coleoptera, Coccinellidae) and its acclimatization in Adjar ASSR. *In The Role of Insects in the Biocoenoses of Far East*. DVO AN SSSR, Vladivostok. pp. 48–54. (In Russian.)

Latham, D. R. and N. J. Mills. 2009. Quantifying insect predation: a comparison of three methods for estimating daily per capita consumption of two aphidophagous predators. *Environ. Entomol.* 38: 1117–1125.

Laubertie, E., X. Martini, C. Cadena et al. 2006. The immediate source of the oviposition-deterring pheromone produced by larvae of *Adalia bipunctata* (L.) (Coleoptera, Coccinellidae) J. *Insect Behav.* 19: 231–240.

Lederberg, J. 1992. The interface of science and medicine. *Mount Sinai J. Med.* 59: 380–383.

Lee, J. H. and T. J. Kang. 2004. Functional response of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) to *Aphis gossypii* Glover (Homoptera: Aphididae) in the laboratory. *Biol. Contr.* 31: 306–310.

Legrand, A. and P. Barbosa. 2003. Plant morphological complexity impacts foraging efficiency of adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Environ. Entomol.* 32: 1219–1226.

Le Rü, B. and A. Mitsipa. 2000. Influence of the host plant of the cassava mealybug *Phenacoccus manihoti* on life-history parameters of the predator *Exochomus flaviventris*. *Entomol. Exp. Appl.* 95: 209–212.

Lei, H. and N. Vickers. 2008. Central processing of natural odor mixtures in insects. *J. Chem. Ecol.* 34: 915–927.

Liere, H. and I. Perfecto. 2008. Cheating on a mutualism: Indirect benefits of ant attendance to a coccidophagous coccinellid. *Environ. Entomol.* 37: 143–149.

Lin, J.-T. and C.-Y. Wu. 1992. A comparative study on the color vision of four coleopteran insects. *Bull. Inst. Zool., Acad. Sinica* 31: 81–88.

Lin, J.-T., C.-Y. Wu and Y.-T. Chang. 1992. Semifused rhabdom of the ladybird beetle *Coccinella septempunctata* Linnaeus (Coleoptera: Coccinellidae). *Bull. Inst. Zool., Acad. Sinica* 31: 261–269.

Lin, K., K. Wu, Y. Zhang and Y. Guo. 2008. Naturally occurring populations of *Bemisia tabaci*, biotype B and associated natural enemies in agro-ecosystems in northern China. *Biocontr. Sci. Techn.* 18: 169–182.

Liu, C. L. 1950. Contribution to the knowledge of Chinese Coccinellidae. X. Occurrence of *Perilitus coccinellae* (Schrank), a parasite of adult Coccinellidae in North China (Hymenoptera, Braconidae). *Entomol. News* 61: 207–208.

Liu, T. and P. A. Stansly. 1999. Searching and feeding behavior of *Nephaspis oculatus* and *Delphastus catalinae* (Coleoptera: Coccinellidae), predators of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Environ. Entomol.* 28: 901–906.

Liu, T.-X., P. A. Stansly, K. A. Hoelmer and L. S. Osborne. 1997. Life history of *Nephaspis oculatus* (Coleoptera: Coccinellidae), a predator of *Bemisia argentifolii* (Homoptera: Aleyrodidae). *Ann. Entomol. Soc. Am.* 90: 776–782.

Lohman, D. J., Q. Liao and N. E. Pierce. 2006. Convergence of chemical mimicry in a guild of aphid predators. *Ecol. Entomol.* 31: 41–51.

Lopez, V. F., M. T. K. Kairo and J. A. Irish. 2004. Biology and prey range of *Cryptognatha nodiceps* (Coleoptera: Coccinellidae), a potential biological control agent for the coconut scale, *Aspidiotus destructor* (Hemiptera: Diaspididae). *Biocontr. Sci. Techn.* 14: 475–485.

Lorenzetti, F., J. T. Arnason, B. J. R. Philogene and R. I. Hamilton. 1997. Evidence for spatial niche partitioning in predaceous aphidophaga: use of plant colour as a cue. *Entomophaga* 42: 49–56.

Lu, W. H. and M. E. Montgomery. 2001. Oviposition, development, and feeding of *Scymnus* (*Neopullus*) *sinuanodulus* (Coleoptera: Coccinellidae): A predator of *Adelges tsugae* (Homoptera: Adelgidae). *Ann. Entomol. Soc. Am.* 94: 64–70.

Lucas, E., S. Demougeot, C. Vincent and D. Coderre. 2004. 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.

Lundgren, J. G. 2009. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biol. Contr.* 51: 294–305.

Lundgren, J. G. and D. C. Weber. 2010. Changes in digestive rate of a predatory beetle over its larval stage: Implications for dietary breadth. *J. Insect Physiol.* 56: 431–437.

Lundgren, J. G. and R. N. Wiedenmann. 2004. Nutritional suitability of corn pollen for the predator *Coleomegilla maculata* (Coleoptera: Coccinellidae). *J. Insect Physiol.* 50: 567–575.

Lundgren, J. G., A. A. Razzak and R. N. Wiedenmann. 2004. Population responses and food consumption by predators *Coleomegilla maculata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. *Environ. Entomol.* 33: 958–963.

Mack, T. P. and Z. Smilowitz. 1978. Diurnal, seasonal, and relative abundance of *Myzus persicae* (Sulzer) predators. *J.N.Y. Entomol. Soc.* 86: 305.

Maelzer, D. A. 1978. The growth and voracity of larvae of *Leis conformis* (Boisd.) (Coleoptera: Coccinellidae) fed on the rose aphid *Macrosiphum rosae* (L.) (Homoptera: Aphididae) in the laboratory. *Aust. J. Zool.* 26: 293–304.

Maeta, Y. 1965. Some observations of the habits od two predacious coccinellid beetles, *Harmonia axyridis* Pallas and *Coccinella septempunctata bruckii* Mulsant. *Tohoku Konchu Kenkyu* 1: 83–94. (In Japanese.)

Magro, A., J. N. Téné, 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. 1994. *Ladybirds*. Harper Collins, London. 367 pp.

Majerus M. E. N. 2006. The impact of male-killing bacteria on the evolution of aphidophagous coccinellids. *Eur. J. Entomol.* 103: 1–7.

Majerus, M. E. N. and G. D. D. Hurst. 1997. Ladybirds as a model system for the study of male-killing symbionts. *Entomophaga* 42: 13–20.

Majerus, M. E. N. and P. Kearns. 1989. *Ladybirds*. Richmond Publishing Co., London. 103 pp.

Majerus, M. E. N. and T. M. O. Majerus. 1996. Ladybird population explosions. *Brit. J. Entomol. Nat. Hist.* 9: 65–76.

Majerus, M. E. N., J. J. Sloggett, J.-F. Godeau and J.-L. Hemptinne. 2007. Interactions between ants and aphidophagous and coccidophagous ladybirds. *Popul. Ecol.* 49: 15–27.

Malcolm, S. B. 1990. Chemical defence in chewing and sucking insect herbivores: plant-derived cardenolides in the monarch butterfly and oleander aphid. *Chemoecology* 1: 12–21.

Mallampalli, N., F. Gould and P. Barbosa. 2005. Predation of Colorado potato beetle eggs by a polyphagous ladybeetle in the presence of alternate prey: potential impact on resistance evolution. *Entomol. Exp. Appl.* 114: 47–54.

Mandour, N. S., N. A.-S. El-Basha and T.-X. Liu. 2006. Functional response of the ladybird, *Cydonia vicina nilotica* to cowpea aphid, *Aphis craccivora* in the laboratory. *Insect Sci.* 13: 49–54.

Mani, M. and A. Krishnamoorthy. 1990. Evaluation of the exotic predator *Cryptolaemus montrouzieri* Muls. (Coccinellidae, Coleoptera) in the suppression of green shield scale, *Chloropulvinaria psidii* (Maskell) (Coccidae, Hemiptera) on guava. *Entomon* 15: 45–48.

Mansfield, S., J. R. Hagler and M. E. A. Whitehouse. 2008. A comparative study on the efficacy of a pest-specific and prey-marking enzyme-linked immunosorbent assay for detection of predation. *Entomol. Exp. Appl.* 127:199–206.

Maredia, K. M., S. H. Gage, D. A. Landis and J. M. Scriber. 1992. Habitat use patterns by the seven-spotted lady beetle (Coleoptera: Coccinellidae) in a diverse agricultural landscape. *Biol. Contr.* 2: 159–165.

Marks, R. J. 1977. Laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae. *Bull. Entomol. Res.* 67: 235–341.

Martini, X., P. Haccou, I. Olivieri and J.-L. Hemptinne. 2009. Evolution of cannibalism and female's response to oviposition-deterring pheromone in aphidophagous predators. *J. Anim. Ecol.* 78: 964–972.

Martos, A., A. Givovich and H. M. Niemeyer. 1992. Effect of DIMBOA, an aphid resistance factor in wheat, on the aphid predator *Eriopis connexa* Germar (Coleoptera: Coccinellidae). *J. Chem. Ecol.* 18: 469–479.

Matsura, T. 1976. Ecological studies of a coccinellid, *Aiolocaria hexaspilota* Hope. I. Interaction between field populations of *A. hexaspilota* and its prey, the walnut leaf beetle (*Gastrolina depressa* Baly). *Jap. J. Ecol.* 26: 147–156. (In Japanese with English summary.)

McAllister, M. K. and B. D. Roitberg. 1987. Adaptive suicidal behaviour in pea aphids. *Nature* 328: 797–799.

McConnell, J. A. and T. J. Kring. 1990. Predation and dislodgment of *Schizaphis graminum* (Homoptera: Aphididae), by adult *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 19: 1798–1802.

McKenzie, H. L. 1932. The biology and feeding habits of *Hyperaspis lateralis* Mulsant (Coleoptera–Coccinellidae). *Univ. Calif. Publ.* 6: 9–20.

McMillan, S., A. K. Kuusk, A. Cassel-Lundhagen and B. Ekbom. 2007. The influence of time and temperature on molecular gut content analysis: *Adalia bipunctata* fed with *Rhopalosiphum padi*. *Insect Sci.* 14: 353–358.

Mehrnejad, M. R. and M. A. Jalali. 2004. Life history parameters of the coccinellid beetle, *Oenopia conglobata contaminata*, an important predator of the common pistachio psylla, *Agonoscena pistaciae* (Hemiptera: Psylloidea). *Biocontr. Sci. Techn.* 14: 701–711.

van den Meiracker, R. A. F., W. N. O. Hammond and J. J. M. van Alphen. 1990. The role of kairomones in prey finding by *Diomus* sp. and *Exochomus* sp., two coccinellid predators of the cassava mealybug, *Phenacoccus manihoti*. *Entomol. Exp. Appl.* 56: 209–217.

Mendel, Z. and D. Blumberg. 1991. Colonization trials with *Cryptochaetum iceryae* and *Rodolia cardinalis* for improved biological control of *Icerya purchasi* in Israel. *Biol. Contr.* 1: 68–74.

Mendel, Z., D. Blumberg, A. Zehavi and M. Weisenberg. 1992. Some polyphagous Homoptera gain protection from their natural enemies by feeding on the toxic plants *Spartium junceum* and *Erythrina corallodendrum* (Leguminosae). *Chemoecology* 3: 118–124.

Mensah, R. K. 1997. Local density responses of predatory insects of *Helicoverpa* spp. to a newly developed food 'Envirofeast' in commercial cotton in Australia. *Int. J. Pest Manage.* 43: 221–225.

Mensah, R. K. 2002a. Development of an integrated pest management programme for cotton. Part 1: Establishing and utilizing natural enemies. *Int. J. Pest Manage.* 48: 87–94.

Mensah, R. K. 2002b. Development of an integrated pest management programme for cotton. Part 2: Integration of a lucerne/cotton interplant system, food supplement sprays with biological and synthetic insecticides. *Int. J. Pest Manage.* 48: 95–105.

Mensah, R. K. and J. L. Madden. 1994. Conservation of two predator species for biological control of *Chrysophtharta bimaculata* (Col., Chrysomelidae) in Tasmanian forests. *Entomophaga* 39: 71–83.

Mensah, R. K. and A. Singleton. 2003. Optimum timing and placement of a supplementary food spray Envirofeast® for the establishment of predatory insects of *Helicoverpa* spp. in cotton systems in Australia. *Int. J. Pest Manage.* 49: 163–168.

Messina, F. J. and J. B. Hanks. 1998. Host plant alters the shape of the functional response of an aphid predator (Coleoptera: Coccinellidae). *Environ. Entomol.* 27: 1196–1202.

Meyhöfer, R. 2001. Intraguild predation by aphidophagous predators on parasitized aphids: the use of multiple video cameras. *Entomol. Exp. Appl.* 100: 77–87.

Meyhöfer, R. and T. Klug. 2002. Intraguild predation on the aphid parasitoid *Lysiphlebus fabarum* (Marshall) (Hymenoptera: Aphidiidae): mortality risks and behavioral decisions made under the threats of predation. *Biol. Contr.* 25: 239–248.

Michaud, J. P. 2000. Development and reproduction of ladybeetles (Coleoptera: Coccinellidae) on the citrus aphids *Aphis spiraecola* Patch and *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae). *Biol. Contr.* 18: 287–297.

Michaud, J. P. 2001. Numerical response of *Olla v-nigrum* (Coleoptera: Coccinellidae) to infestations of Asian citrus psyllid (Hemiptera: Psyllidae) in Florida. *Florida Entomol.* 84: 608–612.

Michaud, J. P. 2003. A comparative study of larval cannibalism in three species of ladybird. *Ecol. Entomol.* 28: 92–101.

Michaud, J. P. 2005. On the assessment of prey suitability in aphidophagous Coccinellidae. *Eur. J. Entomol.* 102: 385–390.

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 A. K. Grant. 2005. Suitability of pollen sources for the development and reproduction of *Coleomegilla maculata* (Coleoptera: Coccinellidae) under simulated drought conditions. *Biol. Contr.* 32: 363–370.

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.

Michaud, J. P. and J. L. Jyoti. 2008. Dietary complementation across life stages in the polyphagous lady beetle *Coleomegilla maculata*. *Entomol. Exp. Appl.* 126: 40–45.

Michaud, J. P. and L. E. Olsen. 2004. Suitability of Asian citrus psyllid, *Diaphorina citri*, as prey for ladybeetles. *BioControl* 49: 417–431.

Michaud, J. P. and J. A. Qureshi. 2005. Induction of reproductive diapause in *Hippodamia convergens* (Coleoptera: Coccinellidae) hinges on prey quality and availability. *Eur. J. Entomol.* 102: 483–487.

Michaud, J. P. and J. A. Qureshi. 2006. Reproductive diapause in *Hippodamia convergens* (Coleoptera: Coccinellidae) and its life history consequences. *Biol. Contr.* 39: 193–200.

Michels, G. J. and R. V. Flanders. 1992. Larval development, aphid consumption and oviposition for five imported coccinellids at constant temperature on Russian wheat aphids and greenbugs. *Southw. Entomol.* 17: 233–243.

Michels, G. J. and A. C. Bateman. 1986. Larval biology of two imported predators of the greenbug, *Hippodamia variegata* Goeze and *Adalia flavomaculata* DeGeer, under constant temperatures. *Southw. Entomol.* 11: 23–30.

Michels, G. J. and R. W. Behle. 1991a. Effects of two prey species on the development of *Hippodamia sinuata* (Coleoptera: Coccinellidae) larvae at constant temperatures. *J. Econ. Entomol.* 84: 1480–1484.

Michels, G. J. and R. W. Behle. 1991b. A comparison of *Coccinella septempunctata* and *Hippodamia convergens* larval development on greenbugs at constant temperatures. *Southw. Entomol.* 16: 73–80.

Michels, G. J., Jr. and J. D. Burd. 2007. IPM Case Studies: Sorghum. *In* H. F. van Emden and R. Harrington (eds). *Aphids as Crop Pests*. CAB International, Wallingford, UK. pp. 627–638.

Michels, G. J., Jr. and J. H. Matis. 2008. Corn leaf aphid, *Rhopalosiphum maidis* (Hemiptera: Aphididae), as a key to greenbug, *Schizaphis graminum* (Hemiptera: Aphididae), biological control in grain sorghum, *Sorghum bicolor*. *Environ. Entomol.* 105: 513–520.

Mignault, M. P., M. Roy and J. Brodeur. 2006. Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *BioControl* 51: 89–106.

Mills, N. J. 1979. Adalia bipunctata *(L.) as a generalist predator of aphids*. PhD thesis, University East Anglia, Norwich.

Mills, N. J. 1981. Essential and alternative foods for some British Coccinellidae (Coleoptera). *Entomol. Gaz.* 32: 197–202.

Mills, N. J. 1982a. Satiation and the functional response: a test of a new model. *Ecol. Entomol.* 7: 305–315.

Mills, N. J. 1982b. Voracity, cannibalism, and coccinellid predation. *Ann. Appl. Biol.* 101: 144–148.

Mills, N. J. and J. M. Kean. 2010. Behavioral studies, molecular approaches, and modelling: Methodological contributions to biological control success. *Biol. Contr.* 52: 255–262.

Mills, N. J. and I. Lacan. 2004. Ratio dependence in the functional response of insect parasitoids: evidence from *Trichogramma minutum* foraging for eggs in small host patches. *Ecol. Entomol.* 29: 208–216.

Minoretti, N. and W. W. Weisser. 2000. The impact of individual ladybirds (*Coccinella septempunctata*, Coleoptera:

Coccinellidae) on aphid colonies. *Eur. J. Entomol.* 97: 475–479.

Miura, T. and S. Nishimura. 1980. The larval period and predaceous activity of an aphidophagous coccinellid, *Harmonia axyridis* Pallas. *Bull. Fac. Agric. Shimane Univ.* 14: 144–148.

Mogi, M. 1969. Predation response of the larvae of *Harmonia axyridis* Pallas (Coccinellidae) to the different prey density. *Jap. J. Appl. Entomol. Zool.* 13: 9–16.

Mondor, E. B. and B. D. Roitberg. 2000. Has the attraction of predatory coccinellids to cornicle droplets constrained aphid alarm signalling behavior? *J. Insect Behav.* 13: 321–329.

Mondor, E. B. and B. D. Roitberg. 2004. Inclusive fitness benefits of scent-marking predators. *Proc. R. Soc. London B* 271: S341–S343.

Mondor, E. B. and J. L. Warren. 2000. Unconditioned and conditioned responses to colour in the predatory coccinellid, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 97: 463–467.

Morales, J. and C. L. Burandt Jr. 1985. Interactions between *Cycloneda sanguinea* and the brown citrus aphid: adult feeding and larval mortality. *Environ. Entomol.* 14: 520–522.

Mori, K., M. Nozawa, K. Arai and T. Gotoh. 2005. Life-history traits of the acarophagous lady beetle, *Stethorus japonicus* at three constant temperatures. *BioControl* 50: 35–51.

Moser, S. E. and J. J. Obrycki. 2009. Non-target effects of neonicotinoid seed treatments; mortality of coccinellid larvae related to zoophytophagy. *Biol. Contr.* 51: 487–492.

Moser, S. E., J. D. Harwood and J. J. Obrycki. 2008. Larval feeding on *Bt* hybrid and non-*Bt* corn seedlings by *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 37: 525–533.

Moura, R., P. Garcia, S. Cabral and A. O. Soares. 2006. Does pirimicarb affect the voracity of the euryphagous predator, *Coccinella undecimpunctata* L. (Coleoptera: Coccinellidae)? *Biol. Contr.* 38: 363–368.

Moursi, A. A. and M. Kamal. 1946. Notes on the biology and feeding habits of the introduced beneficial insect *Leis conformis* Boisd. (Coccinell.) *Bull. Soc. Fouad I. Entomol.* 30: 63–74.

Müller, C. B. and H. C. J. Godfray. 1997. Apparent competition between two aphid species. *J. Anim. Ecol.* 66: 57–64.

Muma, M. H. 1955. Some ecological studies on the twice stabbed lady beetle, *Chilocorus stigma* (Say). *Ann. Entomol. Soc. Am.* 48: 493–498.

Munyaneza, J. and J. J. Obrycki. 1997. Functional response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle eggs (Coleoptera: Chrysomelidae). *Biol. Contr.* 8: 215–224.

Murdie, G. 1971. Simulation on the effects of predators/parasite models on prey/host spatial distribution. *In* G. P. Patil, E. C. Pielou, W. E. Waters (eds). *Statistical Ecology 1.* Pennsylvania State University Press, Harrisburg. pp. 215–223.

Murdoch, W. W. and J. R. Marks. 1973. Predation by coccinellid beetles: experiments on switching. *Ecology* 54: 159–167.

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.

Nakamura, K., N. Hasan, L. Abbas, H. C. J. Godfray and M. B. Bonsall. 2004. Generation cycles in Indonesian lady beetle populations may occur as a result of cannibalism. *Proc. R. Soc. Lond. B* 271: S501–S504.

Nakamura, K., K. Miura, P. De Jong and H. Ueno. 2006. Comparison of the incidence of sibling cannibalism between male-killing *Spiroplasma* infected and uninfected clutches of a predatory ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 103: 323–326.

Nakamuta, K. 1984a. Aphid body fluid stimulates feeding of a predatory ladybeetle, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 19: 123–125.

Nakamuta, K. 1984b. Visual orientation of a ladybeetle, *Coccinella septempunctata* L., (Coleoptera: Coccinellidae), towards its prey. *Appl. Entomol. Zool.* 19: 82–86.

Nakamuta, K. 1985a. Area-concentrated search in adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae): Releasing stimuli and decision of giving-up time. *Jpn. J. Appl. Entomol. Zool.* 29: 55–60. (In Japanese with English summary.)

Nakamuta, K. 1985b. Mechanism of the switchover from extensive to area-concentrated search behaviour of the ladybird beetle, *Coccinella septempunctata bruckii*. *J. Insect Physiol.* 31: 849–856.

Nakamuta, K. 1987. Diel rhythmicity of prey-searching activity and its predominance over starvation in the lady beetle, *Coccinella septempunctata bruckii*. *Physiol. Entomol.* 1: 91–98.

Nakamuta, K. and T. Saito. 1985. Recognition of aphid prey by the lady beetle, *Coccinella septempunctata brucki* Mulsant (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 20: 479–483.

Nakashima, Y. and Y. Hirose. 1999. Effects of prey availability on longevity, prey consumption, and egg production in the insect predators *Orius sauteri* and *O. tantillus* (Hemiptera: Anthocoridae). *Ann. Entomol. Soc. Am.* 92: 537–541.

Nakashima, Y. and N. Senoo. 2003. Avoidance of ladybird trails by an aphid parasitoid *Aphidius ervi*: active period and effects of prior oviposition experience. *Entomol. Exp. Appl.* 109: 163–166.

Nalepa, C. A., S. B. Bambara and A. M. Burroughs. 1992. Pollen and nectar feeding by *Chilocorus kuwanae* (Silvestri) (Coleoptera: Coccinellidae). *Proc. Entomol. Soc. Wash.* 94: 596–597.

Nalepa, C. A., K. R. Ahlstrom, B. A. Nault and J. L. Williams. 1998. Mass appearance of ladybeetles (Coleoptera: Coccinellidae) on North Carolina beaches. *Entomol. News* 109: 277–281.

Napal, G. N. D., M. T. Defago, G. R. Valladares and S. M. Palacios. 2010. Response of *Epilachna paenulata* to two flavonoids, Pinocembrin and Quercetin, in a comparative study. *J. Chem. Ecol.* 36: 898–904.

Naranjo, S. E., R. L. Gibson and D. D. Walgenbach. 1990. Development, survival, and reproduction of *Scymnus frontalis* (Coleoptera: Coccinellidae), an imported predator of Russian wheat aphid, at four fluctuating temperatures. *Ann. Entomol. Soc. Am.* 83: 527–531.

Nault, B. A. and G. G. Kennedy. 2000. Seasonal changes in habitat preference by *Coleomegilla maculata*: implications for Colorado potato beetle management in potato. *Biol. Contr.* 17: 164–173.

Nedvěd, O. and S. Salvucci. 2008. Ladybird *Coccinella septempunctata* (Coleoptera: Coccinellidae) prefers toxic prey in laboratory choice experiment. *Eur. J. Entomol.* 105: 431–436.

Nelson, E. and J. A. Rosenheim. 2006. Encounters between aphids and their predators: the relative frequencies of disturbance and consumption. *Entomol. Exp. Appl.* 118: 211–218.

Ng, S. M. 1986a. Effects of sibling egg cannibalism on the first instar larvae of four species of aphidophagous Coccinellidae. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht, The Netherlands. pp. 69–75.

Ng, S. M. 1986b. The geotactic and phototactic responses of four species of aphidophagous coccinellid larvae. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht, The Netherlands. pp. 57–68.

Ng, S. M. 1988. Observations on the foraging behaviour of starved aphidophagous coccinellid larvae (Coleoptera: Coccinellidae). *In* E. Niemczyk and A. F. G. Dixon (eds). *Ecology and Effectiveness of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 29–33.

Nichols, P. R. and W. W. Neel. 1977. The use of Food Wheast® as a supplemental food for *Coleomegilla maculata* (DeGeer) (Coleoptera: Coccinellidae) in the field. *Southw. Entomol.* 2: 102–105.

Nielsen, F. H., M. S. Hauge and S. Toft. 2002. The influence of mixed aphid diets on larval performance of *Coccinella septempunctata* (Col., Coccinellidae). *J. Appl. Entomol.* 126: 194–197.

Nielson, M. W. and W. E. Currie. 1960. Biology of the convergent lady beetle when fed a spotted alfalfa aphid diet. *J. Econ. Entomol.* 53: 257–259.

Niijima, K. 1979. Further attempts to rear coccinellids on drone powder with field observation. *Bull. Fac. Agric. Tamagawa Univ.* 19: 7–12.

Niijima, K., M. Matsuka and I. Okada. 1986. Artificial diets for an aphidophagous coccinellid, *Harmonia axyridis*, and its nutrition. (Minireview). *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht, The Netherlands. pp. 37–50.

Ninkovic, V., S. AlAbassi and J. Pettersson. 2001. The influence of aphid-induced plant volatiles on ladybird beetle searching behavior. *Biol. Contr.* 21: 191–195.

Nishida, R. and H. Fukami. 1989. Host plant iridoid-based chemical defense of an aphid, *Acyrthosiphon nipponicus*, against ladybird beetles. *J. Chem. Ecol.* 15: 1837–1845.

Nixon, G. E. 1951. *The Association of Ants with Aphids and Coccids*. Commonwealth Inst. Entomol., London. 36 pp.

Nomura, M. and K. Niijima. 1997. Effect of contagion and cannibalism on the abnormal sex ratio in *Menochilus sexmaculatus* (Fabricius)(Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* 32: 501–504.

Nonacs, P. and L. M. Dill. 1993. Is satisficing an alternative to optimal foraging theory? *Oikos* 67: 371–375.

O'Neil, R. J. 1989. Comparison between laboratory and field measurements of the functional response of *Podisus maculiventris* (Heteroptera: Pentatomidae). *J. Kans. Entomol. Soc.* 62: 148–155.

O'Neil, R. J. 1997. Functional response and search strategy of *Podisus maculiventris* (Heteroptera: Pentatomidae) attacking Colorado potato beetle (Coleoptera: Chrysomelidae). *Environ. Entomol.* 26: 1183–1190.

O'Neil, R. J. and R. N. Wiedenmann. 1987. Adaptations of arthropod predators to agricultural systems. *Florida Entomol.* 70: 40–48.

Obata, S. 1986. Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* (Col.: Coccinellidae). *Entomophaga* 31: 303–311.

Obata, S. 1997. The influence of aphids on the behaviour of adults of the ladybird beetle, *Harmonia axyridis* (Col.: Coccinellidae). *Entomophaga* 42: 103–106.

Obata, S. and T. Hidaka. 1987. Ejection and ingestion of the spermatophore by the female beetle, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Can. Entomol.* 119: 603–604.

Obata, S. and Y. Johki. 1990. Distribution and behaviour of adult ladybird, *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae), around aphid colonies. *Jpn. J. Entomol.* 58: 839–845.

Obatake, H. and H. Suzuki. 1985. On the isolation and identification of canavanine and ethanolamine contained in the young leaves of black locus, *Robinia pseudoacacia*, lethal for the lady beetle, *Harmonia axyridis*. *Techn. Bull. Fac. Agr., Kagawa Univ.* 36: 107–115.

Obrycki, J. J. and C. J. Orr. 1990. Suitability of three prey species for Nearctic populations of *Coccinella septempunctata, Hippodamia variegata*, and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae). *J. Econ. Entomol.* 83: 1292–1297.

Obrycki, J. J. and M. J. Tauber. 1984. Natural enemy activity on glandular pubescent potato plants in the greenhouse: an unreliable predictor of effects in the field. *Environ. Entomol.* 13: 679–683.

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. 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. *Oecologia* 117: 279–285.

Ofuya, T. I. and A. E. Akingbohungbe. 1988. Functional and numerical responses of *Cheilomenes lunata* (Fabricius) (Coleoptera: Coccinellidae) feeding on the cowpea aphid, *Aphis craccivora* Koch (Homoptera: Aphididae). *Insect Sci. Applic.* 9: 543–546.

Ohashi, K., Y. Sakuratani, N. Osawa, S. Yano and A. Takafuji. 2005. Thermal microhabitat use by the ladybird beetle, *Coccinella septempunctata* (Col., Coccinellidae), and its life cycle consequences. *Environ. Entomol.* 34: 432–439.

Ohgushi, T. 1996. Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle. *Ecol. Entomol.* 21: 47–55.

Ohgushi, T. and H. Sawada. 1985. Population equilibrium with respect to available food resource and its behavioural basis in a herbivorous lady beetle, *Henosepilachna niponica*. *J. Anim. Ecol.* 54: 781–796.

Ohgushi, T. and H. Sawada. 1995. Demographic attributes of an introduced herbivorous lady beetle. *Res. Popul. Ecol.* 37: 29–36.

Ohgushi, T. and H. Sawada. 1998. What changed the demography of an introduced population of an herbivorous lady beetle? *J. Anim. Ecol.* 67: 679–688.

Okada, I. 1970. A new method of artificial rearing of coccinellid, *Harmonia axyridis* Pallas. *Heredity, Tokyo* 24: 32–35. (In Japanese.)

Okamoto, H. 1961. Comparison of ecological characters of the predatory ladybird *Coccinella septempunctata bruckii* fed on the apple grain aphids, *Rhopalosiphum prunifoliae* and the cabbage aphids, *Brevicoryne brassicae*. *Jap. J. Appl. Entomol. Zool.* 5: 277–278. (In Japanese.)

Okamoto, H. 1966. Three problems of prey specificity of aphidophagous coccinellids. *In* I. Hodek (ed.) *Ecology of Aphidophagous Insects*. Academia, Prague and W. Junk, The Hague. pp. 45–46.

Okamoto, H. 1978. Laboratory studies on food ecology of aphidophagous lady beetles (Coleoptera: Coccinellidae). *Mem. Fac. Agric. Kagawa Univ.* 32: 1–94. (In Japanese.)

Okuyama, T. 2008. Individual behavioral variation in predator–prey models. *Ecol. Res.* 23: 665–671.

Oliver, T. H., J. E. L. Timms, A. Taylor and S. R. Leather. 2006. Oviposition responses to patch quality in the larch ladybird *Aphidecta obliterata* (Coleoptera: Coccinellidae): effects of aphid density, and con- and heterospecific tracks. *Bull. Entomol. Res.* 96: 25–34.

Olszak, R. W. 1988. Voracity and development of three species of Coccinellidae, preying upon different species of aphids. *In* E. Niemczyk and A. F. G. Dixon (eds). *Ecology and Effectiveness of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 47–53.

Omkar and R. B. Bind. 2004. Prey quality dependent growth, development and reproduction of a biocontrol agent, *Cheilomenes sexmaculata* (Fabricius) (Coleoptera: Coccinellidae). *Biocontr. Sci. Techn.* 14: 665–673.

Omkar and B. E. James. 2004. Influence of prey species on immature survival, development, predation and reproduction of *Coccinella transversalis* Fabricius (Col., Coccinellidae). *J. Appl. Entomol.* 128: 150–157.

Omkar and G. Mishra. 2005. Preference–performance of a generalist predatory ladybird: a laboratory study. *Biol. Contr.* 34: 187–195.

Omkar and S. Pathak. 2006. Effects of different photoperiods and wavelengths of light on the life-history traits of an aphidophagous ladybird, *Coelophora saucia* (Mulsant). *J. Appl. Entomol.* 130: 45–50.

Omkar and A. Pervez. 2004. Functional and numerical responses of *Propylea dissecta* (Col., Coccinellidae). *J. Appl. Entomol.* 128: 140–146.

Omkar and S. Srivastava. 2003. Influence of six aphid prey species on development and reproduction of a ladybird beetle, *Coccinella septempunctata*. *BioControl* 48: 379–393.

Omkar, A. Pervez and A. K. Gupta. 2006a. Attack, escape and predation rates of two aphidophagous ladybirds during conspecific and heterospecific interactions. *Biocontr. Sci. Techn.* 16: 295–305.

Omkar, A. Pervez and A. K. Gupta. 2006b. Why do neonates of aphidophagous ladybird beetles preferentially consume conspecific eggs in presence of aphids? *Biocontr. Sci. Techn.* 16: 233–243.

Omkar, A. Pervez and A. K. Gupta. 2007. Sibling cannibalism in aphidophagous ladybirds: its impact on sex-dependent development and body weight. *J. Appl. Entomol.* 131: 81–84.

Omkar, G. Mishra, S. Srivastava, A. K. Gupta and S. K. Singh. 2005. Reproductive performance of four aphidophagous ladybirds on cowpea aphid, *Aphis craccivora* Koch. *J. Appl. Entomol.* 129: 217–220.

Orr, C. J. and J. J. Obrycki. 1990. Thermal and dietary requirements for development of *Hippodamia parenthesis* (Coleoptera: Coccinellidae). *Environ. Entomol.* 19: 1523–1527.

Osawa, N. 1989. Sibling and non-sibling cannibalism by larvae of a lady beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae) in the field. *Res. Popul. Ecol.* 31: 153–160.

Osawa, N. 1992a. A life table of the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae) in relation to the aphid abundance. *Jpn. J. Entomol.* 60: 575–579.

Osawa, N. 1992b. Effect of pupation site on pupal cannibalism and parasitism in the ladybird beetle *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). *Jpn. J. Entomol.* 60: 131–135.

Osawa, N. 1992c. Sibling cannibalism in the ladybird beetle *Harmonia axyridis*: fitness consequences for mother and offspring. *Res. Popul. Ecol.* 34: 45–55.

Osawa, N. 1993. Population field studies of the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): life tables and key factor analysis. *Res. Popul. Ecol.* 35: 335–348.

Osawa, N. 2000. Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. *Popul. Ecol.* 42: 115–127.

Osawa, N. 2002. Sex-dependent effects of sibling cannibalism on life history traits of the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biol. J. Linn. Soc.* 76: 349–360.

Osawa, N. 2003. The influence of female oviposition strategy on sibling cannibalism in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 100: 43–48.

Osawa, N. 2005. The effect of prey availability on ovarian development and oosorption in the ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 102: 503–511.

Osawa N. and K. Ohashi. 2008. Sympatric coexistence of sibling species *Harmonia yedoensis* and *H. axyridis* (Coleoptera: Coccinellidae) and the roles of maternal investment through egg and sibling cannibalism. *Eur. J. Entomol.* 105: 445–454.

Ozder, N. and O. Saglam. 2003. Effects of aphid prey on larval development and mortality of *Adalia bipunctata* and *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Biocontr. Sci. Techn.* 13: 449–453.

Palmer, M. A. 1914. Some notes on life history of lady beetles. *Ann. Entomol. Soc. Am.* 7: 213–238.

Pantyukhov, G. A. 1968. A study of ecology and physiology of the predatory beetle *Chilocorus rubidus* Hope (Coleoptera, Coccinellidae). *Zool. Zh.* 47: 376–386. (In Russian with English summary.)

Papachristos, D. P. and P. G. Milonas. 2008. Adverse effects of soil applied insecticides on the predatory coccinellid *Hippodamia undecimnotata* (Coleoptera: Coccinellidae). *Biol. Contr.* 47: 77–81.

Parajulee, M. N., R. B. Shrestha, J. F. Leser, D. B. Wester and C. A. Bianco. 2006. Evaluation of the functional response of selected arthropod predators on bollworm eggs in the laboratory and effect of temperature on their predation efficiency. *Environ. Entomol.* 35: 379–386.

Park, Y. L. and J. J. Obrycki. 2004. Spatio-temporal distribution of corn leaf aphids (Homoptera: Aphididae) and lady beetles (Coleoptera: Coccinellidae) in Iowa cornfields. *Biol. Contr.* 31: 210–217.

Pasteels, J. M. 2007. Chemical defence, offence and alliance in ants–aphids–ladybirds relationships. *Popul. Ecol.* 49: 5–14.

Perry, J. C. and B. D. Roitberg. 2005. Ladybird mothers mitigate offspring starvation risk by laying trophic eggs. *Behav. Ecol. Sociobiol.* 58: 578–586.

Perry, J. C. and B. D. Roitberg. 2006. Trophic egg laying: hypothesis and tests. *Oikos* 112: 706–714.

Perry, J. C. and L. Rowe. 2008. Neither mating rate nor spermatophore feeding influences longevity in a ladybird beetle. *Ethology* 114: 504–511.

Persad, A. and A. Khan. 2002. Comparison of life table parameters for *Maconellicoccus hirsutus*, *Anagyrus camali*, *Cryptolaemus montrouzieri* and *Scymnus coccivora*. *BioControl* 47: 137–149.

Pervez, A. and Omkar. 2004. Prey dependent life attributes of an aphidophagous ladybird beetle, *Propylea dissecta* (Coccinellidae). *Biocontr. Sci. Techn.* 14: 385–396.

Pervez, A., A. K. Gupta and Omkar. 2005. Kin recognition and avoidance of kin cannibalism by the larvae of co-occurring ladybirds: a laboratory study. *Eur. J. Entomol.* 102: 513–518.

Pervez, A., A. K. Gupta and Omkar. 2006. Larval cannibalism in aphidophagous ladybirds: Influencing factors, benefits and costs. *Biol. Contr.* 38: 307–313.

Peterson, P. G., P. G. McGregor and B. P. Springett. 2000. Density dependent prey feeding time of *Stethorus bifidus* (Coleoptera: Coccinellidae) on *Tetranychus lintearius (*Acari: Tetranychidae). *N. Z. J. Zool.* 27: 41–44.

Pettersson, J., V. Ninkovic, R. Glinwood et al. 2008. Chemical stimuli supporting foraging behaviour of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae): volatiles and allelobiosis. *Appl. Entomol. Zool.* 43: 315–321.

Pfannenstiel, R. S. and K. V. Yeargan. 2002. Identification and diel activity patterns of predators attacking *Helicoverpa zea* (Lepidoptera: Noctuidae) eggs in soybean and sweet corn. *Environ. Entomol.* 31: 232–241.

Phoofolo, M. W., N. C. Elliott and K. L. Giles. 2009. Analysis of growth and development in the final instar of three species of predatory coccinellids under varying prey availability. *Entomol. Exp. Appl.* 131: 264–277.

Phoofolo, M. W., K. L. Giles and N. C. Elliott. 2007. Quantitative evaluation of suitability of the greenbug, *Schizaphis graminum*, and the bird cherry-oat aphid, *Rhopalosiphum padi*, as prey for *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biol. Contr.* 41: 25–32.

Phoofolo, M. W., K. L. Giles and N. C. Elliott. 2008. Larval life history responses to food deprivation in three species of predatory lady beetles (Coleoptera: Coccinellidae). *Environ. Entomol.* 37: 315–322.

Pickett, C. H., K. A. Casanave, S. E. Schoenig and K. M. Heinz. 1999. Rearing *Delphastus catalinae* (Coleoptera: Coccinellidae): Practical experience and a modeling analysis. *Can. Entomol.* 131: 115–129.

Pickett, J. A. and R. T. Glinwood. 2007. Chemical ecology. *In* H. F. van Emden and R. Harrington (eds). *Aphids as Crop Pests*. CABI, UK. pp. 235–260.

Pilipjuk, V. I., L. N. Bugaeva and E. V. Baklanova. 1982. On the possibility of breeding of the predatory beetle *Cryptolaemus montrouzieri* Muls. (Coleoptera, Coccinellidae) on the eggs of *Sitotroga cerealella* Ol. *Entomol. Obozr.* 1: 50–52. (In Russian.)

Pilorget, L., J. Buckner and J. G. Lundgren. 2010. Sterol limitation in a pollen-fed omnivorous lady beetle (Coleoptera: Coccinellidae). *J. Insect Physiol.* 56: 81–87.

Piñol, J., X. Espalader, N. Canellas and N. Perez. 2009. Effects of the concurrent exclusion of ants and earwigs on aphid abundance in an organic citrus grove. *BioControl* 54: 515–527.

Pinto, D. M., J. D. Blande, R. Nykaenen et al. 2007. Ozone degrades common herbivore-induced plant volatiles: does this affect herbivore prey location by predators and parasitoids? *J. Chem. Ecol.* 33: 683–694.

Podoler, H. and J. Henen. 1986. Foraging behavior of two species of the genus *Chilocorus* (Coccinellidae: Coleoptera): a comparative study. *Phytoparasitica* 14: 11–23.

Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* 12: 225–251.

Ponsonby, D. J. and M. J. W. Copland. 1996. Effect of temperature on development and immature survival in the scale insect predator, *Chilocorus nigritus* (F.) (Coleoptera: Coccinellidae). *Biocontr. Sci. Techn.* 6: 101–109.

Ponsonby, D. J. and M. J. W. Copland. 1998. Environmental influences on fecundity, egg viability and egg cannibalism in the scale insect predator, *Chilocorus nigritus*. *BioControl* 43: 39–52.

Ponsonby, D. J. and M. J. W. Copland. 2000. Maximum feeding potential of larvae and adults of the scale insect predator, *Chilocorus nigritus* with a new method of estimating food intake. *BioControl* 45: 295–310.

Ponsonby, D. J. and M. J. W. Copland. 2007a. Aspects of prey relations in the coccidophagous ladybird *Chilocorus nigritus* relevant to its use as a biological control agent of scale insects in temperate glasshouses. *BioControl* 52: 629–640.

Ponsonby, D. J. and M. J. W. Copland. 2007b. Influence of host density and population structure on egg production in the coccidophagous ladybird, *Chilocorus nigritus* F. (Coleoptera: Coccinellidae). *Agr. Forest Entomol.* 9: 287–296.

Poutiers, R. 1930. Sur le comportement du *Novius cardinalis* vis-à-vis de certain alcaloides. *C. R. Séanc. Soc. Biol.* 103: 1023–1025.

Powell, B. E. and J. Silverman. 2010. Impact of *Linepithema humile* and *Tapinoma sessile* (Hymenoptera: Formicidae) on three natural enemies of *Aphis gossypii* (Hemiptera: Aphididae). *Biol. Contr.* 54: 285–291.

Prasad, R. P. and W. E. Snyder. 2010. A non-trophic interaction chain links predators in different spatial niches. *Oecologia* 162: 747–753.

Pratt, C., T. W. Pope, G. Powell and J. T. Rossiter. 2008. Accumulation of glucosinolates by the cabbage aphid *Brevicoryne brassicae* as a defense against two coccinellid species. *J. Chem. Ecol.* 34: 323–329.

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.

Pruszynski, S. and J. J. Lipa. 1971. The occurrence of predatory Coccinellidae on alfalfa crops. *Ekol. Pol.* 19: 365–386.

Pulliam, H. R. 1975. Diet optimization with nutrient constraints. *Am. Nat.* 109: 765–768.

Putman, W. L. 1955. Bionomics of *Stethorus punctillum* Weise in Ontario. *Can. Entomol.* 87: 9–33.

Putman, W. L. 1957. Laboratory studies on the food of some coccinellids (Coleoptera) found in Ontario peach orchards. *Can. Entomol.* 89: 527–579.

Putman, W. L. 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. *Can. Entomol.* 96: 1149–1155.

Puttarudriah, M. and G. P. Channabasavanna. 1952. Two giant ladybird beetles predaceous on aphids in Mysore. *Indian J. Entomol.* 14: 1.

Puttarudriah, D. M. and B. M. Maheswariah. 1966. Biology, fecundity and rate of feeding of *Synonycha grandis* Thunberg. *Proc. 2nd All-Ind. Congress*, Varanasi 1962, pt. 2.

Qin, J. 1988. Effect on the performance of *Coccinella septempunctata* of altering the components in a simplified diet devoid of insect material. *In* E. Niemczyk and A. F. G. Dixon (eds). *Ecology and Effectiveness of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 55–59.

Quezada, J. R. and P. DeBach. 1973. Bioecological and population studies of the cottony-cushion scale, *Icerya purchasi* Mask., and its natural enemies, *Rodolia cardinalis* Mul. and *Cryptochaetum iceryae* Will., in southern California. *Hilgardia* 41: 631–688.

Quilici, S. and G. Iperti. 1986. The influence of host–plant on the searching ability of first instar larvae of *Propylea quatuordecimpunctata*. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht, The Netherlands. pp. 99–106.

Racioppi, J. V., R. L. Burton and R. Eikenbary. 1981. The effects of various oligidic synthetic diets on the growth of *Hippodamia convergens*. *Entomol. Exp. Appl.* 30: 68–72.

Radcliffe, E. B., R. W. Weires, R. E. Stucker and D. K. Barnes. 1976. Influence of cultivars and pesticides on pea aphid, spotted alfalfa aphid, and associated arthropod taxa in a Minnesota alfalfa ecosystem. *Environ. Entomol.* 5: 1195–1207.

Radwan, Z. and G. L. Lövei. 1983. Aphids as prey for the coccinellid *Exochomus quadripustulatus*. *Entomol. Exp. Appl.* 34: 283–286.

Rana, J. S. 2006. Response of *Coccinella septempunctata* and *Menochilus sexmaculatus* (Coleoptera: Coccinellidae) to their aphid prey, *Lipaphis erysimi* (Hemiptera: Aphididae) in rapeseed-mustard. *Eur. J. Entomol.* 103: 81–84.

Rana, J. S., A. F. G. Dixon and V. Jarosik. 2002. Costs and benefits of prey specialization in a generalist insect predator. *J. Anim. Ecol.* 71: 15–22.

Rand, T. A. and S. M. Louda. 2006. Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragmented landscapes. *Conserv. Biol.* 20: 1720–1729.

Raubenheimer, D. and S. J. Simpson. 1999. Integrating nutrition: a geometrical approach. *Entomol. Exp. Appl.* 91: 67–82.

Raubenheimer, D., S. J. Simpson and D. Mayntz. 2009. Nutrition, ecology and nutritional ecology: toward an integrated framework. *Func. Ecol.* 23: 4–16.

Raymond, B., A. C. Darby and A. E. Douglas. 2000. The olfactory responses of coccinellids to aphids on plants. *Entomol. Exp. Appl.* 95: 113–117.

Ren, S.-X., P. A. Stansly and T.-X. Liu. 2002. Life history of the whitefly predator *Nephaspis oculatus* (Coleoptera: Coccinellidae) at six constant temperatures. *Biol. Contr.* 23: 262–268.

Reynolds, A. M. 2007. Avoidance of conspecific odour trails results in scale-free movement patterns and the execution of an optimal searching strategy. *Europhysics Lett.* 79.

Rhamhalinghan, M. 1985. Intraspecific variations in ovariole number/ovary in *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Ind. Zool.* 9: 91–97.

Ricci, C. 1979. L'apparato boccale pungente succhiante della larva di *Platynaspis luteorubra* Goeze (Col., Coccinellidae). *Boll. Lab. Entomol. Agr. 'F. Silvestri'* 36: 179–198. (In Italian with English summary.)

Ricci, C. 1982. Constitution and function of the mandibles in *Tytthaspis sedecimpunctata* (L.) and *Tytthaspis trilineata* (Weise) larvae. *Frustula Entomol.* 3: 205–212. (In Italian with English summary).

Ricci, C. 1986a. Food strategy of *Tytthaspis sedecimpunctata* in different habitats. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht, The Netherlands. pp. 311–316.

Ricci, C. 1986b. Seasonal food preferences and behaviour of *Rhyzobius litura*. *In* I. Hodek (ed.). *Ecology of Aphidophaga*. Academia, Prague and W. Junk, Dordrecht, The Netherlands. pp. 119–123.

Ricci, C. and L. Ponti. 2005. Seasonal food of *Ceratomegilla notata* (Coleoptera: Coccinellidae) in mountain environments of northern Italian Alps. *Eur. J. Entomol.* 102: 527–530.

Ricci, C., G. Fiori and S. Colazza. 1983. Regime alimentare dell'adulto di *Tytthaspis sedecimpunctata* (L.) (Coleoptera Coccinellidae) in ambiente a influenza antropica primaria: prato polifita. *Atti XIII Congr. Naz. Ital. Entomol.*, Sestriere-Torino, 691–698. (In Italian with English summary.)

Ricci, C., L. Ponti and A. Pires. 2005. Migratory flight and pre-diapause feeding of *Coccinella septempunctata* (Coleoptera) adults in agricultural and mountain ecosystems of Central Italy. *Eur. J. Entomol.* 102: 531–538.

Ricci, C., A. Primavera and V. Negri. 2006. Effects of low temperatures on *Chilocorus kuwanae* (Coleoptera: Coccinellidae) trophic activity. *Eur. J. Entomol.* 103: 547–551.

Richards, A. M. 1980. Defensive adaptations and behaviour in *Scymnodes lividigaster* (Coleoptera: Coccinellidae). *J. Zool. Lond.* 192: 157–168.

Richards, A. M. 1981. *Rhyzobius ventralis* (Erichson) and *R. forestieri* (Mulsant) (Coleoptera: Coccinellidae), their biology and value for scale insect control. *Bull. Entomol. Res.* 71: 33–46.

Richards, A. M. 1985. Biology and defensive adaptations in *Rodatus major* (Coleoptera: Coccinellidae) and its prey, *Monophlebulus pilosior* (Hemiptera: Margarodidae). *J. Zool. Lond.* 205: 287–295.

Richards, A. M. and C. Goletsos. 1991. Feeding behaviour in Australian aphidophagous Coccinellidae. *In* L. Polgar, R. J. Chambers, A. F. G. Dixon and I. Hodek (eds). *Behaviour and Impact of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 227–234.

Riffell, J. A., L. Abrell and J. G. Hildebrand. 2008. Physical processes and real-time chemical measurement of the insect olfactory environment. *J. Chem. Ecol.* 34: 837–853.

Risch, S. J., R. Wrubel and D. Andow. 1982. Foraging by a predaceous beetle, *Coleomegilla maculata* (Coleoptera: Coccinellidae), in a polyculture: effects of plant density and diversity. *Environ. Entomol.* 11: 949–950.

Robinson, A. G. 1951. Annotated list of predators of Tetranychid mites in Manitoba. *Rep. Entomol. Soc. Ont.* 82: 33–37.

Robinson, J. 1992. Predators and parasitoids of Russian wheat aphid in Central Mexico. *Southw. Entomol.* 17: 185–186.

Roger, C., D. Coderre and G. Boivin. 2000. Differential prey utilization by the generalist predator *Coleomegilla maculata lengi* according to prey size and species. *Entomol. Exp. Appl.* 94: 3–13.

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.

Rogers, D. J. 1972. Random search and insect population models. *J. Anim. Ecol.* 41: 369–383.

Roitberg, B. D. 1993. Towards a general theory of host acceptance by aphid parasitoids. *Eur. J. Entomol* 90: 369–376.

Roitberg, B. D. and J. H. Myers. 1978. Effect of adult coccinellidae on the spread of a plant virus by an aphid. *J. Appl. Ecol.* 15: 775–779.

Roitberg, B. D., J. H. Myers and B. D. Frazer. 1979. The influence of predators on the movement of apterous pea aphids between plants. *J. Anim. Ecol.* 48: 111–122.

Rolley, F., I. Hodek and G. Iperti. 1974. Influence de la nourriture aphidienne (selon l'âge de la plante–hôte à partir de laquelle les pucerons se multiplient) sur l'induction de la dormance chez *Semiadalia undecimnotata* Schn. (Coleoptera: Coccinellidae). *Ann. Zool.-Écol. Anim.* 6: 53–60.

Rothschild, M., J. von Euw and T. Reichstein. 1970. Cardiac glycosides in the oleander aphid *Aphis nerii*. *J. Insect Physiol.* 16: 1191–1195.

Rott, A. S. and D. J. Ponsonby. 2000. The effects of temperature, relative humidity and host plant on the behaviour of *Stethorus punctillum* as a predator of the two-spotted spider mite, *Tetranychus urticae*. *BioControl* 45: 155–164.

Roy, H. E., H. Rudge, L. Goldrick and D. Hawkins. 2007. Eat or be eaten: prevalence and impact of egg cannibalism on two-spot ladybirds, *Adalia bipunctata*. *Entomol. Exp. Appl.* 125: 33–38.

Roy, M., J. Brodeur and C. Cloutier. 2003. Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey. *BioControl* 48: 57–72.

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: Aphidiidae) as food for *Coccinella septempunctata* and *Hippodamia convergens* (Coleoptera: Coccinellidae). *Biol. Contr.* 47: 82–88.

Rudolf, V. H. W. 2008. Consequences of size structure in the prey for predator–prey dynamics: the composite functional response. *J. Anim. Ecol.* 77: 520–528.

Rutledge, C. E. and S. D. Eigenbrode. 2003. Epicuticular wax on pea plants decreases instantaneous search rate of *Hippodamia convergens* larvae and reduces attachment to leaf surfaces. *Can. Entomol.* 135: 93–101.

Rutledge, C. E., S. D. Eigenbrode and H. Ding. 2008. A plant surface mutation mediates predator interference among ladybird larvae. *Ecol. Entomol.* 33: 464–472.

Rutledge, C. E., R. J. O'Neil, T. B. Fox and D. A. Landis. 2004. Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240–248.

Ruzicka, Z. 1994. Oviposition-deterring pheromone in *Chrysopa oculata* (Neuroptera: Chrysopidae). *Eur. J. Entomol.* 91: 361–370.

Ruzicka, Z. 1996. Oviposition-deterring pheromone in Chrysopidae (Neuroptera): Intra- and interspecific effects. *Eur. J. Entomol.* 93: 161–166.

Ruzicka, Z. 1997. Recognition of oviposition-deterring allomones by aphidophagous predators (Neuroptera: Chrysopidae, Coleoptera: Coccinellidae). *Eur. J. Entomol.* 94: 431–434.

Ruzicka, Z. 2001. Oviposition responses of aphidophagous coccinellids to tracks of ladybird (Coleoptera: Coccinellidae) and lacewing (Neuroptera: Chrysopidae) larvae. *Eur. J. Entomol.* 98: 183–188.

Ruzicka, Z. 2002. Persistence of deterrent larval tracks in *Coccinella septempunctata*, *Cycloneda limbifer* and *Semiadalia undecimnotata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 99: 471–475.

Ruzicka, Z. 2003. Perception of oviposition-deterring larval tracks in aphidophagous coccinellids *Cycloneda limbifer* and *Ceratomegilla undecimnotata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 100: 345–350.

Ruzicka, Z. 2006. Oviposition-deterring effects of conspecific and heterospecific larval tracks on *Cheilomenes sexmaculata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 103: 757–763.

Ruzicka, Z. and I. Hodek. 1978. Observations prèliminaires sur l'halophilie chez *Coccinella undecimnotata* L. *Ann. Zool.-Ecol. Anim.* 10: 367–371.

Ruzicka, Z. and R. Zemek. 2003. Effect of conspecific and heterospecific larval tracks on mobility and searching patterns of *Cycloneda limbifer* (Coleoptera: Coccinellidae) females. *Arquipélago (Life Mar. Sci) Suppl* 5: 85–93.

Ruzicka, Z. and R. Zemek. 2008. Deterrent effects of larval tracks on conspecific larvae in *Cycloneda limbifer*. *BioControl* 53: 763–771.

Saito, T. and S. Bjornson. 2006. Horizontal transmission of a microsporidium from the convergent lady beetle, *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae), to three coccinellid species of Nova Scotia. *Biol. Control* 39: 427–433.

Sakuratani, Y., Y., Sugiura, M. Isida, S. Kuwahara and T. Sugimoto. 1983. Aggregative response of adults of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) to aphid population density. *Mem. Fac. Agric. Kinki Univ.* 16: 49–54.

Sallée, B. and J. Chazeau. 1985. Cycle de développement, table de vie, et taux intrinsèque d'accroissement en conditions contrôlées de *Coelophora mulsanti* (Montrouzier), Coccinellidae aphidiphage de Nouvelle-Calédonie (Coleoptera). *Annls Soc. Entomol. France* 21: 407–412.

Samways, M. J. 1986. Combined effect of natural enemies (Hymenoptera: Aphelinidae and Coleoptera: Coccinellidae) with different niche breadths in reducing high populations of red scale, *Aonidiella aurantii* (Maskell) – (Hemiptera: Diaspididae). *Bull. Entomol. Res.* 76: 671–683.

Samways, M. J. and B. A. Tate. 1986. Mass-rearing of the scale predator *Chilocorus nigritus* (F.) (Coccinellidae). *Citrus Subtrop. Fruits J.* 1986: 9–14.

Samways, M. J. and S. J. Wilson. 1988. Aspects of the feeding behaviour of *Chilocorus nigritus* (F.) (Col., Coccinellidae) relative to its effectiveness as a biocontrol agents. *J. Appl. Entomol.* 106: 177–182.

Santi, F. and S. Maini. 2007. Ladybirds mothers eating their eggs: is it cannibalism? *Bull. Insectol.* 60: 89–91.

Santos, S. A. P., J. A. Pereira, M. C. Rodrigues et al. 2009. Identification of predator–prey relationships between coccinellids and *Saissetia oleae* (Hemiptera: Coccidae), in olive groves, using an enzyme-linked immunosorbent assay. *J. Pest Sci.* 82: 101–108.

Sarmento, R. A., A. Pallini, M. Venzon et al. 2007a. Functional response of the predator *Eriopis connexa* (Coleoptera:

Coccinellidae) to different prey types. *Brazilian Arch. Biol. Tech.* 50: 121–126.

Sarmento, R. A., M. Venzon, A. Pallini, E. E. Oliveira and A. Janssen. 2007b. Use of odours by *Cycloneda sanguinea* to assess patch quality. *Entomol. Exp. Appl.* 124: 313–318.

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. *Agr. 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.

Savastano, L. 1918. Talune notizie sul *Novius* e l'*Icerya* riguardanti l'arboricoltore. *Boll. R. Staz. Sper. Agrum. Fruttic.* 32: 1–2.

Savoiskaya, G. I. 1966. The significance of Coccinellidae in the biological control of apple-tree aphids in the Alma-Ata fruit-growing region. *In* I. Hodek (ed.). *Ecology of Aphidophagous Insects*. Academia, Prague and W. Junk, The Hague. pp. 317–319.

Savoiskaya, G. I. 1970a. Coccinellids of the Alma-Ata reserve. *Trudy Alma-Atin. Gos. Zapov.* 9: 163–187. (In Russian.)

Savoiskaya, G. I. 1970b. Introduction and acclimatisation of some coccinellids in the Alma-Ata reserve. *Trudy Alma-Atin. Gos. Zapov.* 9: 138–162. (In Russian.)

Savoiskaya, G. I. 1983. *Kokcinellidy*. Izdatelstvo Nauka Kazachskoi SSR, Alma-Ata. 246 pp. (In Russian.)

Schaefer, P. W. 1983. Natural enemies and host plants of species in the Epilachninae (Coleoptera: Coccinellidae). A world list. *Agric. Exp. Stn., Univ. Delaware Bull.* 445: 42.

Schaller, M. and W. Nentwig. 2000. Olfactory orientation of the seven-spot ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae): attraction of adults to plants and conspecific females. *Eur. J. Entomol.* 97: 155–159.

Schanderl, H., A. Ferran and V. Garcia. 1988. L'élevage de deux coccinelles *Harmonia axyridis* et *Semiadalia undecimnotata* à l'aide d'oeufs d'*Anagasta kuehniella* tués aux rayons ultraviolets. *Entomol. Exp. Appl.* 49: 235–244.

Schanderl, H., A. Ferran and M.-M. Larroque. 1985. Les besoins trophiques et thermiques des larves de la coccinelle *Harmonia axyridis* Pallas. *Agronomie* 5: 417–421.

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) larvae and pupae when prey become scarce. *Environ. Entomol.* 28: 1092–1100.

Schellhorn, N. A. and D. A. Andow. 2005. Response of coccinellids to their aphid prey at different spatial scales. *Popul. Ecol.* 47: 71–76.

Schenk, D., L. F. Bersier and S. Bacher. 2005. An experimental test of the nature of predation: neither prey- nor ratio-dependent. *J. Anim. Ecol.* 74: 86–91.

Schiefelbein, J. W. and H. C. Chiang. 1966. Effects of spray of sucrose solution in a corn field on the populations of predatory insects and their prey. *Entomophaga* 11: 333–339.

Schlacher, T. A. and G. Cronin. 2007. A trophic cascade in a macrophyte-based food web at the land-water ecotone. *Ecol. Res.* 22: 749–755.

Schuder, I., M. Hommes and O. Larink. 2004. The influence of temperature and food supply on the development of *Adalia bipunctata* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 101: 379–384.

Schuster, M. F., M. J. Lukefahr and F. G. Maxwell. 1976. Impact of nectariless cotton on plant bugs and natural enemies. *J. Econ. Entomol.* 69: 400–402.

Schwartzberg, E. G., G. Kunert, C. Stephan et al. 2008. Real-time analysis of alarm pheromone emission by the pea aphid (*Acyrthosiphon pisum*) under predation. *J. Chem. Ecol.* 34: 76–81.

Seagraves, M. P. 2009. Lady beetle oviposition behavior in response to the trophic environment. *Biol. Contr.* 51: 313–322.

Seagraves, M. P. and K. V. Yeargan. 2006. Selection and evaluation of a companion plant to indirectly augment densities of *Coleomegilla maculata* (Coleoptera: Coccinellidae) in sweet corn. *Environ. Entomol.* 35: 1334–1341.

Semyanov, V. P. 1965. Fauna, biology and usefulness of coccinellids (Coleoptera: Coccinellidae) in Belorus SSR. *Zap. Leningr. SelKhoz. Inst.* 95: 106–120. (In Russian.)

Semyanov, V. P. 1970. Biological properties of *Adalia bipunctata* L. (Coleoptera: Coccinellidae) in conditions of Leningrad region. *Zashch. Rast. Vredit. Bolez.* 127: 105–112. (In Russian.)

Semyanov, V. P. 1980. Biology of *Calvia quatuordecimguttata* L. (Coleoptera, Coccinellidae). *Entomol. Obozr.* 59: 757–763. (In Russian.)

Semyanov, V. P. 1999. Biology of coccinellids (Coleoptera) from Southeast Asia. I. *Leis dimidiata* (Fabr.) *Entomol. Obozr.* 78: 537–544. (In Russian with English summary.)

Semyanov, V. P. 2000. The biology of the coccinellids (Coleoptera) from Southeast Asia. II. *Harmonia sedecimnotata* F.). *Entomol. Obozr.* 79: 3–9. (In Russian with English summary).

Semyanov, V. P. and N. P. Vaghina. 2001. The odor of aphids as a signal for termination of the trophic diapause in the lady beetle *Harmonia sedecimnotata* (Fabr.) (Coleoptera, Coccinellidae). *Proc. Zool. Inst. Russ. Acad. Sci.* 289: 161–166.

Sengonca, C. and B. Liu. 1994. Responses of the different instar predator, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), to the kairomones produced by the prey and non-prey insects as well as the predator itself. *Z. PflKrankh. PflSchutz.* 101: 173–177.

Sengonca, C., J. Kranz and P. Blaeser. 2002. Attractiveness of three weed species to polyphagous predators and their influence on aphid populations in adjacent lettuce cultivations. *J. Pest Sci.* 75: 161–165.

Sethi, S. L. and A. S. Atwal. 1964. Influence of temperature and humidity on the development of different stages of *Coccinella septempunctata* (Coleoptera, Coccinellidae). *Ind. J. Agric. Sci.* 34: 166–171.

Shah, M. A. 1982. The influence of plant surfaces on the searching behaviour of Coccinellid larvae. *Entomol. Exp. Appl.* 31: 377–380.

Shands, W. A., R. L. Holmes and G. W. Simpson. 1970. Improved laboratory production of eggs of *Coccinella septempunctata*. *J. Econ. Entomol.* 63: 315–317.

Shands, W. A., M. K. Shands and G. W. Simpson. 1966. Technique for massproducing *Coccinella septempunctata*. *J. Econ. Entomol.* 59: 102–103.

Shannag, H. K. and W. M. Obeidat. 2006. Voracity and conversion efficiency by larvae of *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) on *Aphis fabae* Scop. (Homoptera: Aphididae) reared on two faba bean cultivars with different levels of resistance. *Appl. Entomol. Zool.* 41: 521–527.

Shannag, H. K. and W. M. Obeidat. 2008. Interaction between plant resistance and predation of *Aphis fabae* (Homoptera: Aphididae) by *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Ann. Appl. Biol.* 152: 331–337.

Shantibala, K., L. S. Singh and T. K. Singh. 1992. Development and larval voracity of a coccinellid predator, *Synonycha grandis* (Thunberg) on bamboo aphid, *Paraoregma alexandri* (Takahashi). *Manipur J. Agric. Sci.* 1: 55–57.

Shirai, Y. and H. Katakura. 1999. Host plants of the phytophagous ladybird beetle, *Epilachna vigintioctopunctata* (Coleoptera: Coccinellidae) in Southeast Asia and Japan. *Appl. Entomol. Zool.* 34: 75–83.

Shirai, Y. and H. Katakura. 2000. Adaptation to a new host plant, *Centrosema pubescens* (Fabales: Leguminosae), by the phytophagous ladybird beetle, *Epilachna vigintioctopunctata*. Coleoptera: Coccinellidae), in tropical Asia. *Popul. Ecol.* 42: 129–134.

Shirai, Y. and N. Morimoto. 1997. Life history traits of pest and non-pest populations in the phytophagous ladybird beetle, *Epilachna niponica* (Coleoptera, Coccinellidae). *Res. Popul. Ecol.* 39: 163–171.

Shirai, Y. and N. Morimoto. 1999. A host shift from wild blue cohosh to cultivated potato by the phytophagous ladybird beetle, *Epilachna yasutomii* (Coleoptera, Coccinellidae). *Res. Popul. Ecol.* 41: 161–167.

Shirai, Y. and K. Yara. 2001. Potential distribution area of the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae) in Japan, estimated from its high-temperature tolerance. *Appl. Entomol. Zool.* 36: 409–417.

Siddiqui, A., A. Kumar, N. Kumar and C. P. M. Tripathi. 1999. Prey–predator relationship between *Lipaphis erysimi* Kalt. (Homoptera: Aphididae) and *Coccinella septempunctata* Linn. (Coleoptera: Coccinellidae): III. Effect of host plants on the searching strategy, mutual interference and killing power of the predator. *Biol. Agric. Hort.* 17: 11–17.

Sighinolfi, L., G. Febvay, M. L. Dindo et al. 2008. Biological and biochemical characteristics for quality control of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) reared on a liver-based diet. *Arch. Insect Biochem. Physiol.* 68: 26–39.

da Silva, P. G., K. S. Hagen and A. P. Gutierrez. 1992. Functional response of *Curinus coeruleus* (Col.: Coccinellidae) to *Heteropsylla cubana* (Hom.: Psyllidae) on artificial and natural substrates. *Entomophaga* 37: 555–564.

Silva, R. B., J. C. Zanuncio, J. E. Serrao et al. 2009. Suitability of different artificial diets for development and survival of stages of the predaceous ladybird beetle *Eriopis connexa*. *Phytoparasitica* 37: 115–123.

Simmons, A. M. and J. C. Legaspi. 2004. Survival and predation of *Delphastus catalinae* (Coleoptera: Coccinellidae), a predator of whiteflies (Homoptera: Aleyrodidae), after exposure to a range of constant temperatures. *Environ. Entomol.* 33: 839–843.

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. 2008a. Habitat and dietary specificity in aphidophagous ladybirds (Coleoptera: Coccinellidae): Explaining specialization. *Proc. Neth. Entomol. Soc. Meet.* 19: 95–113.

Sloggett, J. J. 2008b. Weighty matters: Body size, diet and specialization in aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 105: 381–389.

Sloggett, J. J. and A. J. Davis. 2010. Eating chemically defended prey: alkaloid metabolism in an invasive ladybird predator of other ladybirds (Coleoptera: Coccinellidae). *J. Exper. Biol.* 213: 237–241.

Sloggett, J. J. and M. W. Lorenz. 2008. Egg composition and reproductive investment in aphidophagous ladybird beetles (Coccinellidae: Coccinellini): egg development and interspecific variation. *Physiol. Entomol.* 33: 200–208.

Sloggett, J. J. and M. E. N. Majerus. 1994. *The Cambridge Ladybird Survey* 17: 13–14.

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. and M. E. N. Majerus. 2003. Adaptations of *Coccinella magnifica*, a myrmecophilous coccinellid to aggression by wood ants (*Formica rufa* group). II. Larval behaviour, and ladybird oviposition location. *Eur. J. Entomol.* 100: 337–344.

Sloggett, J. J., K. F. Haynes and J. J. Obrycki. 2009a. Hidden costs to an invasive intraguild predator from chemically defended native prey. *Oikos* 118: 1396–1404.

Sloggett, J. J., J. J. Obrycki and K. F. Haynes. 2009b. Identification and quantification of predation: novel use of gaz chromatography-mass spectrometric analysis of prey alkaloid markers. *Func. Ecol.* 23: 416–426.

Sloggett, J. J., A. Manica, M. J. Day and M. E. N. Majerus. 1999. Predation of ladybirds (Coleoptera, Coccinellidae) on ants

Formica rufa L. (Hymenoptera, Formicidae). *Entomol. Gaz.* 50: 217–221.

Sloggett, J. J., W. Völkl, W. Schulze, J. H. G. Schulenburg and M. E. N. Majerus. 2002. The ant-associations and diet of the ladybird *Coccinella magnifica* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 99: 565–569.

Sloggett, J. J., I. Zeilstra and J. J. Obrycki. 2008. Patch residence by aphidophagous ladybird beetles: Do specialists stay longer? *Biol. Contr.* 47: 199–206.

Smirnoff, W. A. 1958. An artificial diet for rearing coccinellid beetles. *Can. Entomol.* 90: 563–565.

Smith, B. C. 1960. A technique for rearing Coccinellid beetles on dry foods, and influence of various pollens on the development of *Coleomegilla maculata lengi* Timb. (Coleoptera: Coccinellidae). *Can. J. Zool.* 38: 1047–1049.

Smith, B. C. 1961. Results of rearing some coccinellid (Coleoptera: Coccinellidae) larvae on various pollens. *Proc. Entomol. Soc. Ont.* 91: 270–271.

Smith, B. C. 1965a. Differences in *Anatis mali* Auct. and *Coleomegilla maculata lengi* Timberlake to changes in the quality and quantity of the larval food. *Can. Entomol.* 97: 1159–1166.

Smith, B. C. 1965b. Growth and development of coccinellid larvae on dry foods (Coleoptera, Coccinellidae). *Can. Entomol.* 97: 760–768.

Snyder, W. E. and G. M. Clevenger. 2004. Negative dietary effects of Colorado potato beetle eggs for the larvae of native and introduced ladybird beetles. *Biol. Contr.* 31: 353–361.

Snyder, W. E. and E. W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. *Annu. Rev. Ecol. Evol. Syst.* 37: 95–122.

Snyder, W. E., S. N. Ballard, S. Yang et al. 2004. Complementary biocontrol of aphids by the ladybird beetle *Harmonia axyridis* and the parasitoid *Aphelinus asychis* on greenhouse roses. *Biol. Contr.* 30: 229–235.

Snyder, W. E., S. B. Joseph, R. F. Preziosi and A. J. Moore. 2000. Nutritional benefits of cannibalism for the lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae) when prey quality is poor. *Environ. Entomol.* 29: 1173–1179.

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., D. Coderre and H. Schanderl. 2002. Effect of temperature and intraspecific allometry on predation by two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Environ. Entomol.* 32: 939–944.

Soares, A. O., D. Coderre and H. Schanderl. 2004. Dietary self-selection behaviour by the adults of the aphidophagous ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *J. Anim. Ecol.* 73: 478–486.

Soares, A. O., D. Coderre and H. Schanderl. 2005. Influence of prey quality on the fitness of two phenotypes of *Harmonia axyridis* adults. *Entomol. Exp. Appl.* 114: 227–232.

Solomon, M. E. 1949. The natural control of animal populations. *J. Anim. Ecol.* 18: 1–35.

Solomon, M. E. 1964. Analysis of processes involved in the natural control of insects. *Adv. Ecol. Res.* 2: 1–58.

Specty, O., G. Febvay, S. Grenier et al. 2003. Nutritional plasticity of the predatory ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae): comparison between natural and substitution prey. *Arch. Insect Biochem. Physiol.* 52: 81–91.

Spellman, B., M. W. Brown and C. R. Mathews. 2006. Effect of floral and extrafloral resources on predation of *Aphis spiraecola* by *Harmonia axyridis* on apple. *BioControl* 51: 715–724.

Srikanth, J. and N. H. Lakkundi. 1990. Seasonal population fluctuations of cowpea aphid *Aphis craccivora* Koch and its predatory coccinellids. *Insect Sci. Applic.* 11: 21–26.

Stadler, B. 1991. Predation success of *Coccinella septempunctata* when attacking different *Uroleucon* species. *In* L. Polgár, R. J. Chambers, A. F. G. Dixon and I. Hodek (eds). *Behaviour and Impact of Aphidophaga*. SPB Acad. Publ., The Hague. pp. 265–271.

Staley, A. C. and K. V. Yeargan. 2005. Oviposition behavior of *Coleomegilla maculata* (Coleoptera: Coccinellidae): Diel periodicity and choice of host plants. *Environ. Entomol.* 34: 440–445.

Stathas, G. J. 2000. The effect of temperature on the development of the predator *Rhyzobius lophanthae* and its phenology in Greece. *BioControl* 45: 439–451.

Staubli Dreyer, B., P. Neuenschwander, J. Baumgartner and S. Dorn. 1997b. Trophic influences on survival, development and reproduction of *Hyperaspis notata* (Col., Coccinellidae). *J. Appl. Entomol.* 121: 249–256.

Staubli Dreyer, B., P. Neuenschwander, B. Bouyjou, J. Baumgartner and S. Dorn. 1997a. The influence of temperature on the life table of *Hyperaspis notata*. *Entomol. Exp. Appl.* 84: 85–92.

Stewart, L. A., J.-L. Hemptinne and A. F. G. Dixon. 1991. Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. *Funct. Ecol.* 5: 380–385.

Storch, R. H. 1976. Prey detection by fourth stage *Coccinella transversoguttata* larvae (Coleoptera: Coccinellidae). *Anim. Behav.* 24: 690–693.

Strauss, R. E. 1982. Influence of replicated sub-samples and sub-sample heterogeneity on the linear index of food selection. *Trans. Am. Fisheries Soc.* 111: 517–522.

Strouhal, H. 1926a. Die Larven der Palaearktischen Coccinellini und Psylloborini (Coleopt.). *Arch. Naturgesch.* 92(A)3: 1–63.

Strouhal, H. 1926b. Pilzfressende Coccinelliden (Tribus Psylloborini) (Col.). *Z. Wiss. Insekt-Biol.* 21: 131–143.

Stuart, M. K. and M. H. Greenstone. 1990. Beyond ELISA: a rapid, sensitive, specific immunodot assay for identification of predator stomach contents. *Ann. Entomol. Soc. Am.* 83: 1101–1107.

Stubbs, M. 1980. Another look at prey detection by coccinellids. *Ecol. Entomol.* 5: 179–182.

Sundby, R. A. 1966. A comparative study of the efficiency of three predatory insects, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), *Chrysopa carnea* St. (Neuroptera: Chrysopidae) and *Syrphus ribesii* L. (Diptera: Syrphidae) at two different temperatures. *Entomophaga* 11: 395–404.

Sunderland, K. D., N. E. Crook, D. L. Stacey and B. J. Fuller. 1987. A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. *J. Appl. Ecol.* 24: 907–933.

Sutherland, A. M. and M. P. Parrella. 2009. Mycophagy in Coccinellidae: review and synthesis. *Biol. Contr.* 51: 284–293.

Suzuki, N. and T. Ide. 2008. The foraging behaviors of larvae of the ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae) towards ant-tended and non-ant-tended aphids. *Ecol. Res.* 23: 371–378.

Svoboda, J. A. and W. E. Robbins. 1979. Comparison of sterols from a phytophagous and predacious species of the family Coccinellidae. *Experientia* 35: 186–187.

Szumkowski, W. 1952. Observations of Coccinellidae. II. Experimental rearing of *Coleomegilla* on a non-insect diet. *Proc. 9th Int. Congr. Entomol. Amsterdam* 1951: 781–785.

Szumkowski, W. 1961a. Aparicion de un coccinelido predato nuevo para Venezuela. *Agronomía Trop. (Venezuela)* 11: 33–37.

Szumkowski, W. 1961b. Dietas sin insectos vivos para la cria de *Coleomegilla maculata* Deg. (Coccinelllidae, Coleoptera). *Agronomía Trop. (Venezuela)* 10: 149–154.

Taghizadeh, R., Y. Fathipour and K. Kamali. 2008. Influence of temperature on life-table parameters of *Stethorus gilvifrons* (Mulsant) (Coleoptera: Coccinellidae) fed on *Tetranychus urticae* Koch. *J. Appl. Entomol.* 132: 638–645.

Takahashi, K. 1987. Cannibalism by the larvae of *Coccinella septempunctata bruckii* Mulsant (Coleoptera: Coccinellidae) in mass-rearing experiments. *Jap. J. Appl. Entomol. Zool.* 31: 201–205. (In Japanese with English summary.)

Takahashi, K. 1989. Intra- and inter-specific predations by lady beetles in spring alfalfa fields. *Jpn. J. Entomol.* 57: 199–203.

Takeda, S., S. Hukusima and H. Yamada. 1964. Seasonal abundance in coccinellid beetles. *Res. Bull. Fac. Agric. Gifu Univ.* 19: 55–63. (In Japanese with English summary.)

Takeuchi, M., Y. Sasaki, C. Sato et al. 2000. Seasonal host utilization of mycophagous ladybird *Illeis koebelei* (Coccinellidae: Coleoptera). *Jpn. J. Appl. Entomol. Zool.* 44: 89–94.

Tanaka, M. 1981. Biological control of arrowhead scale, *Unaspis yanonensis* (Kuwana), in the implementations of IPM programs of citrus orchards in Japan. *Proc. Int. Soc. Citriculture* 2: 636–640.

Tanaka, M. and Y. Maeta. 1965. Rearing of some predacious coccinellid beetles by artificial diets. *Bull. Hort. Res. Stn. (D)* 63: 17–35. (In Japanese with English summary.)

Tao, C. C. and S. C. Chiu. 1971. Biological control of citrus, vegetables and tobacco aphids. *Spec. Publ. Taiwan Agr. Res. Inst.* 10: 1–110.

Telenga, N. A. and M. V. Bogunova. 1936. The most important predators of coccids and aphids in the Ussuri region of Far East and their utilisation. *Zashch. Rast.*, 1939(10): 75–87. (In Russian.)

Thompson, W. R. 1951. The specificity of host relations in predaceous insects. *Can. Entomol.* 83: 262–269.

Timms, J. E., T. H. Oliver, N. A. Straw and S. R. Leather. 2008. The effect of host plant on the coccinellid functional response: Is the conifer specialist *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae) better adapted to spruce than the generalist *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae)? *Biol. Contr.* 47: 273–281.

Triltsch, H. 1997. Contents in field sampled adults of *Coccinella septempunctata* (Col.: Coccinellidae). *Entomophaga* 42: 125–131.

Triltsch, H. 1999. Food remains in the guts of *Coccinella septempunctata* (Coleoptera: Coccinellidae) adults and larvae. *Eur. J. Entomol.* 96: 355–364.

Tsaganou, F. C., C. J. Hodgson, C. G. Athanassiou, N. G. Kavallieratos and Z. Tomanovic. 2004. Effect of *Aphis gossypii* Glover, *Brevicoryne brassicae* (L.), *and Megoura viciae* Buckton (Hemiptera: Aphidoidea) on the development of the predator *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). *Biol. Contr.* 31: 138–144.

Tschanz B., L. F. Bersier and S. Bacher. 2007. Functional responses: a question of alternative prey and predator density. *Ecology* 88: 1300–1308.

Turchin, P. and P. Kareiva. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology* 70: 1008–1016.

Turian, G. 1969. Coccinelles micromycétophages (Col.). *Mit. Schweiz. Entomol. Ges.* 42: 52–57.

Turian, G. 1971. *Thea 22-punctata* et autres Coccinelles micromycétophages. Nature du pigment élytral jaune. *Bull. Soc. Entomol. Suisse* 44: 277–280.

Turlings, T. C. J., J. H. Tumlinson and W. J. Lewis. 1990. Exploitation of herbivore-induced plant odors by host seeking parasitic wasps. *Science* 250: 1251–1253.

Turlings, T. C. J., M. Bernasconi, R. Bertossa et al. 1998. The induction of volatile emissions in maize by three herbivore species with different feeding habits: possible consequences for their natural enemies. *Biol. Contr.* 11: 122–129.

Turnock, W. J. and I. L. Wise. 2004. Density and survival of lady beetles (Coccinellidae) in overwintering sites in Manitoba. *Can. Field-Nat.* 118: 309–317.

Ueno, H. 2003. Genetic variation in larval period and pupal mass in an aphidophagous ladybird beetle (*Harmonia axyridis*) reared in different environments. *Entomol. Exp. Appl.* 106: 211–218.

Ueno, H., N. Fujiyama, K. Irie, Y. Sato and H. Katakura. 1999. Genetic basis for established and novel host plant use in a herbivorous ladybird beetle, *Epilachna vigintioctomaculata*. *Entomol. Exp. Appl.* 91: 245–250.

Ueno, H., Y. Hasegawa, N. Fujiyama and H. Katakura. 2001. Comparison of genetic variation in growth performance on normal and novel host plants in a local population of a herbivorous ladybird beetle, *Epilachna vigintioctomaculata*. *Heredity* 87: 1–7.

Underwood, N., W. Morris, K. Gross and J. R. Lockwood. 2000. Induced resistance to Mexican bean beetles in soybean: variation among genotypes and lack of correlation with constitutive resistance. *Oecologia* 122: 83–89.

Unsicker, S. B., A. Oswald, G. Köhler and W. W. Weisser. 2008. Complementarity effects through dietary mixing enhance the performance of a generalist insect herbivore. *Oecologia* 156: 313–324.

Uygun, N. and N. Z. Elekcioglu. 1998. Effect of three diaspididae prey species on development and fecundity of the ladybeetle *Chilocorus bipustulatus* in the laboratory. *BioControl* 43: 153–162.

Van der Werf, W., E. W. Evans and J. Powell. 2000. Measuring and modelling the dispersal of *Coccinella septempunctata* (Coleoptera: Coccinellidae) in alfalfa fields. *Eur. J. Entomol.* 97: 487–493.

Van Rijn, P. C. J., F. M. Bakker, W. A. D. van der Hoeven and M. W. Sabelis. 2005. Is arthropod predation exclusively satiation-driven? *Oikos* 109: 101–116.

Vandenberg, N. J. 2002. Family 93. Coccinellidae Latreille 1807. *In* R. H. Arnett Jr., M. C. Thomas, P. E. Skelley and J. H. Frank (eds). *American Beetles. Polyphaga: Scarabaeoidea through Curculionoidea*, Vol. 2. CRC Press, Boca Raton, FL. pp. 371–389.

Varley, G. C. and G. R. Gradwell. 1970. Recent advances in insect population dynamics. *Annu. Rev. Entomol.* 15: 1–24.

Verheggen, F. J., Q. Fagel, S. Heuskin et al. 2007. Electrophysiological and behavioral responses of the multicolored Asian lady beetle, *Harmonia axyridis* Pallas, to sesquiterpene semiochemicals. *J. Chem. Ecol.* 33: 2148–2155.

Vet, L. E. M. and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37: 141–172.

Vinson, S. B. 1977. Behavioral chemicals in the augmentation of natural enemies. *In* R. L. Ridgway and S. B. Vinson (eds). *Biological Control by Augmentation of Natural Enemies*. Plenum Press, New York. pp. 237–279.

Vinson, S. B. and T. A. Scarborough. 1989. Impact of the imported fire ant on laboratory populations of cotton aphid (*Aphis gossypii*) predators. *Florida Entomol.* 72: 107–111.

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. and K. Vohland. 1996. Wax covers in larvae of two *Scymnus* species: Do they enhance coccinellid larval survival? *Oecologia* 107: 498–503.

Waage, J. and D. Greathead (eds). 1986. *Insect Parasitoids*. Academic Press, London. 389 pp.

Wade, M. R., M. P. Zalucki, S. D. Wratten and K. A. Robinson. 2008. Conservation biological control of arthropods using artificial food sprays: current status and future challenges. *Biol. Contr.* 45: 185–199.

Wagner, J. D., M. D. Glover, J. B. Moseley and A. J. Moore. 1999. Heritability and fitness consequences of cannibalism in *Harmonia axyridis*. *Evol. Ecol. Res.* 1: 375–388.

Wajnberg, E., C. Bernstein and J. van Alphen. 2008. *Behavioral Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications*. Blackwell, Oxford. 445 pp.

Waldbauer, G. P. 1968. The consumption and utilization of food by insects. *Adv. Insect Physiol.* 5: 229–288.

Waldbauer, G. P. and S. Friedman. 1991. Self-selection of optimal diets by insects. *Annu. Rev. Entomol.* 36: 43–63.

Wallace, M. S. and F. P. Hain. 2000. Field surveys and evaluation of native and established predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United States. *Environ. Entomol.* 29: 638–644.

Wang, Y. Z. and F. Ba. 1998. Study on optimum control of the soybean aphid. *Acta Phyt. Sinica* 25: 152–155.

Ward, D. 1992. The role of satisficing in foraging theory. *Oikos* 63: 312–317.

Ward, D. 1993. Foraging theory, like other fields of science, needs multiple working hypotheses. *Oikos* 67: 376–378.

Ware, R. L., B. Yguel and M. E. N. Majerus. 2008. Effects of larval diet on female reproductive output of the European coccinellid *Adalia bipunctata* and the invasive species *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 105: 437–443.

Ware, R., B. Yguel and M. 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.

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.

Watson, J. R. and W. L. Thompson. 1933. Food habits of *Leis conformis* Boisd. (Chinese lady-beetle). *Florida Entomol.* 17: 27–29.

Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annu. Rev. Entomol.* 8: 307–344.

Weber, D. C. and J. G. Lundgren. 2009. Assessing the trophic ecology of the Coccinellidae: their roles as predators and as prey. *Biol. Contr.* 51: 199–214.

Weber, R. G. and M. V. Holman. 1976. *Coleomegilla maculata* (DeGeer), (Coleoptera: Coccinellidae), a new coleopteran predator of the elm leaf beetle, *Pyrrhalta luteola* (Müller), (Coleoptera: Chrysomelidae). *J. Kansas Entomol. Soc.* 49: 160.

Wells, M. L., R. M. McPherson, J. R. Ruberson and G. A. Herzog. 2001. Coccinellids in cotton: population response to pesticide application and feeding response to cotton aphids (Homoptera: Aphididae). *Environ. Entomol.* 30: 785–793.

White, C. and S. D. Eigenbrode. 2000. Effects of surface wax variation in *Pisum sativum* on herbivorous and entomophagous insects in the field. *Environ. Entomol.* 29: 773–780.

Wiebe, A. P. and J. J. Obrycki. 2004. Quantitative assessment of predation of eggs and larvae of *Galerucella pusilla* in Iowa. *Biol. Contr.* 31: 16–28.

Wigglesworth, V. B. 1953. *The Principles of Insect Physiology*. 5th ed. with add. Methuen, London. 546 pp.

Wipperfuerth, T., K. S. Hagen and T. E. Mittler. 1987. Egg production by the coccinellid *Hippodamia convergens* fed on two morphs of the green peach aphid, *Myzus persicae*. *Entomol. Exp. Appl.* 44: 195–198.

With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecol. Appl.* 12: 52–65.

Witte, L., A. Ehmke and Th. Hartmann. 1990. Interspecific flow of pyrrolizidine alkaloids. *Naturwissenschaften* 77: 540–543.

Wratten, S. D. 1973. The effectiveness of the Coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the lime aphid, *Eucallipterus tiliae* L. *J. Anim. Ecol.* 42: 785–802.

Wratten, S. D. 1976. Searching by *Adalia bipunctata* (L.) (Coleoptera: Coccinellidae) and escape behaviour of its aphid and cicadellid prey on lime (*Tilia x vulgaris* Hayne). *Ecol. Entomol.* 1: 139–142.

Wright, E. J. and J. E. Laing. 1980. Numerical response of coccinellids to aphids in corn in southern Ontario. *Can. Entomol.* 112: 977–988.

Wright, E. J. and J. E. Laing. 1982. Stage-specific mortality of *Coleomegilla maculata lengi* Timberlake on corn in southern Ontario. *Environ. Entomol.* 11: 32–37.

Wu, Z., D. Schenk-Hamlin, W. Zhan, D. W. Ragsdale and G. E. Heimpel. 2004. The soybean aphid in China: A historical review. *Ann. Entomol. Soc. Am.* 97: 209–218.

Wylie, H. G. (1958) Observations on *Aphidecta obliterata* (L.) (Coleoptera: Coccinellidae), a predator of conifer-infesting Aphidoidea. *Can. Entomol.* 90: 518–522.

Yadava, C. and F. R. Shaw. 1968. The preference of certain coccinellids for pea aphids, leafhoppers and alfalfa larvae. *J. Econ. Entomol.* 61: 1104–1105.

Yan, F.-S., J. Qin and X.-F. Xiang. 1982. The fine structure of the chemoreceptors on the labial palps of *Coccinella septempunctata*. *Acta Entomol. Sinica* 25: 135–140. (In Chinese with English summary.)

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 behaviour of the predatory ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 97: 551–553.

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.

Yasuda, H., T. Kikuchi, P. Kindlmann and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. *J. Insect Behav.* 14: 373–383.

Yigit, A. 1992. Method for culturing *Serangium parcesetosum* Sicard on *Bemisia tabaci* Genn. (Hom.: Aleyrodidae). *J. Plant Dis. Prot.* 99: 525–527.

Yigit, A., R. Canhilal and U. Ekmekci. 2003. Seasonal population fluctuations of *Serangium parcesetosum* (Coleoptera: Coccinellidae), a predator of citrus whitefly, *Dialeurodes citri* (Homoptera: Aleyrodidae) in Turkey's eastern Mediterranean citrus groves. *Environ. Entomol.* 32: 1105–1114.

Yinon, U. 1969. Food consumption of the armored scale ladybeetle, *Chilocorus bipustulatus* (Coleoptera, Coccinellidae). *Entomol. Exp. Appl.* 12: 139–146.

Yoneya, K., S. Kugimiya and J. Takabayashi. 2009. Can herbivore-induced plant volatiles inform predatory insect about the most suitable stage of its prey? *Physiol. Entomol.* 34: 379–386.

Yoon, C., D.-K. Seo, J.-O. Yang, S.-H. Kang and G.-H. Kim. 2010. Attraction of the predator *Harmonia axyridis* (Coleoptera: Coccinellidae), to its prey, *Myzus persicae* (Hemiptera: Aphididae), feeding on Chinese cabbage. *J. Asia Pac. Entomol.* 13: 255–260.

Yu, J.-H., H. Chi and B.-H. Chen. 2005. Life table and predation of *Lemnia biplagiata* (Coleoptera: Coccinellidae) fed on *Aphis gossypii* (Homoptera: Aphididae) with a proof on relationship among gross reproduction rate, net reproduction rate, and preadult survivorship. *Ann. Entomol. Soc. Am.* 98: 475–482.

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. Contr.* 41: 142–150.

Zeleny, J. 1969. A biological and toxicological study of *Cycloneda limbifer* Casey (Coleoptera, Coccinellidae). *Acta Entomol. Bohemoslov.* 66: 333–344.

Zhang, Z. Q. 1992. The natural enemies of *Aphis gossypii* Glover (Hom., Aphididae) in China. *J. Appl. Entomol.* 114: 251–262.

Zheng, Y., K. S. Hagen, K. M. Daane and T. E. Mittler. 1993. Influence of larval dietary supply on the food consumption, food utilization efficiency, growth and development of the lacewing *Chrysoperla carnea*. *Entomol. Exp. Appl.* 67: 1–7.

Zhu, J. and K.-C. Park. 2005. Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. *J. Chem. Ecol.* 31: 1733–1746.

Zhu, J., A. A. Cosse, J. J. Obrycki, K. S. Boo and T. C. Baker. 1999. Olfactory reactions of the twelve-spotted beetle, *Coleomegilla maculata* and the green lacewing, *Chrysoperla carnea* to semiochemicals released from their prey and host plant: electroantennogram and behavioral responses. *J. Chem. Ecol.* 25: 1163–1177.

Zuest, T., S. A. Haerri and C. B. Müller. 2008. Endophytic fungi decrease available resources for the aphid *Rhopalosiphum padi* and impair their ability to induce defences against predators. *Ecol. Entomol.* 33: 80–85.