Chapter 8

NATURAL ENEMIES OF LADYBIRD BEETLES

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8.1 INTRODUCTION

The term **natural enemy** is often used to denote an organism that draws nutrition from another organism, such as a predator (or herbivore), parasitoid, parasite or pathogen (e.g. DeBach & Rosen 1991, Thacker 2002). In this review, we consider natural enemies in a broader sense and define them after Flint and Dreistadt (1998) as 'organisms that kill, decrease the reproductive potential, or otherwise reduce the numbers of another organism'. Such a definition would include some organisms that interact with the prey organism in ways other than exploitation, e.g. through competition or self-defence. Most interactions between ladybirds and their competitors, including intra-guild predation, are discussed elsewhere (Chapter 7). Here, we consider the relations of predatory Coccinellidae with Hemiptera-tending ants, and devote a short section to mites phoretic on Coccinellidae. Although this phoretic relationship has not been shown to be detrimental to ladybirds, the shared food resources of mites and ladybirds (both prey on the same hemipterans) make them competitors. Another unusual interaction that may harm ladybirds is that with some of their prey, i.e. social aphids which produce aggressive soldiers defending their colonies against predators. This is also briefly discussed here. All remaining organisms considered as natural enemies of ladybirds in this review behave in an exploitative manner.

8.2 PREDATION AND RELATED PHENOMENA

8.2.1 Anti-predator defences

Ladybirds display a range of general defence reactions, from escape (by flying away, running away or dropping to the ground) to immobilization (so-called thanatosis) and also other more specific anti-predator adaptations.

8.2.1.1 Aposematic colouration and other visual signals

Adults of many members of Coccinellidae are conspicuously coloured, often with contrasting red-and-black or yellow-and-black patterns on their elytra. Such patterns usually serve as aposematic (warning) colouration (Moore et al. 1990, Joron 2003). Larvae and pupae may also be aposematically coloured with dark and bright areas on their surface (e.g. Richards 1985, Holloway et al. 1991). The function of warning colouration is to advertise to potential predators that the bearer is unpalatable, toxic or nutritionally unprofitable (Joron 2003, Blount et al. 2009). Indeed, ladybirds are often distasteful and toxic to vertebrate and invertebrate predators (Daloze et al. 1995). A recent experimental study by Dolenska et al. (2009) suggests that not only warning colours but also any spotted pattern and general ladybird appearance (oval and convex body shape) may be signals of prey unprofitability for some optically oriented vertebrate predators, such as the great tit (*Parus major*).

8.2.1.2 Reflex bleeding

The bitter taste and toxic properties of many ladybird beetles can be attributed to a variety of **defensive alkaloids** (Daloze et al. 1995). About 50 different alkaloids have been identified in coccinellids (Laurent et al. 2005). The alkaloids are produced in ladybird haemolymph and are distributed by the haemolymph throughout the insect's body. When disturbed, ladybirds secrete droplets of haemolymph through tibiofemoral articulations. The released fluid is called 'reflex blood' and the corresponding defence mechanism – 'reflex bleeding'. Reflex bleeding is commonly used by adults of many ladybird species and by larvae and/or pupae of some species, but in the latter cases, the fluid is usually released from pores in the dorsal body surface (Holloway et al. 1991, Daloze et al. 1995). The pupae of some Epilachninae are known to exude the droplets of defensive fluid by specialized, glandular hairs (Schroeder et al. 1998). In adult ladybirds, reflex bleeding is often associated with thanatosis (Daloze et al. 1995, Ceryngier & Hodek 1996).

Various ladybird species have been shown to exert differing degrees of response and harmful effects on predators which is attributed to differences in their alkaloid composition. Marples et al. (1989) reported that blue tit (*Cyanistes caeruleus*) nestlings suffer severe mortality when supplied with food containing homogenized *Coccinella septempunctata* beetles, but no toxic effect was observed when homogenized *Adalia bipunctata* were added to the nestlings' food. *Adalia decempunctata* also had no apparent toxic effect on blue tit nestlings (Marples 1993). The high toxicity of *C. septempunctata* was associated with severe pathological changes in the blue tits' livers (Marples et al. 1989), and this was probably caused by coccinelline, the main

C. septempunctata alkaloid. In contrast to coccinelline, the major alkaloid compound of *Adalia* species, adaline, appears rather benign to young tits. These striking differences led the authors to the conclusion that light-coloured (typical) *A. bipunctata* and *A. decempunctata* are Batesian mimics of their toxic relative, *C. septempunctata.* Melanic *Adalia* individuals are, according to this hypothesis, the mimics of another model species, *Exochomus quadripustulatus*.

Elytra colouration in *Harmonia axyridis* (at least in its light form *succinea*) seems to represent a true aposematic signal. Bezzerides et al. (2007) found that the proportion of light areas on light-and-black patterned elytra of this form was positively correlated with the concentration of the alkaloid harmonine in ladybird bodies.

Reflex blood also contains **methylalkylpyrazines**, which are involved in ladybird defence. In contrast to alkaloids, pyrazines are volatile, so they can be olfactorily detected by predators. They are responsible for the odour that, in addition to aposematic colouration, acts as a signal in highlighting the unprofitability of a ladybird as food. It was found that pyrazines tend to be absent from cryptically coloured Coccinellidae, but are often present in aposematic species (Moore et al. 1990, Daloze et al. 1995).

Reflex bleeding may also act as a **mechanical defence** against some invertebrate predators. The fluid coagulates quickly on exposure to air and may stick to a predator's legs, antennae and mouthparts (Eisner et al. 1986).

8.2.1.3 Morphological anti-predator adaptations

Adult Coccinellidae, like most beetles, are relatively well protected against many predators by their exoskeleton and elytra. Ladybird pupae also have relatively hard cuticles and, in many species, are additionally protected by the final larval skin. Larvae, and sometimes pupae, may be defended by spiny projections or wax covers (Pope 1979, Richards 1980, Majerus et al. 2007). Pupae of many Coleoptera, including Coccinellidae, have deep intersegmental clefts with heavily sclerotized margins between some of the abdominal tergites. These devices, called 'gin traps', act as jaws when a disturbed pupa rapidly raises and drops its body. Gin traps of *Cycloneda sanguinea* pupae have been found an effective defence against ant attacks (Eisner & Eisner 1992).

8.2.2 Vertebrate predators

Despite being distasteful and toxic, ladybird beetles have been reported to be eaten by various vertebrate and invertebrate predators. Predation by vertebrates concerns virtually all the main groups: fish (e.g. Gomiero et al. 2008), amphibians (e.g. Cicek & Mermer 2007), reptiles (e.g. Pal et al. 2007), birds (e.g. Mizer 1970) and mammals (e.g. Chapman et al. 1955).

Predation of Coccinellidae by **birds** has been analyzed in detail. The contribution of Coccinellidae to the diet of birds was highlighted by Mizer (1970) in Ukraine through analysis of food remnants in almost 7000 stomachs of birds belonging to 234 species. Mizer (1970) detected ladybirds in the diet of 20% of bird species, but only in 2% of the stomachs (individuals) examined (Fig. 8.1). Ladybirds found in bird stomachs belonged to 23 species, of which two, *C. septempunctata* and *Hippodamia variegata*, accounted for more than a half of the total number (Fig. 8.2).

Mean numbers of ladybirds per bird stomach are given in Fig. 8.3, for those bird species which were represented in Mizer's data by at least 20 individuals. For almost all bird species considered, there was less than half a ladybird per stomach. The only exception was the house martin (*Delichon urbica*) with the average number of 0.75 ladybirds per stomach, which is consistent with the findings of other researchers, that birds feeding on the wing such as swifts, swallows and martins often ingest ladybirds (Muggleton 1978, Majerus & Majerus 1997a).

From Fig. 8.3, it is apparent that the tree sparrow (*Passer montanus*) is the next most frequent bird predator of Coccinellidae. This species is partly granivorous in its adult life, but feeds its nestlings mostly with insects. In the surroundings of Bratislava (Slovakia), and several localities in Poland, coccinellid larvae, pupae and adults were found to constitute one of the major fractions of the nestling diet of tree sparrows and house sparrows (*Passer domesticus*) (Wieloch 1975, Kristin 1986, Kristin et al. 1995).

8.2.3 Invertebrate predators

Spiders are frequently reported as preying on ladybirds, especially **web-building spiders** (e.g. Nentwig 1983, Laing 1988, Richardson & Hanks 2009, Sloggett 2010). However, the experimental study by Nentwig

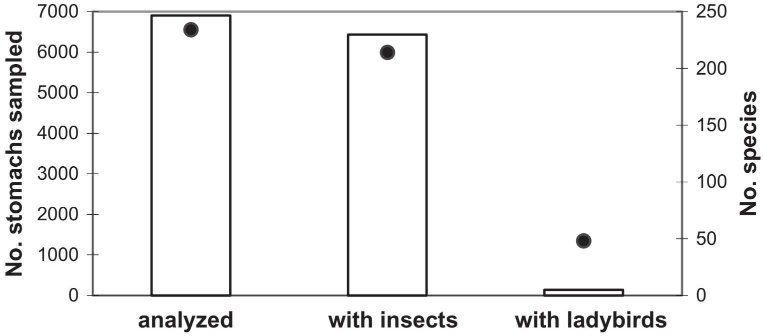

Figure 8.1 Analysis of stomach contents of Ukrainian birds (data extracted from Mizer 1970). Bars, numbers of stomachs; dots, numbers of bird species.

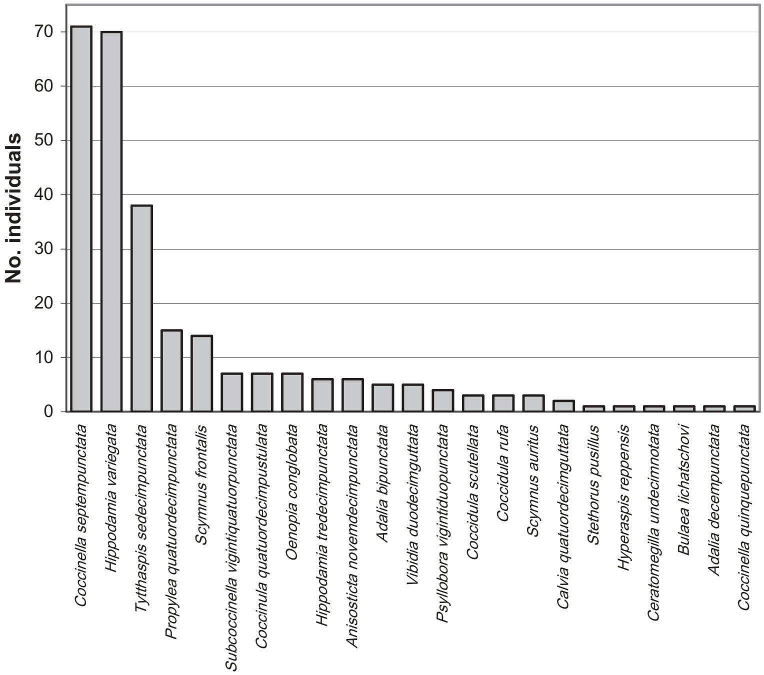

Figure 8.2 Species composition of Coccinellidae found in stomachs of Ukrainian birds (data extracted from Mizer 1970).

(1983) suggests that ladybird beetles, even if caught in a spider web, may be not eaten.

In contrast to web-builders, **actively hunting spiders** can capture their prey in a more targetted manner. It was found that these predators relatively rarely attack coleopterans because of their thick and hard cuticle (Nentwig 1986, Nyffeler 1999). In the case of Coccinellidae, defensive alkaloids may act as additional protection (Eisner et al. 1986; Camarano et al. 2006).

Insects of various orders (e.g. Hemiptera, Diptera, Coleoptera, Neuroptera) have been reported to prey on Coccinellidae, and many of them are intraguild predators (Chapter 7). Insects not belonging to the same

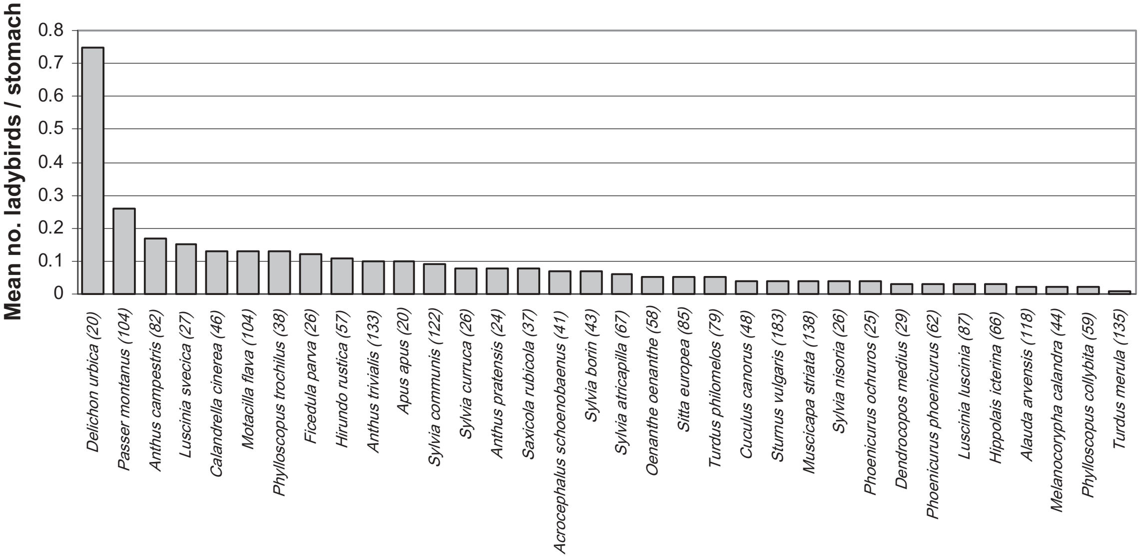

Figure 8.3 Mean numbers of ladybirds in the stomachs of individual bird species (data extracted from Mizer 1970). The number of stomachs analysed is given in brackets.

guild as their predatory ladybird prey include gomphid dragonflies (Odonata: Gomphidae) (Conrad 2005), robber flies (Diptera: Asilidae) (Ghahari et al. 2007) or vespid wasps (Hymenoptera: Vespidae) (Gambino 1992).

Predatory insects known to hunt **phytophagous ladybirds** include beetles (entomophagous Coccinellidae, Carabidae, Cantharidae), true bugs (Anthocoridae, Nabidae, Reduviidae, Pentatomidae, Lygaeidae), neuropterans (Chrysopidae, Myrmeleontidae), butterflies (larvae of some Noctuidae), earwigs (Forficulidae) and ants (Formicidae) (Howard & Landis 1936, Ohgushi 1986). Ants are also known as occasional predators of predatory coccinellids (Sloggett et al. 1999, Majerus et al. 2007), but the majority of interactions between these two groups of insects are of a competitive nature.

8.2.4 Hemiptera-tending ants

The mutualistic relationship in which ants tend honeydew-producing Hemiptera is a very common and widespread phenomenon (Styrsky & Eubanks 2007). The great majority of ants taking part in such associations belong to phylogenetically advanced subfamilies Dolichoderinae, Formicinae and Myrmicinae. The hemipterans most frequently attended are aphids (Aphididae), soft scales (Coccidae) and mealybugs (Pseudococcidae) (Delabie 2001). Ants benefit from this association mainly by feeding on honeydew, a predictable and renewable source of carbohydrates and other compounds. The most important gains of hemipterans are sanitation of their colonies and the protection from natural enemies (Delabie 2001, Majerus et al. 2007, Styrsky & Eubanks 2007).

By protecting honeydew producers, ants come into antagonistic interactions with potential enemies of the former, including ladybirds (Majerus et al. 2007). The level of ant aggression towards enemies of the tended hemipterans increases with increasing proximity to the tended colonies (Hanks & Sadof 1990, Sloggett et al. 1998, Dejean et al. 2002, Sloggett & Majerus 2003, Majerus et al. 2007). As a consequence of a high ant aggression, ladybird adults and especially their soft-bodied larvae are sometimes killed when feeding on ant-tended resources (Cochereau 1969, Majerus 1989, Dejean et al. 2002). More often, adults are chased from the colony, while larvae may be picked up and carried away or dropped off the plant (Hanks & Sadof 1990, Majerus et al. 2007). The number of coccinellids is usually lower in the presence of ants than in their absence (Bradley 1973, Reimer et al. 1993, Takizawa & Yasuda 2006).

Many ladybird species can reduce the effects of ant aggression using various kinds of behavioural, physical and chemical defences. Mechanisms of ladybird defence against ants were recently reviewed by Majerus et al. (2007) and include running or flying away, dropping to the ground, taking a 'clamp down' posture, reflex bleeding, mechanical protection by hard exoskeleton or structures such as spines or wax filaments.

More specific adaptations allowing avoidance of ant aggression can be found in those ladybird species that specialize in feeding on ant-tended hemipterans (Table 8.1). Some of these **myrmecophilous ladybirds**

Table 8.1 Ladybirds adapted to feed on prey tended by ants.

Ladybird	Ant	Tended prey group	Region	Adaptations to ant aggression	References
COCCINELLINAE					
Coccinellini					
Coccinella magnifica	*Formica* spp.	aphids	Palaearctic	possibly chemical and/or behavioural protection	2, 11, 12, 13
SCYMNINAE					
Scymnini					
Scymnus interruptus	*Lasius niger*	aphids	Germany	smeary, adhesive wax cover of the larva repels ant attack	15
Scymnus nigrinus	*Formica polyctena*	aphids	Germany	smeary, adhesive wax cover of the larva repels ant attack	15
Scymnus (Pullus) posticalis	*Lasius niger, Pristomyrmex pungens*	aphids	Japan	larvae ignored by ants (wax cover may function as chemical camouflage)	3, 4
Hyperaspidini					
Hyperaspis conviva	*Formica obscuripes*	coccid	Manitoba (Canada)	larvae rarely attacked, wax cover and reflex bleeding – sufficient protection	1
Hyperaspis reppensis	*Tapinoma nigerrimum*	fulgorid (Auchenorrhyncha)	Italy	larvae not attacked, adults – 'cowering behaviour' when attacked	10
Brachiacanthadini					
Brachiacantha quadripunctata	*Lasius umbratus*	coccids	Massachusetts (USA)	larvae covered with waxy tufts resemble giant coccids	16
Brachiacantha ursina	*Lasius claviger*	aphids	Washington DC (USA)	larvae with waxy cover not attacked by ants	9

Table 8.1 (*Continued*)

Ladybird	Ant	Tended prey group	Region	Adaptations to ant aggression	References
Platynaspidini					
Phymatosternus lewisii	*Pristomyrmex pungens*	aphids	Japan	coccid–like larvae not attacked by ants	4
Platynaspis luteorubra	*Lasius niger*, *Myrmica rugulosa*, *Tetramorium caespitum*	aphids	Europe	larvae – morphological adaptations (flattened shape, long setae, short legs) and presumably chemical camouflage pupae – dense hair cover adults – 'cowering behaviour'	6, 14
ORTALIINAE					
Ortaliini					
Apolinus lividigaster	*Crematogaster* sp., *Paratrechina* sp.	aphids	eastern Australia	very long body projections and wax cover in larva and pupa, defensive behaviour of larva, waxy smear around pupa	7
COCCIDULINAE					
Coccidulini					
Rodatus major	*Iridomyrmex* sp.	margarodid (Coccoidea) eggs	eastern Australia	larval feeding inside margarodid ovisac, wax cover and defensive behaviour of the larva, wax shroud resembling margarodid ovisac produced by prepupa	8
Azyini					
Azya orbigera	*Azteca instabilis*	coccid	Mexico	sticky, waxy filaments of the larva prevent effective ant attack	5

References: 1, Bradley (1973); 2, Godeau et al. (2009); 3, Kaneko (2002); 4, Kaneko (2007); 5, Liere & Perfecto (2008); 6, Majerus et al. (2007); 7, Richards (1980); 8, Richards (1985); 9, Schwarz (1890); 10, Silvestri (1903); 11, Sloggett et al. (1998); 12, Sloggett et al. (2002); 13, Sloggett & Majerus (2003); 14, Volkl (1995); 15, Volkl & Vohland (1996); 16, Wheeler (1911).

(or their particular life stages) are ignored by the ants and, hence, have access to prey resources effectively defended from other predators. To avoid ant aggression, myrmecophilous ladybirds may use chemical camouflage and/or may morphologically mimic their ant-tended prey. Wax filaments produced by the larvae of many ladybird species make them very similar to some of their prey, e.g. coccids or mealybugs. According to Pope (1979), protection against ants is one of the main functions of the larval wax.

8.2.5 Social aphids with a soldier caste

Some aphids in the subfamilies Hormaphidinae (mainly of the tribe Cerataphidini) and Pemphiginae are known to produce morphologically distinct 'soldiers' that defend reproducing individuals in the colony from natural enemies (Stern & Foster 1996). Soldier-producing species are usually those that form long-lived galls or large, exposed colonies (Aoki et al. 2001). In most species, soldiers are a sterile caste constituting first or second instar nymphs which do not moult to older instars. They often differ from normal nymphs by having a more elongate body, a shorter proboscis and enlarged, sclerotized legs (Ito 1989, Stern & Foster 1996, Ijichi et al. 2005, Kurosu et al. 2008). To fight with potential enemies, soldiers of certain aphids use their stylets, through which some of them inject paralyzing venom (Kutsukake et al. 2004). In other aphids, heads of the soldiers are equipped with a pair of frontal horns which are used to pierce their victims. Characteristics of soldiers found in different aphid groups are given in Table 8.2.

A single soldier aphid can rarely cause fatal damage to a ladybird. Shibao (1998) found that individual soldiers of the bamboo aphid, *Pseudoregma bambucicola*, can destroy (with their frontal horns) a small victim such as a syrphid egg or hatchling, but are unable to kill even a first instar larva of predatory ladybird, *Synonycha grandis*. Therefore, soldiers attack in unison; up to three soldiers have been observed to attack a newly hatched *S. grandis* larva, and up to 16 soldiers with an older larva. Very large (20–25 mm in length) fourth instar larvae of *S. grandis*, even if attacked by many soldiers, are usually thrown down to the ground rather than killed. Nevertheless, experiments performed by Shibao (1998) showed that the mortalities of first and third–fourth instar larvae of *S. grandis* were positively correlated with the density of *P. bambucicola* soldiers.

The developmental stage of a ladybird that is most vulnerable to attack from soldier aphids is the egg. Some ladybirds feeding on soldier-producing aphids have developed adaptations to protect their eggs from soldiers. Females of *Sasajiscymnus kurohime*, for example, cover their eggs with a layer of faeces-like secretion, which supposedly serves as a protection against the soldiers of *Ceratovacuna lanigera* and *P. bambucicola* (Arakaki 1988, 1992, Joshi & Viraktamath 2004). Other ladybird species, *S. grandis* and *Megalocaria dilatata*, lay their eggs a safe distance from aphid colonies (Arakaki 1992, Joshi & Viraktamath 2004). Larvae and adults of the latter two species have been observed to reflex bleed in response to soldier attacks (Joshi & Viraktamath 2004). Interestingly, larvae of *S. kurohime* are not attacked by the soldiers of *C. lanigera* (Arakaki 1992).

Table 8.2 Characteristics of aphid soldiers and colonies they defend.

Aphid group	Colony type	Developmental stage of soldiers	Soldier weapon	References
Cerataphidini on primary host plants (*Styrax* spp.)	in galls	2nd instar	stylets	4, 7, 9, 10, 11, 14
Cerataphidini on secondary host plants (monocotyledons)	exposed	1st instar	frontal horns	2, 5, 7, 8, 12, 13, 14
Pemphiginae	in galls or exposed	usually 1st instar	stylets	1, 3, 6, 7, 14

References: 1, Aoki et al. (2001); 2, Aoki et al. (2007); 3, Aoki & Kurosu (1986); 4, Aoki & Kurosu (1989); 5, Arakaki (1988); 6, Ijichi et al. (2005); 7, Ito (1989); 8, Joshi & Viraktamath (2004); 9, Kurosu & Aoki (2003); 10, Kurosu et al. (2008); 11, Kutsukake et al. (2004); 12, Shibao (1998); 13, Stern (1998); 14, Stern & Foster (1996).

8.3 PARASITOIDS

Ladybirds are attacked by a wide array of insect parasitoids. Some are specific for limited ranges of taxa within the Coccinellidae, while others are broad polyphages, which can parasitize members of various insect families and orders. Furthermore, there are also many secondary parasitoids or hyperparasitoids associated with the primary parasitoids. Summarized data on primary and secondary ladybird parasitoids and their host and distribution records are presented in Tables 8.3 and 8.4, but these lists are certainly far from comprehensive. Many taxa are probably still omitted, some should perhaps be removed as misidentifications, and others transferred to another group of parasitoids of ladybirds. In particular it is often not easy to determine whether a particular parasitoid is primary or secondary, or even tertiary, especially as in most cases we only know its taxonomic position.

Hereafter, we first describe the characteristics of parasitoids reported from Coccinellidae, as based on this imperfect set of data in Tables 8.3 and 8.4 and the other tables referred to in Table 8.3. Then we review the available information on selected parasitoid taxa.

Table 8.3 Primary and presumed primary parasitoids of Coccinellidae.

Parasitoid types: I, imaginal; P, pupal; L–P, larval–pupal (oviposition into host larva, emergence from host pupa); L, larval; E, egg parasitoid.

Parasitoid taxon	Reported ladybird host taxa	Parasitoid type	Distribution records	References*
GENERA SPECIFIC FOR COCCINELLIDAE				
Hymenoptera: Braconidae				
Dinocampus				
D. coccinellae	see Table 8.5	I	cosmopolitan	see Table 8.5
Hymenoptera: Chalcididae				
Uga				
several species, see Table 8.8	Epilachninae	L–P	Asia, Africa, Australia, Indonesia	see Table 8.8
Hymenoptera: Encyrtidae				
Cowperia				
several species, see Table 8.9	see Table 8.9	P	Europe, Asia, Indonesia	see Table 8.9
Homalotylus				
many species, see Table 8.10	see Table 8.11	L, L–P	cosmopolitan	see Table 8.10
Hymenoptera: Proctotrupidae				
Nothoserphus				
several species, see Table 8.12	see Table 8.12	L	Europe, Asia, Indonesia	see Table 8.12
Hymenoptera: Pteromalidae				
Metastenus				
M. concinnus	*Cryptognatha signata, Cryptolaemus montrouzieri, Scymnus impexus*, *Scymnus apetzi, Scymnus* sp.	P	Europe, Asia, Argentina	23

(*Continued*)

Table 8.3 (*Continued*)

Parasitoid taxon	Reported ladybird host taxa	Parasitoid type	Distribution records	References*
M. townsendi	*Azya orbigera, Cryptognatha nodiceps, Cryptognatha simillima, Hyperaspis lateralis, Hyperaspis* sp.*, Microweisea* sp., *Nephus guttulatus, Pentilia insidiosa, Pseudoazya trinitatis, Scymnus otohime, Scymnus* sp.	P	Carribean, Mexico, USA, Japan	23
SPECIES SPECIFIC FOR COCCINELLIDAE				
Diptera: Phoridae				
Phalacrotophora several species, see Table 8.13	Coccinellinae, Chilocorinae	P	see Table 8.13	see Table 8.13
Diptera: Tachinidae				
Euthelyconychia epilachnae (syn. *Paradexodes epilachnae*)	*Epilachna varivestis, Epilachna defecta, Henosepilachna vigintisexpunctata*	L, P	Mexico	11, 15, 28
Pseudebenia epilachnae	*Epilachna quadricollis*	L	South Korea	33
Hymenoptera: Braconidae				
Centistes scymni	*Scymnus* (*Pullus*) *impexus*	I	Switzerland, Germany	9
Centistes subsulcatus	*Propylea quatuordecimpunctata*	I	Belgium	13
Hymenoptera: Encyrtidae				
Anagyrus australiensis	*Diomus pumilio*	P	Australia	23
Ooencyrtus azul	*Chilocorus nigripes*	P	Kenya	23
Ooencyrtus bedfordi	*Chilocorus cacti, Chilocorus discoideus, Chilocorus distigma*	P	South Africa, Uganda	23
Ooencyrtus camerounensis	*Epilachna eckloni, Chnootriba similis*	E	Cameroon, Ethiopia, Senegal, South Africa	4, 23
Ooencyrtus epilachnae	*Epilachna dregei*	E	South Africa, Uganda	23
Ooencyrtus puparum	*Platynaspis* sp.	P	Senegal	23
Ooencyrtus sinis	*Exochomus flavipes, Exochomus flaviventris*	P	South Africa	23
Prochiloneurus nigriflagellum	*Orcus australasiae*	L	Queensland (Australia)	23
Hymenoptera: Eulophidae				
Aprostocetus neglectus	Chilocorini, Scymnini, ?Coccinellini	L–P	Europe, Asia, Nearctic	23
Chrysocharis johnsoni	*Henosepilachna vigintioctopunctata*	?	India	23
Chrysonotomyia appannai	*Henosepilachna vigintioctopunctata*	E	India	23
Oomyzus mashhoodi	undet. Coccinellidae	L	India	16
Oomyzus scaposus	Coccinellini, Chilocorini, Scymnini	L–P	cosmopolitan	23
Pediobius foveolatus	Epilachninae	L, L–P, P	Africa, Asia, Australia, Pacific islands, Nearctic (introduced)	23
Pediobius nishidai	*Epilachna mexicana*	L	Costa Rica	23

Table 8.3 (*Continued*)

Parasitoid taxon	Reported ladybird host taxa	Parasitoid type	Distribution records	References*
Quadrastichus ovulorum	Epilachninae	E	Africa, India, Sri Lanka, Melanesia	23
Sigmoepilachna indica[†]	*Epilachna* sp.	E	India	23
Tetrastichus decrescens	*Henosepilachna vigintioctomaculata*	?	China	23
Tetrastichus epilachnae	Epilachninae, Coccinellini, Chilocorini, Scymnini	L–P	Europe, Asia, Morocco	23
Hymenoptera: Eupelmidae				
Eupelmus vermai	*Epilachna* sp.	L	India	23
Hymenoptera: Pteromalidae				
Inkaka quadridentata	*Cryptolaemus montrouzieri*	?	Australia, New Zealand	23
Merismoclea rojasi	*Coccidophilus citricola*	?	Argentina, Chile	23
Mesopolobus secundus	undet. Scymninae, *Hyperaspis senegalensis*	L	Uganda, Kenya	8, 9
Ophelosia bifasciata	undet. Coccinellidae	L	Australia	5
Oricoruna orientalis	*Rodolia fumida*	L	India	23
Oricoruna sp.	*Exochomus* sp., *Rodolia occidentalis*	?	Nigeria	23
TAXA REPORTED FROM VARIOUS HOSTS INCLUDING COCCINELLIDAE				
Diptera: Phoridae				
Megaselia spp.	*Chilocorus distigma*	P	East Africa	10
	Chilocorus quadrimaculatus	P	Kenya	10
	Epilachna varivestis	L, P	USA	10, 15
Diptera: Sarcophagidae				
Boettcheria latisterna (syn. *Sarcophaga latisterna*)	*Epilachna varivestis*	I	Ohio (USA)	11, 15, 28
Helicobia rapax (syn. *Sarcophaga helicis*)	*Epilachna varivestis*	L	Alabama (USA)	11, 15, 28
Ravinia errabunda (syn. *Sarcophaga reinhardii*)	*Epilachna varivestis*	L	Mexico	11, 15, 28
Diptera: Tachinidae				
Chetogena claripennis	*Epilachna borealis, Epilachna varivestis*	L, P	North America	11, 15, 24, 28
Lydinolydella metallica	*Epilachna eusema, Epilachna marginella, Epilachna* sp.	L	South America	3, 11, 28
Lypha slossonae	*Epilachna varivestis*	?	North America	11, 24, 28
Medina spp. incl. *M. separata*, *M. collaris* and *M. melania*[‡]	Epilachninae, Coccinellinae, Chilocorinae	I	Palaearctic	2, 6, 29
Myiopharus doryphorae (syn. *Doryphorophaga doryphorae*)	*Epilachna varivestis*	I	North America	15, 24
Policheta unicolor	*Subcoccinella vigintiquatuorpunctata*	?	France	14

(*Continued*)

Table 8.3 (*Continued*)

Parasitoid taxon	Reported ladybird host taxa	Parasitoid type	Distribution records	References*
Strongygaster triangulifera	*Coccinella trifasciata, Coleomegilla maculata, Harmonia axyridis, Epilachna varivestis*	I	North America	21, 24
Hymenoptera: Encyrtidae				
Anagyrus sp.	*Telsimia* sp.	L	Australia	23
Cerchysiella sp.	*Chilocorus bipustulatus*	L	Israel	36
Eupoecilopoda perpunctata	*Scymnus* sp.	P	Iran	19
Isodromus niger	*Chilocorus similis*	?	SE Europe, Asia, USA	23
Hymenoptera: Eulophidae				
Baryscapus thanasimi	*Chilocorus stigma*	L	USA	23
Omphale sp.§	*Henosepilachna vigintioctopunctata*	E	India	26
Oomyzus sempronius	*Chilocorus bipustulatus*	L	Europe, Egypt, Turkey	23
Parachrysocharis sp.	*Hippodamia variegata*	?	India	23
Pnigalio agraules	*Chilocorus bipustulatus*	?	Palaearctic	23
Tetrastichus cydoniae	*Cheilomenes propinqua vicina, Chnootriba similis*	P	western Africa	23, 31
Tetrastichus orissaensis	*Epilachna* sp, *Subcoccinella vigintiquatuorpunctata*	?	India, Hungary, Italy, former Yugoslavia	23
Hymenoptera: Eupelmidae				
Anastatus spp.	*Chilocorus bipustulatus, Hyperaspis* sp.	?	Israel, Nigeria	23, 36
Eupelmus urozonus	*Chilocorus bipustulatus*	?	?	23
Eupelmus sp.	*Chilocorus bipustulatus*	?	Israel	36
Hymenoptera: Pteromalidae				
Austroterobia sp.	*Rodolia iceryae*	?	Kenya	23
Mesopolobus sp.	*Chnootriba similis*	P	Ethiopia	4
Pseudocatolaccus sp.	*Chilocorus bipustulatus, Cryptolaemus montrouzieri*	?	Russia	23
Trichomalopsis acuminata	*Propylea quatuordecimpunctata*	P	Hungary	27
Hymenoptera: Trichogrammatidae				
Trichogramma sp.	*Epilachna* sp.	E	Indonesia	23

*See Table 8.4 for list of references

†*Sigmoepilachna indica* is the only described species of the recently erected genus *Sigmoepilachna* and its only known host is *Epilachna* sp. In our opinion, however, placing *Sigmoepilachna* among the genera specific for Coccinellidae would be premature, taking into account the highly insufficient data on this genus.

‡Most older records on the parasitization of ladybirds by *Medina* spp. erroneously refer to *Medina luctuosa*.

§This record of *Omphale* sp. as an egg parasitoid of *Henosepilachna vigintioctopunctata* may refer to *Chrysonotomyia appannai* (syn. *Omphale epilachni*) considering that both were reported from the same region (southern India) and host species.

Table 8.4 Hyperparasitoids and presumed hyperparasitoids of Coccinellidae.

Parasitoid taxon	Primary host	Secondary (coccinellid) host	Distribution records	References
Hymenoptera: Ceraphronidae				
Aphanogmus sp.	?	*Chilocorus bipustulatus*	Israel	36
Hymenoptera: Chalcididae				
Brachymeria carinatifrons	*Euthelyconychia epilachnae, Lydinolydella metallica*	*Epilachna mexicana, Epilachna varivestis, Epilachna* sp.	Texas (USA), Mexico, Venezuela, Brazil	3, 23
Conura porteri	*Dinocampus coccinellae, Perilitus stuardoi*	?	Chile	23
Conura paranensis	*Dinocampus coccinellae*	*Cycloneda sanguinea*	Argentina	23
Conura petioliventris	*Dinocampus coccinellae*	*Hippodamia convergens*	California (USA)	23
Conura sp.	?	*Adalia deficiens*	South America	23
	Lydinolydella metallica	*Epilachna eusema, Epilachna* sp.	Argentina	3, 23
Hymenoptera: Encyrtidae				
Cheiloneurus carinatus	*Homalotylus* sp.	?	Africa	23
Cheiloneurus cyanonotus	*Homalotylus* spp., Tetrastichinae	Epilachninae, Chilocorinae, Coccinellinae	Africa	23
Cheiloneurus liorhipnusi	?	*Chnootriba similis*	Kenya, Senegal	23
Cheiloneurus orbitalis	*Homalotylus* sp.	undet. Coccinellidae	South Africa	7
Coccidoctonus trinidadensis	?*Homalotylus* sp.	*Cryptolaemus* sp.	Central America	11, 23
Homalotyloidea dahlbomii	*Homalotylus* spp.	*Chilocorus bipustulatus*, ?*Rhyzobius litura*	Europe, Canary Islands, Israel	23, 35
Ooencyrtus distatus	*Homalotylus* sp.	*Scymnus morelleti*	South Africa	23
Ooencyrtus polyphagus	?	*Chnootriba similis, Henosepilachna elaterii, Exochomus flavipes, Platynaspis* sp.	Cameroon, Mali, Senegal	23
Prochiloneurus aegyptiacus	*Homalotylus* spp.	*Chilocorus bipustulatus, Exochomus flavipes, Hyperaspis aestimabilis*	Africa, Asia, southern Europe	23
	Metastenus sp.	*Exochomus* sp., *Hyperaspis* sp.	Israel	36

(*Continued*)

Table 8.4 (*Continued*)

Parasitoid taxon	Primary host	Secondary (coccinellid) host	Distribution records	References
Hymenoptera: Eulophidae				
Aprostocetus esurus	?	*Chilocorus similis*	USA	20
Elasmus sp.	?	*Henosepilachna vigintioctopunctata*	India	35
Pediobius amaurocoelus	?	*Chnootriba similis*	Ghana	17
Pediobius sp.	Tetrastichinae	*Henosepilachna vigintioctopunctata*	India	35
	?	*Exochomus* sp.	Ghana, Nigeria, Zambia	23
Tetrastichinae	*Pediobius foveolatus*	*Henosepilachna vigintioctopunctata*	India	35
Hymenoptera: Eupelmidae				
Eupelmus sp.	?	*Henosepilachna vigintioctopunctata*	India	35
Hymenoptera: Eurytomidae				
Aximopsis sp.	*Pediobius foveolatus*	*Henosepilachna vigintioctopunctata*	India	23, 35
Hymenoptera: Ichneumonidae				
Gelis agilis (syn. *Gelis instabilis*)	*Dinocampus coccinellae*	*Coccinella septempunctata*	Poland	6
Gelis melanocephalus	?	*Coccinella septempunctata*	England	12, 32
Gelis sp.	*Dinocampus coccinellae*	*Coleomegilla maculata*	Ontario (Canada)	6
Syrphoctonus tarsatorius	?	*Coccinella septempunctata*	?	12, 32
Phygadeuon subfuscus	*Euthelyconychia epilachnae*	*Epilachna varivestis*	North America	11
Hymenoptera: Megaspilidae				
Dendrocerus spp. (syn. *Lygocerus, Atritomellus*), incl. *D. ergensis*	*Homalotylus* spp.	*Chilocorus bipustulatus, Coccinella septempunctata, Pharoscymnus numidicus, Pharoscymnus ovoideus, Scymnus* sp.	Japan, Israel, France, Italy, Spain, North Africa	1, 6, 11, 34, 36
Hymenoptera: Pteromalidae				
Catolaccus spp.	?	*Henosepilachna vigintioctopunctata*	China	23
	Oomyzus scaposus	*Coccinella septempunctata*	Poland	25
Dibrachys microgastri	*Dinocampus coccinellae*	*Coleomegilla maculata, Coccinella septempunctata*	Illinois (USA), England	23, 37
Ophelosia crawfordi	*Homalotylus* sp.	?	?	11

Table 8.4 (*Continued*)

Parasitoid taxon	Primary host	Secondary (coccinellid) host	Distribution records	References
Pachyneuron albutius (syn. *P. syrphi*)	?	*Chilocorus bipustulatus, Chilocorus renipustulatus, Exochomus quadripustulatus, Coccinella septempunctata*	Former USSR	22, 23
Pachyneuron altiscuta	?	*Harmonia axyridis*	North Carolina (USA)	30
Pachyneuron chilocori	*Homalotylus* sp.	*Chilocorus bipustulatus*	Italy, Israel	23, 36
Pachyneuron muscarum (syn. *P. concolor, P. siculum*)	*Homalotylus* sp.	*Chilocorus bipustulatus, Coccinella septempunctata*	Europe, Israel	18, 23, 36
Pachyneuron solitarium	*Homalotylus* sp.	*Anatis ocellata, Coccinella septempunctata, Myzia oblongoguttata*	Hungary, Poland, West Siberia	6
Pachyneuron spp.	*Homalotylus* spp., Tetrastichinae	*Calvia quatuordecimguttata, Cheilomenes lunata, Chilocorus inornatus, Exochomus flavipes, Harmonia axyridis, Hippodamia tredecimpunctata, Hippodamia variegata, Hyperaspis senegalensis, Menochilus sexmaculatus, Nephus kiesenwetteri, Nephus ornatus, Nephus soudanensis, Scymnus quadrillum, Subcoccinella vigintiquatuorpunctata*	Asia, Africa, Europe, North America	6, 23
Trichomalopsis dubia	*Dinocampus coccinellae*	*Coleomegilla maculata*	North America	23
	Pediobius foveolatus	*Epilachna varivestis*	North America	23
Trichomalopsis (syn. *Eupteromalus*) sp.	*Dinocampus coccinellae*	*Coccinella undecimpunctata, Coleomegilla maculata*	Egypt, Ontario (Canada)	6
	Oomyzus scaposus	*Coccinella septempunctata*	Poland	25
Hymenoptera: Signiphoridae				
Chartocerus subaeneus	?	*Nephus* sp.	?	23

References to Tables 8.3 and 8.4: 1, Alekseev & Radchenko (2001); 2, Belshaw (1993); 3, Berry & Parker (1949); 4, Beyene et al. (2007); 5, Boucek (1988); 6, Ceryngier & Hodek (1996); 7, Compere (1938); 8, Crawford (1912); 9, Delucchi (1954); 10, Disney et al. (1994); 11, Domenichini (1957); 12, Elliott & Morley (1907); 13, Hemptinne (1988); 14, Hodek (1973); 15, Howard & Landis (1936); 16, Husain & Khan (1986); 17, Kerrich (1973); 18, Klausnitzer (1967); 19, Lotfalizadeh (2010); 20, Marlatt (1903); 21, Nalepa & Kidd (2002); 22, Nikol'skaya (1934); 23, Noyes (2011); 24, O'Hara (2009); 25, Pankanin–Franczyk & Ceryngier (1999); 26, Patnaik & Mohapatra (2004); 27, Radwan & Lovei (1982); 28, Richerson (1970); 29, Richter (1971); 30, Riddick et al. (2009); 31, Risbec (1951); 32, Schaefer & Semyanov (1992); 33, Shima et al. (2010); 34, Smirnoff (1957); 35, Usman & Thontadarya (1957); 36, Yinon (1969); 37, R. Comont (unpublished).

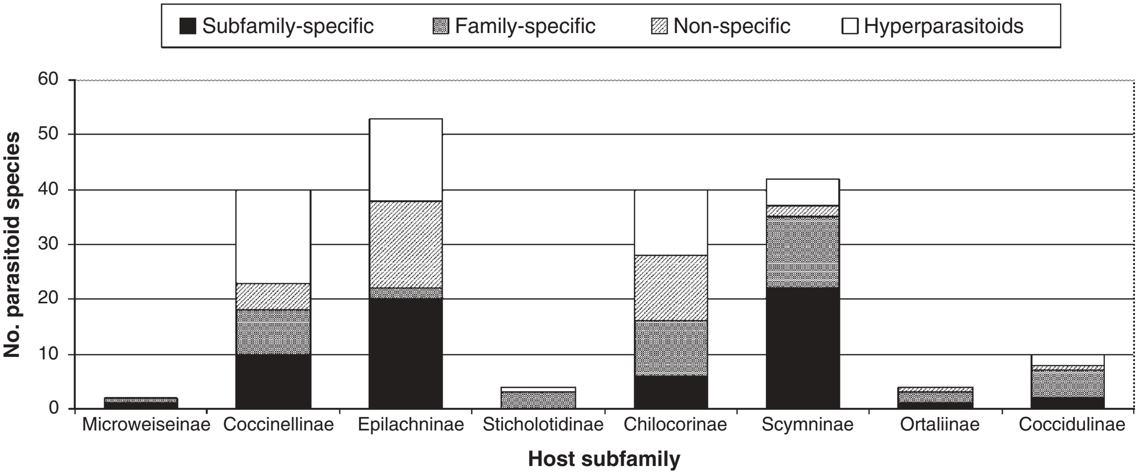

Figure 8.4 Number and host specificity of parasitoid species reported from members of different subfamilies of Coccinellidae. Subfamily-specific species are reported only from hosts belonging to a particular ladybird subfamily; Family-specific species are reported from more than one ladybird subfamily but not from other hosts; Non-specific species are reported from ladybird hosts as well as hosts belonging to other insect families or orders; Hyperparasitoids are species developing in primary ladybird parasitoids.

In allocating the ladybird genera to subfamilies and tribes we have used the system proposed by Nedvěd and Kovář (Chapter 1).

8.3.1 General characteristics of parasitoids of ladybirds

8.3.1.1 Host specificity of parasitoids recorded from Coccinellidae

Of almost 160 parasitoids listed here, about 40 have been classified as **hyperparasitoids**. The remaining 117 taxa, representing three dipteran and eight hymenopteran families, are considered as **primary parasitoids**. The most numerous group among these consists of 46 species belonging to the six genera believed to be entirely specific to Coccinellidae. This number would rise by a further 26 species if we count all described species in these six genera, including those whose hosts have not yet been discovered.

The remaining parasitoid species include a group of about 39 species presumably specific for Coccinellidae, as well as about 32 species of parasitoids not specific for ladybirds but recorded from them. It is possible that some taxa in these two groups are, in fact, hyperparasitoids.

8.3.1.2 Parasitoids of different subfamilies of Coccinellidae

Ladybird hosts of the listed parasitoids belong to eight subfamilies (Fig. 8.4). The majority of records concern four of them, Coccinellinae, Epilachninae, Chilocorinae and Scymninae, with Epilachninae being associated with the highest number (53) of parasitoid species. Interestingly, most parasitoids reported from the Coccinellinae, Epilachninae and Chilocorinae are polyphages and hyperparasitoids, while those of Scymninae, as well as of the remaining four subfamilies (Microweiseinae, Sticholotidinae, Ortaliinae and Coccidulinae), are mainly host subfamily- and family-specific taxa.

8.3.1.3 Parasitism in different developmental stages of Coccinellidae

All developmental stages of ladybirds are subject to attack from parasitoids, though parasitization of eggs and adult beetles is relatively rare and the former is restricted to phytophagous ladybirds of the subfamily Epilachninae. It has been supposed that predatory ladybirds are devoid of **egg parasitoids** due to the cannibalistic habit of the newly hatched larvae. Successful parasitoid development in the eggs prior to being cannibalized is unlikely because egg parasitoids usually emerge from parasitized eggs after the non-parasitized eggs have hatched (Klausnitzer 1969). However, newly hatched larvae of some epilachnine ladybirds are also known to cannibalize unhatched eggs in the batch (Nakamura 1976, Nakamura & Ohgushi 1981).

Parasitization of adult ladybirds, although only a few parasitoid species are involved, has received disproportionately more attention from researchers than parasitization of other stages. Such over-representation is largely due to one species, the euphorine braconid, *Dinocampus coccinellae*, which, since the first systematic studies by Ogloblin (1924) and Balduf (1926), has continuously attracted the attention of successive generations of entomologists.

The predominant group of parasitoids of ladybirds is formed by the **parasitoids attacking larvae and pupae**. However, only very few species in this group, such as the flies *Phalacrotophora fasciata* and *P. berolinensis*, or the wasps *Oomyzus scaposus* and *Pediobius foveolatus*, have been studied in any detail. The biology and ecology of the latter species has been relatively well recognized because of its economic importance as a biological control agent of phytophagous ladybirds.

8.3.2 Review of the more important taxa

Most of the research on ladybird parasitoids concerns a few species found in the Palaearctic region (especially in its European part) and, to a lesser degree, in the Nearctic region. Apart from host and distribution records, we know nearly nothing about the majority of species parasitizing Coccinellidae in the remaining parts of the world.

The intention of this review is not only to discuss the relatively well-known European and North American species, but also to draw the attention of the reader to certain less known but, in our opinion, not less important parasitoids. We applied two criteria in selecting parasitoid taxa for more detailed presentation: (i) the degree of their specificity for ladybirds and (ii) their importance as a mortality factor of Coccinellidae from a more global perspective. Thus, we review the literature for ladybird-specific genera (*Dinocampus*, *Uga*, *Cowperia*, *Homalotylus*, *Nothoserphus* and *Metastenus*) and those species groups (*Phalacrotophora* spp.) or single species (*O. scaposus*, *P. foveolatus*) which play a significant role in limiting ladybird populations in many parts of the world.

8.3.2.1 *Dinocampus* Foerster (Hymenoptera: Braconidae, Euphorinae)

The only known species certainly belonging to the genus *Dinocampus* is ***D. coccinellae*** (Schrank) (synonyms: *Dinocampus terminatus* (Nees), *Perilitus americanus* Riley, *P. coccinellae* (Schrank), *P. terminatus* (Nees)). *Dinocampus nipponicus* recently described from Japan (Belokobylskij 2000) was, soon after its description, transferred to the genus *Centistina* (Belokobylskij 2001). The current taxonomic status of *Perilitus stuardoi*, the other euphorine wasp which might belong to *Dinocampus*, is not known to us. *Perilitus stuardoi* was reported only from Chile as a parasitoid of *Adalia deficiens*, *A. bipunctata*, *Eriopis connexa* and *Cryptolaemus montrouzieri* (Smith 1953) and more recently of *Coleomegilla quadrifasciata* (Gonzales 2006).

Dinocampus coccinellae nowadays has a cosmopolitan **distribution** covering all continents except Antarctica, and many islands (Table 8.5). Although it has most frequently been reported from the temperate zone of the Holarctic, there are also records from the Arctic (Itilleq in Greenland, van Achterberg 2006) as well as from the tropics (e.g. Bangalore in India, Ghorpade 1977; and Planaltina in Brazil, Santos & Pinto 1981) and the temperate regions of the Southern Hemisphere (e.g. south-eastern Australia, Anderson et al. 1986; New Zealand and Tasmania, Alma 1980). The natural geographic range of *D. coccinellae* is difficult to reconstruct. According to Balduf (1926), the wasp might either have been introduced to North America from Europe or may be native to both North America and Eurasia. It is thought that *D. coccinellae* arrived in some parts of its present distribution together with ladybirds released for biological control purposes. It was probably transferred to the Hawaiian islands with the introduced *Olla v-nigrum* (Timberlake 1918), and to New Zealand with another biocontrol agent, *Coccinella undecimpunctata* (Gourlay 1930).

Mode of reproduction

Dinocampus coccinellae usually reproduces by **thelytokous parthenogenesis** (Ceryngier & Hodek 1996). However, as males can sporadically be produced (Muesebeck 1936, Hudon 1959, Wright 1978, Geoghegan et al. 1998a, Shaw et al. 1999, O. Nedvěd,

Table 8.5 Host records of *Dinocampus coccinellae* (from Ceryngier & Hodek 1996 supplemented and updated).

Host	Region	Reference
COCCINELLINAE		
Adalia bipunctata	Europe	4
	USA	4
Adalia decempunctata	Great Britain	4
Anatis ocellata	Great Britain	4
Anisosticta sibirica	Russian Far East	4
Calvia muiri	Japan	4
Calvia quatuordecimguttata	Europe	4
	Russian Far East	4
Ceratomegilla undecimnotata	Europe	4
Cheilomenes sulphurea	South Africa	4
Cheilomenes propinqua	South Africa	4
Cleobora mellyi	Tasmania	1
Coccinella californica	USA	4
Coccinella hieroglyphica	Great Britain	4
Coccinella leonina	Asia	4
	Australia	4
	Hawaii	4
Coccinella magnifica	Europe	4
	India	4
Coccinella novemnotata	North America	4
Coccinella quinquepunctata	Europe	4
	West Siberia	4
Coccinella septempunctata	Europe	4
	Asia	4
	USA	4
Coccinella septempunctata algerica	Tunisia	2
Coccinella septempunctata brucki	Japan	4
Coccinella trifasciata	West Siberia	4
	North America	4
Coccinella undecimpunctata	Europe	4
	Egypt	4
	New Zealand	4
	USA	4
Coccinula quatuordecimpustulata	Europe	4
	West Siberia	4
Coccinula sinensis	Russian Far East	4
Coelophora (=Lemnia) biplagiata	Taiwan	4
Coelophora inaequalis	Australia	4
	Hawaii	4
Coleomegilla maculata	North America	4
	Brazil	14
Cycloneda munda	USA	4
Cycloneda sanguinea	Brazil	13, 14
Eriopis connexa	Brazil	14
Halyzia sedecimguttata	Great Britain	4
Harmonia antipoda	New Zealand	1
Harmonia axyridis	Asia	4
	Japan	4
	North America	6, 8
	Europe	3, 7

Table 8.5 (*Continued*)

Host	Region	Reference
Harmonia conformis	Australia	4
Harmonia dimidiata	Taiwan	5
Harmonia octomaculata	Asia	4
Harmonia quadripunctata	Europe	4
	West Siberia	4
Hippodamia (Adonia) arctica	Russian Far East	4
Hippodamia convergens	USA	4
Hippodamia parenthesis	USA	4
Hippodamia tredecimpunctata	Europe	4
	Asiatic part of Russia	4
	USA	4
Hippodamia (Adonia) variegata	Europe	4
	Asia	4
	Chile	12
Illeis cincta	India	4
Lioadalia flavomaculata	South Africa	4
Macronaemia hauseri	China	4
Menochilus sexmaculatus	India	4
	Taiwan	4
	Japan	4
Micraspis discolor	Taiwan	4
	Vietnam	9
Myrrha octodecimguttata	Great Britain	15
Myzia oblongoguttata	Great Britain	4
Oenopia conglobata	Europe	4
	Russian Far East	4
Olla v–nigrum	USA	4
	Hawaii	4
	Brazil	14
Propylea japonica	Japan	4
	Russian Far East	4
Propylea quatuordecimpunctata	Europe	4
	Asiatic part of Russia	4
Psyllobora vigintiduopunctata	Great Britain	17
Tytthaspis sedecimpunctata	Great Britain	11
CHILOCORINAE		
Exochomus troberti concavus	South Africa	4
Exochomus quadripustulatus	Great Britain	10
Priscibrumus (=Exochomus) lituratus	Himalaya	4
Priscibrumus uropygialis	Himalaya	4
COLEOPTERA: CURCULIONIDAE		
Sitona discoideus	New Zealand	16

References: 1, Alma (1980); 2, Ben Halima–Kamel (2010); 3, Berkvens et al. (2010); 4, Ceryngier & Hodek (1996); 5, Chou (1981); 6, Firlej et al. (2005); 7, Koyama & Majerus (2008); 8, LaMana & Miller (1996); 9, Long & Belokobylskij (2003); 10, Mabbott (2006); 11, Majerus (1997); 12, Rebolledo et al. (2009); 13, Santos & Pinto (1981); 14, Silva et al. (2009); 15, Sloggett & Majerus (2000); 16, Wightman (1986); 17, R. Comont (unpublished).

unpublished), at least some of its strains are actually deuterotokous.

Several ***D. coccinellae* males** (one reared in Ontario, Canada, from *Col. maculata* and four in Scotland from *C. septempunctata*), when placed with females, displayed **courtship behaviour**, involving wing vibration (Wright 1978; Geoghegan et al. 1998a; Shaw et al. 1999) and walking in tight circles (Wright 1978). Moreover, each of those males tried to mount females but the mounting attempts of all but one male were rejected. The exception was the Canadian male, which mated with four females for about 20 minutes per female. Of 74 ladybirds offered to those four mated females, only 24 were parasitized and from 11 of them adult wasps developed, all of them being females (Wright 1978).

Life cycle

From host location to oviposition

Dinocampus coccinellae mostly oviposits into adult ladybird beetles but, especially when adult hosts are scarce, larvae and pupae can also be parasitized (Smith 1960, Maeta 1969, Filatova 1974).

Like some other euphorines, e.g. *Perilitus rutilus* or *Microctonus* spp. (Jackson 1928, Barratt & Johnstone 2001), *D. coccinellae* most frequently parasitizes its hosts when they are mobile (Bryden & Bishop 1945, Walker 1961, Richerson & DeLoach 1972, Orr et al. 1992). **Pre-oviposition and oviposition behaviour** of the parasitoid may be categorized as a sequence of the following activities: (i) pursuit and investigation of the host without extending the ovipositor, (ii) ovipositional stance with the ovipositor extended ventrally and forwards between the legs, and (iii) ovipositional attack, i.e. a thrust into the host with the ovipositor, which, if successful, is followed by egg deposition into the host's body (Richerson & DeLoach 1972, Geoghegan et al. 1998b). The existing evidence indicates that these activities are stimulated both visually (by the movement, colour, and size of potential hosts) and olfactorily (by host derived substances). The importance of **visual stimulation** was shown in tests using artificial hosts such as metal, wooden, plastic or paper models (Walker 1961, Richerson & DeLoach 1972). If such models were moving and were red or black, they caused wasp responses including pursuits, ovipositional stances and ovipositional attacks. Additionally, when the models were smeared with a ladybird's defensive secretion, numbers of the first two responses, but not of ovipositional attacks, increased. This may indicate that **odour** is an important stimulus for host recognition but not for host acceptance (Richerson & DeLoach 1972). More recently, Al Abassi et al. (2001) found that *D. coccinellae* is strongly attracted by some ladybird-produced substances (the alkaloids precoccinelline and myrrhine) but is not attracted by others (hippodamine, pyrazines).

Movement of the host not only facilitates its location by the parasitoid, but also makes **oviposition** easier. When a ladybird is walking, its elytra are slightly raised and the head is extended forward, which gives the female parasitoid better access to the soft membranes between the posterior abdominal segments or between the head and thorax, the host areas into which *D. coccinellae* most often oviposits (Balduf 1926, Iperti 1964, Sluss 1968, Richerson & DeLoach 1972). If a potential host is immobile, the wasp will, before ovipositing, stimulate such a host to walk by palpating it with the antennae, encircling it and probing with the ovipositor (Balduf 1926, Walker 1961, Richerson & DeLoach 1972). Immobilization of a host in response to examination by *D. coccinellae* is a frequently displayed **defensive behaviour against parasitization**. Other behaviours involved in ladybird defence are rapid escape, attacks on the parasitoid with mandibles, and attempts to kick the parasitoid ovipositor with hind legs (Firlej et al. 2010). *Dinocampus coccinellae* oviposition has to be very rapid because of host mobility and defensive reactions, and takes only a fraction of a second (Balduf 1926).

Development

The ripe ovarian **egg of *D. coccinellae*** is elongate and measures about 250 µm by 30 µm. After deposition in a host, it starts to grow and assume a more oval shape. Its average dimensions prior to hatching are 1010 µm by 570 µm (Sluss 1968). The hatched **larva** passes through **three instars** (Ogloblin 1924, Kadono-Okuda et al. 1995, Okuda & Kadono-Okuda 1995). As in many other parasitic wasps (Quicke 1997), the first instar larva, but not later instars, is equipped with grasping mandibles. It is believed that these serve to destroy other parasitoids within the host (Ogloblin 1924). Indeed, although *D. coccinellae* is a **solitary parasitoid**, more than one egg and/or first instar larva, sometimes as many as a few dozen, can be found in a single host (Ogloblin 1913, Balduf

1926, Maeta 1969), but only one larva survives to the second instar (Balduf 1926, Sluss 1968). Also the rate of **superparasitism** (proportion of parasitized hosts harbouring more than one parasitoid individual) in field samples may be quite high. Maeta (1969) found that 33–49% of parasitized *Coccinella septempunctata brucki* in Kurume (Fukuoka Prefecture, Japan) were superparasitized and Ceryngier (2000) recorded a superparasitism rate in *C. septempunctata* in Poland ranging between 22 and 64%. The frequent superparasitization of hosts by *D. coccinellae* may indicate a weak ability of this species to discriminate between unparasitized and already parasitized hosts. This was confirmed in laboratory tests by Okuda & Ceryngier (2000).

At moderate laboratory temperatures (20–26°C), the egg–larva **development of non-diapausing *D. coccinellae*** lasts 2–3 weeks (Sluss 1968, Obrycki & Tauber 1978, Obrycki et al. 1985, Obrycki 1989, Kadono-Okuda et al. 1995, Firlej et al. 2007), of which, 5–10 days are occupied with embryonic development (Balduf 1926, Sluss 1968, Kadono-Okuda et al. 1995). Development time in less suitable hosts, or those parasitized as juveniles, is longer than in suitable adult hosts (Obrycki et al. 1985, Obrycki 1989, Firlej 2007).

When the host stage parasitized is a larva or pupa, parasitoid development is arrested at the first instar larva until the eclosion of the host to adult (Kadono-Okuda et al. 1995). In dormant adult ladybirds, *D. coccinellae* usually diapauses as a first instar larva, and occasionally as an egg (Balduf 1926, Wright & Laing 1982). The **diapause** of *D. coccinellae* and that of its host ladybird are interrelated processes; in diapausing hosts, the parasitoid will not develop beyond the first larval instar (Kadono-Okuda et al. 1995) but causes a decrease in the duration of its host's diapause (Ceryngier et al. 2004).

In the early phase of *D. coccinellae* development, a stimulatory effect of the parasitoid on the maturation of the female host's gonads may be observed. Later, however, vitellin accumulated in the host oocytes is reabsorbed (Kadono-Okuda et al. 1995) and **ovarian maturation is inhibited** (Balduf 1926, Walker 1961, Maeta 1969, Wright & Laing 1978). The gonads of male hosts also seem to be affected by development of *D. coccinellae*, since an **inhibition of spermatogenesis** activity was found in the testes of parasitized *C. septempunctata* males (Ceryngier et al. 1992, 2004).

The **mature *D. coccinellae* larva** emerges from the host ladybird through the membrane between the fifth and sixth or between the sixth and seventh abdominal tergites, and then spins its **cocoon** between the legs of the host and pupates (Balduf 1926, Sluss 1968, Maeta 1969). About 30 minutes before the emergence of the larva, the ladybird becomes immobile and usually stays in this condition until its death, which most often happens within a few days. The legs of the immobilized beetle can only clasp the cocoon and so it is assumed that their extensor muscles are paralyzed (Balduf 1926, Bryden & Bishop 1945, Walker 1961).

The **duration of the pupal stage** of *D. coccinellae* at moderate temperatures (22–26°C) is about 7–10 days (Obrycki 1989, Obrycki et al. 1985, Firlej et al. 2007). After completing its pupal development, the wasp leaves the cocoon by biting through it at the cephalic end (Balduf 1926).

Larval nutrition

During most of its development, the *D. coccinellae* larva does not feed directly on the host tissues. As observed by Sluss (1968), only first instar larvae may directly consume the host's fat body. Later on, larval nutrition is mediated by **teratocytes** – cells derived from the serosa of the parasitoid egg. When the egg hatches, its serosal membrane dissociates into individual teratocytes which are released into the host haemocoel. Although in some hymenopteran parasitoids teratocytes may have functions other than parasitoid nutrition (e.g. host immunosupression, host growth regulation) (Dahlman 1990), it was found by Ogloblin (1924) that in *D. coccinellae* the major function of teratocytes is to provide food for the developing parasitoid larva. More recently, Okuda & Kadono-Okuda (1995) characterized a specific polypeptide synthesized by the teratocytes from amino acids absorbed from the host haemolymph. They detected this polypeptide in the guts of *D. coccinellae* larvae, proving that it was ingested by them. In the course of parasitism, teratocytes grow due to synthesis and accumulation of this specific polypeptide (Okuda & Kadono-Okuda 1995; Kadono-Okuda et al. 1998), and their number decreases as a result of larval feeding (Sluss 1968, Kadono-Okuda et al. 1995). The average initial number of teratocytes in a suitable host, such as adult *C. septempunctata brucki*, or adult *Col. maculata*, is more than 500 (Kadono-Okuda et al. 1995, Firlej et al. 2007). However, that number may be lower in less suitable hosts, e.g. larval *Har. axyridis* (Firlej et al. 2007).

The number of teratocytes gradually decreases with development of the parasitoid, until their complete or almost complete depletion when the larva emerges (Sluss 1968, Kadono-Okuda et al. 1995, Firlej et al. 2007). Meanwhile, the linear size of teratocytes that are not ingested increases more than 10-fold during the course of development from about 46–47 μm in diameter just after egg hatch to about 500 μm in diameter at emergence of the larva (Sluss 1968, Kadono-Okuda et al. 1995). In a less suitable host (*Har. axyridis* parasitized as a larva) the final size of teratocytes may be even larger (up to 900 μm in diameter), perhaps because of their excessive polyploidization and the prolonged development time of the parasitoid (Firlej et al. 2007).

During developmental arrest of the parasitoid larva in a juvenile or diapausing host, teratocyte development is also arrested; the diameter of such 'diapausing' teratocytes was found to be 45–50 μm in diapausing *Hippodamia convergens* adults (Sluss 1968) and 100–150 μm in diapausing *C. septempunctata brucki* adults (Kadono-Okuda et al. 1995).

As a consequence of the indirect feeding of *D. coccinellae* larva, most of the host organs remain intact during the development of the parasitoid larva. The only organs found to be strongly affected are the gonads, the development of which is inhibited, and the fat body that degenerates and considerably decreases in size (Sluss 1968). Due to the relatively little damage, the **ladybirds usually survive the emergence of the parasitoid larva**, although they are considerably weakened and paralyzed. Most of them die within the next few days, but some may recover (Timberlake 1916, Bryden & Bishop 1945, Walker 1961, Anderson et al. 1986, Triltsch 1996). Triltsch (1996) found that some laboratory parasitized *C. septempunctata* females not only survived parasitization but also started laying eggs about 12 days after the emergence of the parasitoid larva.

Host range and host suitability

D. coccinellae is generally considered a parasitoid of ladybirds of the subfamily **Coccinellinae**. It can successfully parasitize a wide array of species belonging to this subfamily, but some evidence indicates that representatives of other subfamilies or even families may also serve as occasional hosts (Table 8.5). Apart from the field records listed in Table 8.5, there are also cases of successful laboratory parasitization by *D. coccinellae* of **non-Coccinellinae hosts.** Richerson & DeLoach (1972) bred a wasp from *Brachiacantha ursina* (Scymninae) and O. Nedvěd (unpublished) from *E. quadripustulatus* (Chilocorinae). However, laboratory tests (Klausnitzer 1969, Ghorpade 1979) showed that ladybirds of subfamilies other than Coccinellinae are not accepted by *D. coccinellae*. This suggests that, either more than one parasitoid species is involved, or different strains of *D. coccinellae* have different ranges of accepted and suitable hosts.

Suitability of ladybird species for development of *D. coccinellae* has usually been quantified as the **rate of successful parasitism** (proportion of hosts attacked to those allowing the emergence of adult parasitoids). Its reported values vary greatly, even within the same species and development stage of host (Table 8.6). Such variability may be a result of different methods used by different authors to determine the rates, but it may also reflect real differences in suitability, related, for example, to the physiological state of the hosts, their colour morphs (Berkvens et al. 2010), or the origin of parasitoid (Koyama & Majerus 2008) and host populations (Orr et al. 1992; Koyama & Majerus 2008).

Juvenile stages (larvae and pupae) of ladybirds are usually less suitable for *D. coccinellae* than adults, and younger larval instars are less suitable than older ones (David & Wilde 1973, Obrycki et al. 1985, Geoghegan et al. 1998b). However, Firlej et al. (2007, 2010) and Berkvens et al. (2010) found fourth instar larvae of *Har. axyridis* to be more suitable than the adults.

Host preferences and parasitization rates

The level of parasitization of ladybirds by *D. coccinellae* may fluctuate considerably depending on the locality, season and host. Sometimes, parasitization rates may reach 70% or more (Geoghegan et al. 1997, Ceryngier 2000), but usually much lower values are reported (for a review see Hodek 1973, pp. 203–204).

Ladybirds are often more heavily affected when aggregating at overwintering sites than when they are active (Iperti 1964, Parker et al. 1977, Anderson et al. 1986). Parasitization rates of such aggregating ladybirds may differ remarkably between different overwintering sites in the same region. In the mountainous region of southwestern Poland, Ceryngier (2000) found parasitization ranging from about 15 to 25% in *C. septempunctata* overwintering on mountain tops,

Table 8.6 Rates of successful parasitism in *Dinocampus coccinellae* of various geographic origins in relation to species, developmental stage and geographic origin of the hosts.

Host species	*D. coccinellae* / host* origin	Host stage parasitized	Rate of successful parasitism	Reference
Coccinella novemnotata	Missouri, USA	A	0.96	Richerson & DeLoach (1972)
Coleomegilla maculata	Missouri, USA	A	0.96	Richerson & DeLoach (1972)
	New Jersey, USA	A	0.80	Cartwright et al. (1982)
	Minnesota, USA	A	0.75	Hoogendoorn & Heimpel (2002)
	Iowa and Georgia, USA	A	0.61	Orr et al. (1992)
	Quebec, Canada	A	0.49	Firlej et al. (2007)
	New York, USA	A	0.40	Obrycki et al. (1985)
	Iowa, USA	A	0.34	Obrycki (1989)
	Quebec, Canada	A	0.18	Firlej et al. (2005)
	New York, USA	P	0.28	Obrycki et al. (1985)
	Quebec, Canada	L4	0.58	Firlej et al. (2007)
	New York, USA	L4	0.26	Obrycki et al. (1985)
	New York, USA	L3	0.19	Obrycki et al. (1985)
	New York, USA	L2	0.08	Obrycki et al. (1985)
	New York, USA	L1	0.00	Obrycki et al. (1985)
Hippodamia convergens	Missouri, USA	A	0.92	Richerson & DeLoach (1972)
	Iowa, USA	A	0.30	Obrycki (1989)
	Kansas, USA	L4	0.34	David & Wilde (1973)
	Kansas, USA	L3	0.13	David & Wilde (1973)
	Kansas, USA	L2	0.23	David & Wilde (1973)
	Kansas, USA	L1	0.10	David & Wilde (1973)
Coccinella septempunctata	UK	A	0.78	Sloggett et al. (2004)
	UK	A	0.64	Koyama & Majerus (2008)
	New Jersey, USA	A	0.58	Cartwright et al. (1982)
	Honshu, Japan / UK	A	0.57	Koyama & Majerus (2008)
	Iowa and Georgia, USA	A	0.49	Orr et al. (1992)
	Iowa, USA	A	0.32	Obrycki (1989)
C. septempunctata brucki	Honshu, Japan	A	0.55	Koyama & Majerus (2008)
	UK / Honshu, Japan	A	0.49	Koyama & Majerus (2008)
Hippodamia parenthesis	Missouri, USA	A	0.72	Richerson & DeLoach (1972)
Cycloneda munda	Iowa, USA	A	0.57	Obrycki (1989)
	Missouri, USA	A	0.12	Richerson & DeLoach (1972)
Coccinella undecimpunctata	New Jersey, USA	A	0.42	Cartwright et al. (1982)
Olla sp.	New Jersey, USA	A	0.39	Cartwright et al. (1982)
Harmonia axyridis	UK / Honshu, Japan	A	0.26	Koyama & Majerus (2008)
	Honshu, Japan	A	0.25	Koyama & Majerus (2008)
	Honshu, Japan / UK	A	0.17	Koyama & Majerus (2008)
	Belgium	A†	0.17	Berkvens et al. (2010)
	Minnesota, USA	A	0.10	Hoogendoorn & Heimpel (2002)
	Belgium	A‡	0.02	Berkvens et al. (2010)
	Belgium	A§	0.00	Berkvens et al.(2010)
	Quebec, Canada	A	0.00	Firlej et al. (2005)
	Quebec, Canada	A	0.00	Firlej et al. (2007)
	UK	A	0.00	Koyama & Majerus (2008)
	Belgium	L4§	0.15	Berkvens et al. (2010)
	Belgium	L4‡	0.07	Berkvens et al. (2010)
	Quebec, Canada	L4	0.12	Firlej et al. (2007)
	Belgium	L3§	0.10	Berkvens et al. (2010)

(Continued)

Table 8.6 (*Continued*)

Host species	*D. coccinellae* / host* origin	Host stage parasitized	Rate of successful parasitism	Reference
Hippodamia variegata	Iowa and Georgia, USA / Canada	A	0.17	Orr et al. (1992)
	Iowa and Georgia, USA / France	A	0.09	Orr et al. (1992)
	Iowa, USA	A	0.00	Obrycki (1989)
Adalia bipunctata	Missouri, USA	A	0.12	Richerson & DeLoach (1972)
	New Jersey, USA	A	0.00	Cartwright et al. (1982)
Brachiacantha ursina	Missouri, USA	A	0.04	Richerson & DeLoach (1972)
Propylea quatuordecimpunctata	Iowa, USA	A	0.02	Obrycki (1989)
	Iowa and Georgia, USA / Canada	A	0.01	Orr et al. (1992)
	Iowa and Georgia, USA / Turkey	A	0.00	Orr et al. (1992)
Coccinella magnifica	UK	A	0.00	Sloggett et al. (2004)

Host stages: A, adult, P, pupa, L1–L4, larval instars.

*Host origin is given only if different from *D. coccinellae* origin.

†Melanic hosts from long–term laboratory population (61–82 generations in the laboratory).

‡Melanic hosts from recently established laboratory population (3–6 generations in the laboratory).

§Non–melanic hosts from recently established laboratory population (3–6 generations in the laboratory).

while it was approximately three times higher at a hibernaculum at the foot of the mountain.

Due to parasitoid preferences, differential parasitization rates in relation to the species, sex, age and developmental stage of the hosts have been recorded. Majerus (1997), while comparing parasitization of adults of various British ladybirds, found mean parasitization rates of about 20% for *C. undecimpunctata*, *Har. quadripunctata* and *C. septempunctata*, the mean rate of 9.7% for *Coccinella quinquepunctata* and rates below 5% for nine other species (Table 8.7).

It was noted by several authors (Maeta 1969, Parker et al. 1977, Cartwright et al. 1982) that female ladybirds are parasitized to a higher degree than males, and Davis et al. (2006) confirmed experimentally the preference of British *D. coccinellae* for ovipositing into female rather than male *C. septempunctata* hosts. Moreover, British *D. coccinellae*, having a choice between young (newly eclosed) and old (overwintered) *C. septempunctata* adults, oviposited preferentially into young ones. Such behaviour was considered adaptive because young hosts are considered more suitable than old hosts due to their longer expected lifespan (Majerus et al. 2000a). *Dinocampus coccinellae* also shows a clear preference for adult over juvenile hosts (Geoghegan et al. 1998b) and for older over younger larval hosts (Obrycki et al. 1985). British strains of the parasitoid appeared reluctant to oviposit in *C. septempunctata* larvae and especially pupae (Geoghegan 1998b), while in North American, Japanese and central European *D. coccinellae*, such a tendency has not been found (Maeta 1969, David & Wilde 1973, Obrycki et al. 1985, Berkvens et al. 2010, P. Ceryngier, unpublished). The reluctance of British *D. coccinellae* to parasitize pre-imaginal hosts is possibly not so strong when immatures of the invasive *Har. axyridis* serve as hosts. Ware et al. (2010) reported emergence of *D. coccinellae* from nine *Har. axyridis* adults collected in the wild as pupae, while in earlier samples of several thousand immatures of *C. septempunctata* no *D. coccinellae* were recovered (Geoghegan et al. 1998b).

It can be assumed that host preferences of a parasitoid are usually adaptive, i.e. positively related with host suitability. An interesting case of an almost certainly maladaptive relationship between host preference and suitability has been found for the system comprising Canadian *D. coccinellae* and invasive *Har.*

Table 8.7 Parasitization of British ladybirds by *Dinocampus coccinellae* measured as the rate of emergence of parasitoid larvae from the host beetles (from Majerus 1997).

Ladybird species	Total of samples	Number parasitized	Mean parasitization rate (%)
Coccinella undecimpunctata	262	58	22.1
Harmonia quadripunctata	284	55	19.4
Coccinella septempunctata	4222	734	17.4
Coccinella quinquepunctata	113	11	9.7
Calvia quatuordecimguttata	98	4	4.1
Hippodamia variegata	113	3	2.7
Myzia oblongoguttata	108	2	1.9
Propylea quatuordecimpunctata	562	10	1.8
Anatis ocellata	244	4	1.6
Tytthaspis sedecimpunctata	10537	148	1.4
Halyzia sedecimguttata	490	4	0.8
Coccinella magnifica	279	1	0.4
Coccinella hieroglyphica	234	1	0.4
Adalia bipunctata	4077	0	0
Adalia decempunctata	185	0	0
Anisosticta novemdecimpunctata	1381	0	0
Aphidecta obliterata	254	0	0
Myrrha octodecimguttata	57	0	0
Psyllobora vigintiduopunctata	143	0	0

axyridis. Although *Har. axyridis* adults are marginal hosts of a very low suitability for *D. coccinellae* (Burling et al. 2010; Table 8.6), in choice tests they were parasitized no less frequently than highly suitable *Col. maculata* adults. Furthermore, the wasps preferred to oviposit into *Har. axyridis* adults than much more suitable larvae of this species (Firlej et al. 2010).

8.3.2.2 *Uga* Girault (Hymenoptera: Chalcididae)

Synonym: *Neotainania* Husain & Agarwal.

Information on these wasps is scant. They form a highly specialized group of ladybird parasitoids and are distributed from Africa through southern Asia to Australia. Of seven described species, six have been proven to be parasitoids of larvae and pupae of phytophagous ladybirds of the subfamily **Epilachninae** (Table 8.8).

Probably the most widely distributed and most common of *Uga* species is *U. menoni* (Fig. 8.5). Kerrich (1960) reports that, in some seasons, this species can almost entirely eliminate *Epilachna* spp. in Orissa (southern India). In the Kyonggido area of Korea, *U. menoni* was found to be a **solitary larval–pupal parasitoid** parasitizing older larvae (third and fourth instars) and pupae of *Henosepilachna vigintioctopunctata*. The wasp was present in the field from June to September and the highest parasitization rate was recorded in July (Lee et al. 1988).

8.3.2.3 *Cowperia* Girault (Hymenoptera: Encyrtidae)

Synonym: *Aminellus* Masi

Three of five described species of the genus *Cowperia* have been found to be **larval and pupal parasitoids** of ladybirds predaceous on mealybugs (Pseudococcidae) (Noyes & Hayat 1984) and whiteflies (Aleyrodidae) (Clausen 1934). Host associations of the remaining two species are not yet known (Table 8.9). *Cowperia* adults have characteristic, stout body form (Fig. 8.6).

More detailed studies on these parasitoids and their effects on host populations are lacking or unknown. Clausen (1934) mentions that, in the locality of Kaban Djahne in Sumatra, larvae and pupae of *Scymnus smithianus* were heavily parasitized by a species of *Aminellus* (= *Cowperia*) subsequently described by Kerrich (1963) as *A. sumatraensis*.

Table 8.8 Host and distribution records of *Uga* species (compiled from Noyes 2011 and Swaine & Ironside 1983 where indicated).

***Uga* species**	**Host records**	**Distribution records**
colliscutellum	*Henosepilachna vigintioctopunctata*, *Henosepilachna guttatopustulata**	Queensland (Australia)
coriacea	*Epilachna canina,* *Epilachna* sp.	South Africa, Uganda
digitata	—	China
hemicarinata	*Henosepilachna vigintioctomaculata*	China
javanica	*Henosepilachna vigintioctopunctata*	Java (Indonesia)
menoni	*Epilachna* sp., *Henosepilachna ocellata*, *Henosepilachna vigintioctomaculata,* *Henosepilachna vigintioctopunctata*	India, Korea, Taiwan
sinensis	*Epilachna* sp.	China

*Host reported by Swaine & Ironside (1983).

Figure 8.5 *Uga menoni* in side view. Note strongly raised scutellum – a very characteristic feature of the genus *Uga* (from Kerrich 1960, Arthur Smith del., with permission).

8.3.2.4 *Homalotylus* Mayr (Hymenoptera: Encyrtidae)

Synonyms: *Anisotylus* Timberlake, *Echthroplectis* Foerster, *Hemaenasioidea* Girault, *Lepidaphycus* Blanchard, *Mendozaniella* Brethes, *Neoaenasioidea* Agarwal, *Nobrimus* Thomson.

This cosmopolitan genus is strictly associated with Coccinellidae (Timberlake 1919, Noyes & Hayat 1984, Trjapitzin & Triapitsyn 2003). Of 63 known species (Noyes 2011), 30 have been shown to develop in ladybirds although it is predicted that the remaining 17 also use ladybirds as a host (Table 8.10). Although there are also many reports of *Homalotylus* parasitizing aphids and coccids, they almost certainly resulted from erroneous host assignment due to mass rearing of the hemipterans together with their ladybird predators.

The majority of data on the biology and ecology of *Homalotylus* have been reported for *H. flaminius*, although most of them probably refer to *H. eytelweinii*. These two widely distributed species were historically regarded as one species (Timberlake 1919), and, for decades, both were usually reported by non-taxonomists as *H. flaminius*. However, most specialists now agree that *H. eytelweinii* is a distinct species (Hoffer 1963, Graham 1969, Trjapitzin & Triapitsyn 2003, Noyes 2011). According to Klausnitzer (1969) *H. eytelweinii* is a parasitoid of ladybirds in the tribes Coccinellini, Psylloborini (= Halyziini) and Chilocorini, and *H. flaminius* parasitizes ladybirds in the Scymnini.

Life cycle

Homalotylus species are **endoparasitoids of ladybird larvae and pupae**. The species that develop in small hosts, e.g. of the tribe Scymnini, are usually **solitary** (Klausnitzer 1969, Vakhidov 1975, Lotfalizadeh & Ebrahimi 2001, Fallahzadeh et al. 2006), while those associated with larger ones are **gregarious** (Iperti 1964, Klausnitzer 1969, Kulman 1971).

Table 8.9 Host and distribution records of *Cowperia* species.

Cowperia species	Ladybird host records	Distribution records	References
areolata	*Cryptolaemus montrouzieri, Scymnus apetzi*	southern Europe, Tadzhikistan, Turkey, Georgia, Armenia	Noyes (2011)
indica	*Cryptolaemus montrouzieri, Jauravia* sp., *Nephus* sp., *Scymnus* sp.	India, Sri Lanka	Noyes (2011)
punctata	—	Singapore, China	Noyes (2011)
subnigra	—	China	Li & Chai (2008)
sumatraensis	*Scymnus smithianus*	Sumatra	Clausen (1934)
Cowperia sp.	*Cryptogonus kapuri*	India	Poorani (2008)

Figure 8.6 *Cowperia indica* (photo courtesy of J. Poorani). (See colour plate.)

Female wasps lay eggs into larvae of young instars (Kato 1968, Filatova 1974, Kuznetsov 1987), often when they are attached to the substrate at ecdysis (Iperti 1964). Larvae of the gregarious *Homalotylus* species avoid direct contact with their siblings and at the end of development they occupy separate chambers with thin walls made of remnants of dry host tissue. In such cases, each emerging adult makes its own opening and emerges from the host (Iperti 1964, Filatova 1974). Some *Homalotylus* species (e.g. *H. eytelweinii*, *H. shuvakhinae*) tend to complete their development in mummified older larvae of ladybirds (Kato 1968, Yinon 1969, Semyanov 1986, Trjapitzin & Triapitsyn 2003), but others (e.g. *H. platynaspidis*, *H. nigricornis*) complete their development in the pupae (Vakhidov 1975, Myartseva 1981, Volkl 1995).

Homalotylus, at least certain species of the *flaminius* group, **overwinter** inside the mummified host as a prepupa, a fully grown larva (Iperti 1964, Filatova 1974), or as a pupa (Smirnoff 1957, Kuznetsov 1987). The reported **duration of development** in non-overwintering wasps ranges, depending on the region, season and host species, from only 7–9 days to 45 days (Telenga 1948, Rubtsov 1954, Smirnoff 1957, Iperti 1964, Kato 1968). The adults are sexually mature at emergence (Filatova 1974) and feed on aphid and coccid honeydew (Rubtsov 1954, Filatova 1974).

Host specificity

Different *Homalotylus* species show varying degrees of host specificity (Table 8.11). Many species are known to be associated with hosts belonging to only one tribe of Coccinellidae, but some (*H. eytelweinii*, *H. africanus*, *H. terminalis*, *H. quaylei*) can parasitize ladybirds of various subfamilies and tribes. Although most data on *Homalotylus* refers to a few species parasitizing ladybirds of the subfamilies Coccinellinae and Chilocorinae (*H. eytelweinii*, *H. terminalis*), the majority of known host associations in *Homalotylus* concern two tribes of the subfamily Scymninae: the Scymnini and Hyperaspidini (Table 8.11).

Table 8.10 Described species of *Homalotylus* with their distribution records and references reporting parasitization of Coccinellidae (compiled from Noyes 2011 and other sources where indicated). Lack of reference means that a given *Homalotylus* species has not so far been reported to parasitize ladybirds.

***Homalotylus* species**	**Distribution**	**Reference reporting parasitization of Coccinellidae**
affinis	USA: California	Noyes (2011)
africanus	central and southern Africa	Noyes (2011)
agarwali	India	—
albiclavatus	India, Iran	Shafee & Fatma (1984), Fallahzadeh & Japoshvili (2010)
albifrons	Japan	Noyes (2011)
albitarsus	USA: Maryland	Timberlake (1919)
aligarhensis	India	—
balchanensis	Turkmenistan	—
brevicauda	Mexico	Timberlake (1919)
cockerelli	Mexico, USA: Texas	Noyes (2011)
ephippium	Europe, Iran, Russia: Yakutia	Noyes (2011)
eytelweinii	Europe, Asia, Africa, Central and South America	Noyes (2011)
ferrierei	India	Shafee & Fatma (1984)
flaminius	cosmopolitan	Noyes (2011)
formosus	India	—
hemipterinus	Europe, Asia, Africa, Indonesia, Malaysia, Fiji, Central and South America	Noyes (2011)
himalayensis	China	—
hybridus	Slovakia	—
hyperaspicola	Japan	Noyes (2011)
hyperaspidis	North and Central America	Noyes (2011)
indicus	India	Noyes (2011)
latipes	Paraguay	—
longicaudus	China	—
longipedicellus	India	Shafee & Fatma (1984)
mexicanus	Mexico	Trjapitzin et al. (1999)
mirabilis	South America	Noyes (2011)
mundus	Philippines, Taiwan	—
nigricornis	Europe, Asia, Canary Islands	Noyes (2011)
oculatus	Philippines	Noyes (2011)
pallentipes	USA: Arizona, Missouri	—
platynaspidis	Europe, western Asia	Noyes (2011)
punctifrons	USA: Florida	—
quaylei	Europe, Africa, Asia, South America	Noyes (2011)
rubricatus	Russian Far East	—
scutellaris	China	—
scymnivorus	India, Japan, Mongolia	Noyes (2011)
shuvakhinae	Mexico	Noyes (2011)
similis	USA	Noyes (2011)
sinensis	China, Iran	Noyes (2011)
singularis	Czech Republic	—
terminalis	North America, Antilles, Uruguay	Noyes (2011)
trisubalbus	China	—
turkmenicus	Turkmenistan, India, Iran	Noyes (2011)
vicinus	Africa, Madagascar, Iran	Noyes (2011), Fallahzadeh & Japoshvili (2010)
yunnanensis	China	—
zhaoi	China	—

After submitting of this Chapter, 17 new species of *Homalotylus* were described from Costa Rica, of which one, *H. hypnos* Noyes, has a known coccinellid host (*Hyperaspis* sp.) (Noyes 2011). These 17 species are not listed here.

Table 8.11 Reported associations of *Homalotylus* species with the subfamilies and tribes of their ladybird hosts (compiled from host records quoted by Noyes 2011 and other sources where indicated).

Homalotylus	**Coccinellinae**		**Epilachninae**	**Sticholotidinae**	**Chilocorinae**	**Scymninae**			**Ortaliinae**	**Coccidulinae**	
species	**Coccinellini**	**Halyziini**	**Epilachnini**	**Sticholotidini**	**Chilocorini**	**Scymnini**	**Hyperaspidini**	**Platynaspidini**	**Noviini**	**Coccidulini**	**Azyini**
affinis	–	–	–	–	–	–	+	–	–	–	–
africanus	–	–	–	–	+	+	+	–	–	+	–
albiclavatus	–	–	–	–	–	+	–	–	–	–	–
albifrons	–	–	–	–	–	+	–	–	–	–	–
brevicauda	–	–	–	–	–	+[†]	–	–	–	–	–
cockerelli	–	–	–	–	–	–	+	–	–	–	–
ephippium	–	–	–	–	+	–	–	–	–	–	–
eytelweinii + *flaminius*[*]	+	+	+	+	+	+	+	+	+	–	–
hemipterinus	+	–	–	–	+	–	–	–	–	–	–
hyperaspicola	–	–	–	–	–	–	+	–	–	–	–
hyperaspidis	–	–	–	–	–	–	+	–	–	–	–
indicus	–	–	–	–	–	+	–	–	–	–	–
mirabilis	+	–	–	–	–	–	+	–	–	–	–
nigricornis		–	–	–	–	+	–	–	–	–	–
oculatus	–	–	–	–	–	+	–	–	–	–	–
platynaspidis	–	–	–	–	–	+	–	+	–	–	–
quaylei	–	–	–	+	–	+	+	–	–	–	–
scymnivorus	–	–	–	–	–	+	–	–	–	–	–
shuvakhinae	–	–	–	–	–	–	–	–	–	–	+
similis	–	–	–	–	–	+	+	–	–	–	–
sinensis	+	–	–	–	+	+	–	–	–	–	–
terminalis	+	+	–	–	+	+	–	–	–	–	–
turkmenicus	+	–	–	–	+[‡]	+[§]	+	–	–	–	–
vicinus	–	–	–	–	–	+	+	–	–	–	–
Number of species	6	2	1	2	7	16	11	2	1	1	1

[*] Data for *H. eytelweinii* and *H. flaminius* are combined because these species have not been differentiated by many authors.

[†] Timberlake (1919).

[‡] Fallahzadeh & Japoshvili (2010).

[§] Lotfalizadeh (2010).

Parasitization rates

In regions with temperate and cold climates, the Old World *Homalotylus* of the *flaminius* group (presumably *H. eytelweinii*) usually show low rates of parasitization. In the Russian Far East, Western Siberia, Turkmenistan and Uzbekistan, it has only been recorded sporadically from several aphidophagous ladybirds (Filatova 1974, Vakhidov 1975, Semyanov 1986, Kuznetsov 1987). In northeastern and central parts of Europe, *Homalotylus* is again not common, although it may sometimes parasitize ladybirds at 20–30% (Klausnitzer 1967, Semyanov 1986, Pankanin-Franczyk & Ceryngier 1999). In the Mediterranean and Black Sea basins, parasitization often reaches moderate or high levels. Stathas et al. (2008) recorded up to 50% parasitization of *Chilocorus bipustulatus* on sour orange trees in southern Greece. In southeastern France, Iperti (1964) noted rates of parasitization exceeding 80% for *C. septempunctata* and 50% for *Propylea quatuordecimpunctata*. Both Stathas et al. (2008) and Iperti (1964) found that parasitization rates tend to increase as the host population develops. According to Smirnoff (1957), 95% of *Chil. bipustulatus* individuals developing on date palms on the Atlantic coast of Morocco were destroyed by the parasitoid. In equatorial Africa (Republic of the Congo), Fabres (1981) found parasitization rates of *Exochomus flaviventris* ranging between 7 and 10% when feeding on the cassava mealybug.

In Germany, Volkl (1995) recorded that parasitization of myrmecophilous *Platynaspis luteorubra* by *H. platynaspidis* may even be higher than 50%. However, the parasitization rate largely depended on the absence of ants (*Lasius niger*) tending aphids exploited by *P. luteorubra* larvae. In ant-tended aphid colonies, especially in simply structured habitats such as plant stems, parasitization rates were significantly lower. Although ants were not found to be aggressive towards *H. platynaspidis*, the searching efficiency of the parasitoid might be highly reduced by continual encounters with ants.

8.3.2.5 *Nothoserphus* Brues (Hymenoptera: Proctotrupidae)

Synonyms: *Thomsonina* Hellen, *Watanabeia* Masner.

The genus *Nothoserphus* seems to be geographically confined to **Palaearctic and Oriental regions** (Johnson 1992). Of 11 species described so far, five have been found to be **solitary parasitoids of ladybird larvae**, while the host records for the remaining six species are lacking (Table 8.12). The genus is divided into **three species-groups** – the *boops*-, *afissae*- and *mirabilis*-groups – and this corresponds with the earlier taxonomic allocation of the *Nothoserphus* species to three distinct genera: *Thomsonina*, *Watanabeia* and *Nothoserphus* (Townes & Townes 1981, Lin 1987). According to the known host records (Table 8.12), species of the *boops*-group are parasitoids of the Scymninae, those of the *afissae*-group parasitize Epilachninae and those of the *mirabilis*-group parasitize Coccinellinae.

Nothoserphus females lay eggs in host larvae. *Nothoserphus afissae* prefers to oviposit in the second and third larval instars of *Henosepilachna vigintioctomaculata*, which are also much more suitable for the development of the parasitoid than either the younger or older larvae (Kovalenko 2002). If the host larvae are parasitized at the first instar, they suffer 100% mortality before the parasitoid larvae has completed development. Oviposition into fourth instar larvae leads to 60% mortality of hosts, and, subsequently no successful development of *N. afissae*. According to Semyanov (1998), females of *N. mirabilis* preferentially parasitize third and fourth instar larvae of *Menochilus sexmaculatus* and do not react to the presence of pupae and first instar larvae.

As a consequence of parasitoid feeding, the host dies at the prepupal stage. The fully grown parasitoid larva emerges from the dead host through the membrane between the two last abdominal sternites and pupates in characteristic posture (Fig. 8.7) on the ventral side of the host's body (Semyanov 1998, Kovalenko 2002).

Kovalenko (2002) and Kovalenko & Kuznetsov (2005) found that *N. afissae* may be an **effective control agent of the herbivorous *H. vigintioctomaculata*** on potato fields in the Russian Far East. During larval development of the beetle population, which takes place between late June and late August, three generations of the parasitoid are produced. **Parasitization rates** gradually increase and may even reach 100% in August. In Japan, however, only 1.5% of the same ladybird species (*H. vigintioctomaculata*) feeding on the same host plant (potatoes) was parasitized (Nakamura 1987). Similarly, low parasitization rates were recorded in relation to two Japanese species feeding on thistles (*Cirsium*) – *Henosepilachna niponica* (Ohgushi 1986) and *H. pustulosa* (Nakamura & Ohgushi 1981).

In a single sample taken from maize field in southeastern China, 19% of larvae of the predatory

Table 8.12 Host and distribution records of *Nothoserphus* species.

***Nothoserphus* species**	**Host records**	**Distribution records**	**References**
***boops*–group (*Thomsonina*)**			
boops	*Scymnus nigrinus*	Scandinavia, Czech Republic	7, 8, 13
fuscipes	—	Taiwan	4
partitus	—	Taiwan	4
scymni	*Scymnus dorcatomoides*, *Scymnus* sp.	Japan	7
townesi	—	Taiwan	4
***afissae*–group (*Watanabeia*)**			
aequalis	—	Nepal, Taiwan	4
afissae	*Epilachna admirabilis, Epilachna varivestis**, *Henosepilachna niponica, Henosepilachna pustulosa, Henosepilachna vigintioctomaculata*	Japan, Korea, Russian Far East	1, 2, 3, 5, 6, 7
debilis	–	Nepal, Taiwan	4
epilachnae	*Epilachna admirabilis*, *Henosepilachna vigintioctopunctata*	Java, China	7
***mirabilis*–group (*Nothoserphus*)**			
admirabilis	—	Taiwan	4
mirabilis	*Coccinella leonina transversalis, Illeis bielawskii, Illeis cincta, Illeis* sp., *Menochilus sexmaculatus, Synona obscura*, undetermined coccinellid	south–eastern China, India, Java, Nepal, Taiwan	4, 9, 10, 11, 12

*Record from the area in Japan invaded by *E. varivestis* (outside its native range).
References: 1, Fujiyama et al. (1998); 2, Kovalenko (2002); 3, Lee et al. (1988); 4, Lin (1987); 5, Nakamura & Ohgushi (1981); 6, Ohgushi (1986); 7, Pschorn–Walcher (1958); 8, Pschorn–Walcher (1971); 9, Poorani (2008); 10, J. Poorani, unpublished; 11, Poorani et al. (2008); 12, Semyanov (1998); 13, Zeman & Vanek (1999).

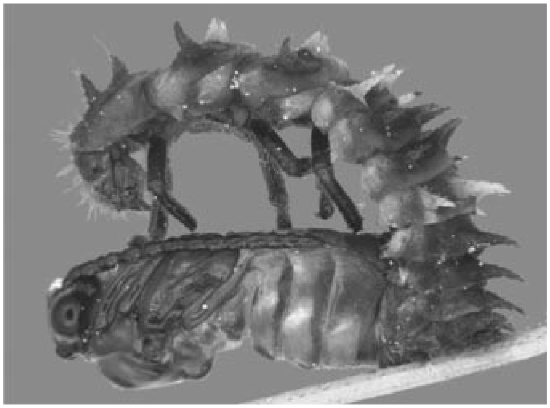

Figure 8.7 A pupa of *Nothoserphus mirabilis* attached to the ventral side of its killed host, a larva of *Menochilus sexmaculatus* (photo courtesy of J. Poorani). (See colour plate.)

M. sexmaculatus were parasitized by *N. mirabilis* (Semyanov 1998).

8.3.2.6 *Metastenus* Walker (Hymenoptera: Pteromalidae)

Synonyms: *Scymnophagus* Ashmead, *Tripolycystus* Dodd.

Five species of the genus *Metastenus* have been described so far, and two of them, *M. concinnus* and *M. townsendi*, appear to be **pupal parasitoids** of ladybirds belonging to the subfamilies Scymninae (tribes Scymnini, Hyperaspidini, Pentiliini and Cryptognathini), Coccidulinae (Azyini) and Microweiseinae (Microweiseini) (Table 8.3). Hosts of the remaining species, i.e. the Australian *M. sulcatus*, the Hungarian

M. caliginosus and the Indian *M. indicus*, are not known (Noyes 2011).

Metastenus concinnus is generally reported from the Palaearctic, with the exception of a single record from Argentina, while the **distribution** of *M. townsendi* includes the Nearctic and Neotropical regions and Japan (Noyes 2011). An undetermined species of *Metastenus* has also been reported as a parasitoid of *Exochomus* and *Hyperaspis* species from several localities in tropical Africa (Neuenschwander et al. 1987). These records possibly relate to *Mesopolobus secundus* – a species reported from Uganda and Kenya (Table 8.3), which resembles *M. townsendi* (Crawford 1912, Delucchi 1954).

Life cycle

Most information on the biology and life cycle of *Metastenus* can be found in Delucchi's (1954) characterization (as *Scymnophagus mesnili*), of *Metastenus concinnus*. Delucchi (1954) reports parasitization of *Scymnus* (*Pullus*) *impexus* by this species in Switzerland and Germany. Female parasitoids were found ovipositing into host pupae in late spring (May and June). The parasitoids either developed directly, emerging as adults between late June and mid-July, or entered larval diapause inside the dead host pupa, emerging the next spring. It is not known which hosts the second generation wasps (the progeny of non-diapausing individuals) developed in.

The pupae of *S. impexus* parasitized by *M. concinnus* are easily distinguishable because they change colour from reddish-brown to light brown. A single parasitized pupa usually contains two parasitoid individuals, which lie face-to-face in their pupal stage (Delucchi 1954).

The recorded impact of *M. concinnus* on *S. impexus* is not very high. Delucchi (1954) mentions **parasitization rates** in three large samples (each of at least 1000 pupae) that range between 0.8 and 12.6%.

M. concinnus probably reproduces by **thelytokous parthenogenesis**, since males of this species are unknown (Delucchi 1954). In *M. townsendi*, however, both sexes are known (Peck 1963, Tachikawa 1972).

8.3.2.7 *Phalacrotophora* Enderlein (Diptera: Phoridae)

The worldwide-distributed genus *Phalacrotophora* comprises more than 50 described species (Brown 2007). Some of them are known as **gregarious endoparasitoids of ladybird pupae** (Table 8.13).

Host ranges

For most of the *Phalacrotophora* species parasitizing ladybirds, records of host species are very scarce (Table 8.13) and thus tell us little about the real host spectra of the flies. The two exceptions are the European *P. fasciata* and *P. berolinensis*. Both have been reported relatively frequently from a variety of ladybirds in the subfamilies Coccinellinae and Chilocorinae (see Disney et al. 1994 and Ceryngier & Hodek 1996). In contrast, another European species, *P. beuki*, was recognized as a monophagous parasitoid of *Anatis ocellata* (Durska et al. 2003).

Life cycle

A sexually mature *Phalacrotophora* female will locate and select a ladybird prepupa, and then start to attract males. As the females in this genus possess complex glands on the abdomen which probably serve for the production of pheromones, Disney et al. (1994) assume that the males are attracted pheromonally. Disney et al. (1994) observed that one or more males may arrive to mate with the female, most often on or near the selected ladybird prepupa. A pair usually spends several minutes *in copula* (Disney et al. 1994).

After mating, the male leaves the female. The female still attends the prepupa and starts to parasitize it, usually at the beginning of its pupation (Disney et al. 1994, Ceryngier & Hodek 1996), although in rare cases it is the prepupa that is parasitized (Filatova 1974, Disney & Chazeau 1990, Disney et al. 1994). It has been shown that females of *P. fasciata* and/or *P. berolinensis* can assess the age of host prepupae and select older ones (Hurst et al. 1998). This is considered adaptive because the female loses less time waiting for a host ecdysis before ovipositing and consequently increases her oviposition rate.

Females of *P. fasciata* and *P. berolinensis* were observed **laying eggs** either on the surface of the pupa or internally. Usually, the ventral thoracic region of the pupa, and less frequently its dorsal surface, was chosen as the areas for oviposition (Disney et al. 1994). Females of *P. quadrimaculata* were seen to attach their eggs to the sides of the host pupa or, to a lesser extent, to its ventral surface (Disney & Chazeau 1990).

Table 8.13 *Phalacrotophora* species reported as ladybird parasitoids.

***Phalacrotophora* species**	**Distribution**	**Reported hosts**	**References**
berolinensis	Europe	many Coccinellinae and Chilocorinae	Disney et al. (1994), Ceryngier & Hodek (1996)
beuki	Europe	*Anatis ocellata*	Durska et al. (2003)
decimaculata	China	unidentified ladybird	Liu (2001)
delageae	Europe	*Adalia bipunctata* *Adalia decempunctata* *Calvia quatuordecimguttata* *Coccinella septempunctata* *Harmonia axyridis* *Sospita vigintiguttata*	Disney & Beuk (1997), Triltsch (1999), Durska et al. (2003), P. Ceryngier, E. Durska & R. H. L. Disney (unpublished), S. Harding, R. H. L. Disney & R. L. Poland (unpublished)
fasciata	Europe, Siberia, Russian Far East, China, Japan	many Coccinellinae and Chilocorinae	Disney et al. (1994), Ceryngier & Hodek (1996), Miura (2010), Lengyel (2011)
indiana	India	*Harmonia eucharis*	Colyer (1961)
nedae	South America	*Neda marginalis* *Neocalvia anastomozans* *Cycloneda sanguinea*	Disney et al. (1994), Aguiar–Menezes et al. (2008)
philaxyridis	Japan (and probably part of continental Asia)	*Harmonia axyridis*	Disney (1997)
quadrimaculata	Taiwan, Sulawesi, New Caledonia, China	*Olla v–nigrum*	Disney & Chazeau (1990), Liu (2001)
Phalacrotophora sp.	Australia	*Harmonia conformis* *Cleobora mellyi*	New (1975), Anderson et al. (1986)
Phalacrotophora sp.	India	*Harmonia expalliata*	Disney et al. (1994)

The eggs hatch within 24 h, and the larvae then enter the host (Wylie 1958, Disney & Chazeau 1990). **Larval development** in *Phalacrotophora* proceeds rapidly. According to Lichtenstein (1920, cited by Disney et al. 1994) and Disney and Chazeau (1990), it may be as short as 2–3 days, but longer times are more often reported. Wylie (1958) indicates 5 days, Filatova (1974) 7–9 days and Kuznetsov (1987) 8–12 days.

Fully grown larvae leave the host through an irregular hole, ventrally between the head and thorax, drop to the ground and **pupate** on its surface or in the upper soil layer (Wylie 1958, Disney & Chazeau 1990). The flies either emerge as adults after 15–25 days or overwinter and emerge the next season (Disney et al. 1994, Ceryngier & Hodek 1996). *Phalacrotophora* **overwinter as fully formed adults within the puparia** (Disney 1994, Durska et al. 2003).

The number of *Phalacrotophora* individuals developing in a single host is related to host size. Generally, larger host species bear a higher number of parasitoid larvae than smaller ones. In pupae of *An. ocellata*, 7–10 larvae were usually reported (Filatova 1974), the average number given for *C. septempunctata* is similar (Semyanov 1986, Disney et al. 1994), but only around two develop from *A. bipunctata* (Disney 1979, Disney et al. 1994).

Many authors (Richards 1926, Colyer 1952, 1954, Delucchi 1953, Disney et al. 1994) have reported that *Phalacrotophora* **feeds on the haemolymph of ladybird** pupae or, less frequently, that of larvae. The fly cuts into either the ventral (Colyer 1952) or dorsal (Disney et al. 1994) surface of the pupa and then imbibes fluid from the wound. This behaviour may allow the fly to obtain appropriate protein-rich food and/or facilitate penetration of the pupa by the hatching larvae (Disney et al. 1994). The small wound and loss of haemolymph, as a consequence of the fly's feeding, do not prevent the development of unparasitized ladybird pupae or the development of flies in parasitized pupae (Disney et al. 1994). Apart from host feeding, adults probably feed on the sap of injured trees. Lengyel (2009) reports high numbers of

Phalacrotophora spp. (mostly *P. beuki*) gathering at the sap exuding from wounds on elm and, less frequently, poplar and maple trees.

Another interesting behaviour of adult *Phalacrotophora* is the **swarming** of the flies around the bases of tree trunks. Early observations of this phenomenon (Colyer 1952, 1954) mostly refer to *P. berolinensis*, but recently Irwin (2006) found a swarm of another species, *P. delageae* in England. It turned out that these swarms, both of *P. berolinensis* and *P. delageae*, exclusively, or almost exclusively, consist of females. Individual flies may temporarily separate from the swarm to settle on the tree trunk with their wings outstretched and the abdomen convulsively expanding and contracting (Schmitz 1929, cited by Colyer 1952), or they may take up a posture in which the wings are vibrating and the membranous patch at the base of the fifth tergite is displayed (Irwin 2006). The function of the swarming and associated 'display postures' is unknown. It could be to attract males (Irwin 2006), but males have not been reported to respond to such female behaviour.

Parasitization rates

Parasitization of ladybird pupae by *Phalacrotophora* may differ greatly depending on the year, season, host species and region, sometimes reaching high values. For example, Disney et al. (1994) and Hurst et al. (1998) recorded combined parasitization rates of *C. septempunctata* by *P. fasciata* and *P. berolinensis* that exceeded 80%.

Distinct differences in parasitization rates of particular host species have been recorded, even for the most polyphagous species *P. fasciata*. In the St. Petersburg region, Lipa and Semyanov (1967) found that parasitization of *Myzia oblongoguttata* might reach 25%, while in other species it was less than 5%. In West Siberia, Filatova (1974) recorded up to 45% parasitization of *C. septempunctata*, *Anatis ocellata* and *Hip. tredecimpunctata*, up to 25–30% parasitization of *Har. axyridis*, *A. bipunctata* and *E. quadripustulatus*, and below 15% parasitization of other species. In Britain, Disney et al. (1994) found, that of the three arboreal species, *A. decempunctata*, *A. bipunctata* and *Calvia quatuordecimguttata*, the most affected by the flies was the least abundant *C. quatuordecimguttata*.

Data on the parasitization rates of ladybird pupae by *Phalacrotophora* species other than *P. fasciata* are scant. Wylie (1958) reports more than 50% parasitization of *Aphidecta obliterata* by *P. berolinensis* on conifers in the Vosges Mountains (eastern France). During three consecutive study seasons in central Poland, Durska et al. (2003) recorded mean parasitization rates of *An. ocellata* by *P. beuki* ranging between 36 and 41%. Parasitization of *Har. axyridis* by *Phalacrotophora* sp. (possibly *P. philaxyridis*) was found to reach up to 17.7% in Kyoto (central Japan) (Osawa 1992a), and to fluctuate between 0.4 and 6.7% during May–October in the Chuncheon area of Korea (Park et al. 1996). In New Caledonia, Disney & Chazeau (1990) noted *P. quadrimaculata* parasitizing 15–79% (39% on average) of an introduced ladybird species, *Olla v-nigrum*.

Multiparasitism

The parasitization of a single host by two species, *P. fasciata* and *P. berolinensis*, has been recorded several times. The host species involved were *A. bipunctata* (Disney 1979, Disney et al. 1994), *M. oblongoguttata* and *C. magnifica* (Ceryngier & Hodek 1996).

Host defence

The usual response of ladybird prepupae and pupae to physical disturbances, including those caused by predators and parasitoids, is 'flicking', i.e. rapid and repeated raising and dropping of their anterior end. Disney et al. (1994) found that this behaviour is relatively ineffective as a defence against *Phalacrotophora* species. Ovipositing *Phalacrotophora* species were only deterred in 17 out of 61 observations by flicking of *A. bipunctata* prepupae and pupae. Disney & Chazeau (1990) reported that flicking by *O. v-nigrum* did not seem to deter *P. quadrimaculata* from oviposition.

The common defensive behaviour of ladybirds against enemies, reflex bleeding, may also be shown by the prepupae defending themselves from *Phalacrotophora*. Disney et al. (1994) found *C. septempunctata* prepupae to reflex bleed in response to ovipositor insertion by the flies. In one instance of five prepupae observed, fluid secreted from the dorsal surface contaminated the legs of the fly, and this deterred it from ovipositing.

8.3.2.8 *Oomyzus scaposus* (Thomson) (Hymenoptera: Eulophidae, Tetrastichinae)

Synonyms: *Tetrastichus coccinellae* Kurdjumov, *T. melanis* Burks, *T. sexmaculatus* Chandy Kurian, *Syntomosphyrus taprobanes* Waterston.

Oomyzus scaposus is probably the most widely distributed and most common species of ladybird larval and pupal parasitoids belonging to the eulophid subfamily Tetrastichinae. Several other species of lesser importance can be found within the genera *Aprostocetus*, *Baryscapus*, *Oomyzus* and *Tetrastichus* (Table 8.3).

According to the **distribution** records quoted by Noyes (2011), *O. scaposus* occurs in the Nearctic, Palaearctic, Oriental and Australasian regions. The reported localities extend from high latitudes in the Northern Hemisphere, even beyond the Arctic Circle (the Murmansk region of Russia), through the tropics (Colombia, southern India, Sri Lanka, Indonesia), to the temperate areas in the Southern Hemisphere (New Zealand). The only big land masses where this species has not been recorded are South America (except Colombia) and sub-Saharan Africa.

The **host range** of *O. scaposus* reported by Noyes (2011) is also quite wide. It mostly includes ladybird species of the tribes Coccinellini (subfamily Coccinellinae) and Chilocorini (Chilocorinae), but there are also single reports of infection of *Scymnus* sp. (Scymninae) and *Chrysopa* spp. (Neuroptera: Chrysopidae).

Tetrastichinae is an extremely difficult group taxonomically (LaSalle 1993) and hence many records concerning *O. scaposus* and related species should be treated with caution.

Life cycle

Females of *O. scaposus* prefer to **lay eggs in third and fourth instar ladybird larvae**, although they have also been reported ovipositing in pupae (Iperti 1964, Klausnitzer 1969), as well as younger larvae (Filatova 1974). According to Semyanov (1986), the eggs are usually inserted between the thorax and abdomen of the host, sometimes between its pleura, and sporadically into the head capsule. The process of oviposition lasts from one to 2.5 minutes. After removing her ovipositor, the **female feeds on the fluid from the wound** (Ogloblin 1913, Semyanov 1986). The female may oviposit up to three times into the same host (Semyanov 1986).

A parasitized ladybird larva usually develops to the pupal stage and then dies and becomes darker. Adult wasps emerge from one, or sometimes more, small openings bitten through the cuticle in the dorsal side of the pupa (Filatova 1974). If young larvae (first and second instar) are parasitized, wasps may emerge before the host pupates (Filatova 1974).

Many *O. scaposus* individuals can develop successfully within a single host; up to 47 were recorded by Semyanov (1986) emerging from individual pupae of *C. septempunctata*. The wasps are sexually mature at emergence and mate within a few minutes of emerging (Iperti 1964, Filatova 1974).

The **development** of *O. scaposus* has been reported to last 20–32 days in southeastern France (Iperti 1964), about 20 days in the Poltava region (Ukraine) (Ogloblin 1913) and 15–26 days in the Russian Far East (Kuznetsov 1987). Filatova (1974) found that wasps developed in 15–18 days at a mean daily temperature of 23°C.

Due to relatively fast development, *O. scaposus* can produce **several generations per year** under favourable conditions (Telenga 1948, Iperti 1964). Parasitoids developing later in the season enter **diapause** to overwinter as prepupae inside their dead hosts (Telenga 1948, Iperti 1964, Filatova 1974).

Parasitization rates

Oomyzus scaposus is sometimes reported as an important mortality factor of ladybirds, especially of multivoltine coccidophagous *Chilocorus* spp. in warmer parts of the Palaearctic region. The level of parasitization of successive generations of these ladybirds tends to rapidly increase, so that, late in the season, high parasitization rates can be observed (Rubtsov 1954, Murashevskaya 1969, Stathas 2001, Stathas et al. 2008).

Aphidophagous ladybirds are more dispersive than species of *Chilocorus* and such time-dependent trends of parasitization rates by *O. scaposus* are more difficult to demonstrate. Nevertheless, Iperti (1964) found that, in southeastern France, parasitization of *C. septempunctata* developing early in the season (April–May) was 0–1%, while later (June–July) it was almost 20%. The rates of parasitization by *O. scaposus* reported for aphidophagous Coccinellidae are generally very variable and may fluctuate considerably from year to year (Dean 1983, Semyanov 1986, Pankanin-Franczyk & Ceryngier 1999).

8.3.2.9 *Pediobius foveolatus* (Crawford) (Hymenoptera: Eulophidae, Entedoninae)

Generic synonym: *Pleurotropis* Foerster.

Species synonyms: *Pediobius epilachnae* (Rohwer), *P. mediopunctata* (Waterston), *P. simiolus* (Takahashi), *Mestocharis lividus* Girault.

Pedobius foveolatus is a **gregarious larval endoparasitoid of phytophagous ladybirds** of the subfamily Epilachninae (Lall 1961, Kerrich 1973). The report on predaceous *C. septempunctata* and *Menochilus sexmaculatus* as hosts of this wasp (Bhatkar & Subba Rao 1976) certainly relates to a different parasitoid species (Bledsoe et al. 1983).

Pedobius foveolatus is widely **distributed** in Afrotropical, Oriental, southern Palaearctic and Australasian regions (Kerrich 1973). Additionally, it was **introduced to the Nearctic** region (USA) to control *Epilachna varivestis*. However, establishment of the parasitoid in that region is impeded in winter. Therefore, laboratory-bred wasps are released annually (Stevens et al. 1975a, 1975b, Schaefer et al. 1983).

Life cycle

Pedobius foveolatus reproduces arrhenotokously (Stevens et al. 1975b). The adults mate soon after emergence from their dead (mummified) hosts (Lal 1946, Lall 1961, Stevens et al. 1975b). The process of mating usually lasts 15–30 seconds (Lal 1946, Lall 1961).

Female *P. foveolatus* oviposit into host larvae, preferentially of older instars (Appanna 1948, Lall 1961, Stevens et al. 1975b), and sometimes into freshly moulted pupae (Appanna 1948). Lall (1961) found that young *Epilachna* larvae (first and second instar) are not suitable for *P. foveolatus* development because, in such hosts, parasitoid larvae die before pupation. Appanna (1948) observed first instar larvae of *Henosepilachna vigintioctopunctata* to be stung by *P. foveolatus*, but without oviposition. Nevertheless, the attack caused the darkening of the larvae that is typical of parasitization.

According to Appanna's (1948) detailed observations of *P. foveolatus* **oviposition behaviour**, the female stings a host larva several times. The first two stings are brief and are not accompanied by oviposition. They cause sudden quick movements of the host; this behaviour is not displayed during later stings, which are associated with oviposition. It is possible that the initial stings inject paralyzing venom into the host's body, so the wasp can begin egg laying, a process lasting 3–4 minutes. An individual female may oviposit three times into the same host at intervals of about 15–20 minutes. Eggs are laid just below the larval skin through the soft intersegmental membranes, usually on the dorsal surface of the larva.

At 25°C, **egg incubation** lasts about 2 days. The hatched **larvae pass through three instars** and pupate inside the host mummy about one week after hatching. The **pupal stage** lasts 4–5 days. **Emergence of adults** takes place approximately 13.5 days after egg deposition (Bledsoe et al. 1983).

Parasitization by *P. foveolatus* leads to the death of the host larva or pupa and its **mummification**. A few days after parasitization, the host larva stops feeding, dies, darkens and hardens (Lal 1946, Lall 1961, Appanna 1948, Stevens et al. 1975b). Adult *P. foveolatus* emerge from the host mummy through one or, more rarely, two, holes on the dorsal side (Appanna 1948). The reported number of individuals emerging from a single field-collected host usually ranges from one or a few to 20–30 (Lal 1946, Appanna 1948, Lall 1961, Barrows & Hooker 1981). As the mean clutch size of *P. foveolatus* in an unparasitized larva of *E. varivestis* was found in laboratory tests to be about 13 (range 5–22) (Hooker & Barrows 1992), the higher values within the reported range might refer to cases of **superparasitism**. It has been shown that females of *P. foveolatus* can superparasitize, in spite of their ability to discriminate between previously parasitized and unparasitized hosts (Shepard & Gale 1977, Hooker & Barrows 1992). **Host discrimination** in this species is expressed by much less frequent ovipositions into parasitized than unparasitized hosts (Shepard & Gale 1977), and by reduction of the clutch size laid in the former (Hooker & Barrows 1992).

Parasitization rates

Pedobius foveolatus has often been reported to limit considerably the populations of epilachnine ladybirds. On potato fields around Bangalore (India), Appanna (1948) recorded average parasitization of *H. vigintioctopunctata* to exceed 40%; it was about 30% in February and March, but reached much higher values (60–77%) later in the season. Parasitization of the same host species and in the same region, reported by Venkatesha (2006) on a medicinal plant, *Withania somnifera*, was similarly high (range 52–70%). In Sumatra, parasitization rates of pupae of *Epilachna* sp. on bitter melon (*Momordica charantia*) were around 25% between March and September, and 60% between October and December (Abbas & Nakamura 1985).

Pedobius foveolatus *as a biocontrol agent*

Pedobius foveolatus can parasitize many phytophagous ladybirds, including those which are serious pests of cultivated plants, and so, attempts have been made to use this parasitoid as a biological control agent. The best-known example involves releases of the wasp in the eastern USA against the notorious pest of soy and other beans, the Mexican bean beetle (*E. varivestis*). It was found that *P. foveolatus* of Indian and Japanese origin can successfully parasitize *E. varivestis* (Angalet et al. 1968, Schaefer et al. 1983), as well as some other American Epilachninae (Romero-Napoles et al. 1987). However, neither Indian nor Japanese wasps can overwinter in the areas where they were released (Schaefer et al. 1983). Schaefer et al. (1983) supposed that it was not climatic constraints, but the lack of a suitable winter host that prevents establishment of *P. foveolatus* in North America. They hypothesized that in its native range, *P. foveolatus* spends the winter months as diapausing larvae inside overwintering larvae of certain Epilachninae, e.g. *Epilachna admirabilis*. Since all eastern North American Epilachninae overwinter as adults, there is no possibility for the parasitoid to survive the winter in the field.

Due to the **inability of *P. foveolatus* to overwinter in North America**, control of the Mexican bean beetle by this species can only be achieved through the releases of laboratory-reared wasps. Preliminary results of such releases in soybean fields and vegetable gardens appeared promising (Stevens et al. 1975a, Barrows & Hooker 1981) and so the wasps became commercially produced for gardeners and farmers (Schaefer et al. 1983).

Less known, but no less successful, was the application of *P. foveolatus* against *Henosepilachna vigintisexpunctata* on Saipan (Mariana Islands). This ladybird was accidentally introduced to the island in 1948 and became a serious pest of solanaceous crops. Releasing *P. foveolatus* in 1985 rapidly suppressed the beetle population. An island-wide survey performed in 1989 revealed that about 80% of *H. vigintisexpunctata* larvae were parasitized (Chiu & Moore 1993).

8.4 PARASITES AND PATHOGENS

8.4.1 Acarina

8.4.1.1 Phoretic mites

Mites found on coccinellids may be divided into those that are parasitic, and those that simply use the coccinellid as a means of transport between hosts. This latter, phoretic group includes species in the families Hemisarcoptidae, Winterschmidtiidae and Acaridae of the order Astigmata, which prey on coccids and other hemipterans. The hypopus stage of the mite does not feed, but attaches itself to the outer surface of an arthropod to be vectored to new host plants and prey colonies. Mites of the genus *Hemisarcoptes* (Hemisarcoptidae) are important predators of diaspidid scale insects (Gerson et al. 1990, Izraylevich & Gerson 1993, Ji et al. 1994), and are generally vectored between prey colonies by members of the genus *Chilocorus*, since these species also prey on coccids (Houck & O'Connor 1991). Four new species of hemisarcoptid mite were discovered in surveys of the mite fauna of coccinellids collected in southern England, Holland and Belgium in the early 1990s (Fain et al. 1995, 1997). It is likely that many new species of mites that are phoretic on coccinellids await discovery.

Although these mites are not actually parasitic on coccinellids and have no known detrimental impact, their phoresy is clearly important in biological control. Species of *Chilocorus* may be selected as biological control agents against coccids, and their efficiency in control programs may be increased by ensuring that released individuals carry hypopi of mites that will also attack the coccids.

A variety of truly parasitic mites have also been recorded from ladybirds. These include some species, such as *Leptus ignotus*, that parasitize a wide variety of arthropods (Hurst et al. 1997a), and mites of the genus *Coccipolipus* that specialize on coccinellids.

8.4.1.2 *Coccipolipus* Husband (Prostigmata: Podapolipidae)

The mite genus *Coccipolipus* was erected by Husband in 1972 and comprises 14 species known to be parasitic upon coccinellids in the subfamilies Coccinellinae, Epilachninae and Chilocorinae (Husband 1984b, Ceryngier & Hodek 1996; Table 8.14). Although many of these species are tropical, the best researched is the widely distributed *Coccipolipus hippodamiae*, which has been recorded from the United States, Russia, central and eastern Europe, and the Democratic Republic of the Congo (Table 8.14). Detailed work on this species in Europe has shown that it is the causative agent of a **sexually transmitted disease** (Hurst et al. 1995, Webberley et al. 2004, Webberley et al. 2006a).

Table 8.14 Described species of the genus *Coccipolipus* and their known host and distribution records (adapted and updated from Ceryngier & Hodek 1996).

***Coccipolipus* species**	**Hosts and distribution**	**References**
africanae	*Epilachna* spp. (DR Congo, Rwanda)	Husband (1984a)
arturi	*Henosepilachna vigintioctopunctata* (Sumatra)	Haitlinger (1998)
benoiti	*Henosepilachna elaterii* (South Africa)	Husband (1981)
bifasciatae	*Henosepilachna bifasciata* (Zimbabwe)	Husband (1984a)
cacti	*Chilocorus cacti* (Mexico)	Husband (1989)
camerouni	*Epilachna nigrolimbata* (Cameroun)	Husband (1984a)
chilocori	*Chilocorus* spp. (DR Congo, Kenya)	Husband (1981)
cooremani	*Cheilomenes* spp. (DR Congo, Rwanda)	Husband (1983)
epilachnae	*Epilachna* spp. (El Salvador, Guatemala, Honduras, Mexico, USA)	Smiley (1974); Schroder & Schroder (1989)
hippodamiae	*Hippodamia convergens* (USA) *Adalia bipunctata* (USA, Russia, Poland, France, Italy, Germany, Austria, Czech Republic, Sweden, Ukraine, Georgia Rep.) *Adalia decempunctata* (Poland, Hungary, Germany, Russia) *Oenopia conglobata* (Poland) *Calvia quatuordecimguttata* (Poland) *Harmonia quadripunctata* (France) *Harmonia axyridis* (Poland, USA) *Coccinella magnifica* (UK) *Exochomus troberti concavus* (DR Congo) *Exochomus fulvimanus* (DR Congo) *Coccinella septempunctata* (Ukraine)	McDaniel & Morrill (1969); Husband (1981); Eidelberg (1994); Majerus (1994); Hurst et al. (1995); Zakharov & Eidelberg (1997); Webberley et al. (2004, 2006b); Rhule & Majerus (2008); Rhule et al. (2010); Riddick (2010); J. J. Sloggett, unpublished
macfarlanei	*Cycloneda sanguinea* (Trinidad, El Salvador) *Coccinella leonina transversalis* (Australia, New Hebrides) *Coccinella transversoguttata* (USA) *Coccinella septempunctata* (Iran, Ukraine, Poland) *Coccinella undecimpunctata* (Iran)	Husband (1972, 1981, 1984b, 1989); Smiley (1974); Eidelberg (1994); Hajiqanbar et al. (2007); R. W. Husband & P. Ceryngier, unpublished
micraspisi	*Micraspis* spp. (DR Congo) *Declivitata* spp. (DR Congo, Rwanda)	Husband (1983, 1984a)
oconnori	*Chilocorus stigma* (USA)	Husband (1989)
solanophilae	*Epilachna karisimbica* (DR Congo)	Cooreman (1952)

Life cycle

All stages of *C. hippodamiae* live on the underside of the elytra of coccinellids (Husband 1981, Majerus 1994; Fig. 8.8). The mouthparts of adult females become embedded into the host's elytra, or occasionally into the dorsal surface of the abdomen, allowing them to feed on host haemolymph. It is thought that female mites are fertilized in their final larval instar, since colonies of egg-laying females have resulted from the artificial transfer of just one larva to a previously uninfected host (E.L. Rhule, unpublished.). Eggs hatch into motile larvae, and these migrate between hosts (Knell & Webberley 2004). Webberley and Hurst (2002) report that **transmission** almost always occurs through sexual contact, although, on rare occasions, larvae may be transferred through close physical contact during host overwintering. Once on a novel host, larvae embed their mouthparts and metamorphose into adults. Thereafter, adult mites are entirely sedentary. Establishment and subsequent maintenance of the mite within a host coccinellid

Figure 8.8 The underside of the elytron of an *Adalia bipunctata* infected with *Coccipolipus hippodamiae* (six large adult female mites and their eggs are visible) (photo courtesy of Emma Rhule). (See colour plate)

population is dependent on two key factors: high levels of promiscuity to permit horizontal transmission between host individuals, and overlapping generations to facilitate vertical transmission down generations (Majerus 1994).

Prevalence

Webberley et al. (2006a) report an increase in the prevalence of *C. hippodamiae* in *A. bipunctata* populations through the year, with up to 90% of some populations of the beetle being infected by the latter part of the breeding season. This is thought to be a direct consequence of mating rate and the extent that matings occur between individuals of successive generations.

Variation in the prevalence of the mite on different host species has also been attributed to the frequency of mating of the hosts (Webberley et al. 2004). Highest prevalence is seen in *A. bipunctata*, which is more promiscuous than the less commonly infected *A. decempunctata* and *Oenopia conglobata*. Lowest prevalence was recorded in *Calvia quatuordecimguttata*. This species requires an overwintering diapause before breeding, leading to a lack of consistent sexual activity between generations and hence a barrier to mite vertical transmission. It is suggested that, in some parts of Europe, *C. hippodamiae* is lacking from *A. bipunctata* populations (Britain, coastal areas of northwest continental Europe) or is scarce (Scandinavia), due to limited intergenerational mating of the ladybird (Majerus 1994, Webberley et al. 2006b). In some years in northwest Europe, the old generation dies before the new generation is reproductively mature.

The only coccinellid from which *Coccipolipus* mites have been recorded in Britain is *C. magnifica* (J.J. Sloggett, unpublished). The presence of mites on this species is probably due to the extended longevity of *C. magnifica*, promoted by its symbiotic relationship with ants (Sloggett et al. 1998). This means that some adults always survive until the first of the next generation have eclosed, allowing some intergenerational mating each year, and transmission of the mite down host generations (J.J. Sloggett, unpublished).

Effects on hosts

Infection of coccinellids by *C. hippodamiae* has strong negative effects, whereby female hosts become infertile. This has been particularly well studied in *A. bipunctata*, in which complete sterility was induced within approximately three weeks of infection (Hurst et al. 1995, Webberley et al. 2004). Hurst et al. (1995) speculate that sterility results from mite-infection interfering with the production of the chorion of the egg, since eggs laid by infected females were observed to shrivel and desiccate within 24 hours of being laid. Webberley and Hurst (2002) also demonstrated that infected *A. bipunctata*, especially males, were less likely to survive overwintering.

The interactions between other *Coccipolipus* species and their hosts have been less studied, although it is thought that patterns of transmission are likely to be similar as for *C. hippodamiae*, with similar effects on host fitness. Indeed, Schroder (1982) reports that *C. epilachnae* reduces fecundity of *E. varivestis* by two-thirds, and increases mortality by 40%.

Coccipolipus *in biological control*

Coccipolipus epilachnae has been introduced from Central America into the USA to control *E. varivestis*, which is a pest of soybean, although there is some disagreement in the literature over whether it actually suppresses host populations (Hochmuth et al. 1987, Schroder 1982, Cantwell et al. 1985).

Work is currently being undertaken to assess the potential of using *C. hippodamiae* to control the invasive coccinellid *Har. axyridis* in Britain and Europe (Rhule & Majerus 2008, Rhule et al. 2010). The fact that *C. hippodamiae* has been recovered from its congener, *Har.*

quadripunctata (Rhule & Majerus 2008), led the authors to suppose that *Har. axyridis* may also be a suitable host and, if similar effects on female fertility are found in *Har. axyridis* as were documented in *A. bipunctata*, infection with this mite may represent a promising avenue for controlling invasive *Har. axyridis* populations. Rhule et al. (2010) were able to establish successful mite colonies, consisting of reproducing adult females and their eggs, through artificial transfer onto *Har. axyridis*. Thereafter, infection was transmitted horizontally through copulation, and infected females were found to become completely sterile within 3 weeks of infection. This work demonstrates the potential for *C. hippodamiae* to become established on *Har. axyridis* as a novel host, and to significantly reduce host fitness. Further work is required to ascertain whether the mite would actually regulate host population numbers in the long term. Recent sampling of *Har. axyridis* in Torun, Poland, has revealed natural infection by *C. hippodamiae* (Rhule et al. 2010), so it seems that, even in the absence of human intervention, this mite may naturally propagate through *Har. axyridis* populations, at least in parts of continental Europe.

8.4.2 Nematodes

Nemathelminthes attacking Coccinellidae belong almost exclusively to the Nematoda, with only a single report of a primitive **Nematomorpha** attacking *Coccinella leonina transversalis* (Anderson et al. 1986).

Field and laboratory studies have demonstrated that ladybirds may be susceptible to entomopathogenic nematodes belonging to several families, such as Steinernematidae (Mracek & Ruzicka 1990, Abdel-Moniem & Gesraha 2001, Shapiro-Ilan & Cottrell 2005), Heterorhabditidae (Abdel-Moniem & Gesraha 2001, Shapiro-Ilan & Cottrell 2005), Allantonematidae (Iperti 1964, Hariri 1965, Narsi Reddy & Narayan Rao 1984) or Mermithidae (Delucchi 1953, Iperti 1964, Rhamhalinghan 1986a). However, only the members of the latter two families have been reported to parasitize ladybirds in the wild.

8.4.2.1 Allantonematidae (Tylenchida)

Within the Allantonematidae, *Parasitilenchus coccinellinae* has been reported from *P. quatuordecimpunctata*, *A. bipunctata*, *Oenopia conglobata*, *Hip. variegata* and *Ceratomegilla undecimnotata* in Europe (Iperti 1964, Iperti & van Waerebeke 1968), and *Menochilus sexmaculatus* and *Illeis indica* in India (Narsi Reddy & Narayan Rao 1984).

The **level of parasitization** of coccinellids by *P. coccinellinae* varies with host species. In France, Iperti & van Waerebeke (1968) found that multivoltine species were most heavily parasitized, especially *P. quatuordecimpunctata* (up to 70%), with *O. conglobata* less so (20%), and *A. bipunctata* and *Hip. variegata* the least heavily parasitized. The univoltine species *Cer. undecimnotata* was only found infected occasionally. *Menochilus sexmaculatus* in India was found parasitized at a rate of 22%, while only 2–3% of *I. indica* were attacked (Narsi Reddy & Narayan Rao 1984).

Over 100 adult female *P. coccinellinae* may infest a single host, with up to 10,000 larvae and young adults (Iperti & van Waerebeke 1968, Narsi Reddy & Narayan Rao 1984). The method of transmission from one host to the next is unknown, but it may be sexually transmitted. Certainly, *P. coccinellinae* is common in the reproductive organs of its host. Ceryngier & Hodek (1996) also suggest that transmission may occur through host tracheae or through soft parts of the cuticle between sclerites. They also speculate that transmission may occur in coccinellid overwintering aggregations, where damp conditions may facilitate nematode propagation. Ceryngier & Hodek (1996) provide details of the **life cycle** of *P. coccinellinae*. Within 4 days of penetrating the body cavity, the ovaries of the fertilized female nematode become enlarged and soon the uterus becomes filled with free larvae and developing eggs. The first larval moult occurs inside the mother, while the remaining two occur within the host body cavity. The third moult either gives rise to adult males, or a final instar of larval females with ovarial primordia of 5–9 cells. Larval females are fertilized by the males at this stage and will not undergo their fourth and final moult until penetrating a new host.

Parasitilenchus coccinellinae is not usually fatal to its host, but retards maturation of the ovaries, consumes host resources and is known to have a general debilitating effect (Ceryngier & Hodek 1996).

There is one report of allantonematid nematodes of the genus *Howardula* infesting *A. bipunctata* larvae in England (Hariri 1965). These nematodes did not seem to affect the gonads of their host as other allantonematids do, but did result in a reduction in size of host fat bodies.

8.4.2.2 Mermithidae (Mermithida)

The immature stages of several members of the Mermithidae are known to be **solitary endoparasites** of adult ladybirds, although Delucchi (1953) recorded parasitization of the larvae of *Aphidecta obliterata*. Identification of the worms to species level is difficult because only the juvenile stages are found in coccinellids. Iperti (1964) found nematodes of the genus *Mermis* in four aphidophagous coccinellids in southeast France. From 2.5 to 4.2% of overwintering *Hip. variegata* were infected; aestivating populations of *Cer. undecimnotata* were infected at a prevalence of 1.2%; while active *P. quatuordecimpunctata and C. septempunctata* were only occasionally infected (Iperti 1964).

Rhamhalinghan (1986 a,b,c, 1987 a,b,c, 1988) carried out detailed studies of the infection of *C. septempunctata* by nematodes of the genus *Hexamermis* (= *Coccinellimermis*) in India. These nematodes reduce the weight, respiratory rate and the size of the fat body of their hosts. Host ovary growth and development is retarded and the worm can cause physical damage to vital organs such as the ovaries, tracheae, alimentary canal, Malpighian tubules, nervous system and heart. Parasitized females undergo a marked change in behaviour: they do not mate, eat fewer aphids and become hyperactive. Infection ultimately results in **paralysis and death of the host** within about 17 days, after which the worm exits.

8.4.3 Fungal pathogens

8.4.3.1 Hypocreales (Ascomycota)

Fungal pathogens of the order Hypocreales are widely regarded as important natural enemies of coccinellids, but their role in regulating coccinellid populations is poorly understood (Majerus 1994, Ceryngier & Hodek 1996, Roy & Cottrell 2008). Most research on the interactions between pathogenic hypocrealean fungi and coccinellids has focused on the impacts of fungal-based biorational pesticides on non-target insects such as coccinellids (James et al. 1995, Roy & Pell 2000, Riddick et al. 2009). There is little information on the interactions of coccinellids with naturally occurring fungal pathogens (Ceryngier 2000, Roy & Cottrell 2008, Riddick et al. 2009, Roy et al. 2009, Steenberg & Harding 2009, 2010), even though fungi, such as *Beauveria bassiana*, are reported as major mortality factors of coccinellids particularly during overwintering (Iperti 1966, Ceryngier & Hodek 1996, Barron & Wilson 1998, Ormond et al. 2006).

There are several hypocrealean fungi that have been found infecting ladybirds: *B. bassiana* (James et al. 1995, Ceryngier 2000, Cottrell & Shapiro-Ilan 2003, Roy et al. 2008, Steenberg & Harding 2009), *Metarhizium anisopliae* (Ginsberg et al. 2002), *Isaria farinosa* (syn. *Paecilomyces farinosus*) (Ceryngier & Hodek 1996, Ceryngier 2000, Steenberg & Harding 2009), *I. fumosorosea* (syn. *P. fumosoroseus*) (Ceryngier & Hodek 1996) and *Lecanicillium* (syn. *Verticillium*) *lecanii* (Ceryngier 2000, Steenberg & Harding 2009).

Beauveria

The most well studied genus of hypocrealean fungi infecting coccinellids is *Beauveria* (Roy & Cottrell 2008), and the phylogeny and corresponding taxonomy of this single genus is undergoing major review (Rehner & Buckley 2005, Rehner et al. 2006). It is now thought appropriate to consider *B. bassiana* in the broadest sense as *B. bassiana* sensu lato because recognition and identification of *B. bassiana* as a distinct species has not been possible (Rehner & Buckley 2005). Indeed, *B. bassiana* s.l. appears to exist as non-monophyletic morphospecies and currently it is difficult to resolve separate species with certainty (Rehner & Buckley 2005, Ormond et al. 2010). It is important to keep in mind that the species reported as *B. bassiana* is likely to be one of many from within the species complex *B. bassiana* s.l.

Life cycle

The general life cycles of hypocrealean entomopathogens are remarkably similar despite their taxonomic diversity (Roy et al. 2006). They produce infective spores (conidia) that attach, germinate and penetrate directly through the host cuticle. So, unlike viral and bacterial pathogens, there is no requirement for ingestion of fungal spores. Once within the host, they proliferate as protoplasts, blastospores and hyphal bodies utilizing the host as a nutritional resource. Ultimately, the host is killed, and the fungus produces infective conidia for further transmission, or resting structures, such as sexual or asexual resting spores, chlamydospores or mummified hosts, for survival in the absence of new hosts or under adverse environmental conditions. The life cycles of hypocrealean fungi are **hemibiotrophic**, i.e. they switch from a parasitic, biotrophic phase in the haemocoel to a saprophytic phase colonizing the body after death.

Fungal activity is strongly influenced by abiotic and biotic conditions; high humidity (in excess of 95%) is required for conidium germination, infection, and sporulation, and the speed of kill is influenced by temperature (Vega et al. 2009). Fungal species exhibit a spectrum of adaptations that reflect the need to overcome environmental limitations and the host's defences (Roy et al. 2006, Ormond et al. 2010).

Prevalence of infection

Kuznetsov (1997) reviewed research on natural enemies attacking coccinellids in the Primorsky Territory of Russia (Far East Siberia) and summarized that the population dynamics of coccinellids in that territory are not significantly influenced by entomopathogens. *Henosepilachna vigintioctomaculata*, a serious pest of potato in the Primorsky Territory, was found infected by *Beauveria* species at frequencies of about 5.5–7%. Other coccinellids found in this territory infected by *Beauveria* species included *C. septempunctata*, *Har. axyridis*, *Calvia quatuordecimguttata* and *Hip. tredecimpunctata*.

Cottrell and Shapiro-Ilan (2003) took field-collected adults of *Olla v-nigrum* and *Har. axyridis* to the laboratory during autumn months, and found that 33% of the total mortality in the September sample and 81% in the October sample of *O. v-nigrum* could be attributed to infection by *B. bassiana*. No infection, however, was found in analogous samples of *Har. axyridis*.

Sublethal effects

Sublethal effects of hypocrealean pathogens on host insects are varied (Roy et al. 2006). There has been limited research on the premortality effects of these pathogens on coccinellids. Poprawski et al. (1998) found that moribund *Serangium parcesetosum* larvae infected with *B. bassiana* were less voracious than uninfected larvae, but they did not detect sublethal effects of either *B. bassiana* or *I. fumosorosea* on development of this predator. Roy et al. (2008) measured mortality of *C. septempunctata*, *Har. axyridis* (populations from Japan and Britain) and *A. bipunctata* and fecundity of the two latter species when exposed to *B. bassiana*. Mortality of both *C. septempunctata* and *A. bipunctata* was higher relative to the Japanese and British populations of *Har. axyridis* but an impact of *B. bassiana* on *Har. axyridis* (in Britain) was detected via reduced fecundity at all *B. bassiana* doses tested (10^5, 10^7 and 10^9 conidia/ml).

8.4.3.2 *Hesperomyces* spp. (Ascomycota: Laboulbeniales, Laboulbeniaceae)

Laboulbeniales are **obligate ectoparasites** that infect many insect and non-insect hosts, but especially Coleoptera (Weir & Hammond 1997). They occur from the tropics to the temperate and polar regions on both terrestrial and aquatic hosts (Weir 2002, Harwood et al. 2006). Coccinellids are infected by several species of the genus *Hesperomyces* (Table 8.15; Fig. 8.9).

Most Laboulbeniales do not penetrate the insect cuticle, but *Hesperomyces virescens* (the most commonly reported laboulbenialean on coccinellids) exhibits rhizoidal penetration into the host body by production of a circular appressorium, which attaches and penetrates the host cuticle (Weir & Beakes 1996).

In general, laboulbenialean fungi do not directly cause mortality of their hosts (Weir & Beakes 1996), but a few **negative fitness effects** have been documented including reduced longevity of *Chil. bipustulatus* in Israel (Kamburov et al. 1967). Heavy infections can supposedly impede flight, mating, foraging and feeding but this requires further investigation (Nalepa & Weir 2007).

Hesperomyces virescens is often on the ventroposterior of males and the dorsoposterior of females; a sexual dimorphism that reflects the major **transmission** mechanism which is thought to be direct contact during mating (Weir & Beakes 1996, Welch et al. 2001, Riddick & Schaefer 2005). However, the distribution of *H. virescens* thalli on aggregating beetles are not explained by sexual transmission (Riddick & Schaefer 2005, Riddick 2006, Nalepa & Weir 2007); fungal thalli on overwintering *Har. axyridis* are located on the anterior part of the body which accords with direct contact through aggregation (Nalepa & Weir 2007). A similar pattern was reported for overwintering *A. bipunctata* which had fungal thalli distributed at the margins and front angles of the elytra (Weir & Beakes 1996). Nalepa & Weir (2007) conclude that transmission of this fungus is through contact with conspecifics: sexual contact is of primary importance in the mating season but aggregation in winter also plays a significant role.

Table 8.15 Host and distribution records of *Hesperomyces* species parasitizing Coccinellidae.

***Hesperomyces* species**	**Host**	**Distribution**	**Reference**
chilomenis	*Cheilomenes lunata*	Kenya	Thaxter (1931)
coccinelloides	*Diomus seminulus*	Brazil	Rossi & Bergonzo (2008)
	Diomus sp.	Ecuador	Castro & Rossi (2008)
	Scymnus tardus	Panama	Thaxter (1931)
	Scymnus sp.	Spain	Santamaría (1995)
	Stethorus pusillus	Belgium	De Kesel (2011)
	undet. Coccinellidae	USA	Benjamin (1989) (cited in Castro & Rossi 2008)
	undet. Scymninae	Grenada	Thaxter (1931)
	undet. Scymninae	Jamaica	Thaxter (1931)
	undet. Scymninae	Philippines	Thaxter (1931)
	undet. Scymninae	Borneo	Thaxter (1931)
hyperaspidis	*Hyperaspis* sp.	Trinidad	Thaxter (1931)
virescens	*Adalia bipunctata*	England	Weir & Beakes (1996)
		Austria	Christian (2001)
		France	Webberley et al. (2006b)
		Germany	Webberley et al. (2006b)
		Italy	Webberley et al. (2006b)
		Sweden	Webberley et al. (2006b)
		The Netherlands	Webberley et al. (2006b)
	Adalia decempunctata –	Italy	Castaldo et al. (2004)
	Adalia sp.	Belgium	A. De Kesel, unpublished
	Brachiacantha quadripunctata	USA	Harwood et al. (2006a)
	Chilocorus bipustulatus	Israel	Kamburov et al. (1967)
	Chilocorus renipustulatus	England	Hubble (2011)
	Chilocorus stigma	USA	Thaxter (1931)
	Coccinella septempunctata	USA	Harwood et al. (2006b)
	Coccinula crotchi	Japan	M. E. N. Majerus & R. L. Ware, unpublished
	Coccinula quatuordecimpustulata	Greece	Castaldo et al. (2004)
	Coccinula sinensis	Japan	M. E. N. Majerus & R. L. Ware, unpublished
	Cycloneda munda	USA	Harwood et al. (2006b)
	Cycloneda sanguinea	? England*	Tavares (1979)
	Eriopis connexa	Argentina	Thaxter (1931)
	Harmonia axyridis	USA	Garces & Williams (2004)
		Germany	Steenberg & Harding (2010), K. Twardowska, unpublished
		Belgium	De Kesel (2011)
		The Netherlands	De Kesel (2011)
	Hippodamia convergens	USA	Thaxter (1931)
	Olla v–nigrum	Fiji	Weir & Beakes (1996)
		USA	Roy & Cottrell (2008)
	Propylea quatuordecimpunctata	Spain	Santamaría (2003)
	Psyllobora sp.	France	Tavares (1985)
	Psyllobora vigintiduopunctata	Spain	Santamaría (2003)
		Belgium	De Kesel (2011)
	Psyllobora vigintimaculata	USA	Harwood et al. (2006)
	Tytthaspis sedecimpunctata	Greece	Castaldo et al. (2004)

*The reported locality (Rustington, England) is either erroneous or concerns laboratory culture of the host native to Americas.

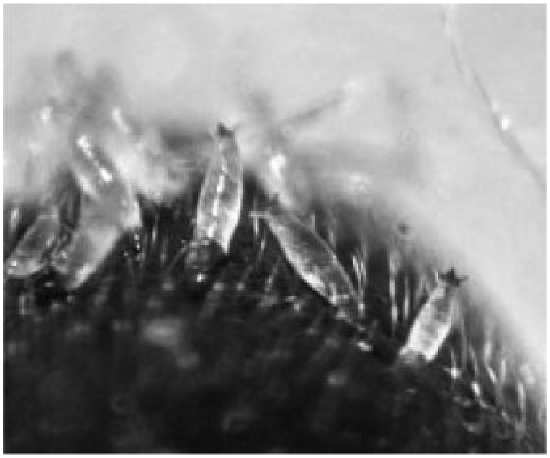

Figure 8.9 Thalli of *Hesperomyces coccinelloides* on the elytra of *Stethorus pusillus* (photo courtesy of Johan Bogaert). (See colour plate.)

Prevalence of infection

Harwood et al. (2006a) examined the prevalence of *H. virescens* on coccinellids in Kentucky, USA, and found that 82.3% of *Har. axyridis* were infected compared with only 4.7, 4.2 and 2.5% of *Psyllobora vigintimaculata*, *Brachiacantha quadripunctata* and *Cycloneda munda*, respectively. This ectoparasitic fungus was not recovered from *Col. maculata* or *Hyperaspis signata*. In Georgia, USA, the prevalence of natural *H. virescens* infection of *O. v-nigrum* is similar as of *Har. axyridis* in Kentucky (T. Cottrell, unpublished data reported in Roy & Cottrell 2008).

The prevalence of infection of *H. virescens* on *A. bipunctata* in London was higher at the centre of the city than at the periphery and, indeed, infection was rare or absent outside the city (Welch et al. 2001). This variation in prevalence over such a short distance (less than 25 km) is unusual, but indicates an association between urbanization and disease dynamics. It is thought that the prevalence of the fungus is linked to elevated urban temperatures which increase the probability of generations of the host overlapping and consequent interbreeding between cohorts.

8.4.3.3 Nosematidae (Microsporidia)

Until recently, microsporidia have been grouped with the protozoa but recent molecular evidence suggests that they should be placed within the fungal kingdom (e.g. Lee et al. 2008). They are intracellular pathogens with fascinating but complex life cycles.

Life cycle

Each microsporidial spore comprises a long, coiled tube called the polar filament. Once a spore is in the host, the polar filament is extruded and acts as a needle injecting the spore contents into the host cell to begin infection. Once inside the appropriate host cell, the intracellular stage (schizont) proliferates asexually and then undergoes an autogamous sexual process producing sporonts. In the genus *Nosema*, each sporont gives rise to one spore (Ceryngier & Hodek 1996). **Transmission** between hosts is dependent on the release of spores into the environment and ingestion by a suitable host. Microsporidian species are often highly specific not just to host species but to specific tissues within the host such as the fat body, midgut wall or the reproductive tissues. Infections by most microsporidia result in chronic diseases and often the host can appear asymptomatic, although body size, longevity and fecundity are often reduced and development time increased (Hajek 2004). These pathogens are often vertically transmitted from mother to egg, a strategy that enables microsporidia to persist in low density or scattered host populations. Some microsporidia are vectored by parasitoids to other insects. There are only a few studies examining the interactions between nosematid microsporidia and coccinellid hosts. There are undoubtedly many more examples yet to be revealed.

Nosematid species infecting Coccinellidae

Brooks et al. (1980) found two microsporidia, subsequently described as *Nosema epilachnae* and *Nosema varivestis* (Brooks et al. 1985), to infect nearly 100% of laboratory colonies of *E. varivestris.* Unusually for a microsporidial infection, the pathogens decimated these colonies. Further investigations revealed both pathogens in field populations of *E. varivestis* in North and South Carolina, USA, with up to 28% infection rates by the more virulent *N. epilachnae*, and a few per cent rates by the less virulent *N. varivestis*. The two *Nosema* species were mechanically transmitted between infected and uninfected hosts by the parasitoid *P. foveolatus*. This parasitoid is highly susceptible to both *N. epilachnae* and *N. varivestis* and so represents a shared host (Brooks et al. 1980).

Another *Nosema* species, *N. henosepilachnae*, has been found infecting various tissues of *Henosepilachna* *elaterii* in Senegal. This microsporidiosis is not directly lethal, but reduces fecundity in adult hosts (Toguebaye & Marchand 1984).

There have been three *Nosema* species identified from predatory coccinellids. *Nosema tracheophila* was found in the tracheal epithelium and connective tissues of *C. septempunctata* (Cali & Briggs 1967) and *Nosema coccinellae* in the midgut epithelium, Malpighian tubules, gonads, nervous and muscle tissues of *C. septempunctata*, *Hip. tredecimpunctata* and *Myrrha octodecimguttata* (Lipa 1968a). *Nosema hippodamiae* was identified from the midguts and fat bodies of *Hip. convergens* in 1959 (Lipa & Steinhaus 1959) and, just after a decade later, microsporidial spores resembling *N. hippodamiae* were observed in the fat body, muscle, gut, Malpighian tubules and testes of 50% of the *Hip. convergens* (Sluss 1968). Interestingly, Sluss (1968) noted that this microsporidium prevented development of *Hip. convergens* parasitoid, *Dinocampus coccinellae*.

Recently, an unidentified nosematid pathogen of *Hip. convergens* was reported by Bjornson and co-authors (Saito & Bjornson 2006, 2008, Joudrey & Bjornson 2007, Bjornson 2008). After ultrastructure and molecular examination, it was described as a new species, *Tubulinosema hippodamiae* (Bjornson et al. 2011). However, it is currently unknown as to whether *T. hippodamiae* actually represents a new species or is one of the coccinellid pathogens already described under the genus *Nosema*. To check this, molecular characterization of type specimens of *N. hippodamiae*, *N. coccinellae* and *N. tracheophila* should be made (Bjornson et al. 2011).

Bjornson (2008) noted rather low prevalence of infection of *Hip. convergens* with *T. hippodamiae*; only 1% of individuals collected in the winter from the field for commercial retail were infected. Infection of *Hip. convergens* by this species has been shown to increase development time and reduce longevity and female fecundity (Joudrey & Bjornson 2007). Saito & Bjornson (2006) demonstrated the efficacy of horizontal transmission of the microsporidium from *Hip. convergens* to larval *C. septempunctata*, *C. trifasciata perplexa* and *Har. axyridis* when these larvae consumed infected eggs in the laboratory. Indeed, the microsporidium was transmitted with 100% efficiency when first instar larvae were fed infected eggs, and, in all cases, larval development was significantly longer for microsporidia-infected individuals than for uninfected individuals, but the microsporidium had no effect on larval mortality (Saito & Bjornson 2008). Therefore, the practice of redistributing *Hip. convergens* from overwintering locations to agricultural ecosystems could facilitate the dispersal of microsporidia to other coccinellids. Laboratory studies demonstrated that invasive non-native species of coccinellid, such as *Har. axyridis*, were less susceptible to infection by *T. hippodamiae* than native species (Saito & Bjornson 2006, 2008); infection was as heavy in *C. trifasciata perplexa* (a native coccinellid) as it was in *Hip. convergens* (original host), but lighter in the introduced species *C. septempunctata* and *Har. axyridis*.

8.4.4 Protozoan pathogens

8.4.4.1 Septate eugregarines (Apicomplexa: Eugregarinida: Septatorina)

Eugregarines are large unicellular organisms (sometimes more than 0.5 mm in length) that inhabit alimentary canals, coelomic spaces or reproductive vesicles of many invertebrates (Rueckert & Leander 2008).

Several species of the eugregarine suborder Septatorina have been reported to inhabit intestines of ladybirds (Table 8.16). Most of them have been placed in the genus *Gregarina* of the family Gregarinidae. However, recent studies by Clopton (2009) showed polyphyly of both Gregarinidae and *Gregarina*, and thus both are likely to be split in the near future.

Life cycle

The direct **transmission** of gregarines usually takes place by the host orally ingesting oocysts. Eight sporozoites emerge from each oocyst, and, using their apical complexes, attach to or invade the epithelial cells of the host. The sporozoites begin to feed and develop into larger trophozoites that subsequently detach from the epithelial cells and live freely in the lumen of the host's gut. Two mature trophozoites pair up in a process called syzygy and develop into gamonts. A gametocyst wall forms around each pair of gamonts and the gamonts begin to divide to produce hundreds of gametes through a process called gametogony. Gamete pairs fuse, form zygotes and become surrounded by an oocyst wall. The process of sporogony, involving meiotic and mitotic divisions within the oocyst, yields eight spindle-shaped sporozoites. Hundreds of oocysts are formed within each gametocyst and these are released in host faeces (Watson 1915, Leander et al. 2006, Rueckert & Leander 2008).

Table 8.16 Eugregarines reported from ladybird hosts (the numbers in brackets apply to references listed below the table).

Eugregarine	Host / region
Brustiophoridae	
Brustiospora indicola	*Stethorus* sp. / India (8)
Gregarinidae	
Anisolobus indicus	*Coccinella septempunctata* / India (5)
Gregarina barbarara	*Adalia bipunctata* / New York, USA (20), Germany (4)
	Coccinella sp. / New York, USA (22)
	Coccinella trifasciata / California, USA (11)
	Exochomus quadripustulatus / Silesia, Poland (3)[*]
	Hippodamia convergens / California, USA (11)
	Hippodamia sinuata / California, USA (11)
	Tytthaspis sedecimpunctata / Silesia, Poland (3)[*]
Gregarina californica	*Coccinella californica* / California, USA (11)
Gregarina chilocori	*Chilocorus rubidus* / Japan (16)
Gregarina coccinellae	*Coccinella quinquepunctata* / St Petersburg region, Russia (12)
	Coccinella septempunctata / Poland (10)
	Exochomus quadripustulatus / Poland (13)
	Harmonia quadripunctata / Poland (13)
	Hippodamia tredecimpunctata / Poland (10)
	Myrrha octodecimguttata / St Petersburg region, Russia (11), Poland (13)
Gregarina dasguptai	*Coccinella septempunctata* / India (14)
Gregarina fragilis	*Coccinella* sp. / Illinois, USA (22)
	Coccinella trifasciata / USA, California (11)
Gregarina hyashii	*Coccinella leonina transversalis* / India (18)
Gregarina katherina	*Aiolocaria hexaspilota* / Japan (21)
	Ceratomegilla undecimnotata / Slovakia (15)
	Coccinella californica / California, USA (11)
	Coccinella novemnotata / New York, USA (22)
	Coccinella septempunctata / Silesia, Poland (3)[†], Slovakia (15)
	Coccinella septempunctata brucki / Japan (21)
	Coccinella trifasciata / California, USA (11)
	Coccinula quatuordecimpustulata / Silesia, Poland (3)[†]
	Pharoscymnus anchorago / Mauretania (9)
Gregarina ruszkowskii	*Adalia bipunctata* / Poland (13)
	Coccinella quinquepunctata / Poland (10)
	Coccinella septempunctata / Poland (10)
	Exochomus quadripustulatus / Poland (13)
Gregarina straeleni	*Epilachna* spp. / DR Congo (20)
Undetermined eugregarines	*Adalia bipunctata* / Nova Scotia, Canada (17)[‡]
	Adalia decempunctata / France (7)
	Coccinella septempunctata / France (7)
	Henosepilachna pustulosa/ Japan (6)
	Hippodamia convergens / California, USA (1)[‡]
	Hippodamia variegata / France (7)
	Oenopia conglobata / France (7)
	Propylea quatuordecimpunctata / France (7)
	Scymnus apetzi / France (19)
	Scymnus (*Pullus*) *impexus* / Switzerland and Germany (2)

[*] According to (10), this record concerns *G. coccinellae*.

[†] According to (10), this record concerns *G. ruszkowskii*.

[‡] Possibly three different gregarine species.

References: 1, Bjornson (2008); 2, Delucchi (1954); 3, Foerster (1938); 4, Geus (1969); 5, Haldar et al. (1988); 6, Hoshide (1980); 7, Iperti (1964); 8, Kundu & Haldar (1981); 9, Laudeho et al. (1969); 10, Lipa (1967); 11, Lipa (1968b); 12, Lipa & Semyanov (1967); 13, Lipa et al. (1975); 14, Mandal et al. (1986); 15, Matis & Valigurova (2000); 16, Obata (1953), cited in Laudeho et al. 1969; 17, Saito & Bjornson (2008); 18, Sengupta & Haldar (1996); 19, Sezer (1969), cited in Laudeho et al. 1969; 20, Theodorides & Jolivet (1959), cited in Laudeho et al. 1969; 21, Tsugawa (1951); 22, Watson (1915); 23, Watson (1916).

Prevalence

Gregarine diseases seem to be more common in regions with warm climates than in colder ones. The prevalence of *Gregarina katherina* in coccinellids occupying palm groves in Mauretania was high: the proportion of infected adult *Pharoscymnus anchorago* fluctuated between 50 and 100% during the year, and two introduced coccinellids (*Chil. bipustulatus* and *Chil. stigma*) were infected to a similarly high degree. No eugregarines, however, were found in *Chil. distigma* (Laudeho et al. 1969). Iperti (1964) reported that five aphidophagous coccinellids in southeastern France harboured eugregarines, and one of them, *P. quatuordecimpunctata*, at a prevalence of about 10%. Lipa and Semyanov (1967) observed only a few per cent of *C. quinquepunctata* and *Myrrha octodecimguttata* infected by *G. coccinellae* in the St Petersburg region of Russia. Similarly low prevalences of *G. coccinellae* and *G. ruszkowskii* were recorded in four ladybird species in Poland (Lipa et al. 1975). Bjornson (2008) has examined the prevalence of eugregarines in commercially available *Hip. convergens* that were collected from their overwintering sites in California. Although only 0.2% of the beeetles were found to be infected, the eugregarines involved probably belonged to three different species, and none of them were similar in size to *Gregarina barbarara*, the only eugregarine reported from *Hip. convergens*.

Effects on hosts

Eugregarines developing in Coccinellidae are considered to be weak pathogens that destroy intestinal cells in coccinellid larvae and adults and derive nourishment from their digestive tracts (Ceryngier & Hodek 1996). However, Laudeho et al. (1969) reported that gregarine infection could cause reduced fecundity and longevity of *P. anchorago* and, in heavily infected individuals, the gametocysts could even cause death by blocking the intestinal tract.

8.4.5 Bacteria

8.4.5.1 General pathogenic bacteria

With the exception of one group of bacteria with a particularly interesting life cycle, rather little is known about the bacterial diseases of coccinellids. Those with experience of culturing coccinellids in the laboratory may have observed mortality in stocks that are not hygienically maintained, with larvae showing symptoms of enteric disease characteristic of bacterial or viral infections of the gut. However, there are only a few empirical studies of bacterial pathogens in coccinellids, and little detail on effects in natural populations. In the quest to find biological methods of controlling some phytophagous Epilachninae, which act as crop pests, a number of authors have found evidence of susceptibility to bacteria. A Chinese strain of *Bacillus thuringiensis* was found to be harmful to larvae, but not adults, of *Henosepilachna vigintioctomaculata* (Ping et al. 2008); and Pena et al. (2006) reported insecticidal activity of a Mexican strain of *B. thuringiensis* against *E. varivestis*. Otsu et al. (2003) found that a chitinase secreting strain of the bacterium *Alcaligenes paradoxus* inhibited feeding and oviposition by *H. vigintioctopunctata* adults, but had no effects on longevity. Rather less is known of the effects of such bacteria on entomophagous species, although Giroux et al. (1994) found no lethal effects of the commercial M-one strain of *B. thuringiensis* on *Col. maculata lengi*.

8.4.5.2 Male-killing bacteria

Most studies of bacterial infections of Coccinellidae concern the male-killing bacteria (Majerus & Hurst 1997). The first observation of a female-biased sex ratio in a coccinellid was reported by Lusis (1947), who noted that some female *A. bipunctata* produced only or predominantly female progeny, and that this trait was maternally inherited. 'Abnormal sex ratios' were also later observed in *Har. axyridis* (Matsuka et al. 1975) and *Menochilus sexmaculatus* (Niijima & Nakajima 1981). Hurst et al. (1992) reported similar findings from a British sample of *A. bipunctata*, and postulated the causative agent of the 'sex ratio' trait to be a cytoplasmically inherited bacterium which kills males, since normal sex ratios were obtained after oral administration of tetracycline to affected females. The male-killing bacterium was later identified as a *Rickettsia* (Werren et al. 1994).

Diversity of male-killing bacteria in the Coccinellidae

Since this first discovery in *A. bipunctata*, male-killing bacteria have now been identified in 13 other coccinellid host species, and are suspected to occur in five others (Table 8.17). Bacteria of five different groups have been identified as male-killers of coccinellids (*Rickettsia*, *Wolbachia*, *Spiroplasma*, Flavobacteria and γ-proteobacteria), suggesting that male-killing has evolved independently many times. Given the still small

Table 8.17 Male–killing bacteria in the Coccinellidae (adapted from Majerus 2006).

Host species	Countries	Agent	Prevalence	Evidence*	References
Adalia bipunctata	England, Scotland, Holland, Denmark, Luxembourg, Belgium, France, Germany, Poland, Russia, Kyrgyzstan, Norway	*Rickettsia*	0.01–0.23	f-bsr, lhr, mi, as, hs, m, sDNA, PCR	Hurst et al. (1992, 1999a); Werren et al. (1994); Majerus et al. (2000b); Schulenburg (2000); Zakharov & Shaikevich (2001); Tinsley (2003)
Adalia bipunctata	Germany, Russia, Sweden	*Spiroplasma* (Group VI)	0.03–0.53	f-bsr, lhr, mi, as, hs, m, sDNA, PCR	Hurst et al. (1999a); Majerus et al. (2000b); Tinsley (2003)
Adalia bipunctata	Russia, Sweden	Two strains of *Wolbachia*	0.02–0.1	f-bsr, lhr, mi, as, hs, m, sDNA, PCR	Hurst et al. (1999c); Majerus et al. (2000b)
Adalia decempunctata	Germany, England	*Rickettsia*	0.09	f-bsr, lhr, mi, as, hs, m, sDNA, PCR	Schulenburg et al. (2001); Majerus (2003)
Anisosticta novemdecimpunctata	England	*Spiroplasma* (Group VI)	0.31	f-bsr, lhr, mi, as, sDNA, PCR	Tinsley & Majerus (2006)
Calvia quatuordecimguttata	England, Canada	Unknown	<0.05	f-bsr, lhr, mi	Majerus (2003)
Coccidula rufa	Germany	*Rickettsia*	0.59	f-bsr, PCR	Weinert et al. (2007)
Coccidula rufa	Germany	*Wolbachia*	0.78	f-bsr, PCR	Weinert et al. (2007)
Coccinella septempunctata	England Germany	Unknown	<0.01	f-bsr, lhr	J. J. Sloggett, unpublished
Coccinella septempunctata brucki	Japan	Unknown	0.13	f-bsr, lhr, mi	M. E. N. Majerus, unpublished
Coccinella undecimpunctata	Egypt	*Wolbachia*	0.5	f-bsr, lhr, mi, sDNA, PCR	Elnagdy (2008)
Coccinula crotchi	Japan	Flavobacterium	0.23	f-bsr, lhr, mi, as, sDNA, PCR	M. E. N. Majerus, unpublished
Coccinula sinensis	Japan	Flavobacterium	0.23	f-bsr, lhr, mi, as, PCR	Majerus & Majerus (2000)
Coleomegilla maculata	USA	Flavobacterium	0.23	f-bsr, lhr, mi, as, sDNA, PCR	Hurst et al. (1996, 1997b)
Harmonia axyridis	Japan, Russia, South Korea	*Spiroplasma* (Group VI)	0.02–0.86	f-bsr, lhr, mi, as, hs, m, sDNA, PCR	Matsuka et al. (1975); Majerus et al. (1998, 1999); Majerus (2001, 2003)

Table 8.17 (*Continued*)

Host species	Countries	Agent	Prevalence	Evidence*	References
Harmonia quadripunctata	France	Flavobacterium	0.11	f-bsr, lhr, mi, as, sDNA, PCR	M. E. N. Majerus & M. C. Tinsley, unpublished
Hippodamia quinquesignata	USA	Unknown	Unknown	f-bsr, lhr, mi	Shull (1948)
Hippodamia variegata	Turkey, England	Flavobacterium	0.07–0.13	f-bsr, lhr, mi, as, sDNA, PCR	Hurst et al. (1999b)
Menochilus sexmaculatus	Japan	γ–proteobacterium	0.13	f-bsr, lhr, mi, as, PCR	Majerus (2001, 2003)
Mulsantina picta	USA	Unknown	Unknown	f-bsr, mi	J. J. Sloggett, unpublished
Propylea japonica	Japan	*Rickettsia*	0.07–0.26	f-bsr, lhr, mi, as, PCR	Majerus (2001, 2003)
Rhyzobius litura	Germany	*Rickettsia*	0.84	f-bsr, PCR	Weinert et al. (2007)
Rhyzobius litura	Germany	*Wolbachia*	0.89	f-bsr, PCR	Weinert et al. (2007)

*Evidence given as: f-bsr, female biased sex ratio; lhr, low egg hatch rate in infected lines; mi, maternal inheritence; as, antibiotic sensitive; hs, heat sensitive; m, microscopy; sDNA, DNA sequencing; PCR, detection of symbiont using symbiont–specific PCR reaction.

number of coccinellid species in which male-killing has been sought and identified, it is unlikely that the full taxonomic diversity of male-killers in coccinellids has yet been revealed (Weinert et al. 2007).

Evolutionary rationale of male-killing in the Coccinellidae

For cytoplasmic symbionts, the existence within a male is an evolutionary 'dead-end', since there is no opportunity for vertical transmission to the next generation. Instead, such symbionts may increase their fitness indirectly by killing male hosts and in doing so preferentially favour female hosts, which carry clonally identical copies of themselves. In coccinellids, this is achieved by causing death early in male embryonic development, and thereby 'reallocating' resources that would have been used by males to their female siblings (Hurst 1991, Majerus 2003). **Resource reallocation** in coccinellids comes in two forms. First, infected females suffer less from competition than they would when growing up with male siblings. In addition, upon hatching, they are able to consume the dead embryos of their brothers, which provide a substantial nutritional advantage.

Majerus and Hurst (1997) identified a number of behavioural and ecological **properties of aphidophagous coccinellids** that make this group particularly prone to male-killer infection. First, aphidophagous coccinellids lay their eggs in clutches, meaning that the likelihood of fitness compensation accruing to hosts harbouring the same male-killer is high. Secondly, populations of their aphid prey are highly unstable in space and time. And finally, coccinellids are highly cannibalistic and indulge in sibling egg consumption (Majerus & Majerus 1997b). **Cannibalistic behaviour** (5.2.8) is of particular relevance in male-killer infected clutches, in which half of the eggs will fail to develop as they are male. Daughters of infected females gain a significant survival advantage by feeding upon the unused soma and dead embryos of their brothers since, on average, each female larva has one dead egg to feed on before dispersal from the clutch (Fig. 8.10), giving significant increase in larval survival time.

Evolutionary dynamics of male-killing in the Coccinellidae

In considering the dynamics of early male-killers, Hurst (1991) and Hurst et al. (1997c) showed that

Figure 8.10 A clutch of *Adalia bipunctata* eggs and young larvae in which only half the offspring have hatched, due to the action of a male-killing *Rickettsia* (Photo: Remy Poland). (See colour plate.)

three parameters affect the spread of a male-killer in a host population. These are: the level of fitness compensation accrued to infected females (to offset the cost of male losses), the vertical transmission efficiency of the male-killer, and any direct cost that infection imposes on infected females.

In coccinellids **fitness compensation** results chiefly from resource reallocation to sisters through consumption of the dead males, the relative level of which will depend largely on the availability of prey. However, the vertical transmission efficiency and direct costs of male-killers vary as a result of interactions between different male-killers and their various hosts. In most species, **vertical transmission** is not 100%. Values obtained from laboratory cultures vary from 72% for a *Rickettsia* from a Russian population of *A. bipunctata* (Majerus et al. 2000) to 99.98% for a *Spiroplasma* from a Japanese population of *Har. axyridis* (Majerus et al. 1999).

The **cost to females of bearing a male-killing bacterium**, in addition to the loss of male progeny, has been assessed in five species of coccinellid (Matsuka et al. 1975, Hurst et al. 1994, Hurst et al. 1999b, Majerus 2001). Each case has shown some negative fitness effects, such as decreased oviposition rates, lower overall fecundity, higher infertility levels or shorter adult life-span.

Adalia bipunctata is a particularly interesting species in which to study male-killing, as it has been shown to be host to four different male-killers (a *Rickettsia*, two *Wolbachia*s and a *Spiroplasma*), with all four occurring together within a single sample from Moscow (Majerus et al. 2000). Weinert et al. (2007) provide evidence for the co-infection of German *Rhyzobius litura* and *Coccidula rufa* populations with both *Rickettsia* and *Wolbachia.* Theoretical models of the evolution of male-killing suggest that two or more male-killers cannot coexist in a single host population at equilibrium, except in the presence of male-killer suppressors (Randerson et al. 2000).

A recent study has demonstrated that the vertical transmission of a γ-proteobacterium to *Menochilus sexmaculatus* is influenced by the male; the prevalence of the male-killing trait varies depending on the male a female has mated with (Majerus & Majerus 2010). Further analysis demonstrated that a single dominant allele (rescue gene) functions to rescue male progeny of infected females from the male-killing effects of this microbe (Majerus & Majerus 2010). Furthermore, presence of the rescue gene in either parent does not significantly affect the inheritance of the symbiont.

Evolutionary implications of male-killing in the Coccinellidae

Male-killer infection can have significant evolutionary implications on host populations, resulting both from the presence of the male-killer itself, and the female-biased population sex ratios that it produces. Since both male-killing bacteria and host mitochondria are maternally inherited, an invading male-killer will be in linkage disequilibrium with the mitotype of the first host that it invades. Johnstone & Hurst (1996) described how the invasion of a male-killer can cause mitotype selective sweeps in the host population. This will be the case when the population is host to a single male-killer. For populations co-infected with more than one male-killer, mitochondrial polymorphism would be expected. Indeed, Jiggins & Tinsley (2005) have linked an ancient mitochondrial polymorphism in *A. bipunctata* to the presence of multiple *Rickettsia* strains. The association between male-killers and host mitotypes should be remembered by those working on coccinellid population genetics and phylogenetics, since mtDNA sequences are likely to show significant deviations from neutrality (Chapter 2).

The maternal inheritance of male-killing bacteria means that they are in direct conflict with the rest of the host genome. Since most nuclear genes are biparentally inherited, they will be under selection to resist

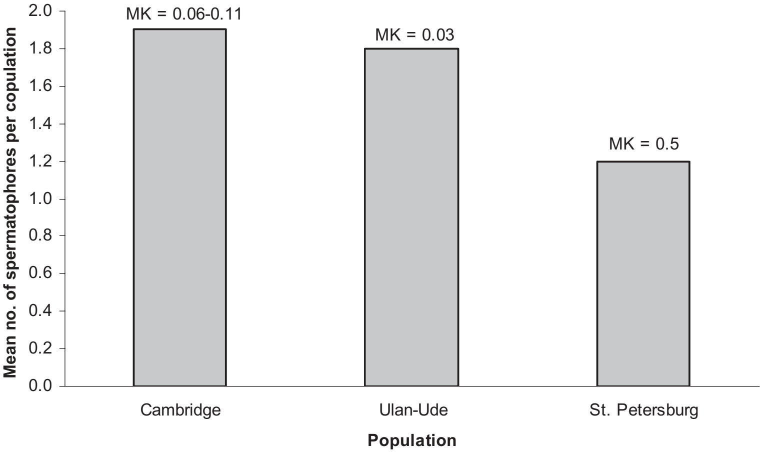

Figure 8.11 Number of spermatophores produced per copulation by male *Adalia bipunctata* from three populations (Cambridge, UK; Ulan Ude, Russia; and St. Petersburg, Russia). Male-killer prevalences (MK) of each population are shown above. Adapted with permission from Majerus (2003).

the mortality imposed on them by the pathological action of the male-killer. This intra-genomic conflict may lead to the evolution of suppressor systems acting against the male-killer. Majerus (2003, 2006) suggested that suppression may be achieved by killing the male-killer itself, reducing its vertical transmission efficiency or blocking its action. Unpublished data reported in Majerus (2003) indicated the presence of a male-killer rescue gene in *M. sexmaculatus* infected with a γ–proteobacterium.

It may be expected that, in populations that have a female-biased operational sex ratio due to the presence of a male-killer, the strength of selection for males to compete and females to choose will be reduced. In very strongly female-biased populations, in which males rather than females become the limiting sex, full sex role reversal may result. Reduction or reversal of sexual selection may be manifest in a number of ways. These effects have been most comprehensively studied in the *Wolbachia*-infected butterfly *Acraea encedon* (Jiggins et al. 1999), and limited published data is available for coccinellids. However, some interesting effects on female mating preferences have been documented in some species. Osawa & Nishida (1992) reported varying levels of female choice in Japanese populations of *Har. axyridis*, and it has been suggested that this is correlated with the presence of male-killing *Spiroplasma* (Majerus 2006).

A female-bias in the operational sex ratio may select for males to invest less in each mating than they would when the sexes are closer to parity. This has been demonstrated in *A. bipunctata*, in which males insert variable numbers of spermatophores during copulation. Majerus (2003) found that males from a strongly female-biased population were observed to pass significantly fewer spermatophores per copulation than those from less female-biased populations (Fig. 8.11).

Finally, female-biased sex ratios can affect the way in which sexually transmitted diseases spread through the host population. Coccinellids are highly promiscuous and so the rate of spread of a sexually transmitted disease will be increased in populations exhibiting a sex ratio bias. An association between prevalence of the sexually transmitted mite *C. hippodamiae* and male-killer prevalence has been documented in Scandinavian *A. bipunctata* populations (Tinsley 2003). Further investigation into the association between male-killer infection and sexually transmitted diseases is warranted.

8.5 IMPACT OF NATURAL ENEMIES ON LADYBIRD POPULATIONS

In the last part of the chapter we discuss the role of natural enemies in influencing numerical changes in the populations of phytophagous and predatory ladybirds.

8.5.1 Impact on phytophagous Coccinellidae

There are several field studies investigating the causes of **mortality of juvenile epilachnine** ladybirds by means of life table construction and key factor analysis. Some of these studies were performed in the tropical regions of Sumatra (Indonesia) (latitude 1° S) (Abbas & Nakamura 1985, Nakamura et al. 1988, Inoue et al. 1993) and Ethiopia (7° N) (Beyene et al. 2007), and others from the temperate Japanese islands Honshu (35–36° N) (Nakamura 1976, 1987, Nakamura & Ohgushi 1981, Shirai 1987, 1988) and Hokkaido (43° N) (Kimura & Katakura 1986). The most striking difference between the mortality factors affecting tropical and temperate epilachnines concerns parasitoids. Tropical ladybirds suffered high mortality from egg parasitoids (Tetrastichinae in Sumatra and *Ooencyrtus camerounensis* in Ethiopia) but egg parasitoids were entirely absent from temperate regions (Fig. 8.12a). Similarly, larval and pupal parasitoids, although present in tropical and temperate zones, tended to exert a much stronger effect on host populations in the tropics than in temperate regions (Fig. 8.12 b, c).

Quantification of the impact of predators is more difficult than that of parasitoids. Two phenomena, inter- and intraspecific predation (cannibalism), are usually indistinguishable and categories such as 'disappearance' or 'unknown causes' are frequently found among mortality factors in the life tables. In Fig. 8.12d–f, the maximum possible rates of predation on tropical and temperate Epilachninae are juxtaposed. In calculating these rates, we combined rates of intra- and interspecific predation, and assumed that every individual that 'disappeared' had been consumed. Although differences between tropical and temperate populations were not very clear, maximum predation rates for eggs and larvae of temperate ladybirds tended to be quite high (Fig. 8.12d and e). Indeed, the role of predators, especially an earwig, *Anechura harmandi*, in reducing the numbers of eggs and larvae of *Henosepilachna* spp. is often emphasized in Japanese studies (Nakamura & Ohgushi 1981, Nakamura 1983, Kimura & Katakura 1986, Ohgushi 1986, Shirai 1987).

Depletion of food resources due to feeding of epilachnine larvae is often reported in the tropics (Abbas & Nakamura 1985, Nakamura et al. 1988, Inoue et al. 1993), but also in temperate regions (Nakamura 1976, 1983, 1987, Kimura & Katakura 1986), indicating inability of natural enemies to regulate herbivore populations in a density-dependent manner. However, in temperate latitudes of the Russian Far East (44° N), Kovalenko and Kuznetsov (2005) found good synchronization between population dynamics of *H. vigintioctomaculata* and its parasitoid, *N. afiss*ae, hinting at a density-dependent regulatory mechanism.

A parasitoid, *P. foveolatus*, used in classical and augmentative biological control programmes, has been found to provide an effective suppression of the populations of certain noxious Epilachninae (8.3.2.9).

Although reported **mortality of adult phytophagous Coccinellidae** during dormancy may exceed 95% (Nakamura 1983, Inoue et al. 1993), little is known about the factors responsible for this mortality.

8.5.2 Impact on predatory Coccinellidae

Japanese studies on the mortality of *Aiolocaria hexaspilota* (Matsura 1976) and *Har. axyridis* (Osawa 1992b, 1993), with the field data structured in the form of life tables, suggest negligible role of parasitoids and interspecific predators as mortality factors of these ladybirds. The most important impact on the numbers of **immature stages** of both species was cannibalism of eggs and larvae, and prey shortage during larval feeding. Of the three mentioned papers, only one (Osawa 1993) reported any effect of parasitoids. According to this paper, parasitism of *Har. axyridis* pupae by *Phalacrotophora* sp. in two study years accounted for 4.9% and 18.6% mortality of pupae.

On maize crops in Ontario (Canada), egg predation (without distinguishing between interspecific predation and cannibalism) was recognized as an important mortality factor of *Col. maculata*. By conducting daily observations of selected egg clusters, Wright & Laing (1982) found the predation rate of eggs to be 45% in one year and 49% in another.

The majority of available data do not allow reliable estimation of the regulatory effects of enemies on the populations of predatory ladybirds. However, high

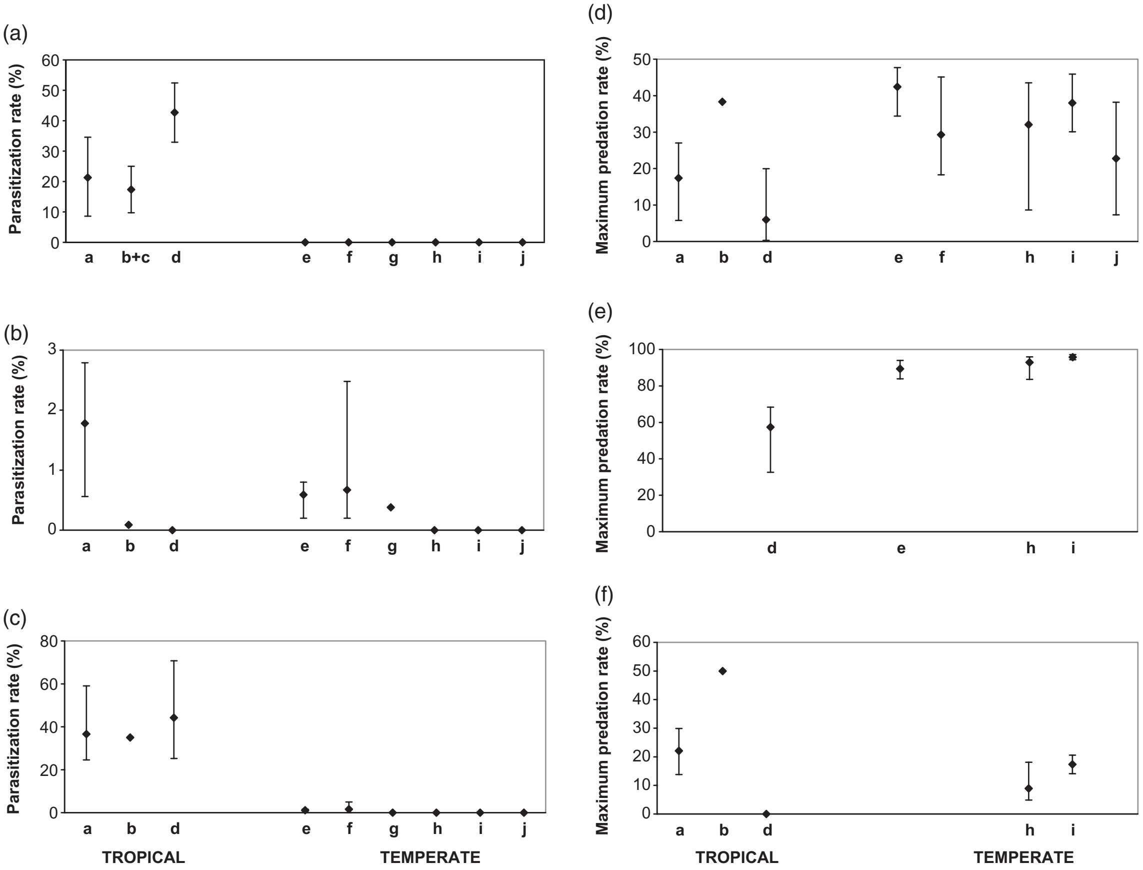

Figure 8.12 Impact of parasitoids and predators on immature stages of various Epilachninae species in tropical and temperate regions (square, mean value; bar, recorded range).
(a) Parasitization of eggs; (b) proportion of hatched larvae dying from parasitoids during larval development; (c) proportion of pupae dying from parasitoids; (d) maximum predation rates of eggs; (e) maximum predation rates of larvae; (f) maximum predation rates of pupae.
Maximum predation rate equals pooled rates of recorded predation (incl. cannibalism) and 'disappearance'.
a, *Henosepilachna septima* on Sumatra (latitude 1ºS) (after Abbas & Nakamura 1985).
b and c, *Henosepilachna vigintioctopunctata* on Sumatra (1ºS) (after Nakamura et al. 1988 (b) and Inoue et al. 1993 (c)).
d, *Chnootriba similis* in Ethiopia (7ºN) (after Beyene et al. 2007).
e, *Henosepilachna pustulosa* on Honshu (35ºN) (after Nakamura & Ohgushi 1981).
f, *Henosepilachna vigintioctopunctata* on Honshu (35ºN) (after Nakamura 1976).
g, *Henosepilachna vigintioctomaculata* on Honshu (36ºN) (after Nakamura 1987).
h, *Henosepilachna niponica* on Honshu (36ºN) (after Shirai 1987).
i, *Henosepilachna yasutomii* on Honshu (36ºN) (after Shirai 1988).
j, *Henosepilachna pustulosa* on Hokkaido (43ºN) (after Kimura & Katakura 1986).

parasitization rates of larvae and pupae, recorded in many studies, especially by *Homalotylus* spp. (8.3.2.4), *Phalacrotophora* spp. (8.3.2.7) and *O. scaposus* (8.3.2.8), indicate that, in certain circumstances, larval and pupal parasitoids may be important mortality factors.

Several generalisations can be made concerning parasitization of immature entomophagous Coccinellidae by hymenopterans (*Homalotylus* spp., *O. scaposus*): (i) relatively sedentary coccidophagous species tend to be parasitized to a higher degree than their more dispersive aphidophagous relatives, (ii) parasitization rates are usually higher in warmer regions than in colder ones, (iii) parasitization rates tend to increase with the progress of host population development and (iv) successive host generations tend to be more and more affected by the parasitoids. Thus, in warm regions of Morocco and southeastern Europe, larvae and pupae of late generations of coccidophagous *Chilocorus* spp. can be parasitized at rates of up to 80–95% (Rubtsov 1954, Smirnoff 1957, Murashevskaya 1969, Stathas et al. 2008).

Parasitization of predatory species by flies of the genus *Phalacrotophora* may also reach high values (around 80%), although rates of parasitization are very variable (Disney & Chazeau 1990, Disney et al. 1994, Hurst et al. 1998).

Two biotic factors are often ranked among the most important causes of mortality in **adult predatory ladybirds**: the braconid parasitoid *D. coccinellae*, and entomopathogenic fungi particularly of the genus *Beauveria*.

Parasitization rates by *D. coccinellae* are sometimes quite high, especially in overwintering ladybird populations. However, the rates of host mortality caused by parasitoid development are clearly lower than the parasitization rates. For example, parasitization rates of *C. septempunctata* recorded in early dormancy in two overwintering sites in Poland were 15 and 74%, while the rates of parasitoid emergence were only 4 and 24%, respectively (Ceryngier 2000).

Fungal pathogens are the organisms most frequently reported as responsible for high winter mortality of Coccinellidae (Iperti 1966, Lipa et al. 1975, Olszak 1986, Ceryngier 2000, Ormond et al. 2006). Evaluation of their effects on naturally overwintering ladybirds is also complex. The susceptibility of an insect to the pathogen largely depends on the condition of the host and its associated immunity. It was found that various entomopathogenic fungi may opportunistically infect moribund ladybirds, while healthy ones are resistant to their attack (Ceryngier & Hodek 1996, Ceryngier 2000).

8.5.3 Concluding note

Some data suggest that natural enemies may exert stronger and more persistent effects on the populations of phytophagous than entomophagous Coccinellidae, and, of the latter, coccidophagous species may be more affected than aphidophagous ones. This may be related to differences in the prevalent lifestyles within these groups. Riddick et al. (2009) suppose that phytophagous species, which are typically sedentary, are more easily located by natural enemies, especially parasitoids, than are more mobile predatory species. However, regardless of which group of Coccinellidae is considered, there is little evidence for top-down regulation of their populations. Further studies are needed to clarify the role that natural enemies play in population dynamics of both phytophagous and predatory ladybirds.

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