

For a long time, information on predators, parasites and pathogens attacking coccinellids accumulated more or less haphazardly, mostly in a form of faunistic communications. In fact, a study of biology was undertaken only for the parasite *Perilitus coccinellae*. Only during the last 15 years have the natural enemies of coccinellids become a subject of systematic study on a wider scale. Because of this it is now possible to present preliminary ideas about the effectiveness of the enemies of coccinellids, which in some cases appears great and considerably endangers the beneficial activity of these important entomophagous insects.

Because detailed studies are really only just beginning, and because their regional distribution is rather disjointed (Italy — Domenichini, south-eastern France and north-western Africa — Iperti, the surroundings of Leningrad (USSR) — Semyanov and Lipa, central Europe — Klausnitzer and Fukuoka region of Japan — Maeta) a survey of the accumulated knowledge cannot yet provide a complete picture of the enemies of coccinellids. Many more systematic studies in more regions are needed in this field.

8.1 Ants

Several species of ants attend honeydew producing *Homoptera*. Aphids are often associated with *Lasius* and *Formica spp.*, coccids with *Iridomyrmex humilis* and *Oecophylla spp.* The observations and experiments of many authors that the attending ants are hostile to enemies (including *Coccinellidae*) of attended aphids or coccids have been summarized by Nixon (1951) and particularly by Way (1963)¹). Nixon supposed that the ants do not protect the *Homoptera* actively as a source of food, but merely incidentally, since they attack swift or erratic moving organisms.

Way (1963) considers this view to be an oversimplification; ants may attack other insects at various instances. (1) Predatory ants attacking most insects, which they discover within their foraging territories, protect the attended *Homoptera* incidentally from natural enemies. This is in concert with Nixon's concept. (2) The ants, however, attack other insects also if they intrude on the nest or on food sources which the ant is monopolizing. They are then aggressive towards intruders which, away from the food source, would be tolerated. Thus, *Lasius niger* workers were not hostile to coccinellid adults which they met away from attended aphids. When food is scarce, the aggressiveness of ants at the food source and hence their protection of *Homoptera* is enhanced.

¹) The reader is referred to this review for the quotations of original papers.

Thus, the protection given by ants to *Homoptera* is related to their value as a food source. Moreover, the attendant workers of predatory ant species are too young to behave as predators and yet protect actively their brood and *Homoptera* from intruders.

An exceptional case is that of the **myrmecophilous** *Coccinella divaricata* which is associated with *Formica* spp. This coccinellid is not attacked although ants do react to its movement by tapping it with their antennae (Pontin 1960). This author supposed that *Platynaspis luteorubra* is also myrmecophilous; he found one larva of this species in underground galleries of *Lasius niger*. The shape of the larva (Pl. XXXIV), untypical of other coccinellid species resembles the shape of other myrmecophiles, e. g. of *Lycaenids* and *Microdon* (*Syrphidae*).

8.2 Predators of Coccinellidae and coccinellid defense mechanism

There have been numerous reports of predation by both arthropods and vertebrates on *Coccinellidae*. Older observations are listed in the survey by Schilder and Schilder (1928).

Coccinellids which are disturbed fall into thanatosis (a stupor, during which the legs and antennae are pressed closely into depressions on the abdomen) and exude a yellowish fluid from the femorotibial articulations ("reflex bleeding"). This phenomenon is also known in other insects (Heikertinger 1932, Rothschild 1961). The bitter taste and quinolene-like smell (Rothschild 1961) of the secretion has been regarded as protecting the coccinellids against their vertebrate and insect predators. This view has been strongly opposed by Heikertinger (1932) who succeeded in feeding coccinellids to several vertebrate and insect predators. Frazer and Rothschild (1960) and Lane and Rothschild (1960), however, found experimentally that coccinellids were unacceptable to some predators (6 species of mammals, 6 species of birds, several lizards and terrapins and one toad). Gas chromatography showed (Rothschild 1961) that the secretion of coccinellids is similar to that of certain insects generally rejected by predators and even to the exudation of nettles (*Urtica dioica*).

Relevant to the discussion as to whether defence mechanisms do or do not exist in coccinellids (i. e. whether the special taste and smell have protective value) is the theory that coccinellids show aposematic Müllerian mimicry. This theory has been rejected by Heikertinger (1932), but stressed by Rothschild (1961).

Several authors express a strong belief that some of the predators have a great impact on population change in coccinellids and in the case of spiders and birds as predators this is very likely so. However, no tangible evidence has as yet been published. This is a dangerous shortcoming, which limits the value both of the utilization of *Coccinellidae* and of all evaluations and prognoses of their impact.

8.3 Parasites

The recorded insect parasites of coccinellids belong to 3 genera of *Diptera* (*Phalacrotophora*, *Degeeria*, *Hyalomyodes*) and 6 genera of *Hymenoptera* (*Perilitus*, *Centistes*, *Metastenus*, *Pachyneuron*, *Tetrastichus*, *Homalotylus*). In principle, they attack only larvae, pupae and adults of coccinellids, and there exist only two records of egg parasites.

Ooencyrtus johnsoni from North America (Peck 1963) and *Tetrastichus ovulorum*, parasitizing eggs of various *Epilachna* spp. (Schmidt 1954). Although 7 species of *Ooencyrtus* are known in central Europe, Klausnitzer (1969b) failed to rear a single parasite from 5000 coccinellid eggs collected in the field. He supposes that the adaptation of egg parasites to coccinellids may have been impeded by the circumstance that coccinellid larvae soon after hatching eat yet unhatched eggs of the same batch. It is indeed known that the egg parasites emerge from parasitized eggs mostly after the larvae have hatched from nonparasitized eggs.

8.31 Diptera

Phalacrotophora spp. (Phoridae)

Two species are known of this gregarious endoparasite of larvae and pupae of European coccinellids. The adults may be determined according to Colyer (1952):

- 1 (2) Posterior metatarsae very dark and considerably broadened, especially in females. *fasciata* Fallen
- 2 (1) Posterior metatarsae yellowish white and of normal shape. *berolinensis* Schmitz.

What follows refers to *P. fasciata*, which is nearly always the species mentioned.

This species is reported by many authors as parasitizing a number of coccinellid species in the tribes *Chilocorini*, *Hippodamiini*, *Coccinellini* and *Psylloborini*; these reports are listed by Klausnitzer (1969b). A single pupa of *Coccinella septempunctata* may contain as many as 7 parasites, a pupa of *Adonia variegata* as many as 4 (Iperti 1964), that of *Adalia bipunctata* an average of 2, and that of *Anatis ocellata* an average of 8.4 (Klausnitzer 1969b). Maeta (1969b) found averages of 4 and 5 (range 2—7) parasites per host in *Harmonia axyridis* over two years in Japan (Nagano region). Clausen (1940) reports 8—14 parasites per single specimen of the genus *Coccinella*.

Life cycle. — In central Europe the development of a 2nd generation is possible (Klausnitzer 1969b). If *C. septempunctata* is used as a host, the total development time of the parasite from egg to adult emergence amounts to 30 days in May and to about 25 days in June in southeastern France. In pupae of *A. variegata*, development time is shortened by 5—6 days (Iperti 1964).

If the adults are reared on an artificial diet based on sugar, agar, honey and water, they mature sexually in 15 days. Each ovary contains only one egg (Iperti 1964). The eggs are laid on prepupae or freshly moulted pupae between the legs. Embryonic development is already advanced by the time the egg is laid, so that the larva hatches in a few hours and immediately bores into the host at the base of its leg.

Percentage parasitization. — In southeastern France, Iperti (1964) found by dissection of pupae of *C. septempunctata* that 9.1 % were parasitized in the region of Antibes in June 1961, whereas round Giens the figure was 6 % in May 1961 and 2.5 % in June 1962. In contrast, *A. variegata* was much more heavily parasitized: 26.6 % in July 1962 round Digne. In central Europe, Klausnitzer (1969b) reared 90 *P. berolinensis* from 1111 pupae (several parasites may emerge from one pupa) of *A. bipunctata*, and of 212 pupae of *A. ocellata* 14 (= 6.6 %) were parasitized. Clausen (1940) reports parasitization as high as 48 % of coccinellids of the genus *Adalia* by this dipteran. In Japan (Nagano region) the parasitization of *Harmonia axyridis* ranged between 7 and 18 % (Maeta 1969b).

Degeeria luctuosa (Tachinidae)

This endomonoparasite of adult *Coleoptera* has only been recorded from 5 species of coccinellids. Banks (1956) and Walker (1962) report two isolated cases from *Adalia decempunctata* in England. In south-eastern France Iperti (1964 and unpubl.) recorded this parasite mainly on *Adalia bipunctata* and *Synharmonia conglobata*. *Propylaea quatuordecimpunctata* had a low parasitization (0.75 — 3.5 %) in summer. Hibernating *Synharmonia conglobata* were rather more attacked in the region of Bautzen, G. D. R.: dissection of 209 specimens, collected in November 1965, revealed larvae of *Degeeria* in 8 males and 21 females (13.9 %). When breeding 226 hibernating coccinellids collected in March and April 1966, Klausnitzer (1969a) found only 14 (6.2 %) puparia of *Degeeria*. Klausnitzer (1969b) only obtained 3 puparia from 567 coccinellids of 15 species collected near the end of hibernation near Dresden and Tharandt: 2 from *Exochomus quadripustulatus* and 1 from *Myrrha octodecimguttata*.

A single larva of the parasite develops in the body cavity of the coccinellid. In the third and last larval stage, the parasite consumes all fundamental organs of the coccinellid; it finally escapes through the dorso-abdominal wall of the beetle and pupates in the soil. The adult already emerges after a week. Adult parasites emerged from both parasitized specimens of *Adalia decempunctata* found in England, whereas emergence failed to occur from puparia obtained from *Propylaea quatuordecimpunctata* in France (Iperti 1964). Domenichini (1953) describes the larval stages.

Hyalomyodes triangulifera (Tachinidae)

This parasite was reared by Howard and Landis (1936) and Smith (1960) from adults of *Coleomegilla maculata*. Smith (1960) records this parasite also from *Coccinella trifasciata perplexa*.

Pericheta unicolor (Tachinidae)

was found in May and June on *Subcoccinella vigintiquatuor punctata* (Iperti unpubl.).

8.32 Hymenoptera

Perilitus coccinellae (Braconidae, Euphorinae)

The subfamily *Euphorinae* includes a group of endoparasites of adult *Coleoptera* of which those belonging to the genus *Perilitus* parasitize *Coccinellidae* and *Curculionidae*. Domenichini (1956) records two species which are exclusive parasites of coccinellids in the subfamily *Coccinellinae*: *Perilitus stuardoi*, parasitizing *Scymnini* and *Coccinellini* in South America; and the cosmopolitan *P. coccinellae*, parasitizing coccinellids in the tribes *Coelophorini*, *Hippodamiini* and *Coccinellini*.

Both are solitary endoparasites (endomonoparasites) of adult coccinellids. *P. coccinellae* is by far the best studied of all parasites. Not only have a fair number of studies been devoted to its biology, from classical works by Ogloblin (1913) and Balduf (1926) to recent studies from France (Iperti 1964), central Europe (Klausnitzer 1969b) and from Japan (Maeta 1969a), but also the changes caused by the parasite larva in the body of the coccinellid have been studied in detail (Ogloblin 1924, Sluss 1968).

Host range. — The list presented in table 8.01 shows a very wide range of hosts within the three coccinellid tribes mentioned above.

However, the table also shows that the parasite has a distinct preference for certain coccinellid species. *Coleomegilla maculata* is most frequently attacked in the USA (Balduf 1926, Smith 1960), *Coccinella septempunctata* in Europe (Walker 1962, Iperti

Tab. 8.01 Hosts of *Perilitus coccinellae*

Host species	Region	References
<i>Adalia bipunctata</i> (?)	Europe	Telenga 1948
<i>Adonia variegata</i>	Europe, China	Ogloblin 1913, Liu 1944 (2), 1950, Telenga 1948, Walker 1961, Ipert 1964
<i>Coccinella divaricata (distincta)</i>	Europe	Sem'yanov and Lipa 1967 (5)
<i>Coccinella novemnotata</i>	USA, Canada	Riley 1888 (1), Folsom 1909 (1), Hudon 1959 (3)
<i>Coccinella quinquepunctata</i>	Europe	Walker 1961, Sem'yanov and Lipa 1967 (5), Klausnitzer 1969b
<i>Coccinella repanda</i>	Formosa	Sonan 1939 (2)
<i>Coccinella sanguinea</i>	USA	Balduf 1926
<i>Coccinella septempunctata</i>	Europe, China	Ogloblin 1913, Goriainov 1917 (1), Tullgren 1916 (1), Sonan 1939 (2), Liu 1944 (2), Bryden and Bishop 1945, Telenga 1948, Cavalloro 1949, Liu 1950, Walker 1961, Ipert 1964, Sem'yanov and Lipa 1967, Klausnitzer 1969b
<i>Coccinella septempunctata bruckii</i>	Japan	Koide 1961 (4), Maeta 1969a
<i>Coccinella trifasciata perplexa</i>	Canada	B. C. Smith 1960b
<i>Coccinella undecimpunctata</i>	Europe	Bryden and Bishop 1945, Walker 1961
<i>Coccinella undecimpunctata aegyptiaca</i>	Egypt	Ibrahim 1955b
<i>Coleomegilla maculata</i> (= <i>Ceratomegilla fuscilabris</i>)	USA, Canada	Riley 1888 (1), Weed and Hart 1889 (1), Folsom 1909 (1), Cushman 1922 (1), Balduf 1926, Hudon 1959 (3), B. C. Smith 1960b, Timberlake 1918 (1)
<i>Coelophora inaequalis</i>	Hawaii	Timmerlake 1918 (1)
<i>Eocaria muiri</i>	Japan	Koide 1961 (4), Maeta 1969a
<i>Harmonia arcuata</i>	Formosa	Sonan 1939 (2)
<i>Harmonia axyridis</i>	China, Japan	Liu 1950, Koide 1961 (4), Maeta 1969a
<i>Harmonia quadripunctata</i>	Europe	Ipert 1964
<i>Hippodamia convergens</i>	USA	Timberlake 1916 (1), Cushman 1922 (1), Balduf 1926, Sluss 1968,
<i>Hippodamia parenthesis</i>	USA	Balduf 1926
<i>Hippodamia tredecimpunctata</i>	USA, USSR	Cutright 1924 (1), Balduf 1926, Sem'yanov and Lipa 1967
<i>Lemnia biplagiata</i>	Formosa	Sonan 1939 (2)
<i>Macronaemia hauseri</i>	China	Liu 1944 (2)
<i>Menochilus sexmaculatus</i>	Formosa, Japan	Sonan 1939, (2), Maeta 1969a
<i>Micraspis discolor</i>	Formosa	Sonan 1939 (2)
<i>Olla abdominalis</i>	USA, Hawaii	Timberlake 1918 (1)
<i>Propylaea japonica</i>	Japan	Koide 1961 (4), Maeta 1969a
<i>Propylaea quatuordecimpunctata</i>	Europe	Ogloblin 1913, Walker 1961, Ipert 1964
<i>Semiadalia undecimnotata</i>	Europe	Ipert 1964
<i>Synharmonia conglobata</i>	Europe	Ipert 1964
!! <i>Epilachninae</i>	never parasitized	Balduf 1926, Liu 1950

(1) (2) (3) (4) (5) References marked in this way are not included in the list of references in this book; they are quoted by the following authors: (1) Balduf 1926, (2) Liu 1950, (3) B. C. Smith 1960b, (4) Maeta 1969a, (5) Klausnitzer 1969b.

1964, Klausnitzer 1969b) and *Coccinella septempunctata bruckii* in Japan (Maeta 1969a). On the other hand, some coccinellid species (within the three tribes mentioned) are not parasitized by *Perilitus*, or at least the parasite does not develop in them. *Adalia bipunctata* and *A. decempunctata* apparently rank among such species, although *P. coccinellae* females readily attack the adults in experiments (Bryden and Bishop 1945,

Walker 1962, Klausnitzer 1969b). It is also very difficult, although not impossible, to obtain emergence of an adult parasite from the cocoon following parasitization of *Pro-pylaea quatuordecimpunctata* (Iperti 1964). According to Klausnitzer (1969b) the parasitization of *Anatis ocellata* is impeded by the size of this coccinellid.

Life cycle. — *Perilitus coccinellae* has thelytokous parthenogenesis (i. e. unfertilized eggs hatch, but give rise only to females). The female inserts her eggs into coccinellid adults. Only very rarely has it been demonstrated (in *Coleomegilla maculata* — Cushman 1922, Smith 1960) that parasite adults can result if eggs are laid in coccinellid larvae. The parasite has also been reported to lay eggs in pupae of *Hippodamia convergens* (Sluss 1968) and of *Coccinella septempunctata bruckii* (Maeta 1969a).

The female especially attacks moving coccinellids, pursues them in its typical posture, i. e. with the abdomen flexed to the front between the legs and the ovipositor extending slightly forward of the head. After several minutes of antennal palpating and probing with the ovipositor, an attempt to oviposit follows involving a powerful forward thrust of the ovipositor. About one-half of the attempts result in actual egg deposition (Sluss 1968). The female inserts its ovipositor in the gap between the elytra and abdominal sternites, or according to Iperti (1964), into the intersegmental seam, most often between the head and the thorax, or again according to Sluss (1968), in the coxae or in the abdomen at a ratio of about 1 : 2. The rather petiolate egg (Fig. 8.01) deposited first increases in size for about 3 days, during which period its length increases four times. The egg hatches in about 5 days, releasing the first-instar larva and the trophic cells (see chapter Response of the host to parasitism, p. 204).

In a single coccinellid, many first-instar larvae can be found (superparasitism), as many as 47 in *Coccinella septempunctata bruckii* (Maeta 1969a), but always just one single second-instar larva is eventually left. The grasping mandibles, with which first-instar larvae (but not the larvae of other instars) are equipped, apparently serve to destroy the surplus larvae (Ogloblin 1924).

The larva passes through four instars, and, as in any insect, the length of larval development depends on temperature. In south-eastern France (Iperti 1964) this takes about 12—14 days in summer, and 20—21 days in spring. Under $21^{\circ} \pm 3^{\circ} \text{C}$ in the laboratory the egg hatches in about 5 days and larval development in *Hippodamia convergens* lasts 8—9 days (Sluss 1968). The morphology and anatomy of the larva has been described in detail by Ogloblin (1913, 1924).

The adult larva escapes from the coccinellid through the membrane between the 5th and 6th (Cushman 1922) or between the 6th and 7th abdominal tergites (Sluss 1968, Maeta 1969a). The beetle does not move about half-an-hour before the escape of the parasite larvae; its body and appendages tremble and jerk at times (Balduf 1926). The emerged larva spins a cocoon on the side of the abdomen of the host. The behaviour of spinning has been described in detail by Balduf (1926), who also specified the shape and structure of the cocoon. The caudal end is broadly rounded, whereas the cephalic end is pointed, hard and thick. The wall of the cocoon has two layers: (1) the outer, loose, meshwork and loops of silk which are directly attached to (2) the inner, solid and continuous layer. The development of the pupa takes 7—9 days in southeastern France (Iperti 1964) and 5—9 days in Japan (Fukuoka) (Maeta 1969a).

After completing its development inside the pupa and after escaping from it, the adult parasite bites through the cocoon at the cephalic end by means of elongated rectangular mandibles with terminal and post-terminal teeth. It is an exacting activity which takes about 24 hr and has been described by Balduf (1926) who writes admiringly: “. . . the labor is so protracted and energetic that one marvels at the endurance of the insect”.

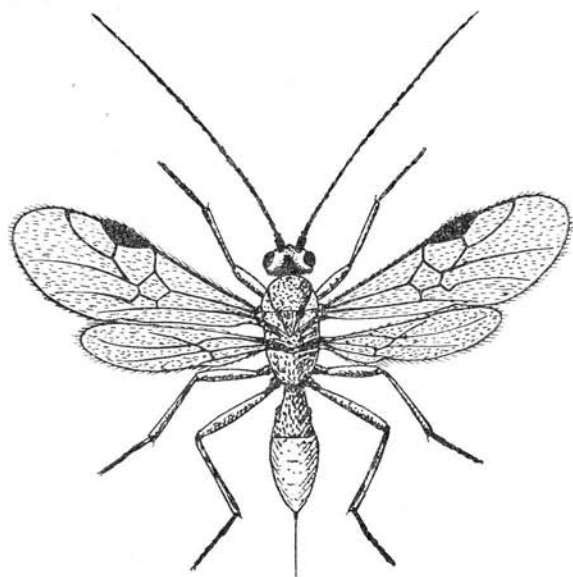
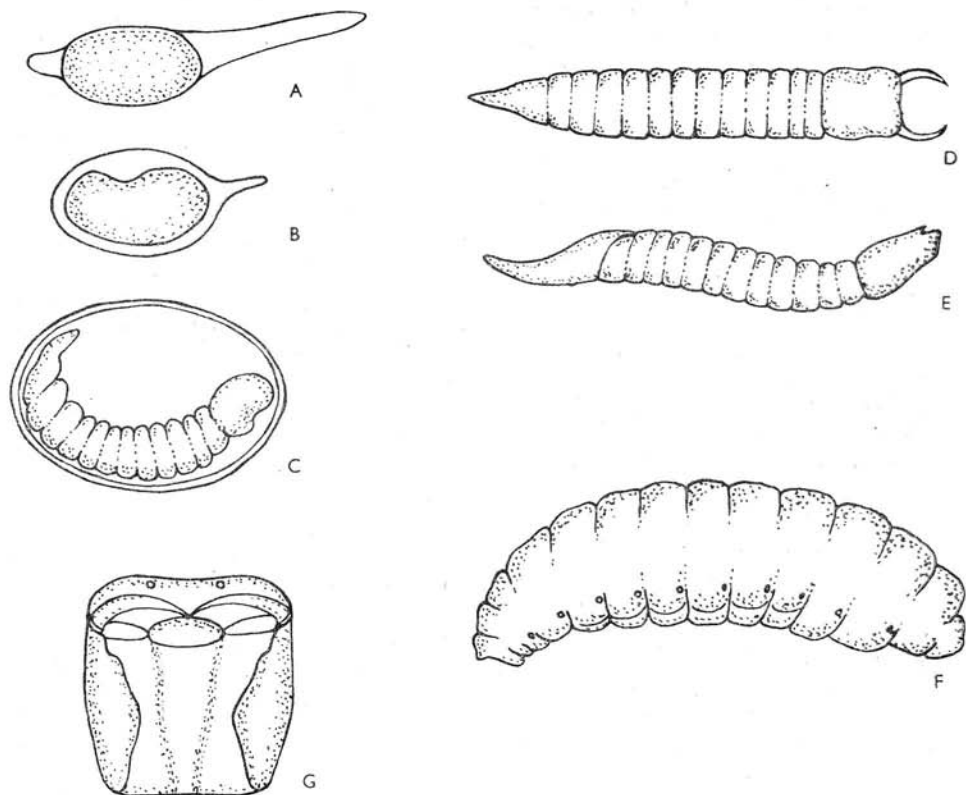


Fig. 8.01 I. Developmental stages of *Perilitus coccinellae*. A — egg newly deposited in host; B — egg aged four days; C — egg shortly before hatching; D — 1st-instar larva, dorsal view; E — lateral view; F — mature larva; G — head capsule of the 1st instar larva (the approximate relation of lengths A or G : B : C : D or E : F = 1 : 1.5 : 2 : 6 : 13).

II. Female of *Perilitus coccinellae* (del. J. Zelený).

Of the imagos, virtually only females have been recorded. In the literature there are only a few references to males. One of the references cannot be checked and the other specimen turned to be the male of another insect (Balduf 1926). When it leaves the cocoon, the female already contains ripe eggs and is able to parasitize immediately (Ogloblin 1924, Iperti 1964). The adults may live actively in the laboratory for about 5 days, if fed on honey solution and attacking coccinellids, but as long as 18 days when isolated in the dark although also fed on honey (Balduf 1926). Iperti (1964) recorded a maximum longevity of 21 days at 14 °C and 85 % relative humidity. Maeta (1969a) obtained a longevity of 2–6 days for starved adult parasites and 2–8 days for parasites fed on honey solution, apparently at normal laboratory temperatures.

Voltinism. — *Perilitus coccinellae* is a multivoltine species. Klausnitzer (1969b) reports that a second generation possibly develops in central Europe, where, according to Ogloblin (1924), there ought to be three generations. Iperti (1964) considers there are probably 3–4 generations in southeastern France. 4–5 generations are suggested for Illinois, USA, by Balduf (1926), and also for Italy by Goidanich (1943) and Cavalloro (1949). In Japan (Fukuoka), Maeta (1969a) reports the development of 3 generations of the parasite in *Coccinella septempunctata bruckii*, while the first generation of coccinellids is parasitized by the 1st and 2nd parasite generations.

The **percentage parasitization** fluctuates considerably according to regions, seasons of the year and the host. It is of doubtful value to compare data from the literature, as it is not always clear whether percentage parasitization has been ascertained by breeding — so that it is the percentage of emerged parasites (as cocoons or adults) which has been recorded — or whether the parasitization has been revealed by dissection. Moreover, some authors (Walker 1961) do not mention the total number of coccinellid individuals studied.

Balduf (1926) reports — on the basis of dissections — a range in parasitization of 1.3 — 36.0 % in *Coleomegilla maculata*, 4.0 — 21.1 % in *Hippodamia convergens* and 9.5 — 12.8 % in *H. parenthesis* (Table 8.03). According to Sluss (1968) the degree of parasitization of *H. convergens* rarely exceeds 10 % in California. In Italy, Goidanich (1943) ascertained a parasitization rate as high as 25 % for *Adonia variegata*, but usually a figure nearer 10–15 %. In Ontario, Canada, *Coccinella trifasciata perplexa* was parasitized at a rate of approximately 7 %, and *Coleomegilla maculata lengi* at 16 % (Smith 1960). Iperti's (1964) dissections of *Adonia variegata* in southeastern France in 1950–61 gave 5–25 % parasitization which is similar to the figure Goidanich gave for Italy.

Tab. 8.02 Parasitization of *Harmonia axyridis* and *Coccinella septempunctata bruckii* by *Perilitus coccinellae* in Japan (Maeta 1969a).

Host		Date of sampling		Number dissected		Percentage parasitized		Locali- lity ¹⁾
Species	Gener.	pupae	adults	♀ ♀	♂ ♂	♀ ♀	♂ ♂	
<i>H. a.</i>	1	June	—	64	65	10.9	4.6	Kurume
<i>H. a.</i>	0	—	November	106	58	0.9	1.7	Ina
<i>C. s.</i>	1	May	—	133	132	30.1	21.2	Kurume
<i>C. s.</i>	1	June	—	29	28	3.4	7.1	Ina
<i>C. s.</i>	1	—	June	33	37	18.2	3.0	Ina
<i>C. s.</i>	1	—	August — September	96	86	37.5	25.6	Kurume
<i>C. s.</i>	0	—	November, January, March	35	31	11.1	3.2	Ina

¹⁾ Kurume, Fukuoka or Ina, Nagano.

Tab. 8.03 Parasitization of *Coleomegilla maculata*, *Hippodamia convergens* and *H. parenthesis*, by *P. coccinellae* in Urbana, Illinois, USA (Balduf 1926)

Host species	Date of sampling	Number dissected	Percent parasitized	Locality
<i>C. m.</i>	March —	400	14.8	winter quarter in a woods margin
<i>C. m.</i>	April	51	36.0	winter quarter along a fence in town
<i>C. m.</i>	April	104	23.0	active near winter site
<i>C. m.</i>	August —	157	1.3	sewage disposal plant
<i>C. m.</i>	September	349	2.5	corn; West Lafayette, Ohio
<i>H. c.</i>	June	32	18.8	} various plants
<i>H. c.</i>	July — August	19	21.1	
<i>H. c.</i>	September	100	4.0	
<i>H. p.</i>	June	86	12.8	
<i>H. p.</i>	July	111	10.8	
<i>H. p.</i>	August	95	11.6	
<i>H. p.</i>	September	21	9.5	

Iperti found a higher parasitization rate in *Coccinella septempunctata* (10–27 %) and lower rates in *Semiadalia undecimnotata* and *Propylaea quatuordecimpunctata* (never > 8 %). Walker's (1962) result of 20 % parasitization of *Coccinella septempunctata* for England (Berkshire) is very similar to Iperti's figure for this species. Klausnitzer (1969b) reared 4 specimens of *Perilitus* from 1500 coccinellids collected in spring 1967 — 3 from *Coccinella septempunctata* and 1 from *Coccinella quinquepunctata*. In Japan, parasitization by *P. coccinellae* ranged between 1 and 11 % in *Harmonia axyridis*, and between 3 and 38 % in *Coccinella septempunctata bruckii* (Maeta 1969a, Tab. 8.02).

Balduf (1926) estimated that, in the area of Urbana in 1925, *Perilitus coccinellae* decreased the efficiency of coccinellids by 1/8. Iperti (1964) regards *Perilitus coccinellae* as the main parasite of migrating coccinellids (e. g. *Coccinella septempunctata* and *Semiadalia undecimnotata*). The relatively high potential fecundity (100 eggs), parthenogenesis and polyvoltinism of this parasite suggest that it could potentially be still much more effective. Its efficiency is apparently decreased mainly by superparasitism and by its preference for migrating coccinellid species which already enter diapause in summer (see chapter 7), and simultaneously cause a developmental arrest of the 1st instar parasite larvae.

Response of the host to parasitism. — Sometimes superparasitism or parasitization of a small host results in the premature death of the host. In the course of normal parasitism, the developing larva prevents the ovaries from developing (Balduf 1926). If females with ripe ovaries are parasitized, it takes some time before the developing larva of *P. coccinellae* causes ovarian regression. Parasitized females of *Coleomegilla maculata* lay fertile eggs up to 10 days before the emergence of *P. coccinellae* (Smith 1960).

On the other hand, the parasitization had no effect on mating behaviour of males until after the parasite emerged, and viable sperms were transferred to the female beetles at each mating. This fact does not in itself prove that testes had not been

affected, because viable sperm can be stored for a long time. However, no changes were indeed found in the tissue of the testes of parasitized males.

The feeding of parasitized *Hippodamia convergens* was significantly less than that of non-parasitized beetles, while there was no significant effect on respiration rate. Although the gut, muscle, nerve and other tissues were examined, only the fat body showed structural changes as a result of parasitism (Sluss 1968).

Opaque globules of various sizes, which serve as nourishment for the parasite larva, are conspicuous when parasitized coccinellids are dissected. Such globules have been described in *Coccinella septempunctata* by Ogloblin (1924) and in *H. convergens* by Sluss (1968).

When a parasite larva hatches from the egg, clumps of unseparated trophic cells are released; each clump consists of 30 to 100 cells. These cells constitute one of the embryonic membranes (Ogloblin 1924, Sluss 1968). In the literature they are designated as "trophamnion" cells, although it is not certain if they in fact originate from the amniotic membrane. Next day they divide into individual, spherical opaque cells, about 50 μ in diameter. In the course of larval development they keep growing, so that 2 days before emergence of the larva from the host body they already measure 370 μ by 440 μ . The surface of the trophic cells is covered by many microvillae. The profuse mitochondria suggest that these cells are very active metabolically. Their main function is to absorb and store nutrients from the host beetles (Sluss 1968). At first there are about 500 trophic cells (Ogloblin 1924). The strongly mandibulate first-instar larva apparently feeds directly on the fat body. The larvae of later instars eat the trophic cells (Ogloblin 1924, Sluss 1968). Most of the trophic cells present are ingested by the parasite larva during its development. The remaining few disintegrate, so that none are apparent 1 day after the parasite has emerged (Sluss 1968).

As long as the trophic cells are still small, the haemolymph distributes them into the whole body, even to the legs. They can be found even in the drop of haemolymph produced by 'reflex bleeding' at the articulation between femur and tibia (see chapter 8.2). 'Reflex bleeding' can thus be used to prove the presence of a *P. coccinellae* larva without dissecting the host (Ogloblin 1924).

After emergence of the parasite, the host coccinellid is considerably weakened and usually remains attached both to the cocoon of the parasite and to the substrate. Most observations suggest that the host coccinellid dies within the next few days (Balduf 1926: after 2–5 days, Smith 1960: within 10 days, Sluss 1968: 3–4 days). Bryden and Bishop (1945) and Walker (1962) detached parasitized individuals of *C. septempunctata* from the cocoons of *Perilitus* and fed them. The coccinellids recovered the use of their legs and appeared healthy. However, other workers who repeated these experiments found that the beetles were nevertheless so weakened by parasitization that they died within 1–2 weeks in any case (Iperti 1964, Klausnitzer 1969b). Thus death is not the result of the coccinellid's imprisonment by the cocoon fibres and starvation as Balduf (1926) had thought. Total recovery of a parasitized host has only been described by Timberlake (1918), who records the case of the large coccinellid *Olla abdominalis*. Five out of nine individuals escaped the wrapping up in connection with the cocoon: they recovered, resumed feeding and were subsequently reparasitized, one individual giving issue to a second mature larva of *Perilitus*! It is probable that the degree to which the host is damaged depends on its size.

Homalotylus spp. (Chalcidoidea, Encyrtidae)

This genus contains several species of endoparasites of the larvae and pupae of coccinellids.

According to Hoffer (1963), Graham (1969) and Klausnitzer (1969b), the nomenclature of two species, *H. flaminus* and *H. eytelweini*, is confused. The data on *H. flaminus* in the literature may partly refer to *H. eytelweini*. According to Hoffer (1963) Graham

(1969) and Klausnitzer (1969b) it is possible to distinguish the two species by the following characters:

- 1 (2) Hind tarsi white, radial vein short and curving away from the front edge of the wing. *flaminus* Dalm.
- 2 (1) Hind tarsi black, radial vein longer and not curving away from the front edge of the wing (i. e. almost parallel with it). *eytelweini* Ratzb.

Klausnitzer (1969b) thinks that *H. flaminus* is a solitary parasite of *Scymnini*, whilst *H. eytelweini* is a gregarious parasite of *Coccinellini*, *Chilocorini*, *Hippodamiini* and *Psylloborini*.

H. platynaspidis, which as yet has been reared solely as a solitary parasite from *Platynaspis luteorubra* (Hoffer 1963, Klausnitzer 1969b), is apparently monophagous.

Life cycle. — Eggs are laid in young (Rubtsov 1954) or even mature (Telenga 1948) coccinellid larvae, mostly while the host is attached to the substrate at ecdysis (Iperti 1964). After several days the parasitized larva again attaches itself to the substrate as at ecdysis, but instead of casting a skin it swells and the cuticle becomes hard and dark. The adult parasite leaves the host through a small round opening. When polyparasitism is involved, individual parasite larvae pupate in chambers separated from each other by remnants of dry host tissue and each adult makes its own opening through which it leaves the host. In larvae of the genus *Chilocorus* there usually develop 1–3 parasites (Telenga 1948, Domenichini 1956), about 3 parasites develop in *Propylaea quatuordecimpunctata* larvae, and 4–6 in older larvae of *C. septempunctata* (Iperti 1964). The adults are already sexually mature at emergence, and longevity in the laboratory is 6–11 days (Iperti 1964). In the open the adults feed on honeydew of aphids and coccids (Rubtsov 1954).

Homalotylus hibernates as a pre-nymph inside the host. In south-eastern France the parasites took as long as 97–145 days to emerge from several parasitized larvae of *Coccinella septempunctata* collected in May at an altitude of 600–1000 m (Iperti 1964).

The length of development in non-hibernating generations fluctuates with temperature during the year. Development thus takes between 25 and 45 days for *C. septempunctata* and is shorter for *Propylaea quatuordecimpunctata* (Iperti 1964). Rubtsov (1954) reports about one month. Telenga (1948) from the Ukraine SSR gives 17–19 days in summer.

Voltinism. — *Homalotylus* is polyvoltine. For south-eastern France, 5–6 generations per year are reported by Iperti (1964), 3 generations for the Black Sea coast of USSR by Rubtsov (1954) and 5 generations for the region of Krasnodar (Ukraine SSR) by Telenga (1948).

The percentage parasitization. — Parasitization by *Homalotylus* may be as high as 90–95% in *Chilocorus bipustulatus* (at the Black Sea coast — Rubtsov 1954, the same as in North Africa — Smirnoff 1957, ref. in Yinon 1969b) and as high as 100% in *Rodolia cardinalis* in India (Subramanyam 1950, ref. in Yinon 1969b). *Homalotylus* is therefore generally considered as a very significant mortality factor which limits the entomophagous efficiency of coccinellids. Other coccinellids, where *Homalotylus* has been specifically stressed as an important agent, are *C. septempunctata* and *Propylaea quatuordecimpunctata* in south-eastern France — Iperti 1964, and *Chilocorus bipustulatus* in the coastal plain of Israel — Yinon 1969b.

Hyperparasites. — Iperti (1964) reared adults of a proctotrupid of the genus *Lygocerus* from *C. septempunctata* larvae which had been parasitized by *Homalotylus*. Yinon (1969) reared two species of hyperparasites (an encyrtid *Achrysocephalus aegyptiacus* and a pteromalid *Pachyneuron siculum* from parasitized *Chilocorus bipustulatus* larvae by *Homalotylus*. Domenichini (1956) reared a pteromalid *Pachyneuron chilocori* from parasitized *Chilocorus bipustulatus* (hyperparasitization 86%).

Tetrastichus spp. (Chalcidoidea, Eulophidae)

According to Klausnitzer (1969b), 4 species of this genus parasitize *Coccinellidae*. It is very difficult to identify the species of the genus *Tetrastichus*, so that it is possible that not all data attributed to *Tetrastichus coccinellae* really concern this species.

Tab. 8.04 Survey of the *Tetrastichus* species which parasitize *Coccinellidae* (after Klausnitzer 1969b).

<i>Tetrastichus</i>	Parasitized stage of the host	Food specialization
<i>coccinellae</i> Kurdj. <i>epilachnae</i> (Giard.) <i>neglectus</i> Domenichini	larvae, pupae larvae, pupae larvae, pupae	<i>Chilocorini</i> , <i>Coccinellini</i> <i>Epilachninae</i> <i>Chilocorini</i> , <i>Coccinellini</i> , <i>Scymnini</i>
<i>sempronius</i> Erdoes	larvae	mainly <i>Chrysopa</i> spp., but also <i>Chilocorus bipustulatus</i>

Tetrastichus is a gregarious parasite. As many as 25 *T. coccinellae* can develop in one *Coccinella septempunctata*, but more often only 10—15 parasites are found (Iperti 1964, Klausnitzer 1969b). Fewer parasites develop in *Adalia bipunctata*. For 103 parasitized pupae Klausnitzer (1969b) ascertained an average of 10.2 (minimum 3, maximum 14) *T. neglectus* per pupa. In coccinellids of the genus *Chilocorus*, Telenga (1948) usually found 6—8 parasites but sometimes even more, as many as 18.

Life cycle. — The female lays eggs in 3rd and 4th instar larvae; the 4th instar larvae manage to pupate (Telenga 1948). According to Iperti (1964), eggs are also laid in pupae. In the host's body the developing larvae are not in separate chambers (contrast *Homalotylus*). All the adult parasites which emerge from the host do so through the same single opening. Parasites of one sex only emerge from any one host pupa (Klausnitzer 1969b). The females are mature at emergence; several minutes later they copulate and so can immediately (Iperti 1964) or the next day (Telenga 1948) parasitize another host. In the laboratory at 20—25 °C and 70 % relative humidity, the longevity of the adult fluctuated between 5 and 20 days, at 14 °C it may reach 25 days (Iperti 1964).

Depending on temperature the whole development of the parasite lasts 20—32 days; Telenga (1948) reports as little as 12—16 days for the Krasnodar region (Ukraine SSR), while Iperti (1964) reports a minimum value of about 20 days for south-eastern France in July.

Voltinism. — Owing to the very fast development of *Tetrastichus* the annual number of generations is high. Both Telenga (1948) and Iperti (1964) report 7 generations for the Ukraine and south-eastern France. In the Ukraine, however, diapausing larvae (= prepupae) could be found from the 4th generation onwards.

Percentage parasitization. — There is general agreement that parasites of the genus *Tetrastichus*, similarly to *Homalotylus*, considerably limit the population increase of aphidophagous and coccidophagous coccinellids. The maximum parasitization that Iperti (1964) recorded in *Adalia bipunctata* reached 60 % in July 1962. According to Telenga (1948), *Tetrastichus coccinellae* is even more significant than *Homalotylus flaminus* in the Krasnodar region. Rubtsov (1954) complains of the ruinous effect of both these parasites on coccinellids of the genus *Chilocorus* on the Black Sea coast. The coccinellids of the 1st (= spring) generation are parasitized at 10 %, by the 2nd

(= summer) generation the parasitization has already risen to 50—70 %, and by the 3rd generation often 90 % or more are parasitized. As a result, only 1—10 % of the beetles hibernate, thus permitting an intense reproduction in the following spring by the coccids which are their prey.

8.33 Acarina

Apart from *Acarina* showing phoresis (e. g. *Pediculoides ventricosus*), coccinellids are attacked also by parasitic *Acarina* of the genus *Podapolipus* (*Podapolipodidae*). The parasite develops on the inner side of elytra. 4—5 females fix themselves, lose their appendages, feed on haemolymph and lay several hundred eggs. The hatched nymphs fill the space between the tergites and the elytra. Mostly *Adalia bipunctata* is attacked (up to 40 %), but also *Coccinella septempunctata* and *Synharmonia conglobata*. *Semiadalia undecimnotata* does not suffer from the attacks of this parasite. Although the parasitization of coccinellids by *Podapolipus* is not lethal, it causes an important fall in vitality of coccinellids.

8.34 Nematoda

Parasitylenchus coccinellinae (Tylenchida, Allantonematidae)

This nematode has been found as an endoparasite of the adults of multivoltine coccinellids in south-eastern France (Iperti 1964) and described as a new species (Iperti and van Waerebeke 1968). In dissections of coccinellids, nematodes were found from May to October with the maximum in late summer and early autumn. Either only adult female nematodes were found which had not yet oviposited, or ovipositing females together with female larvae and males. From 1 to 140 adult females could be found in one host; the number of larvae and young adults could amount to about 10,000 individuals.

Life cycle. — The young migrating fertilized female penetrates into the body cavity of the coccinellid. How this penetration occurs is not yet certain — there are three possible ways: (1) through the tracheae, (2) during coccinellid copulation through the sexual organs (where *P. coccinellinae* is abundant) or (3) through the softer cuticle between the sclerites (in a young infesting female the stylet is particularly well developed). The aerial environment of coccinellids is disadvantageous for the propagation of nematodes. Infection may occur in aggregations, when rain or dew can create the damp environment favourable for parasites among the coccinellids.

Within 4 days after penetration into the beetle, the body of the nematode female is almost entirely filled with ovaries, and after a short time the uterus is filled with free larvae and developing eggs containing coiled larvae. The larvae undergo their first moult while still in the uterus, then they moult twice more in the body cavity of the host. The third moult gives rise to males which are already adult, whereas the female gonads are still ovarian primordia of 5—9 cells. At this stage the larval females are fertilized. These young females evidently moult for the last (fourth) time immediately after penetrating into the host.

At the onset of the hibernation of the coccinellids, the development of *P. coccinellinae* eggs ceases and the female nematode becomes an ovisac.

Percentage parasitization. — Multivoltine species of coccinellids are most often attacked, especially *Propylaea quatuordecimpunctata* which is highly parasitized (up to

70 %), *Synharmonia conglobata* rather less (20 %), and least *Adalia bipunctata* and *Adonia variegata* (less than 10 %). In monovoltine species, *P. coccinellinae* has been found only incidentally in *Semiadalia undecimnotata* (Iperti and van Waerebeke 1968).

Although the nematodes are not quickly lethal to their host, they will reduce and may even completely stop the maturation of ova. They certainly also consume the reserves of the host.

Howardula sp. (Tylenchida, Allantonematidae)

In England, Hariri (1965) found adults and larvae of nematodes in 9 individuals of *Adalia bipunctata*; the nematodes were determined by Dr. G. O. Poinar as probably a new species of *Howardula*. The gonads of coccinellids were little affected by the parasite, but the fat bodies were much smaller than those of unparasitized beetles.

Mermis sp. (Mermitidae)

This endomonoparasite was found in south-eastern France by Iperti (1964) in four aphidophagous coccinellids during both diapause and activity. Hibernating *Adonia variegata* (2.5—4.2 %) and the aestivating *Semiadalia undecimnotata* (1.2 %) were attacked most often while the nematode was found only occasionally in active *Propylaea quatuordecimpunctata* and *Coccinella septempunctata*.

8.4 Pathogens

8.41 Protozoa

Gregarinidae (Sporozoa)

Laudého et al. (1969) have recently provided a literature review surveying the occurrence of these protozoa in coccinellids. A number of species, whose synonymy has not been reliably clarified, are involved. They destroy intestinal cells of coccinellid larvae and adults. Digestive troubles increase in the host with the number of gregarines which can, within a month, rise from only 10 individuals to several thousands in the central intestine of each infected coccinellid. A great number of gametocysts are then formed, and these may cause death of the beetle by blocking the intestine near the rectal pouch. In adults of *Pharoscygnus anchorago* which survive the danger of blockage, longevity is then reduced to one-half and fecundity to one-third. Laudého et al. found a high infection rate (more than 50 %) in two coccidophagous coccinellids inhabiting palm groves of Mauretania; these were the indigenous *P. anchorago*, and *Chilocorus bipustulatus* introduced from Iran. Two other introduced species showed different sensitivities. *Chilocorus stigma* was very sensitive to infestation by gregarines, whereas these protozoa were never found in *C. distigma*.

In areas with a milder climate, infections by gregarines are less massive. Iperti (1964) located them in 5 aphidophagous coccinellids in south-eastern France and, for example, in *Propylaea quatuordecimpunctata* infection was only around 10 % infestation during the whole year.

8.42 Fungi

Beauveria group *bassiana*

The coccinellids hibernating in aggregations are very often infected and killed by the pathogenous fungi of the genus *Beauveria*, group *bassiana*. The body cavity of the attacked coccinellids is then filled with a homogeneous cheese-like mass where the individual coccinellid organs cannot be discerned.

In *Semiadalia undecimnotata* the occurrence of mycosis is related to the type of hibernation shelter and its altitude (Iperti in Hodek 1966, p. 189). Below 1000 m the rate of mortality which was registered at three different sites for 4 years amounted to 19.7%. At three other sites elevated above 1000 m the mortality rate was only 1.5% at the same period. The incidence of mycosis was much lower in rock cracks or in piles of stones (1.3 and 8.6%) than when the coccinellids hibernated among plants (34%). To reduce the high mycosis, Iperti (in Hodek 1966, p. 189) placed artificial traps simulating rock cracks (Photo 4) on the mountain tops lacking rocks. The coccinellids preferred the artificial "hibernation quarters" over the original sites between plants and their mortality was substantially reduced.

Hibernating adults of *Coccinella septempunctata* are also often attacked by *B. bassiana*; Iperti (pers. comm. 1971) reports a mean 50% infection in south-eastern France.

Laboulbenia

Iperti (unpubl.) found a non-pathogenous fungus of the genus *Laboulbenia*, very bizarre in form, on the body surface of adult coccinellids. In south-eastern France, *Adalia bipunctata* and *A. decempunctata* are attacked in spring, *Pharoscyminus semiglobosus* in Morocco all over the year.

8.5 Comparison of parasitization and disease

Iperti (1964 and unpubl.) made a detailed study of the parasitization of 5 coccinellid species (*Adonia variegata*, *Semiadalia undecimnotata*, *Coccinella septempunctata*, *Adalia bipunctata*, *Propylaea quatuordecimpunctata*) in south-eastern France (Alpes-Maritimes and Basses-Alpes). He observed parasitization in all the three developmental stages and for some coccinellid species in both active and diapausing adults.

The abundant material (7617 specimens) which he acquired over 4 years (1961-64) makes possible an interesting comparison of different coccinellid species and stages, though at certain points such comparison relies on limited numbers — e. g. the data for *P. quatuordecimpunctata* pupae obtained from only 22 specimens must be regarded as preliminary.

Total parasitization. — The above mentioned 5 coccinellid species can be divided into 3 groups on the basis of the parasitization of larvae and pupae (fig. 8.02). (1) *A. variegata* and especially *S. undecimnotata* show low parasitization of these stages, and exclusively by the phorid *Phalacrotophora fasciata*. (2) In one coccinellid species, *A. bipunctata*, chiefly the pupae were strongly parasitized by the eulophid *Tetrastichus coccinellae*. (3) In *P. quatuordecimpunctata* and *C. septempunctata* it was the larvae which were strongly parasitized and the main parasite was the encyrtid *Homalotylus flaminus*. Parasitization of pupae was lower than that of larvae and included all three preimaginal parasite species.

From the above, it can be seen that the pre-imaginal stages are parasitized only by insects. By contrast, the adults are also heavily attacked not only by *Nematoda*,

P. quatuordecimpunctata is often strongly infected by a new species of the genus *Parasitylenchoides* and *A. variegata* rather less by *Nematoda* belonging to the genus *Mermis*, but in addition by pathogens (protozoans and fungi). *Gregarina* occurred in active adults of all observed species, but were no more than rare in *A. bipunctata* and *S. undecimnotata*.

In adults the only generalization which can be made is that a rather intense parasitization by the braconid *Perilitus coccinellae* occurs in hibernating individuals of all three species studied. In addition, hibernating *S. undecimnotata* were infected heavily also by fungi of the genus *Beauveria*. By contrast with active adults (see below) *Gregarina* have not been found in hibernating coccinellids.

When comparing parasitization of active coccinellids, we find a unique situation in *P. quatuordecimpunctata*. The contribution of a massive nematode (*Parasitylenchus*) infection raises the overall level of infestation by all agencies to 35 % which is much higher than is found in any other coccinellid species.

Next most infested are *C. septempunctata* and *A. variegata* with 20 % and 12 %. Active adults of *A. bipunctata* and *S. undecimnotata* may be considered by comparison as rather "healthy", as total infestation is only 6 %. Of the insect parasites, the braconid *Perilitus coccinellae* is strikingly abundant in active *C. septempunctata*, whereas in other species it forms only a negligible percentage (1—2 %) and in *A. bipunctata* it is completely missing. The other insect parasite of adults, the tachinid *Degeeria luctuosa* is completely absent from *C. septempunctata* and only parasitizes the other four species to a small extent (0.3—2.1 %).

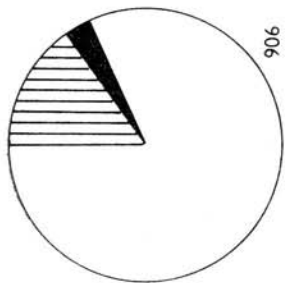
If we compare all the five coccinellid species according to the total sum of parasitization and disease of the nonhibernating stages, *S. undecimnotata* would appear to be the 'healthiest' species. If we regard this species as the standard for 'health', *P. quatuordecimpunctata* stands out as by far the most sickly by a factor of 10. Intermediate are *C. septempunctata* (a factor of 5) and *A. variegata* (a factor of 3).

All the above figures used for comparison are the averages. In the course of every season, the percentage of parasitization increases. Thus, about 70 % of coccinellids die instead of entering dormancy (Iperti unpubl.).

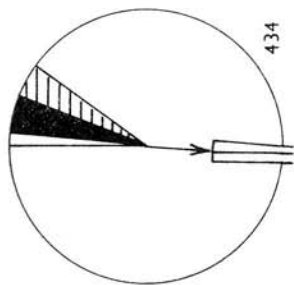
Differences between individual years. — Percentage of infection by individual parasites and pathogens often varies from year to year (Iperti 1964 and unpubl.). Exceptions are perhaps seen in the rather constant attack of *A. bipunctata* pupae by *Tetrastichus coccinellae*, of larval and pupal *A. variegata* by *Phalacrotophora fasciata* and of *P. quatuordecimpunctata* larvae by *Homalotylus flaminus*. By contrast, parasitization of *C. septempunctata* larvae by *T. coccinellae* which had risen considerably in May and June 1961, was very low in the same period of 1962, and in 1963 *Tetrastichus* did not occur at all before July. Infection of *C. septempunctata* by *Gregarina* also differed from season to season: in 1961 they were not found in a single sample, in 1962 they were found only in May, and in 1963 the infection by gregarines showed a gradual rise from June to August.

The comparisons which have been presented here are probably limited to the one region (south-eastern France) where such studies have been carried out. Unfortunately, similar data are not yet available from other regions, although they would be very useful, especially from the point of view of employing coccinellids in biological and integrated control. The task of accumulating such data is one of the projects of international cooperation in aphid predator studies within the framework of I. B. P. (see chapter 9). The only other extensive data comes from two regions of the USSR and from Israel (see 2.32) but unfortunately concerns only one genus of coccinellid (*Chilocorus*) and is limited to insect parasites only.

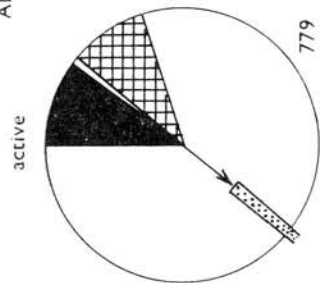
LARVAE



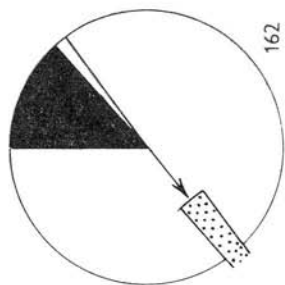
PUPAE



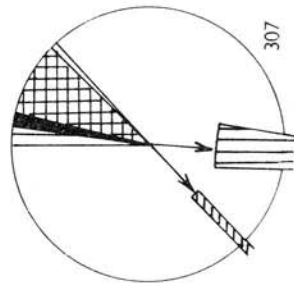
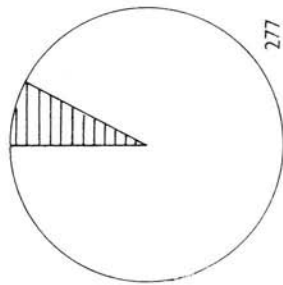
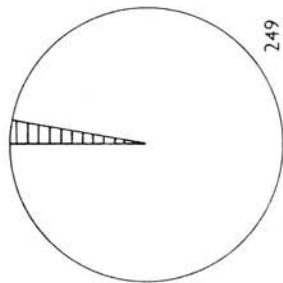
ADULTS



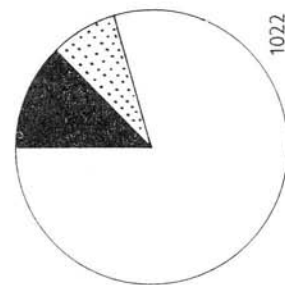
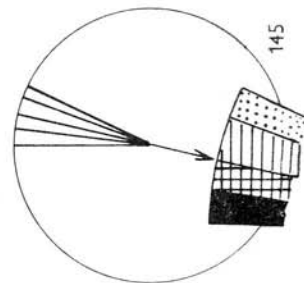
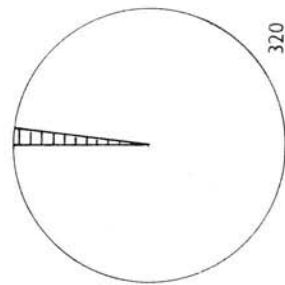
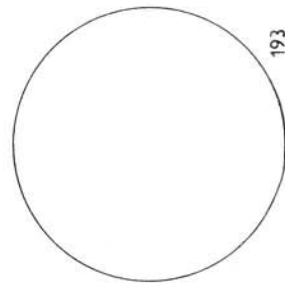
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Coccinella septempunctata



Adonia variegata



Semiadalia undecimnotata

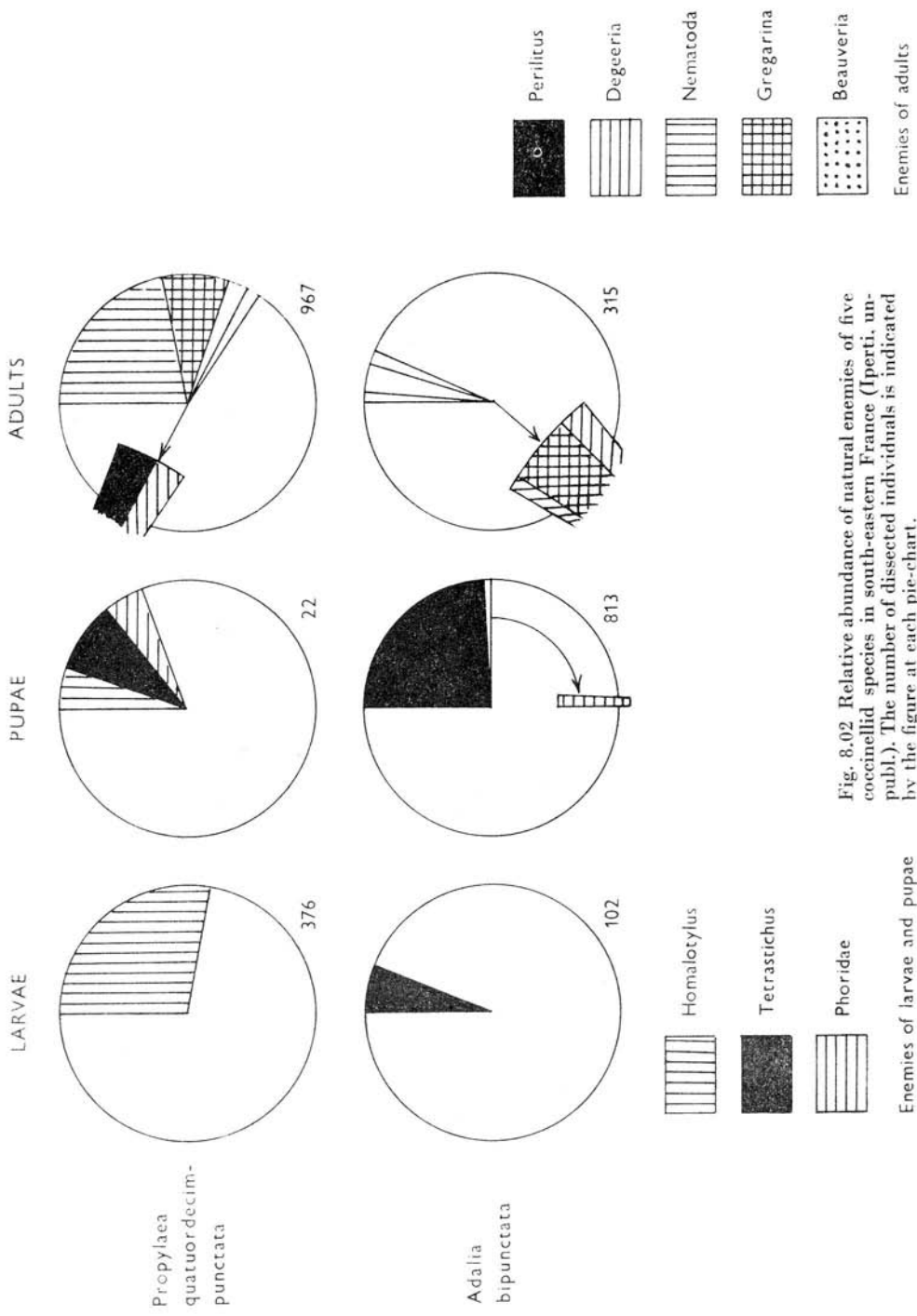


Fig. 8.02 Relative abundance of natural enemies of five coccinellid species in south-eastern France (Iperiti, unpubl.). The number of dissected individuals is indicated by the figure at each pie-chart.

Tab. 8.05 Parasitization of coccinellid predators of the sorghum aphid in N. Transvaal (van Rensburg unpubl.)¹⁾

Coccinellid species	Parasitization	
	of larvae by <i>Homalotylus</i> <i>flaminus</i> [%]	of adults by <i>Perilitus</i> <i>coccinellae</i> [%]
<i>Cheilomenes propinqua</i>	19.8	24.0
<i>Cheilomenes lunata</i>	81.3	10.4
<i>Lioadalia flavomaculata</i>	69.5	36.2
<i>Exochomus concavus</i>	68.6	6.6
<i>Scymnus moreletti</i> ²⁾	54.9	

¹⁾ Neither the eggs nor the pupae of any of the coccinellid species studied were attacked by parasites.

²⁾ *S. moreletti* larvae were parasitized by an unidentified *Homalotylus* sp.

The use of predaceous coccinellids for the control of pests differs with climatic area (the contrast between the temperate zone and the tropics and subtropics) and with the type of prey (aphids, coccids, mites). A further important consideration is whether an indigenous or imported exotic prey is involved.

As is true in other examples of biological control, comparatively the easiest way is, of course, to import a missing coccinellid against a prey which has been unintentionally introduced into a new area without its predator. This was the basis of the almost miraculous success with *Rodolia cardinalis* (see 9.21). This success was further assured by the fact that the rate of increase ratio between predator and prey was in favour of the coccinellid. In general it can be said that this ratio is much more favourable for the multivoltine coccidophagous coccinellids in the tropics and subtropics than it is for the usually univoltine (or only partially bivoltine) aphidophagous coccinellids in temperate areas. This is evidently the reason why coccids are particularly successful subjects for biological control (DeBach 1964) (see 9.21).

In temperate zones there is a major difference in strategy for utilizing aphidophagous coccinellids between the permanent habitats (forests, orchards) and the fields, especially annual crops. The coccinellids which breed in forests also hibernate there (see 7.324); it would therefore be comparatively easier than in annual crops to use supporting procedures to augment their numbers in the long term. No attempts in this direction have been reported, for the simple reason that aphids in forests are generally considered as economically neutral within that habitat. Orchards somewhat resemble forests in that at least a part of the population of some coccinellid species (e. g. *Stethorus punctillum*, *Adalia bipunctata*) both breed and hibernate there (see 7.323). However, the majority of coccinellids which are of economic significance in orchards move to other habitats even in the course of the breeding season (see 5.32), and they also hibernate elsewhere. Thus the coccinellid fauna in an orchard is, to a large extent, re-formed every year and is influenced by conditions in neighbouring habitats.

This applies to annual field crops to a much greater extent. As a rule, they are secondary host plants of pest aphids. Whether the coccinellids will or will not have an impact on the aphid populations is often determined within a short period of time, and the deciding factors are: the previous development of aphids on their primary hosts, the proximity to the crop of the hibernation sites of coccinellids (see 5.33), the meteorological conditions in the critical period (see 9.1), etc.

The most frequent problem which applies generally in all habitats is to provide coccinellids on the crop in sufficient numbers during the critical period to have an impact on the pest population. This can be achieved in a variety of ways:

- (1) by the release of sufficient numbers of coccinellids
 - (a) collected elsewhere, e. g. in hibernation quarters;
 - (b) cultured in the laboratory;
- (2) by attracting coccinellids from other habitats or by retaining them on the crop
 - (a) by providing alternative food;
 - (b) by disturbing the adjacent habitats or strata;
- (3) by the general support of coccinellids in the longer term and over larger areas. Here may be suggested
 - (a) in the period after the population crash of aphids the provision of some alternative food to enable the coccinellids to lay down sufficient reserves before hibernation (see 6.111 and 7.311),
 - (b) the planting of suitable hibernation sites, protection of hibernation sites (especially against burning), or the erection of artificial shelters to prevent mycosis (see 8.421) and mammalian predation.

In spite of the considerable study devoted to coccinellids, there are still **gaps in our knowledge** which must be filled before coccinellids can be utilised or supported rationally:

- (1) the mobility of coccinellid adults in terms of distance and direction of migration;
- (2) the qualities of a habitat that attracts the immigrant coccinellid adults;
- (3) the influence of meteorological factors, mainly temperature, on the searching efficiency and feeding rate of the predator in comparison with the rate of reproduction of the prey (see 9.1);
- (4) the population density of the prey
 - (a) necessary to retain the predator;
 - (b) to enable reproduction;
 - (c) to assure a high survival of first instar larvae which are least efficient in searching for prey;
- (5) the composition of artificial essential food to enable economic mass production;
- (6) the composition of cheap alternative foods
 - (a) for attracting and maintaining coccinellids in the habitat during the critical period;
 - (b) for the nutrition of coccinellids before hibernation;
- (7) methods of treating coccinellids to reduce their tendency to fly and thus disperse at the end of hibernation. If they are collected and transported to crops, dispersal will nullify attempts at mass release.

Coccinellids are, of course, only one segment — even though a significant one — in a whole complex of factors utilizable in pest management. A variety of other known predators (*Anthororidae* and other *Heteropteran* families, *Syrphidae*, *Itionididae*, *Chrysopidae*, *Hemerobiidae*) belong to this complex. There is some evidence that some other aphid predators are being overlooked because of their nocturnal feeding activities. The *Dermaptera*, for example, also apparently prey on aphids (Schlinger et al. 1959, Skuhrový 1960, Smith 1966, Asgari 1966, Way and Banks 1968). Furthermore, it seems probable that some *Carabidae* (Skuhrový 1959) visit plants at night and prey on aphids, chiefly those which have fallen from the plants. Some *Cantharidae* (Smith 1966, Way and Banks 1968) and spiders are other overlooked aphid predators. Other important factors are parasites and pathogens (Hagen and van den Bosch 1968), also the other tools of integrated control, e. g. modification of cultivation schemes, premature defoliation of host plants, breeding plants resistant to aphids, etc.

In addition, the prey of coccinellids is hardly ever the only pest in a crop. Coccinellids must, therefore, be incorporated into the complex of the **integrated control** measures for a given crop. "Integrated pest control is a pest population management system that utilizes all suitable techniques in a compatible manner to reduce pest populations

and maintain them at levels below those causing economic injury" (Smith and Reynolds 1966). This approach is being recognized as essential for the sound future of agricultural production. Other approaches may give dramatic results on a short-term basis, but in the long run we must learn how best to apply basic ecological principles to the inherently artificial crop environment. However, these basic principles are expressed differently in every ecosystem and therefore no general scheme can be designed — integrated control procedures must be specific for each crop and for each climatic area. Each agroecosystem must be analyzed for the most serious "key pests", their competitors and natural enemies and the main alternative food supplies of the pest.

9.1 Evaluation of the impact

There still exists only little concrete, numerical evidence of the impact of coccinellids (Smith 1966, Hagen and van den Bosch 1968, van Emden et al. 1969, Hodek et al. 1971). This, in fact, also applies to other entomophagous insects. More reliable data on the efficiency of coccinellids (and other natural enemies acting synergistically) are highly desirable, particularly for two reasons:

- (1) we must know to what extent and at what period we can rely upon their action;
- (2) we should be able to calculate the cost efficiency ratio of supporting procedures (e. g. mass production, import, spraying with artificial food, etc.). To do this, we must be able to evaluate the effect of such treatments.

The control potential of coccinellids can be examined from several angles. The significance of coccinellids (and natural enemies in general) in the full population dynamics of aphids, i. e. in the long-term regulation of aphid numbers, is not yet sufficiently understood. This is because, with the exception of a few aphids (see 9.11), most evidence relates to short-term population dynamics restricted to a small area (R. F. Smith 1966). But even such studies enable us to recognize which factors determine the impact of natural enemies at individual phases of the aphid cycle (see 9.12). Very often the impact is judged by hindsight from a co-incidence of events observed from the sampling data of both prey and natural enemy populations; this method is not very likely to yield reliable conclusions. There is a need for much more extensive use of the more efficient experimental methods (see 9.13). In most cases it appears that coccinellids on their own are unable to check pest infestations effectively and must be helped in various ways (see 9.2 and 9.3).

9.11 Role of coccinellids in the regulation of aphid numbers

Our ideas on the efficiency of aphidophagous insects have broadly remained unchanged for 40 years, since Blatný (1925) hypothesized that the alternation of years with an overpopulation by aphids and years with lower aphid population is caused by the action of natural enemies. In a year with many aphids the enemies have suitable conditions for rapid multiplication, and thus the next year the large number of enemies can keep the aphid population at a low level. Because numbers of prey are thus reduced, the population increase of aphidophagous insects in the second year is inhibited and thus the third year will again be favourable for overpopulation by aphids (Fig. 9.01 b). Similar assumptions are still generally accepted, though they are now much more sophisticated (Müller 1966, Behrendt 1969). However, the hypothesis has still not been proved unequivocally.

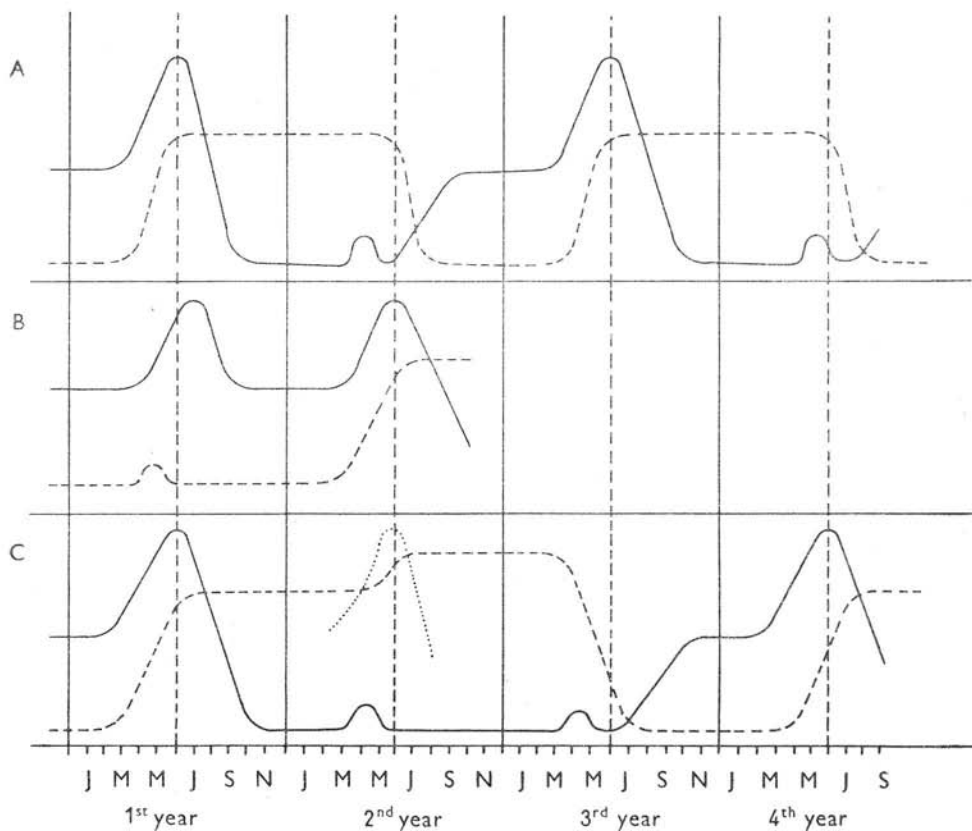


Fig. 9.01 Scheme of predator/prey relationships between coccinellids (---) and aphids (—) (Müller 1966).

A: the normal case with an alternation of aphid and coccinellid peaks:

B: cold weather delays the aphid peak; the coccinellid population remains low, and therefore the aphid is again abundant in the following year:

C: during low population levels of the main host aphid the coccinellids can prey on another aphid (.....) and thus show high population levels in two successive years; this results in a low population of aphids.

Müller (1966) includes two modifications of Blatný's hypothesis. Cool weather delays the aphid peak and the population of coccinellids therefore remains low. This enables a repeated outbreak of aphids in the following year and therefore aphid overpopulation can occur in two consecutive years (Fig. 9.01b). The opposite situation holds when, during low population levels of one prey species, the coccinellids can build up a high population by preying on another species. Thus they may prevent the outbreak of the original species of prey for a second year (Fig. 9.01c).

This scheme is relevant to the fluctuations of *Aphis fabae* in a mild climate. Way and Banks (1953) in England, Palyi (1960) in the "Black-soil" region of the USSR and Behrendt (1969) in the German Democratic Republic, are all of the opinion that, in the long-term population dynamics of this aphid, the most important period for the impact of natural enemies follows the aphid peak on crops. In this period, the activity of natural enemies determines the number of overwintering aphid eggs on

primary host-plants (*Euonymus*). A correlation has been found between a low number of eggs and a subsequent low summer occurrence of the aphid on secondary host-plants (sugar-beet etc.). The summer level of aphids is also affected (apart from other factors) directly by the number of natural enemies, mainly overwintered coccinellids (Hodek et al., in Hodek 1966, p. 331, Hodek et al. 1966). The number of the latter is dependent on their survival during hibernation (esp. with respect to mycoses and late frosts). The spring impact of coccinellids is modified by the effect of meteorological conditions on their feeding activity and by the distance between the hibernation sites.

In both these ideas concerning the critical phase for the action of coccinellids, it has been decided already at the beginning of the vegetation season whether or not coccinellids (and other natural enemies) will have an economic impact.

An entirely different pattern of fluctuation in aphid populations holds in California (Hagen and van den Bosch 1968) for alfalfa aphids (*Acyrtosiphon pisum* and *Theorhaphis trifolii*), where there can be two or three population peaks each year. The principal factor responsible for this contrast with mid-Europe is the climate which, in the warmer lowland California, not only speeds aphid development but favours anholocycly. There is a close synchronization between natural enemies and aphids, and less drastic population oscillations occur. All coccinellid species do not have equal impact. The *Hippodamia* species, which only have a facultative adult dormancy, are more sensitive to the occurrence of aphid; they reproduce if there are sufficient aphids and if temperatures are high enough. Most *Coccinella* spp. do not react to summer aphid abundance; they go into diapause anyway. Microclimatic changes caused by harvesting the alfalfa have important effects on both natural enemies and aphids (see 9.232).

In middle lowland California, coccinellids are extremely important in biological control of alfalfa aphids, particularly in spring-time. This knowledge was used effectively in the development of an integrated control of alfalfa aphids, and was largely responsible for chemical treatments in spring-time being abandoned.

9.12 Factors determining the impact of coccinellids

9.121 Theoretical evaluation of coccinellids as predators

Efficiency of a natural enemy as a controlling agent is determined by a variety of characteristics (Bombosch 1963, DeBach 1964, van Emden in Hodek 1966 p. 227, van Emden et al. 1969, Hodek et al. 1966, Hodek 1967). Some of these characteristics appear to indicate that *Coccinellidae* might be effective predators.

The searching capacity of coccinellids in general is quite high (see 6.31), although the adults of some species tend to leave the habitat if the prey density falls below a critical level (see 9.124). The random searching behaviour of coccinellids is an advantage e. g. in the critical period of the arrival of aphids on the secondary host-plants; at the beginning of an infestation the coccinellids will find isolated aphids, to which other predators which orientate to the smell of aphid colonies would not yet be attracted. Coccinellids occupy all the habitats and niches of their prey (see 5.3) and the similarity in taxes (phototaxis, geotaxis) of coccinellids and their prey cause them to occur in the same places (see 6.31).

There is controversy about the relative controlling efficiency of specific and general predators. Whilst specific natural enemies have provided the most successful examples of control using introduced species, a specific predator is more endangered by

prey scarcity than is a more general feeder. Furthermore, if the better utilization of indigenous predators is considered, it seems probable that best results will come from the manipulation of the complex of non-specific or relatively non-specific species of which coccinellids are often outstanding. Coccinellids have as a valuable characteristic a degree of host specificity connected with dependence on certain aphid species for breeding (see 6.11), which is associated with considerable polyphagy in terms of alternative food for the adults (see 6.111 and 6.12). This is a very advantageous characteristic, as far as such ephemeral prey as aphids are concerned. Coccinellids are very voracious (particularly the fourth instar larvae) and their voracity or at least the number of prey killed increases with an increase in prey density (see 6.22). They are at the same time able to adjust their rate of development and adult weight to the abundance of food (see 6.23). Coccinellids can survive periods of scarcity of food by such adjustment and by feeding on alternative food (see 6.111) or by cannibalism (see 6.13).

Coccinellids are amenable to culture (see 9.2), although with some difficulties, particularly in the case of the aphidophagous species. If satisfactory artificial foods can be developed, then the demands on space and labour, which at present limit the amount of culturing possible, will be much reduced. The fact that both larvae and adults of coccinellids are entomophagous is of paramount importance for their impact. It enables them to attack immediately on arrival; some other predators, e. g. *Syrphidae*, are incapable of this.

As regards the rate of increase of coccinellids, fecundity is generally fairly high, and both developmental rate and number of generations (as compared to these characteristics of their prey) are favourable in the case of coccidophagous species (particularly in warmer regions), but unfavourable in aphidophagous ones.

9.122 The phases of prey population, with respect to their sensitivity or insensitivity to coccinellid impact

This section is a simplified generalization of a series of events, which of course vary with different prey, different habitats and climatic conditions. In the relationship between coccinellids and coccids in the subtropics (or tropics), such phases are not discrete. The section is, however, vitally relevant to the relationship between coccinellids and aphids in temperate regions. To facilitate the argument, Smith's (in Hodek 1966, p. 285) division of short term population dynamics of aphids is used with slight modifications.

(A) Initiation phase. — Often it is during this period, when the aphid population establishes itself in a new environment and begins to increase, that its future fate is determined. It has been observed with *Aphis fabae* on secondary host-plants (Way et al. 1954, Hodek et al. 1962, 1966) that a check of the population can occur in this phase. The coincidence of predator and prey in both time and space is the most critical element at the very beginning of this phase (Smith in Hodek 1966 p. 285), and therefore the vicinity of hibernation quarters of *Coccinellidae* to the crops is of special importance (Hodek 1964, Skuhřavý and Novák 1966).

As aphidophagous coccinellids are very mobile, a certain aphid population level will be necessary to keep the predator on the crop in this phase. This crucial factor has largely been neglected and has been evaluated only for *Scymnus minimus* (Kuenen 1947), for *Stethorus punctillum* (Putman 1955), for *Hippodamia convergens* and *Olla abdominalis* (Sluss and Hagen in Hodek 1966, p. 243), and for coccinellids on sugar-beet fields (Skuhřavý and Novák 1966). On carrots (Dunn 1965), the abundan-

ce of coccinellids does not seem to be correlated with the population density of *Cavariella aegopodii*.

Skuhřavý and Novák (1966) found that, at the beginning of the immigration to sugar-beet fields, the coccinellids flew to all fields, regardless of the extent of aphid infestation of these fields. The coccinellids only remained, however, on fields with a sufficient aphid density — 100 or more aphids per 100 plants were sufficient to maintain a non-declining population of coccinellids.

(B) First increase. — If the aphid population is not checked at the very beginning, its increase is then affected mainly by the balance between the rate of reproduction of the aphids and the voracity of the aphidophagous insects (van Emden in Hodek 1966, p. 227); both are governed by weather conditions (Hodek et al. 1965). Dunn (1952) found that only at constant temperatures above 51—52 °F (= 11 °C) can one *Coccinella septempunctata* adult consume more than the number of nymphs produced by one *Acyrtosiphum pisi* mother. Some field confirmation of a similar differential effect of temperature on the reproductive capacity of *Aphis fabae* and on the preying efficiency of *Coccinella septempunctata* adults was obtained in field cage experiments on sugar-beet (Hodek et al. 1965). In the warmer season of 1964 the impact of coccinellids was more than twice as great as in 1963. In 1963 the coccinellids failed to prevent overpopulation by aphids in all cages where the ratio of aphids to beetles was 90: 1 or greater; in 1964, however, the coccinellids destroyed the population of aphids completely within 10 days, even in cages with as many as 200 aphids per beetle (Fig. 9.02). Sometimes it happens that a catastrophic weather event checks the increase of aphids.

(C) Peak phase. — When the population increase of aphids passes a certain limit, further activity of natural enemies makes no contribution to economic impact on that crop, even if the enemies invade in large numbers from neighbouring habitats (Szalay — Marzso 1957, Way and Banks 1958, Hodek et al. 1966). At worst, the aphidophagous insects may in fact even benefit the aphids if they remove sufficient individuals to decrease intraspecific competition (Way, in Hodek 1966, p. 283). At best, the impact of natural enemies shortens the time during which aphids remain at peak density (Sluss and Hagen, in Hodek 1966, p. 243). From the point of view of integrated control, however, this phase is very significant. Chemical treatment should not be carried out as

- (1) it can no longer prevent yield loss;
- (2) the outbreak will anyway cease spontaneously;
- (3) the natural enemies are then usually present in masses and should not be destroyed (see 9.231), but preserved for later phases of the season and for next year (*Aphis fabae* — Hodek et al. 1966).

Similar conclusions were reached by Sluss and Hagen (in Hodek 1966, p. 243) for *Chromaphis juglandicola*.

(D) Crash. — The crash of the prey outbreak is brought about by the complex action of several factors: meteorological conditions (particularly high temperature), changes in the physiological condition of the host plant, mycosis, action of natural enemies. With regard to the last mentioned, the importance of syrphids and parasites increases in this and the previous phase (C), unless the parasites were heavily hyperparasitized earlier. If the numbers of aphids are reduced to very low levels, the coccinellids (and other predators) do not remain in the habitat, and the aphid populations are allowed to resurge later in the season (Sluss and Hagen, in Hodek 1966, p. 243).

(E) Scarcity or absence of aphids. — If after the crash the aphids on a given crop still maintain small population fluctuations, the coccinellids may stay there until the onset of dormancy and produce a further generation, then accumulating enough reserves for overwintering. During the last two phases (D and E) the survival ability

of the predator is of importance, and this depends on the relation of the population density of prey present to the minimum required by the predator. The first larval instar is limiting in such a situation (see 6.31). If all food has disappeared, cannibalism becomes relatively advantageous in that it makes survival possible for at least a part of the population. However, the feeding of old larvae on soft pupae or newly emerged adults has no adaptive advantage (see 6.13).

Very often the aphids disappear completely from the habitat and the coccinellids search for them in other habitats (see 5.32). Usually they find the prey in humid places and on weeds. Where they do not find their essential prey, extensive polyphagy with respect to alternative food (including even different types of phytophagy, see 6.111 and 6.12) increases survival. The last two phases are very critical for the population dynamics of coccinellids and attention should be paid to these phases when searching for ways of utilizing coccinellids fully. During phase (E) coccinellids may be conserved by the provision of alternative, even artificial, food (see 9.233).

9.13 Methods for studying the effectiveness of Coccinellidae¹

The scarcity of real evidence on the impact of natural enemies (Hagen and van den Bosch 1968) arises from the fact that most conclusions have been based on correlations of data obtained by indirect methods (9.131). Wherever possible, direct (9.133) or semi-direct methods (9.132) should be used in preference, in conjunction with long-term ecosystemic studies. A survey of all such methods has been given in detail (Hodek et al. 1972) and is therefore only brief here.

9.131 Indirect methods

At the beginning of this century the collapse of high aphid populations was often attributed to predation by coccinellids, as these were observed in large numbers on the crop at the aphid peak. Unfortunately, observations or even counts of aphids and their natural enemies may merely demonstrate a coincidence of events and they do not prove causal relationships. However, such relationships can be established from a combination of more refined sampling procedures and a detailed knowledge of the biology of the insects concerned. For example, the losses of aphids by emigration can be determined from the proportion of alate nymphs in successive samples. Losses from disease and parasites can also be accurately assessed from sample data.

In order to interpret the population dynamics of prey and predator from sampling data realistically, auxiliary studies on essential biological, ethological and ecological characteristics are required for the predator: essential and alternative prey (see 6.113), prey-searching behaviour (see 6.31), voracity (see 6.2), induction of diapause affecting voltinism (see 7.42), other components of the rate of increase, such as fecundity, rate of development (see 4.12) and longevity (see 4.2), and the impact of natural enemies of the predator (see 8).

The weak point of indirect methods persists through even accurate sampling: causal relationships are being deduced by hindsight from a coincidence of events. The many factors (extremes of weather conditions such as heavy rain or very high temperature,

¹ A comprehensive account of all sampling methods is given by Southwood (1966). Many methods specifically developed for studying the effectiveness of natural enemies are discussed by DeBach (1964).

physiological state of the plant, fungal attacks, emigration of alatae etc.) affecting aphids interrelate in a very complex manner, leaving an intuitive hypothesis as the only course open to the investigator. Sampling can, however, estimate the ratio prey/natural enemies and if we know the critical ratio, it will help us in assessing the feasibility of releasing coccinellids at a particular time, mostly in phase (A) (see 9.122).

Two types of sampling are most used. (1) Numbers on plants may be counted directly in the field, or after transfer of a sample to the laboratory. In both cases some mobile predators may escape. (2) Sweeping on herbaceous plants or beating off trees and shrubs are simple quick methods for large areas but being affected by physical conditions and by the height of plants (Dumas et al. 1964) they give differential results even for related species. Interception traps (mainly special sticky traps) which catch insects more or less at random are important for detecting predator mobility (Ewert and Chiang, in Hodek 1966, p. 195).

The size of populations may be expressed as numbers, biomass (weight) (Szalay-Marzós 1958), or energy content. Graphic methods facilitate understanding of prey/predator relationships. Abundance may be simply plotted arithmetically against a time scale. When comparing several curves, the time scale goes from front to rear and the abscissa indicates the origins of separate curves (Fig. 9.02). Correlations can be expressed directly as a function by a plot of number of prey against number of predators without any time scale. A log scale can be used for a geometrically increasing population (Hughes 1963) (Fig. 9.03). A useful illustration technique has been used by van Emden (in Hodek 1966, p. 227). In two horizontal axes he plotted the number of prey against the number of predators with % of prey eaten on the vertical axis (Fig. 9.04). The horizontal plot was joined up in sequence of time.

A very promising indirect approach is to estimate predator efficiency on the basis of simplified models (Bombosch 1963, Hughes 1963, van Emden in Hodek 1966, p. 227).

9.132 Semi-direct methods

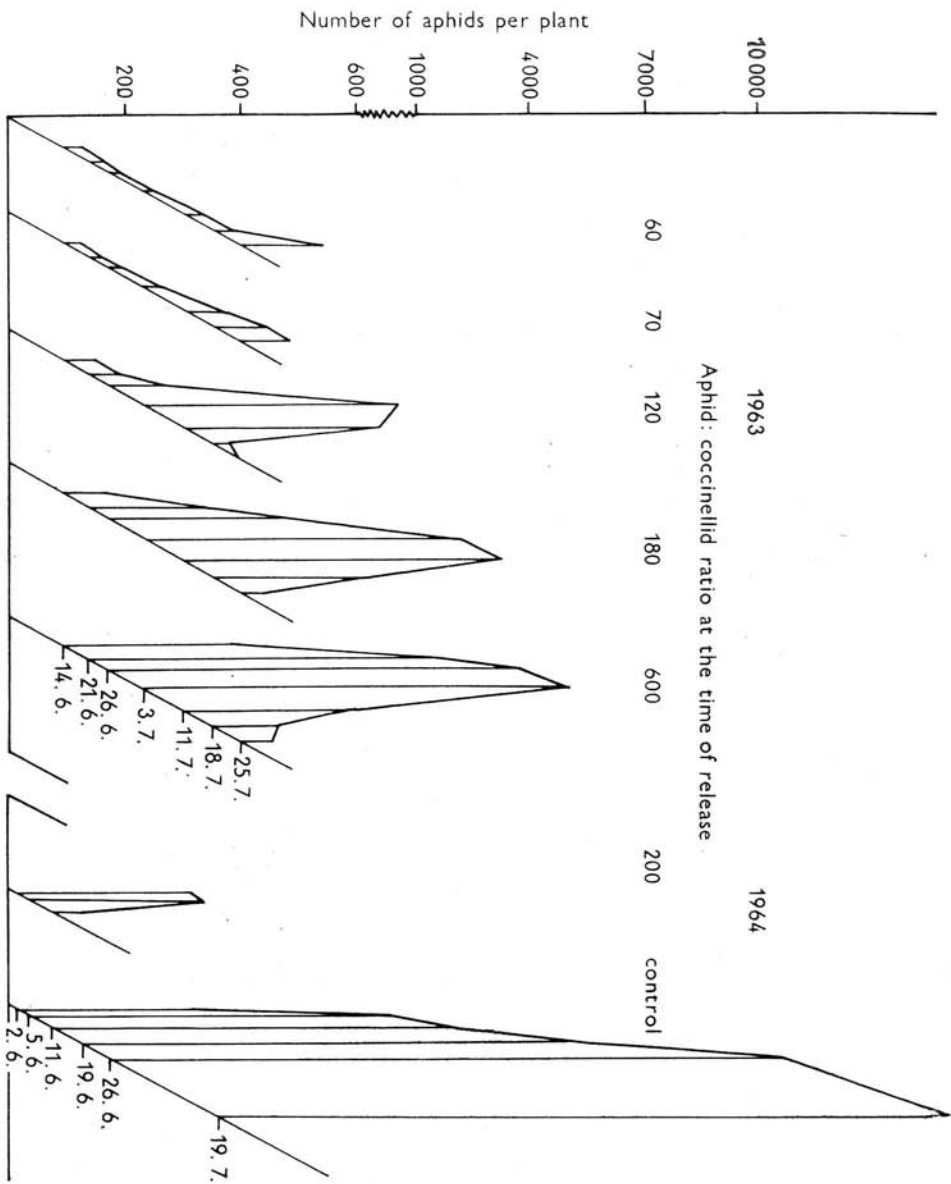
Some methods combine observation or sampling with experimentation. van Emden's (1963) method of inspecting marked aphid colonies of the fairly sessile *Brevicoryne brassicae* was developed to measure mortality factors directly in the field; thus the correlation of prevailing weather conditions and the appearance and abundance of predators with changes in aphid numbers is not assumed vaguely a posteriori, as it inevitably is with indirect methods. Similarly, the influence of predators on marked colonies of the more or less sessile *Adelges piceae* was followed by Karafiat and Franz (1956) and Franz (1958).

An important obstacle in evaluating the role of natural enemies from counts of prey and predator is the changing physiological state of the host-plant. This variable has been standardized by sampling predators on trap plants infested in the laboratory with a constant number of prey (Müller 1966).

9.133 Direct, i. e. experimental methods

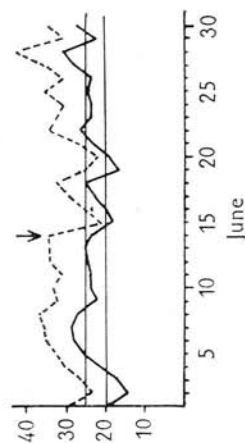
Logically, the most convincing test of predator impact would be a comparison of similar host populations with and without natural enemies.

The idea itself is obvious, but actual experiments are technically difficult. Natural enemies can be killed (insecticides), removed (hand) or excluded (cages). All of these

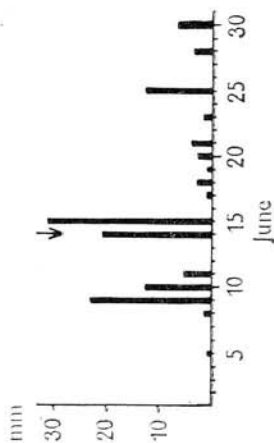


1963

Aver. + max. temperature

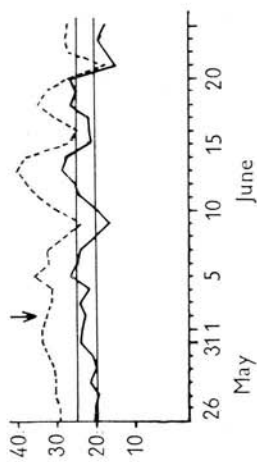


Rainfall



1964

Aver. + max. temperature



Rainfall

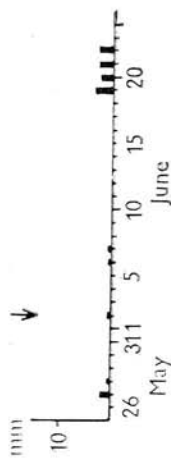


Fig. 9.02 Impact of *Coccinella septempunctata* on *Aphis fabae* on sugar-beet inside nylon cages (Hodek et al. 1965). The arrow shows the date of coccinellid release.

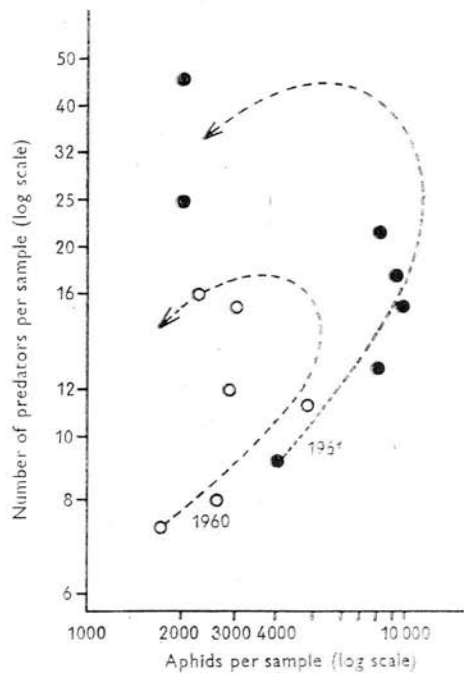
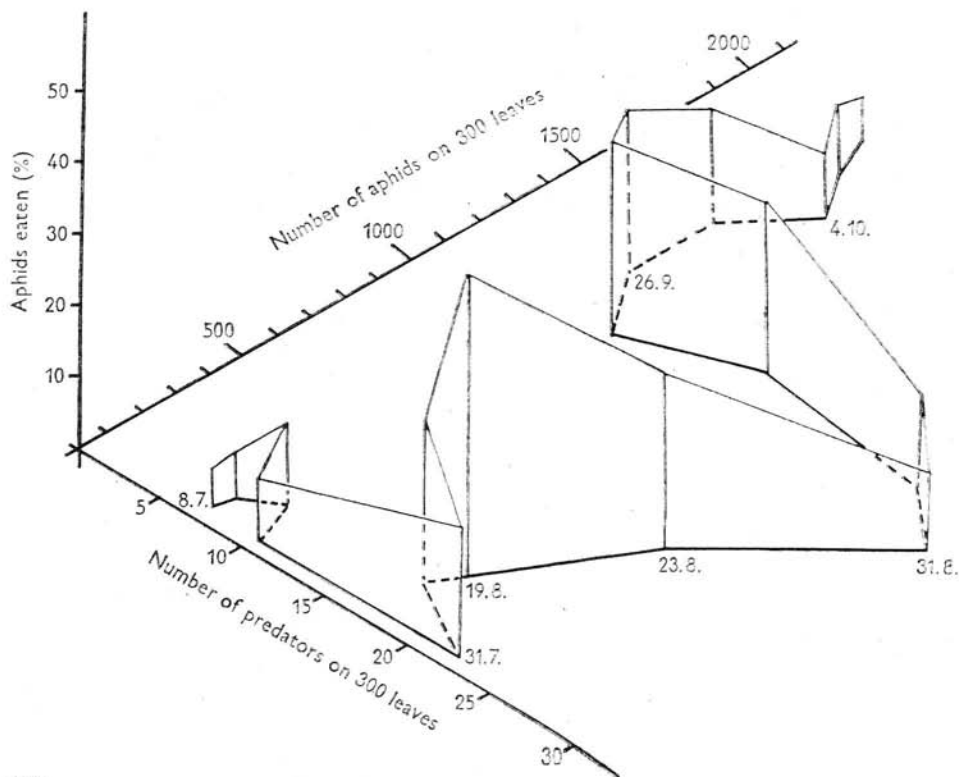


Fig. 9.03 Time trends in the relation between number of aphids and number of predator larvae showing the lag caused (Hughes 1963).

Fig. 9.04 The efficiency of predator action in a field infestation of *Brevicoryne brassicae* (calculated from van Emden 1964, 1965) (van Emden in Hodek 1966, p. 227).



techniques have disadvantages. Chemical exclusion (DeBach 1946, 1964) needs a selective insecticide in absolute terms, i. e. it kills the predator but leaves the prey unaffected. Unfortunately, although DDT has been widely used for the purpose and Sevin has also been found satisfactory (Meier in Hodek 1966, p. 323), insecticides are rarely, if ever, absolutely selective. Also, insecticides must be sufficiently residual to kill immigrating predators. Both these limitations result in a certain underestimation of the role of natural enemies.

Hand picking of natural enemies can be only recommended for calibration of other methods (Fleschner 1958, Matsumoto and Nishida 1966), because it is very tedious. There is also a risk of damaging the host-plant and disturbing the prey.

While both hand removal and insecticides require constant repetition, cages ensure permanent exclusion. They have, however, two important disadvantages: the microclimate inside the cage is changed and the natural emigration of the prey is prevented. Both disadvantages can partly be overcome by adding control cages in the form of a "double cage" (Sparks et al. 1966) or slatted wooden framework (Way and Banks 1968). Both allow some movement of natural enemies and emigrants, and reproduce many of the climatic conditions of cloth-covered cages.

Numbers of natural enemies can also be varied experimentally by reducing them with ants ("biological check" of DeBach et al. 1949) or increasing them by adding artificial food (Schiefelbein and Chiang 1966, Smith in Hodek 1966, p. 19).

A known initial number of prey and natural enemies may be confined together in a simplified artificial system. Natural physical conditions can be retained (within the limitations discussed above) by using outdoor cages and thus the effect of differences between individual years can be studied (Hodek et al. 1965, see Fig. 9.02).

The effectiveness of natural enemies can be studied in a still more simplified system under controlled laboratory conditions. Only the essential "skeleton" of the prey/natural enemy relationship then remains. No long-term laboratory systems with coccinellids have yet been studied.

9.2 Use in biological control

The term biological control has two basic different meanings (DeBach 1964). (1) From the ecological viewpoint, biological control is defined as the action of parasites, predators, or pathogens in maintaining another organism's population density at a lower average than would occur in their absence. Man's manipulation of natural enemies is not implicit in this definition. (2) The same term is, however, more frequently used for "the study and utilization of parasites, predators and pathogens for the regulation of host population densities", i. e. exactly man's activity.

In the previous section (9.1) the biological control function of coccinellids in sense (1) has been discussed as well as the methods by which this activity can be studied. In the old mixed and scattered farming, which affected the ecosystem relatively little, such a spontaneous impact of natural enemies (including *Coccinellidae*) on pests was quite probable. Great acreages of monoculture, although creating ideal conditions for pests, deteriorate the environment for natural enemies, and greatly limit the possibility of their preventing the increase of the pest population above the economic level on their own accord. Because of the danger of the wide use of pesticides, the only sensible pest management is to gradually build a complex system of integrated controls (see 9 Introduction). An important constituent of these measures is the use of natural enemies, i. e. biological control in the sense (2) comprising three types of activity: importation (see 9.21), augmentation and conservation (see 9.22) (DeBach 1964).

9.21 Importation of exotic species

The classical and still most frequent approach to biological control is to import the natural enemy to an area where it is lacking. From the economic point of view it is an extremely efficient procedure: if after a successful establishment the natural enemy reduces the target host population, activity then continues without any further effort from man.

Coccidophagous species. — Most often the missing biotic agent is imported to follow the host which has been unintentionally introduced into a new area. This was the case with the introduction of *Rodolia cardinalis* which has still remained the most spectacular success story of biological control (DeBach 1964). In 1887, the infant citrus industry in California was threatened with destruction by massive infestations of *Icerya purchasi*. In December 1888 and January 1889 the first 129 specimens of *R. cardinalis* were sent from Australia. After propagation in the laboratory, 10,555 specimens were released in June 1889 and established successfully. In one year, the production of oranges increased about three times, and the cost of the project was a mere \$ 1500! *R. cardinalis* was later introduced to other countries [DeBach (1964) listed 29 countries] and produced complete (or at least substantial) control of *I. purchasi* everywhere. It also succeeded in controlling the other species of this genus.

Even though the *Rodolia/Icerya* relationship is more favourable for control than may be encountered with some other coccidophagous coccinellids (e. g. *Cryptolaemus montrouzieri* must be periodically replenished — see 9.222), coccids in the tropics and subtropics seem on the whole to be very suitable subjects for biological control by coccinellids. In the table of "cases of biological control of pest insects by imported entomophagous insects" (DeBach 1964), 11 coccid species in addition to *Icerya spp.* are listed which were controlled by the coccinellids *Chilocorus cacti*, *C. distigma*, *C. nigritus*, *C. politus*, *Cryptognatha nodiceps*, *Cryptolaemus montrouzieri*, *Rhizobius ventralis*, *Rodolia pumilla* and *Telsimia nitida*.

Also the introduction of the coccinellid *Lindorus lophantae* to Italy, North Africa and to the Black Sea coast of the USSR resulted in successful control of coccids, particularly of the subfamily *Diaspidinae* (Yakhontov 1960). The European *Chilocorus bipustulatus* seems only tenuously established in California (Huffaker and Doutt 1965). *Orthezia insignis* attacking ornamentals in Kenya, has been substantially controlled by *Hyperaspis jocosus*, imported from Hawaii (DeBach 1964).

Aphidophagous species. — The 12 successful examples of coccid control by coccinellids contrast strikingly with only two examples available for aphids — *Aphis sacchari* on sugar cane in Hawaii (Pemberton 1948) and *Therioaphis maculata* on alfalfa in California — and even in both examples predators did no more than contribute to control. Moreover, the coccinellids preying on *T. maculata* are native species. The earliest known introduction of an insect for biological control is the importation of *Coccinella undecimpunctata* into New Zealand in 1874 for the control of aphids (Dumbleton 1936, Read 1965). The species is now generally distributed throughout the country, but its impact has been curtailed by the inadvertent introduction of its parasite (Dumbleton 1936).

Aphidecta oblitterata was imported from Germany to North Carolina against *Adelges piceae*, the cause of considerable damage to *Abies spp.* The aphid was accidentally introduced into North America in about 1900 and was discovered in N. Carolina in 1957. The coccinellid was released in 1960 and 1963. After four years of survival, it has been reported as a permanent addition to the predator complex (Amman 1966).

The Palaearctic *Coccinella septempunctata* is reared for repeated mass releases (see 9.222) against potato aphids in Maine (U.S.A.).

Sometimes instances of inadvertent establishment are reported without a known introduction, or instances of belated establishment many years after seemingly unsuccessful importation. Inadvertent establishment is reported by Putman (1955); the native species in Ontario, *Stethorus punctum*, has become replaced by the Palaearctic *S. punctillum*. It would certainly be extremely valuable for the theory of introductions to study such a process as it occurs; it is a pity that this was neglected. *S. punctillum* began to invade North America both from east and west, in both cases probably after accidental importation.

An example of belated establishment concerns *Cryptolaemus montrouzieri*, which is very well established round Bangalore (Futtarudriah et al. 1952), although it had hitherto remained unnoticed. The only reference to importation is in the list of introductions in Washington, D. C.: "imported into India in 1898, not established".

Recent attempts at introduction. — Attempts to control the coccid *Parlatoria blanchardi* infesting the date palm in the region of Adrar in Mauritania (Iperti and Laudého 1968, Iperti and Brun 1969, Iperti and Laudého 1969), have commenced with the importation of four species of coccinellids: *Pharoscyrnus ovoideus* (from Iran), *Chilocorus bipustulatus*¹⁾ (from Iran), *C. stigma* (from California) and *C. distigma* (from Senegal). These coccinellids are propagated in the Valbonne quarantine laboratory in the Station de Lutte Biologique at Antibes. They are reared on *Pseudaulacaspis pentagona* on potatoes and on three coccids on a gourd (pastèque): *Quadraspidiotus perniciosus*, *Chrysomphalus ficus*, and *C. dictyospermi*, and they are sent regularly to Adrar. After release, *C. bipustulatus* (from Iran) reproduces successfully and the infestation by *P. blanchardi* decreases. The dry, hot period of the year, however, is unfavourable for the permanent establishment of *C. bipustulatus*.

In Central Asia, Savoiskaya (1970b) is attempting to introduce four coccinellid species to the Alma-Ata area. Two of the species come from the Far East (*Aiolocaria mirabilis* and *Harmonia axyridis*) and two come from southern Kazakhstan (*Calvia punctata* and *Exochomus undulatus*). *C. punctata* and *H. axyridis* are aphidophagous, *E. undulatus* is coccidophagous (but can also be fed on aphids), and *A. mirabilis* is being introduced against the chrysomelid *Melasoma populi*, a pest of poplars. Both the Far Eastern species have already been released (*H. axyridis* for 3 years), but it would be premature to say whether or not they have successfully established.

General considerations. — Although a long series of successful introductions of various insect species has been made, we still do not understand the conditions which determine the success of establishment of a species in a new area. DeBach (1964) emphasizes that the only valid generalization from "more than 220 cases involving about 110 species of pests being controlled to a greater or less degree by natural enemies" is: "Over a period of time, the number of successes attained will be proportional to the amount of research and importation work carried out". All other hypotheses which have been put forward based on the accumulated evidence are contradicted by exceptions, so that any easy advice may deter potentially successful projects. Wilson (1971) also stresses that there can be no advance certainty of a successful outcome of any particular importation. The importation of natural enemies is thus still doomed to the method of trial and error. This, however, does not imply that researchers should merely rely on luck. The probability of success is much greater, if natural enemy importations are based on deductions from main ecological principles. Thus it is, for instance, advisable

¹⁾ There is an essential difference in the beetles from the Near East and Europe in their biological characteristics. Up to now it is not clear, whether just biotypes or ssp. are involved (Iperti and Brun 1969).

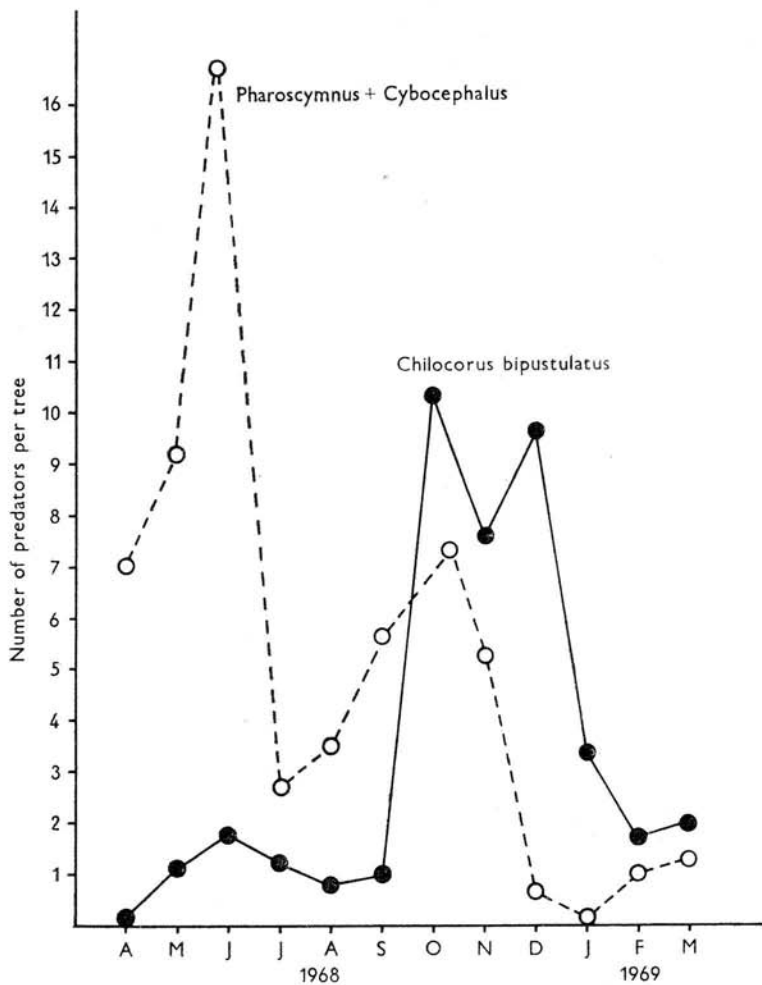


Fig. 905 Occurrence of the introduced *Chilocorus bipustulatus* var. *iranensis* and of endemic predators (*Pharoascymnus anchorage* and *Cybocephalus* sp.) on date palms in Mauretania (Laudého et al. 1970). (Larvae and adults are summed.)

to import insects from areas which are ecologically similar to the region where they are to be introduced. Also genetic studies may help in making decisions about importations. The genetic structure of the source population may differ in marginal and central areas of the species' distribution (Remington 1968). Ecologically marginal populations are small inbred units with high homozygosity and are closely adapted to a narrow range of conditions, while the ecologically central populations are numerous outcrossed units with high heterozygosity and tend to be adapted to a wide range of environments. As these assumptions by Remington seem inconsistent with his own conclusions (esp. his table), the criticism by Lucas (1969) should also be consulted. The best chance of establishment appears to be the importation of a large sample of the ecologically central population.

9.22 Conservation and augmentation

This involves two phases — first, the maintenance of existing natural enemies by avoiding harmful practices, such as use of inappropriate pesticides, and secondly the augmentation of natural enemy populations either directly by releasing them in the environment or indirectly by making the environment more favourable for them.

9.221 Selective breeding

This method has largely been neglected as regards coccinellids. Yakhontov (1957) has succeeded in raising the viability of coccinellids by inducing heterosis through intra-specific cross-breeding of individuals from different climatic regions. This type of breeding does not appear to have large-scale application, as the heterotic effect disappears in the F_2 -generation.

9.222 Colonization in the open

More often *Coccinellidae* have been used for periodic colonizations. In several cases the coccinellids for release have been produced by laboratory mass rearing.

Cryptolaemus montrouzieri was introduced into California in 1892 by Koebele against *Pseudococcus spp.* (mealybugs) infesting citrus. Permanent establishment was achieved only along the coast of southern California; in other areas, *C. montrouzieri* could not survive the winter. Even in the narrow zone of permanent establishment, the coccinellid failed to reduce the mealybug populations in time to prevent damage. The pest can be, however, kept under control by periodic re-colonizations of insectary-cultured *C. montrouzieri* released together with the encyrtid *Leptomastix dactylopii*. The coccinellid is cultured on mealybugs on potato sprouts. About 20 adults per tree are released, and each tree receives 1—5 releases each year. The production of 30 million beetles in 1960 cost 17,000 \$. The annual cost for the co-operating growers in whose groves *Cryptolaemus* and *Leptomastix* are periodically released is about 10 \$ per acre (Fischer 1963, DeBach 1964, p. 441).

Having proved successful in California, *C. montrouzieri* was subsequently imported into several subtropical regions. It has also been used with success on the Black Sea coast of the USSR (Telenga 1948, Rubtsov 1954, Yakhontov 1960).

The Palaearctic *Coccinella septempunctata* has been imported to the USA against aphids on potatoes with the aim of periodic re-colonizations, and is propagated in the laboratory at Maine (Shands et al. 1966, 1970). The recently described method for producing eggs seems to be sufficiently low in cost to be economic and to enable large-scale colonizations. One person can tend and collect the daily eggs from 2800 beetles in 112 cages. If each of ca. 1800 females deposited 25 eggs per day, one technician would then collect 315,000 eggs per week. So far 64 % of the possible production has been achieved, the major limiting factor being diapause. The mass-production technique involves two ingenious improvements. Gelatin-coated, A-fluted, single-phase corrugated cardboard serves as the oviposition substrate, and the eggs can be readily removed by dissolving the gelatin in lukewarm water. The separated eggs are sprayed in water in the field. One piece of corrugated cardboard is laid onto another with the flutes touching, and thus forming a multicelled sandwich. The sandwich appears to attract gravid females and shelters the eggs from cannibalism. Cannibalism is also decreased by a 5 cm layer of fluffy excelsior in the oviposition cages which provides increased room for the movement of non-ovipositing beetles.

In most cases of periodic re-colonization, field-collected coccinellids have been used. Between 1908 and 1914 huge numbers of *Hippodamia convergens* adults were collected from winter aggregations in the Sierra Nevada mountains of California and distributed to cantaloupe growers in the Imperial Valley for the control of melon aphid, *Aphis gossypii* (Carness 1912a, b). Such transfers, however, did not bring about control because the beetles dispersed rapidly. Scarcely any of the marked beetles could be found after three days in the area where they had been released (Hagen 1962, DeBach 1964). Recently, Hagen (in DeBach 1964, p. 444) has observed that feeding synthetic diets to *H. convergens* adults collected from aggregations somehow reduces this tendency to disperse.

Cooke (1963) made 4 massive releases (40,000 to 150,000 of beetles per release) of *H. convergens* against *Acyrtosiphon pisum* on alfalfa fields in the Blue Mountain area, and obtained some reduction in aphid population. However, the reduction was uneconomic in relation to the cost of the releases. Within 4—5 days the coccinellids left the fields with equal rapidity, whether or not they had previously been fed (for a couple of days on a formula containing honey and protein hydrolysates). Iperti (pers. comm. 1963) and Savoiskaya (in Hodek 1966, p. 318) reduced the dispersion of coccinellids after release by the diametrically opposite approach, i. e. by starving the coccinellids.

In the Georgian SSR, Bogdanova (1956) has achieved control of *Chloropulvinaria floccifera* by transferring *Hyperaspis campestris* from tree habitats to tea plantations, where it has then established. In south-eastern Kazakhstan, the release of field-collected *Adalia bipunctata* and *Coccinella septempunctata* (Savoiskaya, in Hodek 1966, p. 318) has reduced aphid infestation of orchards.

Coccinellids have even been released successfully against their alternative food. Yakhontov (1960) reported economic impact of the coccinellids *Brumus octosignatus* and *Semiadalia undecimnotata* against their alternative prey, the weevil *Phytonomus variabilis* on alfalfa in Central Asia (Tab. 9.01). The author evaluated the control achieved as incomplete, although crop yield was increased.

Tab. 9.01 Control of alfalfa weevil *Phytonomus variabilis* after release of *Coccinellidae* in Central Asia (Yakhontov 1960)

Coccinellid species released	<i>Brumus octosignatus</i>	<i>Semiadalia undecimnotata</i>
Number of weevil larvae per coccinellid	20—40	20—80
Increase of dry alfalfa yield [kg/hectare] compared with control plots	by 60—270	by 160—660

Some authors make recommendations on colonization by coccinellids without having attempted it by themselves. Dösse (1957) advises the release of young larvae of *Stethorus gilvifrons* at the beginning of the population increase of tetranychid mites on apple trees in the Lebanon, and Sundby (1968) in Norway similarly recommends the release of *C. septempunctata* against aphids in the fields early in the season.

9.223 Use in glass-houses

A special case of augmentative manipulation of coccinellids is their use in the closed environment of the glass-house. *Cryptolaemus montrouzieri* has been released with success in glass-houses for the control of mealybugs on flower crops (DeBach 1964, p. 443). In

one case, where *C. montrouzieri* was not effective because of low temperature, *Exochomus flavipes* was liberated along with *Anagyrus kivuensis* and *Chrysopa plorabunda*, and this gave effective control of *Pseudococcus citri* (Doutt 1951).

Gurney and Hussey (1970) tested 4 species of coccinellids with the aim of using them for biological control of aphids on cucumbers and chrysanthemums in glasshouses, and arrived at somewhat discouraging conclusions. They apparently also found it too laborious to be economical to rear coccinellids on an aphid diet. It is possible, however, that other species may be more suitable than the species tested. These included *Coleomegilla maculata* which is preferentially pollinivorous (see 6.12), and *Coccinella septempunctata*, which had been collected in the hibernation sites in the Himalayas while in diapause, and therefore was possibly not in the most suitable life-phase.

It is likely that coccinellid species which are small in size and also have an adequate range of optimum temperature will be better suited to breed in glass-houses. The promising results of preliminary tests with *Adonia variegata* in France (Jourdeuil, pers. comm.) seem to support this suggestion.

9.224 Sensible use of pesticides

The application of insecticides has often caused outbreaks of new or old pests previously kept in control by introduced natural enemies. An example was the resurgence of *Icerya purchasi* following destruction of *Rodolia cardinalis* by DDT and malathion (DeBach 1947, Bartlett and Legace 1960).

Natural enemies can to a large extent be conserved by supervised use of chemical control. The ecologically damaging zeal for exterminating pests must be completely abandoned. Pesticides should never be applied as a routine preventative measure; if their application is inevitable, selective compounds should be used at an appropriate time. All aspects of this subject have been discussed by Bartlett (in DeBach 1964, p. 439) and Newsom (1967). Bartlett has also tabulated pesticides in respect of their toxicity to natural enemies. In this list, the pesticides least toxic to coccinellids are: butylpheroxyisopropyl chloroethyl sulphite, captan, chlorfenson, chlorobenzilate, bis (4-chlorophenoxy) methane, 1,1-dichloro-2,2-bis (4-ethylphenyl) ethane, 2,4-dichlorophenyl benzenesulphonate, dicofol, dinocap, ferbam, gamma-BHC, glyodin, ryania, sabadilla, schradan, tetradifon, trichlorophon, zineb.¹⁾ Comparative studies on the sensitivity of coccinellids to pesticides have been carried out by many authors; the most recent are: Atallah and Newsom 1966b, Bartlett 1965, Campbell and Hutchins 1964, Cherry and Pless 1969, Hamilton and Kieckhefer 1968, 1969, Hukusima 1964, Kehat and Swirski 1964, Laster and Brazzel 1968, Lindgren and Ridgway 1967, Meier (in Hodek 1966, p. 323), Nagui 1969, Nohara et al. 1965, Takeda et al. 1965, Wiackowski and Dronka 1968, Wiackowski and Nowacka 1968, Yun and Ruppel 1964, Zelený (in Hodek 1966, p. 337), Zelený 1969.

In general, contact insecticides are highly toxic to coccinellids whereas systemic insecticides are highly selective or are made selective if they are applied via the soil. There is considerable variation in the resistance of individual coccinellid species. Usually larvae are more sensitive than pupae or adults. Some insecticidal compounds may be added to Bartlett's list of pesticides with low toxicity to coccinellids: thiometon (Zelený), demeton and menazon (Wiackowski and Nowacka), and metox (Wiackowski and Dronka). *Coleomegilla maculata* is resistant to DDT; the mechanism was studied by

¹⁾ In order to facilitate reference to the chemical compounds quoted, the standard "chemical names" (Martin 1963) have been used.

Atallah and Nettles (1966) and ascribed at least in part to the ability of this coccinellid to metabolize DDT to DDE (1,1 — dichloro — 2,2- bis/p-chlorophenyl/ ethylene).

Coccinellids can also be preserved by suitable timing of chemical applications. Hodek et al. (in Hodek 1966, p. 331) advise that aphicides are best applied to sugar-beet during the two weeks following the end of the main immigration of *A. fabae* from *Euonymus*. Savoiskaya (in Hodek 1966, p. 317) gives recommendations for the timing of the first two sprays in apple orchards in Alma-Ata. In general, chemical treatments should be avoided during the peak phase of the aphid infestation (see 9.122).

In apple orchards in Japan, Hokusima (1968, 1969) combined applications of selective fungicides and acaricides with the release of the coccinellids *Harmonia axyridis* and *Propylaea japonica* and the spider *Misumena tricuspidata*. The predators appeared to survive. If, however, aphicides must be applied at times when coccinellids should be preserved, intrinsically specific chemicals as nicotin, schradan, menazon or pirimicarb should be used (Way, pers. comm. 1971). Alternatively, specificity can be conferred on an otherwise non-specific chemical if it is applied in granular formulation on the foliage or is placed in the soil.

9.225 Modification of cultural practices

There have been many suggestions for promoting the effectiveness of coccinellids by cultural means. Destruction of the ground cover drives the beetles into orchard trees and has been accomplished by cutting the grass in south-eastern Kazakhstan orchards (Savoiskaya, in Hodek 1966, p. 317) and by cultivating the ground under walnut trees in California (Hagen and Sluss, in Hodek 1966, p. 245). Careful timing can establish a good beetle/aphid ratio in the trees. Adjacent parts of a crop may serve as refuges for coccinellids and enable them to re-invade strips treated with insecticide (Dyadechko 1953, Sem'yanov 1965c) or crops harvested in strips (Schlinger and Dietrick 1960). An example given by the latter authors shows the adverse effects of mowing the entire field of alfalfa at one time (regular farming) in contrast to mowing in alternate strips (strip-farming). Although the aphid occurred at similar densities under both systems early in the season, it rose to densities causing considerable damage in the regular-farmed field, but numbers became negligible in the strip-farmed field (Tab. 9.02). In addition to these numerical differences, several species of parasites which were effective in the strip-farmed field never appeared in the regular-farmed one.

Tab. 9.02 The effect of strip-farming and regular farming on the average number of natural enemies of *Therioaphis maculata* (Schlinger and Dietrick 1960)

Group of natural enemies	Regular farming ¹⁾ (thousands of individuals/acre)	Strip farming ¹⁾ (thousands of individuals/acre]
Coccinellid adults	46	205
Coccinellid larvae	11	232
Chrysopid larvae	195	206
Hymenopterous parasites	70	287
„Big-eyed“ <i>Heteroptera</i>	199	401
An aphidophagous spider	105	1094
Totals	626	2435

¹⁾ June 1959, Brawley, California.

Burning old grass early in spring, which is practised in central Europe, is very detrimental to coccinellids. The burning is done on headlands, dykes and other habitats in arable land which are used by coccinellids as dormancy sites; many coccinellids are thus destroyed.

Tamaki and Halfhill (1968) have used defoliant to suppress *Myzus persicae* on peach trees. The aphids concentrated on the remaining foliage and were then easy prey for predators migrating into the orchards in autumn. The number of overwintering aphid eggs was thus reduced.

9.226 Providing alternative food

A whole range of natural enemies suffer from a lack of pollen and nectar in pure monocultures. Pollen and nectar are particularly required by the adults of hymenopterous parasites and adult syrphids, but this food is also important for coccinellids when essential prey is missing (see 6.111). The artificial provision of certain flowering plants, which has been recommended for other natural enemies, would be valuable for coccinellids also.

It has been shown that populations of predators, including *Coccinellidae*, can also be increased by treating the crops with alternative artificial food (Schiefelbein and Chiang 1966, Smith 1965a, b). This could be used to attract the coccinellids to the required habitats especially at the time when the pest begins to occur; perhaps also after the end of the infestation in order to maintain a high number of coccinellids, mainly for the next season.

9.227 Providing shelter

That adjacent shelter used by coccinellids for hibernation can produce a higher and usually earlier occurrence of the predator on the crop has been demonstrated for sugar-beet (Bombosch 1965), potatoes (Fenjves 1945, Galecka, in Hodek 1966, p. 255) and brussels sprouts (van Emden 1965a, b, c). In Czechoslovakia, it has been recommended (Hodek et al. 1962) that patches and strips of woodland should be planted to compensate for the amalgamation of small fields into large crop acreages.

In south-eastern France, Iperti (in Hodek 1966, p. 189) has used artificial traps which simulate rock cracks to effect a considerable reduction in the high *Beauveria* mortality which takes place in *Semiadalia undecimnotata* sheltering amid vegetation for hibernation. (Photo 50). These traps also facilitate the collection and transport of hibernating coccinellids for use in biological control. On the Black Sea coast in the Caucasus, large moderately heated cages placed around the trees have been used for overwintering *Rodolia cardinalis* and *Cryptolaemus montrouzieri*. The predators from such cages show a greater viability than those bred in the laboratory and the cost of the spring release is reduced (Sysoev 1958).

Nohara (1962) recommends that citrus branches be wrapped in cloth to provide artificial hibernation quarters for *Chilocorus kuwanae*. With the same aim — enabling the predators to overwinter — Tamaki and Weeks (1968) put black painted aluminium bands (lined with thick paper and tarred burlap) on the main branches of peach trees.

Such banding on trees may also benefit the predator in another way. Smith and Armitage (1931) found that bands on the trunks of citrus trees benefited *C. montrouzieri* by attracting both the prey (*Pseudococcus gahani*) and the coccinellid, thereby increasing the intensity of predation.

9.3 Conclusions

There is abundant evidence that coccinellids are often a major cause of mortality of aphids, coccids and spider mites. In regions where coccids are serious pests particular coccinellid species with a high degree of prey specificity may be paramount in the biological control of a pest (e. g. *Rodolia*) and there may be further opportunities for spectacular biological control through introductions of such coccinellids.

Coccinellids that prey on aphids are relatively less specific, and this characteristic, together with the aphids' ephemeral occurrence on particular host-plants, makes it likely that coccinellids will provide their contribution as a major component of the overall biological control complex in integrated control practices. Despite the very considerable amount of work already done on aphidophagous coccinellids much still needs to be done before they can be used to best advantage. In particular much more behavioural and ecological work is required of the type needed for population models in which the quantitative effects of the different natural enemies are separately determined. Such knowledge could then be used to manipulate those coccinellid species which play or could play a key role in depressing aphid numbers.