

Biodiversity of predaceous coccinellidae in relation to bioindication and economic importance

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Abstract

Their pioneering role in the development of biological pest control has rendered the Coccinellidae of great practical and scientific interest. About 90% of the approximately 4200 coccinellid species are considered beneficial because of their predatory activity, mainly against Homopteran insects and mites. Coccinellids live in all terrestrial ecosystems: tundra, forest, grassland, agrosystems, and from the plains to mountains.

Knowledge of coccinellid life history requires investigation of their bio-ecology. Being holometabolous insects, coccinellids present all types of voltinism. They reproduce in different habitats and show a wide range of behaviours, from stenotropism to eurytropism. In spite of their polyphagy, adults tend to prefer certain types of food (or essential prey), which are eaten voraciously. Many aphidophagous and monovoltine coccinellid species migrate in response to unfavourable environmental conditions; however, in most cases adults endure hostile environmental changes by entering a temporary dormant state, i.e., hibernation, aestivation or aestivo-hibernation. Despite these adaptive behaviours, the coccinellids are very vulnerable to several limiting factors, including natural enemies and anthropological influences. Therefore, many precautions must be taken throughout the year to protect them.

Seasonal changes influence the occurrence of aphid outbreaks, the type of plant infested and the behaviour of coccinellids. Reciprocally, the species found in different geographic zones can be recruited as bioindicator insects owing to their climatic and trophic characteristics. In the context of biological control, the coccinellids represent an important cause of mortality of coccids, aphids and mites. The peculiar aggregation behaviour of coccinellids remains to be exploited for acclimatization of a new species in a new country. Their migratory abilities pose challenges and opportunities for the development of effective biological control programs against aphids. Future research on the genetics, physiology and behaviour of coccinellids combined with studies of their flight aerodynamics and interactions with agricultural ecosystems will undoubtedly lead to improvements in coccinellid-based aphid control programs. ©1999 Elsevier Science B.V. All rights reserved.

Keywords: Bio-ecology; Coccinellidae; Taxonomy; Bioindicator; Biological control; Migration

1. Introduction

Beetles of the family Coccinellidae, commonly called ladybirds, Marienkäfer, Mariguaita, Bête à Bon Dieu and many other affectionate nicknames (often referring to the Virgin Mary), are widely considered

to symbolize happiness, good-will and serenity. From a practical point of view, the family includes many important predators of insect pests such as aphids and scales. Taxonomically coccinellids are one of the best known families of Coleoptera because of their distinctive appearance, with many reddish-coloured, black-spotted species. These ubiquitous insects are found from Alaska to Argentina, from Scandinavia to

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South Africa, in the Far East and in Australia. Faunistically, the group is better known in Europe, Japan and North America. Since Linnaeus (1768) till now, about 490 genera and 4200 species of Coccinellidae have been described around the world; among them, 400 species live in North America (Belicek, 1976) and about 110 species in Europe (Iperiti, 1986a) including the species acclimatized in this century, e.g., *Rodolia cardinalis* Muls., *Cryptolaemus montrouzieri* Muls., *Lindorus lophantae* Blaisd., *Rhyzobius forestieri* Muls., and *Serangium paracetosum* Sicard.

The majority of coccinellid species (about 90%) are beneficial predators; others are phytophagous on crops or fungivorous. The feeding habits of larvae and adults are similar. Generally, the brightly coloured species feed on aphids, while the darker colored and smaller species feed on scale insects, mealybugs, whiteflies or spider mites. When their preferred prey is scarce ladybirds rely on alternative food sources such as honeydew, extrafloral nectar, pollen, etc.

Coccinellids live in all the ecosystems of the world including tundra, forest, grass-land and agroecosystems, and at nearly all elevations. Some species periodically move from meadows to forests or from valleys to mountains. To investigate this family it is necessary to study their physiology, biology and ecology, i.e., their microclimatic and trophic specificity, their limiting factors and their possibility to migrate.

Beginning with introduction of *R. cardinalis* from Australia into California during the 1880s to control the cottony cushion scale (*Icerya purchasi* Mask.) on citrus crops, ladybirds have played a significant role in the development of biological control strategies. In fact, the story of *R. cardinalis* is the founding event in classical biological control. Many species of ladybirds have subsequently been acclimatized in attempts to control noxious insects introduced in new areas. While ladybird species that prey upon stationary pests, scale insects or mealybugs have often been successful as biological control agents, aphidophagous species, which migrate over long distances between feeding sites and hibernating shelters, have yielded less satisfying results.

2. General taxonomy

The family Coccinellidae belongs to the coleopterous superfamily Cucujoidea (section Clavicornia).

Historically many authors have proposed systems to classify the coccinellids within subfamilies and tribus. Mulsant (1866, 1950) in 1866 and 1950, Crotch (1874) in 1874 and in this century, Korschefsky (1931, 1932) and Mader (1955) have tried to arrange all the Coccinellidae in a system that has now gained general acceptance. Sasaji (1968) presented a modern system for classifying all coccinellids of the world based on the comparative morphology of the larvae and adults and has described the main subfamilies and the tribus living in the Palaearctic zone. Sasaji divided the family into six subfamilies: the Sticholotinae, Scymninae, Chilocorinae, Coccidulinae, Coccinellinae, and Epilachninae. According to Bielawsky (1959), European species are mainly represented by three subfamilies, the Scymninae, Chilocorinae and Coccinellinae; there are no European Sticholotinae, very few Coccidulinae and only three species of Epilachninae.

Sasaji (1968) concluded that Coccidulinae are undoubtedly extremely primitive, and suggested that the most ancient of the remaining five subfamilies is perhaps Sticholotinae, followed by Chilocorinae and Scymninae, which belong to a monophyletic group. The subfamilies Coccinellinae and Epilachninae include the most advanced tribes, and have evolved from certain Sticholotinae ancestors without any connection to the Scymninae and Chilocorinae stock. Their phylogenetic pattern of divergence is associated with a change of feeding habits from carnivorous to phytophagous. Sasaji's views are not completely accepted by the authors of new phylogeny systems.

It is difficult to identify ladybirds only on the basis of their colour pattern, which is extremely variable in most species. For identification of coccinellids in Europe, it is convenient to refer to the system of Bielawsky (1959), which is adapted to the faunistic diversity of the subfamilies and the tribus living in the palaearctic zone. Detailed keys to the subfamilies, tribus, genera, and species of some larvae of the Palaearctic coccinellids are given by Savoiskaya and Klausnitzer (1973); a simple key for field use is provided by Klausnitzer and Kovar (1973). Additional taxonomy works include those of Belicek (1976), Bielawsky (1959), Dauguet (1949) and Gourreau (1974). The most recent systems to classify coccinellids were presented by Chazeau et al. (1989), Fürsch (1990) and Kovar (1996).

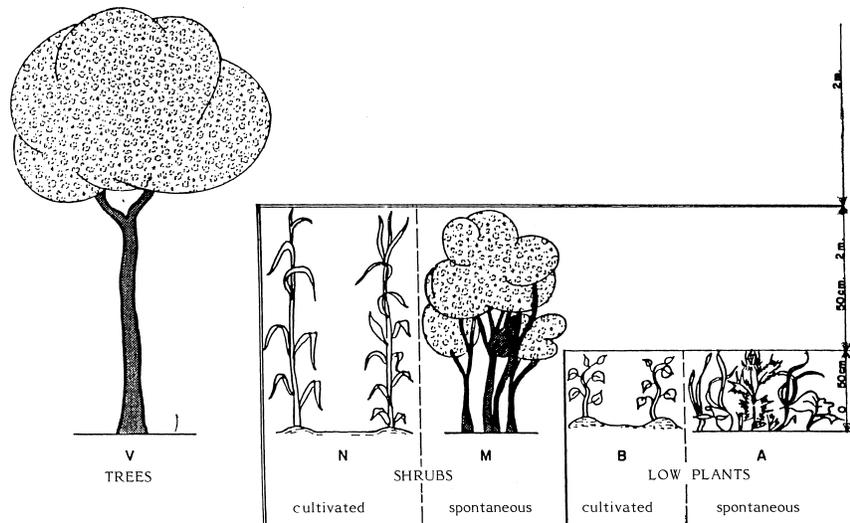


Fig. 1.

It is difficult to precisely identify the coccinellids due to their production of many morphs. Their identification is only possible by looking carefully at morphological characters of the ventral side, especially the colour of epimera I, II and III. Identification in the field requires other criteria based on the most easily distinguishable characteristics such as shape, size, color and pilosity, which are often sufficient to recognize their trophic preference, often the main point of the study (Fig. 1). It is necessary to discriminate between the large beetles (3–9 mm long), which are glabrous, the small ones (less than 3 mm) which are pubescent, and the very small ones (less than 2 mm) which most often eat mites or aleurodes. The three groups represent 60%, 39% and 1% of the coccinellid species, respectively. It is sometimes possible to predict the trophic range of coccinellids from their elytral colour. For example, in Europe, aphidophagous coccinellids have bright red, yellow or pink elytra and constitute 65% of coccinellid species (tribus: Coccinellini, Hippodamini; *Scymnus* spp., *Pullus* spp.). Coccidophagous coccinellids are dark in colour and represent 25% of the coccinellid species (tribus: Chilocorini, Hyperaspini; *Sidis* spp., *Nephus* spp., *Cryptolaemus* spp.). Mycophagous coccinellids are generally light maroon or white or sometimes lemon yellow and represent 8% of coccinellid species (tribus: Psyllorini; *Rhyzobius* spp.). Aphidophagous coccinellids living in forests (tribus: Coccinellini, Hippodamiini)

are fulvous. Phytophagous coccinellids are also fulvous but unlike forest aphids they are pubescent (ca. 1%)(tribus: Epilachnini).

3. Sampling

Different methods can be used to sample populations of coccinellids according to the strata (trees, shrubs or low plants) and the season (period of activity and period of rest). Sampling coccinellids during their period of activity is challenging due to their high mobility. Coccinellids on trees and shrubs can be studied by visual control (useful for appraising the population on a large scale) or by beating the plant's branches to dislodge larvae and adults. Coccinellids on low plants can be studied by visual control, removal sampling (useful for determining the proportion of different instars) or by collecting plants (especially useful for assessing density of eggs) (Lapchin et al., 1987). In spring, the best period to sample are in the morning before 10 a.m. and the afternoon after 5 p.m. when coccinellids are most likely to be found in vegetation. During dormancy, the adults can be sampled from aggregations in different hibernation sites, which are generally located outside cultivated fields, at the base of plants or under rocks. It is important that the sampling repetitions be carried out systematically, i.e., with an adequate and consistent number of beatings, visual scanning for the same amount of time, etc.

These sampling methods give an index of plants frequented by coccinellids and allow assessment of their capacity to control homopterous pests. To give an example, a beating control done on the totality of the branches of one apple tree (in an orchard in the south of France, with 150 trees/ha, 10-years old) gave the following guidelines for pest control: less than 20 coccinellids (*C. bipustulatus* against Diaspinae or *A. bipunctata* against Aphididae) indicated no chance for controlling a spring outbreak; between 30 and 50 coccinellids indicated that the pest population could be maintained at the same level; more than 100 coccinellids indicated efficient biological control.

The best way to assess the efficiency of coccinellids in controlling pests is to compare the biomass of the prey with the voracity of the predators per surface unit. However, this is no easy task, as it is very difficult to sample Coccinellidae. Failing to determine the real density of the coccinellids in relation to the density of the pests, it is possible to indirectly appraise their efficiency by following fluctuations in the pest population (Ipert and Hodek, 1974).

4. Typical habitat

Coccinellid species can be classified as stenotopic or eurytopic (Hodek, 1973). A given area is defined as a typical habitat on the basis of its degree of attraction for adult predators, the quantity of larvae present, and its degree of nutritive suitability, established in the laboratory by comparing the consumption of different types of prey found in the area.

Alimentary factors influence the behaviour and food specificity of coccinellids only within the range of the spatial distribution of adults according to their preferred strata of vegetation. On the contrary, microclimatic conditions appear to be particularly important in determining the habitat specificity of coccinellids (Ipert, 1965a, 1965b). The importance of microclimatic factors is demonstrated by the fact that a range of host plants infested with *Aphis fabae* scop. attract different species of ladybirds. For example, *A. bipunctata* is found on *Evonymus europaeus* L. (a shrub), *C. septempunctata* on *Chenopodium album* L. (a spontaneous low plant), *S. undecimnotata* on *Vicia faba* L. (a cultivated low plant) and *A. variegata* on *Phaseolus vulgaris* L. (a cultivated shrub). In addition, certain

types of vegetation are preferred by certain ladybird species, which sometimes exhibit seasonal preferences for certain strata of the habitat. This is the case with some common aphidophagous predators from European regions (Fig. 2): some species such as *C. septempunctata* and *S. undecimnotata* generally lay eggs on low plants (0–50 cm) infested by aphids; others such as *P. quatuordecimpunctata* and *A. variegata* often occur on shrubs (0.50–2 m); and several species such as *A. bipunctata*, *S. conglobata* and *A. decempunctata* mostly depend on tree dwelling aphids (above 2 m) (Ipert, 1965a, 1965b).

Predators constantly search for a suitable microclimate, preferred plant strata and a plentiful food source. Therefore, the study of habitat specificity is essential for understanding the behaviour of active aphidophagous predators. It is also necessary to differentiate between spring and summer climatic conditions. In spring a large number of aphids infest the young shoots of a great number of plants, thus offering an excellent habitat in which predators may complete their cycle under good feeding conditions. In summer aphid infestation is considerably reduced, and behaviour of the predator is dependent only on the presence of aphids, regardless of the microclimatic conditions and the suitability of food. Apart from their influence on the synchronisation of predators and prey, seasonal changes in climatic conditions substantially affect the distribution of coccinellids by changing the microclimatic characteristics of habitats and by influencing the growth of aphid populations through the physiology of plants.

5. Voltinism and reproduction

In temperate climates, predaceous coccinellids generally reproduce in spring when their prey are abundant and become quiescent in summer. Some species exhibit renewed activity in autumn, and all coccinellids display varying levels of dormancy in winter. All individuals of a given coccinellid species do not react similarly in the same geographical area, nor does one species necessarily produce the same number of generations over its entire distribution range (Hagen, 1962).

Univoltinism is common in many aphidophagous species of the Coccinellini and Hippodamini tribes (Banks, 1954; Delucchi, 1954; Hodek, 1958; Hagen,

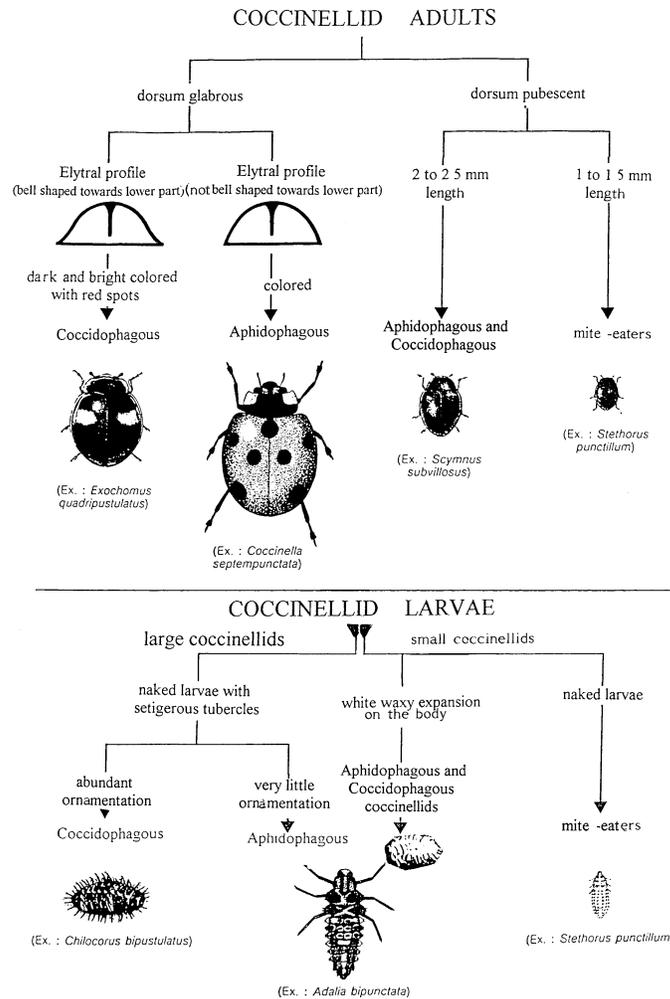


Fig. 2.

1962; Schroeder, 1909) and is sometimes exhibited by some coccidophagous species (Katsoyannos, 1983) and mycophagous species (Evans, 1936). Bivoltinism is observed in aphidophagous species belonging essentially to the Hippodamiini (Hagen, 1962) and Coccinellini tribes (Hagen, 1962; Ongagna et al., 1993). Bivoltinism with an interval of aestivation is characteristic of some aphidophagous species from the Hippodamiini and Coccinellini tribes (Ibrahim, 1955; Hagen, 1962; Quilici, 1981). Multivoltinism with at least three generations per year is the rule for all the coccidophagous insects from the Chilocorini tribes (Ipert et al., 1970; Katsoyannos, 1983), some aphidophagous species from the Coccinellini tribes (Thompson, 1926;

Ipert, 1986a), and for *Scymnus apetzii* Muls. and *S. subvillosus* (Ipert, 1986a, 1986b).

Some coccinellids present successive generations, without dormancy of adults. These are mainly represented by the exotic species introduced from Australia and the Pacific region to California and Europe, especially the coccidophagous predators from the Coccidulini tribes (Poutiers, 1930; Sezer, 1970) and from the Scymnini tribes. In Europe, ladybirds present all types of voltinism. Commonly the large-sized aphidophagous insects develop one generation per year, most often in spring, and the coccidophagous predators produce at least three generations per year in spring, summer and autumn. The small-sized coccinel-

lids reproduce mainly in summer when the temperature is high.

Coccinellids are holometabolous insects which lay eggs, develop through four larval instars (rarely 3 or 5), pupate and become adults. The duration of their development cycle ranges from less than 2 weeks up to 2 months depending on size, thermal conditions and trophic specificity. The ovaries of females mature after the end of hibernation after they have fed on aphids. The gonads of males collected from hibernation sites in autumn reveal some spermatogenesis (e.g., in *C. septempunctata*; Ceryngier et al., 1992). During the initial period of diapause males of *S. undecimnotata* have active testes but their activity decreases with decrease in temperature. Females of this species and of *Adalia bipunctata* have empty spermathecae from the beginning of dormancy until spring (Hodek and Landa, 1971; Hemptinne and Naisse, 1987). Mating occurs mainly in aggregation sites shortly before the beetles disperse or migrate at the termination of dormancy; the preoviposition period most often lasts about 1 week. This behavior is probably important for the survival of migrating species, as only one mating is necessary to fertilize all the eggs laid throughout the female's life. The oviposition rate of females is proportional to the number of ovarioles in the ovaries, which varies greatly among feeding groups and species (e.g., from less than 4 to more than 50; Ipert et al., 1977).

Most aphidophagous coccinellids deposit their eggs in regular clusters containing 10–100 eggs; coccidophagous coccinellids produce smaller clusters.

Laboratory studies showed that the total number of eggs laid by a given female over the study period (about 2 months) varied among species and was influenced by many factors, including seasonal temperature and quantity and quality of food (Quilici, 1981). Vitellogenesis depends on physical and trophic factors. Laboratory experiments demonstrate that, paradoxically, polyvoltine species generally show higher fecundity in spring, and that monovoltine species show higher fecundity in summer.

The small barrel-shaped eggs are initially yellowish in color, and then darken just before hatching. Most of the common species deposit their egg clusters on the undersides of leaves near their prey. The eggs of aphidophagous predators hatch after 2–5 days; incubation requires from 7–9 days in coccidophagous species. The very active larvae are dark in color, with a long

body, long legs and characteristic setae. The larvae of Scymnini are covered with thick waxy white coloured exudations that are easy to remove with simple brushing, which makes them resemble mealybugs (Coccidae). Pupae are naked in aphidophagous species and in Sticholotinae. In coccidophagous species of Chilocorini and Noviini tribes, the pupa develops within the larval skin and in Hyperaspini and Scymnini the larval skin completely covers the pupa.

Adult coccinellids that emerge in spring disperse rapidly from the site of larval development. Less than a week after emergence the adults mate and about 1 week later the females begin to oviposit. In summer and autumn the newly emerged adults enter dormancy (aestivation and hibernation, respectively). The reproductive activity of coccinellids is dependent on the thermal conditions. A mathematical model formulated by Sanderson and Peairs (1913) can be used to calculate the lower development threshold (T_l) and the thermal constant (C) (Table 1). For the coccinellids living in temperate areas, the value of the upper development threshold is above 32–33°C.

Longevity of adults depends on their voltinism, and can range from a few months to years. Coccinellids native to temperate zones estivate or hibernate as adults and enter either simple quiescence or intense diapause. In contrast, exotic species such as *Lindorus lophantae* Blaisd., *Cryptolaemus montrouzieri* Muls. and *Novius cardinalis* Muls. do not estivate or hibernate; instead, their larval stages resist drastic changes in climate, reducing the speed of development during winter but never stopping it entirely.

6. Eating habits

To consume their prey ladybirds insert their mandibles into various parts of the victim's body and sometimes perform a preoral digestion. Generally the adults eat the entire body of the prey, including all solid and liquid parts. The feeding behaviour of larvae varies greatly according to the different species, with some larvae eating only a portion of the prey's body.

Coccinellids accept a wide range of food and the larvae eat the same prey as adults. As adults are polyphagous, lists of prey taken by coccinellids are not sufficiently informative for determining a predator-prey relationship (Balduf, 1935). However, they complete larval development and produce viable

Table 1

Lower development threshold (T1) and thermal constant (C) of the most common European species

<i>Aphidophagous</i>	
<i>Coccinella septempunctata</i>	T1 = 12.8°C; C = 227 (Bodenheimer, 1943)
<i>Propylea quatuordecimpunctata</i>	T1 = 13.3°C; C = 280 (Quilici, 1981)
<i>Adalia bipunctata</i>	T1 = 9°C; C = 390 (Bodenheimer and Neumark, 1955)
<i>Synharmonia conglobata</i>	T1 = 12.4°C; C = 323 (Bodenheimer and Neumark, 1955)
<i>Adonia variegata</i>	T1 = 13°C; C = ? (Ipertí, unpublished observation)
<i>Semiadalia undecimnotata</i>	T1 ≠ 10°C; C = ? (Ipertí, unpublished observation)
<i>Coccidophagous</i>	
<i>Chilocorus bipustulatus</i>	T1 = 10.6°C; C = 697 (Bodenheimer and Neumark, 1955)

progeny only if they consume their 'essential food' (Hodek, 1973). In contrast, adults can survive on 'alternative food' which may consist almost wholly of spores of the lower cryptogams, pollen grains, and plant aphids and varying but little from one genus to another, as observed by Forbes (1876–1883) in his early studies of coccinellid feeding habits (1876–1883).

Despite their polyphagy, adults tend to prefer certain types of food. For example, the adults of *C. septempunctata* prefer aphids attacking wheat (*Metopolophium dirhodum* Walk., *Sitobion avenae* F. and *Rhopalosiphum padi* L.), and adults of *S. undecimnotata* prefer *Aphis fabae* Scop., which attacks beans.

Most coccinellids undergo normal oogenesis only when their essential prey is available. Consumption of certain aphid species does not allow completion of ovarian differentiation, and some prey species are toxic: for example, *Aphis nerii* Boyer de Fonscolombe on *Nerium oleander* (rose-laurel) is unsuitable food for most coccinellids except *Adonia variegata* Goeze. Taking into consideration their degree of evolution, it is interesting to note that the most primitive coccinellids are coccidophagous and that the most evolved species are aphidophagous or surprisingly phytophagous in a few cases. A survey of the food specificity of Coccinellidae has been made by Balduf (1935). The different tribes included in the six subfamilies of Coccinellidae tend to share the same determined food habits, with some exceptions (Sasaji, 1968). Among Sticholotinae tribes, Sukunahikonini, Pharini, and Microweisini eat principally Coccidae, chiefly Diaspinae. One tribe, Serangini, attacks the aleyrodids. Among Coccidulinae, practically all the Coccidulini eat coccids, 51% of Rhizobiini consume Diaspinae, 35% Coccinae and 14% Lecaniinae. Exoplectrini and Noviini are reported to feed mostly on

Icerya spp. and their nearest relatives. Among Chilocorinae, 79% of the species of Chilocorini feed on coccids, mainly Diaspinae. *Brumus* spp., *Aspidimerus* spp., *Stictobura* spp. and *Orcus* spp. eat *Pseudococcus* spp. 71% of the food of European and American *Exochomus* spp. consists of Coccidae, principally Diaspinae and Lecaninae. However, African species of *Exochomus* eat aphids. Among the Scymninae, *Stethorus* spp. eat exclusively phytophagous mites; 62% of the Scymnini feed on scales and 23% on aphids; *Clithostethus* spp. and *Lioscymnus* spp. consume Aleyrodidae; *Diomus* spp., *Nephus* spp., *Sidis* spp., *Parasidis* spp., *Cryptolaemus* spp. and *Pseudoscymnus* spp. eat *Pseudococcus* spp. and their close relatives. *Platyorus* spp., *Pullus* spp. and *Scymnus* spp. live on aphids. Within Coccinellinae, the majority of the aphid-eating coccinellids belong to the large tribes Hippodamiini and Coccinellini. Most Hippodamiini and Coccinellini are in fact aphidophagous (76% and 85%, respectively); a minority (1% in each tribe) feed on plants and the remainder feed on Coleoptera, Heteroptera, Homoptera, and also on Acarina. The tribes of Psylloborini eat fungi (Erisyphe). Among the Epilachninae, all the species of *Epilachnini* are phytophagous. In Europe, Africa and Asia *Epilachna* spp. and *Henosepilachna* spp. have a strong tendency to attack cucurbitaceous plants, while in the USA and South America, *Epilachna varivestis* Muls. (the Mexican bean beetle) is a very important pest comparable in noxiousness to the Colorado beetle on potatoes.

Many factors affect food consumption, including density of the prey (Popov, 1960), temperature (Hodek, 1958), age of the larval stage (Ipertí, 1986a), sex and activity of the adults (Ipertí, 1986b) and size of the species (Hodek, 1973). During the different larval stages, prey consumption increases exponentially according to larval size. In the fourth larval stage food

Table 2
Voracity of some *Coccinellidae*

Aphidophagous species	Average number of small aphids consumed daily by		Average number of medium sized aphids consumed daily by	
	L1	L2	L3	L4
<i>C. septempunctata</i>	8	18	20	35
<i>S. undecimnotata</i>	12	26	25	42
<i>A. bipunctata</i>	13	20	19	35
<i>A. variegata</i>	8	18	16	22
<i>P. quatuordecimpunctata</i>	8	15	18	22
Coccidophagous species	1st and 2nd stage scales consumed daily by		Female scales consumed daily by	
	L1	L2	L3	L4
<i>Chilocorus bipustulatus</i> L.	9–21	31–66	24–30	31–52
<i>Chilocorus elegans</i> Mader	14–20	34–57	19–34	40–58

consumption reaches 80% of weight of the prey eaten during the entire preimaginal period. Data regarding the number of prey animals consumed each day (i.e. voracity) by the most common aphidophagous and coccidophagous species are provided in Ipert (1965a, 1965b); Table 2 summarizes data obtained for instars of several aphidophagous and coccidophagous species maintained at 25°C and 70–80% relative humidity. Temperature influences the duration of developmental instars, and thus also affects the total larval feeding rate.

The only way to compare the feeding rates of various species of coccinellids is to express the quantity of prey consumed in terms of biomass. In adults the daily food intake can equal its body weight. Voracity is usually higher in ovipositing females and always lower in males; adults do not feed during aestivation or hibernation. Predators larger than 3 mm-long are the most voracious. Smaller individuals attack prey which are less numerous, generally later in the season. This is the case with *Scymnus apetzii* Muls., whose fourth instar larvae consume about 15 third instar *Myzodes persicae* Sulzer per day in summer. The small larvae commonly eat the smallest nymphs, and a decline in feeding is observed on the last day before moulting or before pupation. Adults consume less food in the first days of their life than during their reproductive period (Balduf, 1935).

7. Migration and dormancy

Many species of aphidophagous and monovoltine Coccinellidae migrate. Migration of Coccinellidae oc-

curs soon after the first generation adults emerge, during the first warm days of the year, usually at the beginning of summer in the temperate regions. Coccinellidae are well adapted to pursue mobile prey such as aphids and are able to move continuously in search of occasional aphid outbreaks. Therefore, their migratory abilities are only an exaggeration of their normal flight habits.

The photoperiod provides a very precise cue for the initiation of migration (Hodek and Ipert, 1983), hence the famous ‘oogenesis flight syndrome’ of Johnson (1969) (i.e., the general ability of very young adults, less than 2 weeks of age, to migrate) (Rankin et al., 1986). Short photoperiod, unfavorable temperatures and changes in food availability and quality are important factors inducing migration (Hodek, 1958; Johnson, 1969; Ipert and Hodek, 1974; Rolley et al., 1974; Nichols and Nell, 1977; Zaslavski and Sem’yanov, 1983; Obrycki et al., 1987; Ipert et al., 1988). Other cues for migration include endocrine factors (Rankin et al., 1986); wind (Yan et al., 1981; Tsai et al., 1986); rainfall (Yan et al., 1981); natural enemies (Dong et al., 1982; Ruzicka and Hagen, 1985); and disease pressures (Ipert, 1965a, 1965b, 1986b). On the other hand, industrialisation has been shown to interfere with migration of *Coccinella septempunctata* L. (Galecka, 1980).

The mechanisms that control the direction, speed and distance covered by Coccinellidae during their migratory flights are not yet understood. It appears that an astrotaxic cue, i.e., the position of the sun in the sky, is involved in determining the initial direction of migration (Medioni et al., 1975); there is no evi-

dence that coccinellids orient to magnetic cues. The migration of *S. undecimnotata* from cultivated fields to surrounding mountains was observed in the morning when wind speed was less than 3 m/s and temperature exceeded 18°C (i.e., the threshold temperature for coccinellid flight) (Ipert, 1986a); the insects landed when they reached the 18°C isotherm of the first mountain encountered (Ipert, 1986a).

Before migratory flights coccinellids are positively phototactic; after landing, they change their behaviour and walk on the soil searching for shelter, darkness and thigmotactic conditions. Depending on the geological structure and botanic richness of the landing area, they aggregate among rocks, under piles of stones or at the base of plants (Hodek, 1960; Hagen, 1962; Ipert, 1986b). The chosen shelters present certain hygrometrical characteristics offering protection to hibernating beetles, including protection from light, minimal climatic change, good ventilation and high but not excessive humidity.

Migrants to dormancy sites are physiologically similar to diapausing insects, with hypertrophied fat bodies and immature ovaries. During dormancy the individuals are gregarious and aggregate into groups, the size of which varies from a few dozen to thousands depending on the species. The sexual immaturity associated with adult diapause probably gives origin to the behavioral pattern leading to these aggregations.

Adults are usually able to support unfavourable environmental conditions by entering dormancy. Inside hibernating shelters adults enter a dormant state of variable physiological arrest which, depending upon the species, ranges from simple quiescence to diapause. Coccinellids exhibit three main types of dormancy: hibernation (e.g., in *A. bipunctata*), aestivation (e.g. in *P. quatuordecimpunctata*) and estivo-hibernation (e.g. in *S. undecimnotata* and *C. septempunctata*). Although almost all coccinellids in temperate zones hibernate, the intensity of their dormancy varies according to the species. The exotic multivoltine species such as *R. cardinalis* and *C. montrouzieri* simply slow their development and can reproduce during winter. European multivoltine species such as *P. quatuordecimpunctata* enter quiescence, and univoltine species such as *C. septempunctata* enter diapause. Diapause in aphidophagous coccinellids is primarily a response to the ephemeral occurrence of their aphid prey (Hodek, 1986). The induction

of diapause is regulated mainly by the photoperiod, with the newly emerged adult beetle usually the stage showing sensitivity to the photoperiod. The age of the host plant may affect the induction of diapause, and seems to be the principal factor determining the induction of diapause and the onset of migration in *S. undecimnotata* (Rolley et al., 1974). In addition, different genotypes of the same species may differ in their tendency to diapause (Hodek, 1986; Sem'yanov, 1986). During hibernation metabolic activities are low, as indicated by the reduced respiratory rate in *H. axyridis* (Sakurai et al., 1986) and in *C. septempunctata* (Hodek et al., 1989).

Aestivation is apparently triggered in response to hot weather in some species (Bodenheimer, 1943; Ibrahim, 1955; Hagen, 1962; Quilici, 1981). However, according to Sem'yanov (1986), aestivation is induced not by photoperiodic conditions or by temperature but only by the absence of aphid prey. Although ovary and fat body condition in aestivation is analogous to that in winter adult diapause, aestivation is a far more mobile state. The onset of aestivation is accompanied by induction of the migratory state as in the beginning of winter diapause. In some species aestivation is a diapause controlled by the corpora allata, while hibernation is not (Sakurai et al., 1986); in other species hibernation is a diapause whereas aestivation is a quiescence (Sakurai et al., 1988). In Australia *Scymnodes lividigaster* enters dormancy in summer when aphids are scarce. In hot climates, some species such as *Leis conformis* (Hagen, 1962) and *Adonia variegata* (Ipert, 1986b) do not enter a dormant state but remain active and feed on non-insect food.

Estivo-hibernation begins in summer and continues until spring, and thus often lasts about 9 months. It occurs in the univoltine aphidophagous Coccinellidae in temperate and subtropical zones, notably *H. convergens* in the USA and *S. undecimnotata* and *C. septempunctata* in Europe (Hagen, 1962).

8. Natural enemies

The coccinellids are very vulnerable to environmental changes, including events that influence the natural enemies of coccinellids, i.e., predators, parasitoids and pathogens, and are sensitive to the effects of physical and chemical pollution, including microclimatic fluctuations.

Despite their supposed protective secretions in the form of a yellowish fluid exuded from the femorotibial articulations ('reflex breeding'), the Coccinellidae are attacked by lizards, rodents and other mammals, birds, spiders, and other insects such as wasps, ants, mantis, syrphids, chrysopa, and asilid flies (Ipert, 1964).

We can distinguish enemies feeding on the three important development stages of the coccinellids: (i) larvae are preyed upon by *Homalotylus flaminus* Dalm. (Encyrtidae, Hymenoptera) and *H. eytelweini* Ratzb.; (ii) pupae, by *Tetrastichus coccinellae* Kurd. (Eulophidae, Hymenoptera) and *T. epilachnae* Girard, *T. neglectus* Domenichini, *T. sempronius* Erdoes, *Phalacrotophora fasciata* Fall. (Phoridae, Cyclorhapa, Diptera), *P. berlinensis* Schmitz; and (iii) adults, by *Perilitus coccinellae* Schr. (Braconidae, Hymenoptera), *Medina* (=Degeeria) *luctuosa* Meig. (Tachinidae, Diptera), *Parasitylenchoides* spp. (Nematoda, Vermes), *Mermis* spp. (Nematoda, Vermes), *Gregarina katherina* Watson (Sporozoa, Protozoa), *Nosema coccinellae* Lipa, *Podapolipus* spp. (Acarina), *Laboulbenia* spp. (Fungi), and *Beauveria* spp. (Fungi).

The relative importance of the particular parasitoids has been studied in some coccinellids both during activity and rest. The rate of parasitism increases over the course of the active period of every coccinellid studied. Furthermore, depending on the species, certain developmental stages are particularly vulnerable to parasites. The rate of parasitism remains relatively low in early spring but rapidly increases later on, provoking a striking reduction in the next generation (Ipert, 1964).

It is generally agreed that cannibalism is one of the main problems in rearing Coccinellidae, as both larvae and adults may devour all four stages of their own species. This behaviour is regarded by Hawkes (1920) as a biological advantage because it preserves the species during the periods when food is scarce.

During dormancy coccinellids are mainly attacked by the dangerous fungus *Beauveria* of the bassiana group. Prolongation of the aggregation period of hibernating adults greatly increases the risk of mycosis. This is particularly noticeable in *S. undecimnotata*, because the inactive adults form very large aggregations.

A comparison of the rate of parasitism of the different stages of a migratory species (*C. septempunctata*) and a sedentary one (*P. quatuordecimpunctata*) led to the conclusion that most of the parasites kill their respective host. The successive action of para-

sites, specific to each stage of the life cycle of coccinellids, results in the progressive increase of the rate of parasitism. Simultaneous attack by different parasites leads to a considerable decrease in populations of coccinellids prior to hibernation in both migratory and sedentary species, thereby possibly reducing the future efficiency of these predators against spring outbreaks of aphids.

9. Anthropological influences

Domestic pollution combined with intensive urbanization and an inappropriate use of pesticides and fertilizers are the main reasons for the decline of numerous coccinellids, which in general are highly vulnerable toward chemical treatments (Table 3). In highly industrialized regions such as Silesia in Europe, the coccinellid community shows considerable diversity, with a clearly increasing dominance of *C. septempunctata* (Galecka, 1980), a eurytopic species. In addition, these regions have fewer predators and coccinellids are less likely to migrate to overwintering sites. The warmer climate that has occurred over the last few years also plays an important role in the decline of some species. The installation of sophisticated radioelectric instruments on hills and mountain tops is responsible for killing large numbers of migrating adults (Kreiter and Ipert, 1984a).

10. Conservation

A good example of coccinellid protection is given by the measures taken to conserve *S. undecimnotata* in Digne (Alpes de Haute-Provence, France). Since 1972, a marked decrease in the numbers of hibernating *S. undecimnotata* has been observed.

S. undecimnotata is very vulnerable to environmental changes due to: (1) increases in physical and chemical pollution; (2) the increased culture of cereal crops (wheat, oat, maize, etc.) which creates trophic problems for *S. undecimnotata*, whose essential aphid prey (mainly *Aphis fabae* Scop.) live on Leguminosae plants; (3) the impact of climatic fluctuations resulting from mesoclimatic changes caused by industrial pollution in European countries; and (4) the installation of sophisticated radio-electric instruments on mountain tops, which kill large numbers of adults.

Table 3
Pesticides impact on coccinellid beetles in agriculture^a

% Mortality of Coccinellids	Pesticides ^b	Active ingredients	Persistence
Neutral pesticides	Bupirimate	Pyrimidines family	Transient
	Captane	Phtalamide dicarboximide	Very stable
0–10%	Copper		
	Dicofol	Chlorine compound	2–3 weeks
	White oil		
	Thirame	Carbamate	2–3 weeks
	Zinebe	Carbamate	persistant
Low toxicity	Chinometionate	Quinoxaline	persistant
	Isolane	Carbamate	10–20 days
11–40%	Nicotine	Alcaloid	<15 days
	Pirimicarb	Carbamate	some days
	Vamidithion	Organo-phosphorus	4–6 weeks
	Binapacryl	Benzenic compound	15–20 days
Moderate toxicity	Diethion	Organo-phosphorus	3–4 weeks
	Dinocap	Phenol compound	?
	Phosalone	Organo-phosphorus	15–18 days
High toxicity	Azinphos methyl	Organo-phosphorus	15 days
	Diazinon	Organo-phosphorus	8 days
61–80%	Dichlorvos	Phosphoric ester	4–5 days
	Formothion	Organo-phosphorus	3 weeks
	Lindane	Organo-chlorine	>3 weeks
	Malathion	Organo-phosphorus	8 days
	Phosmet	Organo-phosphorus	15 days
	Tetrachlorvinphos	Organo-phosphorus chlorine	1–2 weeks
	Carbaryl	carbamate	15–21 days
	Dimethoate	Organo-phosphorus	2–3 weeks
81–100%	Methidation	Organo-phosphorus	2–3 weeks
	Mevinphos	Organo-phosphorus	3 days
	Parathion	Organo-phosphorus	some days
	Phosphamidon	Organo-phosphorus	some days
	Fenitrothion	Organo-phosphorus	10–15 days
Contradictory opinion on toxicity	Carbophenothion	Organo-phosphorus	15 days
	Cyhexatin	Stanic compound	2 months
	Endosulfan	Organo-chlorine	3–7 days
	Oxydemeton	Organo-phosphorus	3–4 weeks
	Sulfur	–	–
	Toxaphene	Organo-chlorine	2–3 weeks
	Thiometon	Organo-phosphorus	15–20 days

^a Analysis of the published data collected by the 'Union of Plant Protection Industries' and the 'Plant Protection Service of Toulouse' with the collaboration of A.C.T.A. (Association de Coordination Technique Agricole) and I.N.R.A. (Institut National de la Recherche Agronomique) (Iperiti, 1986a).

^b New estimation of the influence of pesticides after 1985. 0–50%: without effect; 50–75%: slight effect; 75–99%: moderate effect; >99% high toxic.

The focus of the measures taken to conserve this species changes during the course of the year. In spring, during the reproductive period, it is important to promote integrated control on cultivated plants. Furthermore, the use of insecticides must be interrupted when young coccinellid larvae are present (Iperiti, 1965b). In summer, during the migra-

tory period, the conservation of some coccinellid species is related to the protection of summits of mountains (Iperiti, 1965b). In winter, during their dormancy, the first priority should be enhancing coccinellid populations, with dormant adults produced in insectaries (Kreiter and Iperiti, 1984a).

In an experiment carried out from 1977 to 1981 to replenish *S. undecimnotata* numbers, individuals were reared in the laboratory under diapause-inducing conditions (at 20.1°C, 70–80% R.H., under 12 h of photophase and provided with *Acyrtosiphon pisum*) and were placed every winter on the dormancy site on the peak of St-Michel de Cousson (1515 m), near Digne. Thus, for five consecutive winters, the resting population of *S. undecimnotata* on the top of Saint-Michel de Cousson was enhanced, resulting in a significant increase in the number of coccinellids overwintering there.

Many additional precautions must be taken to maintain a high density of these predators, the most important of which concerns the use of aphicides. Coccinellids are highly affected by insecticides during every stage of their life cycle, for many reasons. First, their high mobility increases their possibility of meeting plants or aphid colonies recently treated with chemicals. Secondly, they consume prey both as larvae and adults and therefore, are always vulnerable. Thirdly, the young larvae eat the chorion, thereby often ingesting noxious spray immediately after hatching; finally, pupation takes place unprotected on plant or mineral surfaces exposed to chemical treatments. Nevertheless, recommended standards exist and if they are followed, coccinellid populations can be partially protected. The use of pirimicarb, for example, results in a long-lasting decrease in egg laying by *S. undecimnotata*, resulting in a diminution in their predatory efficiency. In order to protect the beneficial fauna, the use of specific products must be recommended. In this field, the solution belongs to the inventors of new pesticides that are more selective for the intended victims. Pyrethrum powder presents a very low toxicity towards aphidophagous adults. For example, pyrethrum-treated *C. septempunctata* become ill for 1 or 2 days but then recover their normal predaceous activity (Ipert, unpublished observations). Chemical pest and disease control treatments should progressively be replaced by biological agents reared in specialized units. However, multiplication of biological agents still faces some problems.

Maintenance and reinforcement of these beneficial organisms are major goals of integrated pest management programs developed in France and elsewhere, especially in Rosaceae orchards. Pest and disease control treatments must be limited in time and space, car-

ried out as much as possible in the absence of the beneficial organisms and coupled with various cultural techniques, for example, preserving refuge areas in the vicinity of fields or abandoning dry farming in spring and autumn (Ipert, 1986b). In order to significantly reduce the rate of mortality due to *Beauveria* (75% reduction), artificial shelters made from fibrocement resembling the crevices of rocks in which coccinellids aggregate have been designed and placed at the base of plants. These shelters, when used in the natural environment next to cultivated areas, allow the local increase of beneficial species. This method could be generalized and integrated with the effective measures of protection taken towards two species: *S. undecimnotata*, preying on aphids of Leguminosae, and *A. bipunctata*, preying on aphids of Rosaceae. In the same way, similar methods could be used to protect coccidiphagous coccinellids, e.g., *C. bipustulatus* and *E. quadripustulatus*, and other aphiphagous predators such as *S. conglobata* or even *C. septempunctata*, which aggregates in the Paris region at the top of huge installations of radio detection equipment used by astronomers and in the radars used for aerial observation of the country. Radioelectric equipment set on top of mountains are preferential targets for coccinellid adults, which settle on them and interfere with the performance of the equipment; conversely, many beneficial insects are killed by these installations. To protect this equipment as well as the insects, the solution would be to build shelters adapted for coccinellids on these installations. Insofar as our industrial civilisation is responsible for a myriad of aggressions against these species during their entire life cycle, it would be reasonable to think that it is time to provide these beneficial insects with safer estivo-hibernation shelters.

Domestic pollution combined with intensive urbanization and inappropriate use of insecticides and fertilizers are the main reasons for the decline of coccinellids. The change in climate that has occurred in recent years is also relevant and might serve as a signal that better management of the environment is necessary to solve this complicated problem before more difficult challenges arise.

11. Ecology of coccinellids in rural landscapes

Seasons influence the occurrence of aphid outbreaks, the type of plant infested and the behaviour

Table 4
The monthly activities of the main European univoltine aphidophagous species in their principal and occasional biotopes of France

Univoltine species	
<i>Coccinella septempunctata</i>	
Larvae and adults	April: <i>Aphis fabae</i> on <i>Capsella bursa pastoris</i> ; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia</i> spp. May: <i>Macrosiphon artemisiae</i> on <i>Artemisia</i> spp.; <i>A. urticae</i> on <i>Vicia</i> spp. <i>Aphis gossypii</i> on <i>Viola odorata</i> , <i>A. fabae</i> on <i>Vicia faba</i> June: <i>A. fabae</i> on <i>Chenopodium</i> spp.; <i>A. urticae</i> on <i>Urtica</i> spp.; <i>A. fabae</i> on <i>Vicia faba</i> ; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Medicago sativa</i> July: <i>Brachycaudus cardui</i> on <i>Carduus</i> spp.; <i>Cavalleria umbellatarum</i> on <i>Pastinaca</i> spp.; <i>A. fabae</i> on <i>Chenopodium</i> spp.; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Medicago sativa</i> ; <i>A. fabae</i> on <i>Phaseolus vulgaris</i> ; <i>Longiunguis donacis</i> on <i>Arundo donax</i> August: <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia</i> spp. and on <i>Medicago sativa</i> ; <i>C. umbellatarum</i> on <i>Pastinaca</i> spp.
Only adults	
<i>Adalia bipunctata</i>	
Adults emerging from hibernation	April: <i>Macrosiphum rosae</i> on <i>Rosa</i> spp.; <i>A. fabae</i> on <i>Vicia faba</i>
Larvae and adults	May: <i>Myzus cerasi</i> on <i>Prunus avium</i> ; <i>Brachycaudus semisubterranea</i> on <i>Prunus domestica</i> , <i>M. rosae</i> on <i>Rosa</i> spp., <i>Disaphis plantaginea</i> on <i>Malus communis</i> and <i>M. persicae</i> on <i>Persica vulgaris</i> June: <i>Aphis pomi</i> on <i>Malus communis</i> ; <i>Brachycaudus persicae</i> on <i>Persica vulgaris</i> July: <i>B. persicae</i> and <i>Hyalopterus pruni</i> on <i>Persica vulgaris</i> August: <i>Rhopalosiphum maidis</i> on <i>Zea mays</i> ; <i>L. donacis</i> on <i>Arundo donax</i> ; <i>C. umbellatarum</i> on <i>Pastinaca</i> spp. September: <i>R. maidis</i> on <i>Zea mays</i>
Only adults	
<i>Semiadalia undecimnotata</i>	
Larvae and adults	May and June: <i>A. fabae</i> on <i>Chenopodium</i> spp.; <i>Vicia faba</i> on <i>Phaseolus vulgaris</i> July and August: <i>A. fabae</i> on <i>Chenopodium</i> spp.; <i>C. umbellatarum</i> on <i>Pastinaca</i> ; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Medicago sativa</i> <i>M. persicae</i> on <i>Solanum tuberosum</i>

of coccinellids. In a given year, the succession of aphid outbreaks in fields varies largely according to the weather. In southeastern France, during a 'normal year' aphidian outbreaks occur as follows: first they appear on spontaneous low plants and shrubs, then they progress to cultivated low plants and early deciduous trees and develop on cultivated shrubs and trees. When the climatic conditions are unfavorable at the beginning of spring (too cold or too warm), the order of occurrence of aphid outbreaks is modified. In this situation, it is difficult to describe the annual behaviour of coccinellids with a model because the number of variables is too great. The monthly activities of the main European aphidophagous species in their different and occasional biotopes on cultivated and spontaneous plants in the plains of southeastern France, separating larval and imaginal behaviour, are summarized in Tables 4–6 (Ipert, 1965a).

The results of these studies can be summarized as follows: (1) The majority of large aphidophagous coccinellids are very polyphagous, with some slight alimentary preferences. Only *S. undecimnotata* shows a

real specificity towards *A. fabae*. *P. quatuordecimpunctata* is polyphagous, and manifests a particular ability to develop its cycle on a large number of aphidian species. (2) On the contrary, many aphidophagous predators are stenotypic; they exhibit a great constancy in choosing their plant strata and then living and reproducing in particular microclimates, when all the aphidian food conditions are qualitatively and quantitatively acceptable. (3) The seasonal weather conditions determine both the growth of plants and aphid outbreaks, thereby influencing the biology and ecology of coccinellids. Unfavorable climatic conditions during the course of a year can entirely change the ecological behaviour of a species, but the presence of sufficient prey remains the main factor. (4) During their period of activity, adults possess an important ability to disperse and show great voracity.

During their period of activity the behaviour of coccinellids varies with the season, and is determined almost exclusively by the abundance of aphids; microclimatic conditions and food quality are of minor importance. In spring, aphid outbreaks occur on various

Table 5

The monthly activities of the main European multivoltine aphidophagous species in their principal and occasional biotopes

Multivoltine species	
<i>Adonia variegata</i>	
Adults emerging from hibernation	April: <i>A. fabae</i> on <i>Capsella bursa pastoris</i> ; <i>A. medicaginis</i> on <i>Vicia</i> spp. and <i>Medicago sativa</i>
Larvae and adults	May: <i>M. artemisiae</i> on <i>Artemisia</i> spp., <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia faba</i> ; <i>M. dirhodum</i> and <i>S. avenae</i> on <i>Hordeum</i> spp.; <i>B. helichrysi</i> on <i>Chrysanthemum</i> spp. June: <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia</i> spp.; <i>S. avenae</i> on <i>Hordeum</i> spp.; <i>A. urticae</i> on <i>Urtica</i> spp.; <i>B. helichrysi</i> on <i>Chrysanthemum</i> spp. July: <i>A. urticae</i> on <i>Urtica</i> spp.; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia</i> spp. and on <i>Medicago sativa</i> ; <i>A. fabae</i> on <i>Phaseolus vulgaris</i> , <i>M. persicae</i> on <i>Solanum tuberosum</i> . August and September: <i>A. nerii</i> on <i>Nerium oleander</i> , <i>A. evonyui</i> on <i>Pittosporum</i> spp. October: <i>R. maidis</i> on <i>Zea mays</i>
<i>Propylea quatuordecimpunctata</i>	
Only adults	April: <i>A. urticae</i> on <i>Urtica</i> spp.; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia</i> spp.; <i>A. fabae</i> on <i>Vicia faba</i> .
Larvae and adults	May: <i>M. artemisiae</i> on <i>Artemisia</i> spp.; <i>A. urticae</i> on <i>Urtica</i> spp.; <i>A. evonymi</i> on <i>Pittosporum</i> spp.; <i>H. pruni</i> on <i>Phragmites</i> spp. June: <i>H. pruni</i> on <i>Phragmites</i> spp.; <i>A. fabae</i> on <i>Chenopodium</i> spp. and on <i>Vicia faba</i> August and September: <i>R. maidis</i> on <i>Zea mays</i> ; <i>A. nerii</i> on <i>Nerium oleander</i> . October: <i>R. maidis</i> on <i>Zea mays</i>
<i>Synharmonia conglobata</i> and <i>Adonia decempunctata</i>	
Larvae and adults	May: <i>B. semisubterranea</i> on <i>Prunus domestica</i> ; <i>A. evonymi</i> on <i>Pittosporum</i> spp. June: <i>A. pomi</i> on <i>Malus communis</i> ; <i>M. rosae</i> on <i>Rosa</i> spp. July: <i>R. maidis</i> on <i>Zea mays</i> ; <i>A. medicaginis</i> and <i>A. craccivora</i> on <i>Vicia</i> spp. <i>M. rosae</i> on <i>Rosa</i> spp. August, September and October: <i>R. maidis</i> on <i>Zea mays</i> .

plants. During this season, predators can always find abundant prey and breed on this ample food in their preferential strata. In summer, the number of aphidian outbreaks decreases sharply. In the absence of aphids, the fecundity of the coccinellids is greatly reduced or even decreases to zero.

In May and June, farmers must control the numerous aphid pests that damage their crops and would be helped by the activities of many efficient natural entomophagous insects. However, during these months, microclimatic factors confine predators to certain preferential strata of vegetation, e.g. *S. undecimnotata* and *C. septempunctata* on herbs, *P. quatuordecimpunctata* and *A. variegata* on shrubs and *A. bipunctata*, *S. conglobata* and *A. decempunctata* on trees.

On the other hand, many aphid outbreaks on spontaneous plants situated in favourable microclimates attract a great number of coccinellids. Last but not the least, particular microclimatic conditions in cultivated fields (maximum exposure to sun, naked soil) prevent the coccinellids from exerting their beneficial activity. In this case coccinellids have great difficulty in finding habitats with favourable temperature and humidity.

In spring, only two coccinellid predators can be efficient in controlling outbreaks of aphids in southeastern France: *A. bipunctata* in orchards and *S. undecimnotata* on cultivated herbaceous plants. In summer and autumn only the multivoltine species efficiently attack aphids, and the aphidophagous potential of coccinellids is diminished by about 50%. However, the crops still in place show an increased frequentation of some predators still in activity because they remain the only plants that offer aphids (Ipert, 1965a).

12. Coccinellidae as bioindicators

To consider a coccinellid as an indicator species one must ask the following questions: Who is to benefit from its entomophagous ability, the farmer or the forester? Which pests are to be controlled: aphids, coccids, mites, aleurodes, fungi? What are its areas of distribution and what are its typical strata within a habitat?

Each continent has a specific fauna of Coccinellidae. Regarding this specificity, Belicek (1976) states that 'many species develop their cycles in life zones delineated by the general physiography of the con-

Table 6
Number of European coccinellid species and their abundances in various environments^a

Useful to farmers	
On low plants	On trees
<i>Aphidophagous</i>	
Gramineous plants	Rosaceous plants
xxx <i>Coccinella septempunctata</i> L.	apple trees
x <i>Coccinella quinquepunctata</i> L.	xxx <i>Adalia bipunctata</i> L.
xx <i>Scymnus apetzi</i> Muls.	x <i>Adalia conglomerata</i> L.
x <i>Sidis biguttatus</i> Muls.	x <i>Adalia rufocincta</i> L.
	peach trees
	xxx <i>C. decempunctata</i> L.
	xx <i>Synharmonia conglobata</i>
	xx <i>Pullus subvillosus</i> Goeze
Legumineous plants (alfalfa, <i>Vicia faba</i> ...)	
xxx <i>Semiadalia undecimnotata</i> Schn.	
xxx <i>Adonia variegata</i> Goeze	
	Citrus plants
	xx <i>Synharmonia conglobata</i> L.
	x <i>Synharmonia doublieri</i> L.
Grasslands	
xx <i>Anisosticta novemdecimpunctata</i> L.	
xx <i>Coccinella undecimpunctata</i> L.	
x <i>Semiadalia notata</i> Laich.	
<i>Coccidophagous</i>	
	Rosaceous plants (apple trees, peach trees, plum tree)
	xx <i>Chilocorus bipustulatus</i> L.
	xx <i>Lindorus lophantae</i> Blaisd.
	xxx <i>Chilocorus renipustulatus</i> Scriba.
	Citrus plants
	xxx <i>Chilocorus bipustulatus</i> L.
	xxx <i>Exochomus quadripustulatus</i> L.
	xx <i>Novius cardinalis</i> Muls.
	xx <i>Cryptolaemus montrouziei</i> Muls.
	x <i>Nephus quadrimaculatus</i> Herbst.
	Olive plants
	xxx <i>Exochomus quadripustulatus</i> L.
	xx <i>Rhyzobius forestieri</i> Muls.
	xx <i>Chilocorus bipustulatus</i> L.
	x <i>Hyperaspis campestris</i> Herbst.
<i>Mite-eating</i>	
None	Different trees
	xxx <i>Stetorus puctillum</i> Weise
<i>Aleyrophagous</i>	
None	Citrus plants
	xx <i>Clitostethus arcuatus</i> Rossi
<i>Mycophagous</i>	
xx <i>Tythaspis sedecimpunctata</i> L.	None
Useful to foresters	Miscellaneous
On coniferous trees	On shrubs and hedge-rows

Table 6. (Continued)

Useful to farmers	
On low plants	On trees
Aphidophagous	Aphidophagous
Pine trees	Phragmites spp., maize
xxx <i>Harmonia quadripunctata</i> Pont.	xxx <i>Propylea quatuordecimpunctata</i> L.
xx <i>Myrrha oblongoguttata</i> L.	xx <i>Scymnus interruptus</i> Goeze.
x <i>Myrrha octodecimpunctata</i> L.	x <i>Platynaspis luteorubra</i> Goeze.
x <i>Myrrha decimpunctata</i> L.	Nerium oleander, Pittosporum spp.
x <i>Chelonitis venusta</i> Weise.	xxx <i>Adonia vareigata</i> Goeze
x <i>Adaliopsis alpina</i> Villa.	Coccidophagous
xx <i>Pullus suturalis</i> Thunb.	Nerium oleander, broom, Pittosporum spp.
x <i>Pullus haemorrhoidalis</i> Herbst.	xx <i>Exochomus quadripustulatus</i> L.
x <i>Scymnus nigrinus</i> Kub.	xx <i>Exochomus flavipes</i> L.
Fire trees and spice trees	x <i>Lindorus lophantae</i> Blaisd
xxx <i>Aphidecta oblitterata</i> Weise.	x <i>Hyperaspis campestris</i> Herbst.
x <i>Adalia congenerata</i> L.	x <i>Hyperaspis reppensis</i> Herbst.
x <i>Anatis ocellata</i> L.	Mite- eating
xxx <i>Pullus impexus</i> Muls.	x <i>Pullus ferrugatus</i> Moll.
xx <i>Scymnus abietis</i> Payk.	Mycophagous
Tamarisk trees	xxx <i>Thea vigintiduopunctata</i> L.
x <i>Nephus kiesenweteri</i> Muls.	
x <i>Nephus redtenbacheri</i> Muls.	
Coccidophagous	
x <i>Chilocorus bipustulatus</i> L.	
Mycophagous	
xx <i>Rhyzobius chrysomeloides</i> Herbst.	
On deciduous trees	On aquatic plants
Aphidophagous	Aphidophagous
Oak trees, willow trees, lime trees,...	xx <i>Hippodamia tredecimpunctata</i> L.
xxx <i>Coccinula quatuordecimpustulatus</i> L.	x <i>Hippodamia septemmaculata</i> De Geer
xxx <i>Harmonia lyncea</i> Ob.	x <i>Coccidula rufa</i> Herbst.
x <i>Coccinula sinuatomarginata</i> Fald.	x <i>Coccidula scutellata</i> Herbst.
x <i>Myrrha quinquedecimguttata</i> Fabr.	x <i>Pullus haemorrhoidalis</i> Herbst.
x <i>Myrrha quatuordecimguttata</i> L.	x <i>Nephus redtenbacheri</i> Muls.
x <i>Myrrha vigintiguttata</i> L.	
x <i>Pullus ater</i> Kug.	
x <i>Pullus testaceus</i> Motsch.	
x <i>Nephus bipunctatus</i> Kug.	
Coccidophagous	
xxx <i>Chilocorus bipustulatus</i> L.	
Mite-eating	
xxx <i>Stethorus punctillum</i> Weise.	
x <i>Pullus ferrugatus</i> Moll.	
x <i>Pullus auritus</i> Thung.	
Mycophagous	
Nut-trees	
xx <i>Vibidia duodecimguttata</i> Poda.	
Hazel trees	
xx <i>Halyzia sedecimguttata</i> L.	

^a xxx: high; xx: moderate; x: low.

tinents (mountainous barriers) and climatic patterns combined with types of vegetation in a given zone'. The species found in the different geographic areas of the world can be utilized as bioindicator insects owing to their climatic and trophic characteristics. The effects of glaciation on the distribution of coccinellids were profound and the level of endemism is most probably controlled by ecological factors such as temperature, food and natural enemies.

With regard to climatic and trophic characteristics it is possible to differentiate among zones with characteristic coccinellid species. The temperate zones of Europe and North America tend to be heavily infested by Aphidae. Grasslands in these areas contain coccinellids from the tribus Coccinellini (*Coccinella* spp., *Adalia* spp., *Harmonia* spp.), Cheilomenini and Scymnini (*Pullus* spp., *Scymnus* spp.). Open deciduous and coniferous forests in this zone contain other genera of Coccinellini (*Anatis* spp., *Myrrha* spp., *Mysia* spp.) and Hippodamiini (*Aphidecta* spp., *Hippodamia* spp.).

Tropical zones in central and southern Africa, South America, India and China that are infested by Coccidae are occupied by many coccinellids from the tribus Chilocorini, (*Chilocorus* spp., *Exochomus* spp., *Brumus* spp.) Scymnini (*Nephus* spp., *Sidis* spp., *Cryptolaemus* spp., etc.) Hyperaspini, Coccidulini and Novini. In the Mediterranean area, aphids and coccids are found together and are attacked by coccinellid species coming from temperate and tropical regions, especially *Rhyzobius* spp. and *Novius* spp. The mite eaters of the genus *Stethorus* and the predators of whiteflies of the genera *Clitostethus* and *Serangium* reach their greatest diversity in the Pacific zone. Two environments, desert and mountain, possess typical coccinellid fauna. Deserts contain many phytophagous Epilachnini species and some coccidophagous Pharini species (*Pharoscymnus* spp.); Hippodamiini are by far the most important coccinellids found on mountains (e.g., the Alps and Rocky Mountains).

13. Intensification of biological control with coccinellids and landscape manipulation

According to De Bach (1964) "more than 220 cases involving about 110 species of pests are controlled to a greater or lesser degree by native enemies". About half of the cases studied concerned scales, 40% of

which resulted in complete or substantial control (8 completely controlled and 15 substantially controlled). There were 42 programs for biological control of scale insects using ladybirds, with a success rate approaching 55%.

The introduction of *Novius* (*Rodolia*) *cardinalis* Muls. into 33 countries to control *Icerya purchasi* has yielded the following levels of control:

complete control in 26 countries e.g., the USA, Argentina, Chile, Peru, Portugal, Uruguay, Venezuela, France, Italy, Spain, Greece, Morocco, Tunisia, Turkey, Egypt, India, Japan, New-Zealand;

substantial control in four countries: Russia, Libia, the Bahamas, Ecuador; also Bermuda;

and partial control in two countries: Seychelles Islands and Mauritius.

Nearly the same rate of success was achieved with the acclimatization of *Cryptolaemus montrouzieri* Muls. to control *Pseudococcus* spp.

There are only two cases demonstrating successful control of aphids: *Melanaphis sacchari* Zehntner on sugar cane in Hawaii with *Coleophora inaequalis* F. and *Therioaphis maculata* Brukton on alfalfa in California with a native coccinellid species. Since its introduction in eastern North America, *C. septempunctata* has colonized the western part of the USA and Canada (Horn, 1992).

In the author's opinion, the main reason explaining the unsatisfactory results obtained with the exotic aphidophagous coccinellids is the absence of an essential sequence of reproduction in the migrating aphidophagous species. Their ability to disperse and migrate makes it very difficult for pairs to form; without mating the females cannot lay fertilized eggs and produce a new generation. On the contrary, coccidophagous coccinellids tend to stay in the same area throughout their life cycle; therefore, pair formation and mating is not a problem. Another explanation stresses the relation between the voltinism of prey and the predator: while many aphidophagous coccinellids in moderate climates are univoltine, their aphid prey produce many generations and can thus quickly build up an outbreak. In contrast, in the subtropics the voltinism of coccids and coccidophagous coccinellids is similar (Hodek, 1973; Hodek and Honek, 1996).

Habitat improvement measures can increase the efficiency of coccinellid-based control programs: cultural practices such as cutting grass in orchards

(Savoiskaya, 1966) and strip harvesting of crops (Sem'yanov, 1965) maintain refuges for coccinellids in portions of the farmed environment. Alternative food sources for coccinellids (e.g., a mixture of yeast and proteins; Smith, 1965) are still in the experimental stages. Artificial shelters for hibernation of *S. undecimnotata* have been placed on top of some mountains of southeastern France to reduce mortality of the adults infected and killed by the pathogenic fungi *Beauveria* group *bassiana* (Ipert, 1965b).

14. Conclusion

The coccinellids are important predators of aphids, coccids and spider mites. They currently play an important role in controlling scale insects but have been less successful in controlling aphids. The fact that aphidophagous (and to a lesser extent coccidophagous) coccinellids form aggregations during dormancy can be very useful in biological control programs, by providing a supply of reproductively active predators that can be mass-released against aphid populations (Davidson, 1924; Zaslavskii and Sem'yanov, 1983). Hodek et al. (1989) proposed that adults of *C. septempunctata* collected in hibernating quarters could be brought to reproduction prematurely in early winter in warm greenhouses where the natural photoperiod is not modified. In addition, sampling well known aggregation sites in mountains can be very useful for predicting the future abundance of ladybirds in agricultural areas (Honek, 1989) and for determining the moment when they disperse in the crop (Zaslavskii and Sem'yanov, 1983; Kreiter and Ipert, 1984a) in order to prevent the use of inappropriate insecticides.

The peculiar aggregation behaviour of coccinellids has not yet been exploited to facilitate acclimatization of a new species in a new country. In collaboration with A. Ferran, the author is experimenting with this method for introducing *Harmonia axyridis* Pallas to control aphids in rosaceous orchards in southeastern France (Schanderl et al., 1985).

Migration is very important for the survival of the aphidophagous coccinellids. Therefore, knowledge gained from observational studies of migration and ecological experimentation should be applied to better protect the hibernating or estivo-hibernating sites of main aphidophagous species (Ipert, 1986b),

to survey the moment of their dispersion from aggregation (Kreiter and Ipert, 1984b; Honek, 1989), and to experimentally introduce new species to new areas from dormant sites instead of simply releasing the coccinellids in fields (Ipert et al., unpublished). Future research on the genetics, physiology and behaviour of coccinellids, combined with studies of their flight aerodynamics and interactions with agricultural ecosystems, will undoubtedly lead to improvements in coccinellid-based aphid control programs.

Acknowledgements

The author thanks Mrs. Nadine Clave' and Mrs. Paulette Gradone (INRA, Antibes, France) for typing the manuscript, and Mrs. Anne Dufay (INRA, Antibes, France) and Mr. Jean-Louis Hemptinne (Faculte' Agronomique de Gembloux, Belgique) for English editing of the manuscript.

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