Structure of Ladybird (Coleoptera: Coccinellidae) Assemblages in Apple: Changes through Developmental Stages

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ABSTRACT Larvae, pupae, and adults of ladybird beetles were observed in an insecticide-free and an insecticide-treated block in an apple orchard near Budapest, Hungary during 1980–1982. Species numbers and densities in all developmental stages were higher and species turnover was lower in the insecticide-free block. Diversity and similarity indices showed more diverse and constant assemblages in the insecticide-free block. The adult assemblage was the most rich in species, with 19 species in the insecticide-free and 12 species in the treated block. The most common species overall were *Coccinella septempunctata*, *Adonia variegata*, *Adalia bipunctata*, and *Exochomus quadripustulatus*. The larval assemblage included nine and eight species for the untreated and treated blocks respectively, whereas the pupal assemblage had eight species in both blocks. Immature stages of 11 species were found in at least 1 yr and 10 of these was able to complete development in the orchard. The rate of success was higher in the insecticide-free block for most species. Only *A. bipunctata* reproduced successfully in both blocks in all three years but *A. decempunctata* and *C. septempunctata* were often successful.

KEY WORDS Insecta, Coccinellidae, apple, species assemblage

COCCINELLIDS are probably the best studied natural enemies of aphids (Hodek 1973, Niemczyk & Dixon 1988). The coccinellid fauna of cultivated areas has received considerable interest, especially in crops on which aphids and coccids are important pests. Apple trees support several species of homopteran pests and consequently, the ladybird fauna of apple orchards is well studied in Europe (Hodek 1973) and elsewhere (Niemczyk & Dixon 1988). However, only a few of these studies include developmental stages other than adults (Skanland 1981, Radwan & Lövei 1982, Carroll & Hoyt 1984, Lövei & Radwan 1988). Even these typically consider larvae or pupae as a group and do not distinguish species within them.

In the current paper we report on the composition of all coccinellid developmental stages on apple trees in an orchard in central Hungary. We describe the structure of the assemblage of larvae, pupae, and adults and show that although 20 ladybird species were present as adults and ten species laid eggs, subsequent developmental stages of these species were not found in all years.

Materials & Methods

Study Orchard. The study site was a 5.8-ha experimental apple orchard at the Juliannamajor Experimental Farm of the Plant Protection Institute near Budapest, Hungary. The natural vegetation of this hilly area is composed of oak–hornbeam forests and dry meadows, cleared and cultivated in the valleys and hillsides. The cultivated areas consist of orchards and fields of small grains, legumes, and forage crops.

The experimental orchard, established in 1967, was sprayed 4–6 times a year until 1976, when a treated and an untreated block of equal size was established. Both blocks had three apple varieties, 'Jonathan', 'Starking', and 'Red Delicious', in equal proportions. The 'insecticide-free' block received no insecticide sprays since 1976 but was sprayed with fungicides, herbicides, or both. Weeds were controlled by mowing and spraying with herbicides (three sprays in 1980 and 1982, five in 1981). The 'treated' block received the same management but was also sprayed with insecticides. There were three insecticide applications in 1980 (28 April, with Novenda 2.0% (AI) dinitrophenol; 23 June and 5 August, with Ditrifon 50, 0.2% [AI] ditrifon), three in 1981 (the methylparathion Wofatox SPP, 0.4% on 31 March and 29 June, Ditrifon 50 on 16 May) and two in 1982 (Wofatox SPP on 7 May and 16 August).

Observation Methods. Ladybirds were visually observed weekly from early spring (March) until late autumn (October) in 1980–1982, 32 wk/yr. Fifty branches (five randomly selected major branches of each on ten trees) per block were censused. Half of these trees were selected randomly at the first census and were 'constant' afterwards;

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Table 1. Composition and characteristics of the larval assemblages in the apple orchard, Juliannamajor, 1980–1982

Species	Treated block				Insecticide-free block			
	1980	1981	1982	Total	1980	1981	1982	Total
Adalia bipunctata	0	10	217	227	84	126	147	357
A. decempunctata	0	2	26	28	16	36	1	53
Anatis ocellata	0	0	0	0	0	1	0	1
Calvia quatuordecimguttata	0	0	16	16	43	65	16	124
Coccinella septempunctata	0	2	39	41	1	47	46	94
Exochomus quadripustulatus	2	6	3	11	21	21	20	62
Propylea quatuordecimpunctata	0	9	4	13	0	0	1	1
Scymnus subvillosus	0	0	0	0	0	0	7	7
Semiadalia undecimnotata	0	0	1	1	0	1	0	1
Stethorus punctillum	0	49	1	50	0	0	0	0
Identified, total	2	78	307	387	165	297	238	700
Unidentified	0	7	259	266	392	279	170	850
Species number	1	6	8	8	5	7	7	9
Dominance	—	0.63	0.71	—	0.51	0.42	0.62	—
Q diversity	—	1.86	1.56	—	1.09	1.31	1.39	—

Numbers are yearly totals (32 weekly samples) observed on 50 branches.

the other five were randomly selected before every census. This design was recommended throughout the Agroecology Project as a result of spatial analysis of apple arthropods (Szentkirályi, unpublished). All coccinellid developmental stages were counted and identified if possible. To ascertain the validity of observations on reproduction, eclosion events and the presence of teneral adults was noted. Samples of unidentified larvae and pupae were taken to the laboratory for rearing and confirmation as necessary. This was difficult with small larvae and consequently, many of these were not identified to species. Densities are given as the totals observed on 50 branches for each year.

Analysis. The species rank–abundances were fitted to the logarithmic distribution using the linear regression subroutine of the BIOM package (Rohlf 1987) on log-transformed data. To compare the diversity of the assemblages, we used the dominance index (Southwood 1978) and the midrange diversity (Kempton & Taylor 1976), both of which are superior for comparisons than the more popular Shannon–Wiener index of diversity (Kempton & Wedderburn 1978). The dominance index, d, is

$$d = N_1/N_{total}, \quad (1)$$

where N_1 is the number of individuals of the most common species, N_{total} is the number of individuals in the sample, and d is the relative abundance of the most common species. The midrange or Q-diversity was calculated as:

$$Q = 0.371\ S/\sigma, \quad (2)$$

where S is the number of species and σ is the standard deviation of the natural logarithm of the abundances (Kempton & Taylor 1976).

The similarities were evaluated by Renkonen's percentage similarity (Renkonen 1938):

$$PS = \Sigma \min (p_{1i}, p_{2i}), \quad (3)$$

where $p_{ji} = n_{ji}/N_j$, the proportion of species i in sample j.

As a measure of stability of species composition, we calculated species turnover, the sum of the number of species 'acquired' and 'lost' in a given year, compared to the previous one:

Species turnover for year n = number of species present in year n but not in year n-1 + number of species not present in year n but present in year n-1. (4)

Results

Larval Assemblages. The number of larvae observed in the insecticide-free block (1,550 in 3 yr) was twice that in the treated block (653). About half of these, mainly newly hatched larvae, were not identified to species. More species and more individuals in the insecticide-free block than in the treated block were observed in 1980 and 1981 but not in 1982 (Table 1). Species turnover was higher in the treated block (3.5 species/yr versus 2.67 species/yr in the insecticide-free block). Densities among years varied widely in the treated block (1980–1981, 39× increase; 1981–1982, 3.9×), less so in the insecticide-free block (1980–1981, 1.8×; 1981–1982, 0.8×).

In the insecticide-free block, 5 the 9 species were present in all 3 yr; all others were found in 1 yr only. These five species made up 98.6% of all the individuals identified.

Larvae of eight species were observed in the treated block over the 3 yr studied. Only *Exochomus quadripustulatus* (L.) was found in all 3 yr. Five of the remaining seven species were present in both remaining years; *Calvia quatuordecimguttata* (F.) and *Semiadalia undecimnotata* (Schneider) were observed in 1982 only. The constant six species found in two or more years accounted for 95.6% of all identified larvae.

Most species present in the treated block in a given year were also present in the insecticide-free block. Exceptions to this were: *Stethorus punctil-*

Table 2. Renkonen similarities of the larval assemblages in the apple orchard, 1980–1982

	TR 1982	IF 1980	IF 1981	IF 1982
TR 1981	0.205	0.237	0.250	0.239
TR 1982		0.662	0.701	0.815
IF 1980			0.817	0.671
IF 1981				0.725

Because only a single species was present, TR 1980 was omitted from the calculations. TR, treated block; IF, insecticide-free block.

lum Weise, present in the treated block in 2 yr, and not observed in the insecticide-free block at all; *Propylea quatuordecimpunctata* (L.), 1981, relatively common in the treated block, but absent from the insecticide-free block; and *S. undecimnotata*, observed in 1982 in the treated block but absent from the insecticide-free block. Because of the richer larval assemblages, there were eight species–year occurrences in the insecticide-free block that were not paralleled by an observation in the treated block (Table 1).

The structure of the assemblages in both blocks fitted the logarithmic distribution. The fit was very good in all cases (r = 0.919–0.988, P = 0.027 to P = 0.00002). The diversity index Q indicated that the treated block was more diverse, whereas the dominance index showed that the insecticide-free block was more diverse. The large numbers of some medium abundance species caused the Q index, which is sensitive to the abundance ratios of these species, to drop below the values of the treated block assemblages.

The similarity of the larval assemblages (Table 2) among years was much higher in the insecticide-free block ($\bar{x} \pm$ SD, 0.74 ± 0.07) than for the treated block (PS = 0.21). Because of the few larvae of only one species in the treated block in 1980, this year was not included in the comparisons. In 1982, when many larvae were found in both blocks, the similarity value was high (PS = 0.82).

Pupal Assemblages. Pupae of 10 species were found in the orchard (Table 3). Although the two blocks supported the same number of species, only six species were common. In the treated block, a single pupa of *Adalia bipunctata* (L.) was found in 1980. The situation in 1981 was not different, except for the large number of *Stethorus* pupae (Table 3). More pupae were observed in 1982 and there was little difference in abundance or species numbers between the insecticide-free and the treated block.

The most abundant pupal species was *A. bipunctata* in both treatments and in all years except in the treated block in 1981, when *S. punctillum* was the most common. Apart from this, there was no consistency in the abundance rank among years.

The number of species in the insecticide-free block was higher than in the treated block for each year. As measured by the dominance index, diversity of the pupal assemblage was low in both years in the treated block and in 1980 in the insecticide-free block. Contrary to this, the Q index indicated a higher than average diversity in the treated block in 1982, a medium value in the insecticide-free block in 1980–1981 and a low one in the treated block in 1981. Only in 1982 did the rank–abundance curves fit the logarithmic distribution (treated block: r = 0.879, P = 0.009; insecticide-free block: r = 0.979, P = 0.00002).

In the treated block, only *A. bipunctata* pupae were found in all 3 yr, comprising 48.5% of all pupae found. *P. quatuordecimpunctata* was present in 2 yr. *S. punctillum* pupae were observed only in the treated block in 1981 but in such numbers that they made up 31.7% of all pupae found in all 3 yr. The five newly found species in the treated block in 1982 were also present in the insecticide-free block. Only *Adonia variegata* Goeze appeared first in 1982 in both blocks; the other four species were previously found in the insecticide-free block.

There were no species 'lost' in the insecticide-free block. The four species present in the first year persisted through the study period and accounted for 92.6% of all pupae observed. These were *A. bipunctata*, *Adalia decempunctata* (L.), *C. quatuordecimguttata*, and *E. quadripustulatus*. The two additional species *Anatis ocellata* (L.) and *Coccinella septempunctata* L. were found in 1981 and again in 1982. Although *P. quatuordecimpunctata* successfully pupated in 2 yr in the treated block, it was not found in the insecticide-free block.

Adult Assemblages. The total number of adults observed on the trees was 1,595 (the insecticide-free block) and 845 (the treated block), belonging to 19 and 12 species, respectively (Table 4). There were more individuals and more species in the insecticide-free block than in the treated block in all 3 yr. Differences in abundance between different years were higher in the treated block, as was found for larvae and pupae.

The most common species was *C. septempunctata* in both blocks in all years. Other common species included *A. bipunctata*, *A. variegata*, and *E. quadripustulatus* in the insecticide-free block, and the same species plus *S. punctillum* in the treated block (Table 4). The three most common species in any year made up the majority of the individuals observed, more so in the treated block (84.9–93.0%) than in the insecticide-free block (77.7–91.4%).

All the assemblages closely fitted the logarithmic distribution (r = 0.907 - 0.988; $P = 1.1 \times 10^{-5}$ to $P = 2.9 \times 10^{-8}$). The diversity index Q of the assemblages was higher in the insecticide-free block in all years. The dominance index also indicated a more diverse assemblage in the insecticide-free block except in 1982 (Table 4).

The between-year similarities were significantly higher in the insecticide-free block (Table 5) ($\bar{x} \pm$ SD, 0.849 ± 0.047) than either in the treated block between years (0.626 ± 0.133) (t = 5.66, $P < 0.005$) or between the two blocks in the same year (0.725

Table 3. Composition and characteristics of coccinellid pupal assemblage in the Juliannamajor apple orchard, 1980–1982

Species	Treated block				Insecticide-free block			
	1980	1981	1982	Total	1980	1981	1982	Total
Adalia bipunctata	1	1	47	49	49	48	38	135
A. decempunctata	0	0	6	6	4	25	6	35
Adonia variegata	0	0	1	1	0	0	1	1
Anatis ocellata	0	0	0	0	0	1	2	3
Calvia quatuordecimguttata	0	0	2	2	9	10	3	22
Coccinella septempunctata	0	0	3	3	0	5	8	13
Exochomus quadripustulatus	0	0	2	2	6	12	14	32
Propylea quatuordecimpunctata	0	3	3	6	0	0	0	0
Scymnus subvillosus	0	0	0	0	0	0	2	2
Stethorus punctillum	0	32	0	32	0	0	0	0
Total	1	36	64	101	68	101	74	242
Species number	1	3	7	8	4	6	8	8
Dominance	—	0.89	0.73	—	0.72	0.47	0.51	—
Q diversity	—	0.63	2.09	—	1.35	1.65	2.48	—

Numbers are yearly totals observed on 50 branches.

± 0.089) (t = 6.11, P < 0.005). This showed that the adult assemblages in the treated block did not reach the degree of stability in composition observed for coccinellids in the orchard habitat.

Life Cycle Completion. The presence of eggs or larvae was categorized as 'attempted reproduction' by a species; the presence of both pupae and teneral adults as 'successful reproduction'. Observation of eclosion from pupae was used as supporting evidence for 'successful reproduction'. Immature stages of 11 species were found in at least 1 yr in the orchard (Table 6). Although adults of five species were present in both blocks in all years, only *A. bipunctata* and *E. quadripustulatus* laid eggs each year as well. Eggs, larvae, pupae, and teneral adults of *A. bipunctata* were found in all years, indicating successful reproduction. Similar records show only 50% success for *E. quadripustulatus* (Table 6). Four other species were always successful when reproduction was attempted—*C. quatuordecimguttata* on four occasions, *A. ocellata* and *A. variegata* on two occasions, and *Scymnus subvillosus* once (Table 6). Immature stages of *A. decempunctata* and *C. septempunctata* were often found as well. Reproductive attempts by other species were rare. Among them, *S. undecimnotata* is the only one without successful reproduction (Table 6).

Inter-Block Differences in Life Cycle Completion. Coccinellids in Hungary have one full generation per year (Lövei 1989). Each of the 11 species had three opportunities to attempt reproduction, for a possible total of 33 reproduction occasions in each block. Reproductive effort as well as success was lower in the treated block: 51.5% (17 of 33) of the opportunities were taken up by adults of the 11 species in the treated block, versus 70.0% (23 of 33) in the insecticide-free block. Of these attempts, 64.7% were categorized 'successful' in the treated block and 78.3% in the insecticide-free block; overall, the success in relation to opportunities was 33% in the treated block and 54.5% in the insecticide-free block.

Five species attempted reproduction in the insecticide-free block more often than in the treated block, and six others had equal numbers of attempts in the two blocks (Table 6). *A. bipunctata* and *E. quadripustulatus* laid eggs or had larvae in all 3 yr in the treated block and three more species did so in at least 2 yr (Table 6). Only *S. punctillum* had more attempts in the treated than in the insecticide-free blocks.

Eggs, larvae, and pupae as well as adults of *A. bipunctata*, *A. decempunctata*, *C. quatuordecimguttata*, and *E. quadripustulatus* were found in all 3 yr in the insecticide-free block. *C. septempunctata* successfully completed its development cycle in 1981 and 1982, but not in 1980. The success rate was equal in the two blocks for *A. bipunctata*, *C. quatuordecimpunctata* and *A. variegata*. For *P. quatuordecimpunctata* and *S. punctillum*, the success rate was higher in the treated block (Table 6).

Discussion

Compared with other apple orchards in Europe, the species richness of this orchard was high. Twenty-one species were found as adults and this is a large proportion of the ladybird fauna of central Europe (87 species in Fürsch [1966]). An earlier study found 12 species in the same orchard (Lövei 1981). Three to five species were reported from apple orchards in Belgium (Malevez 1976), Finland (Clayhills & Markkula 1974), Norway (Skanland 1981), and Yugoslavia (Ciglar 1985). A 5-yr study of 9 orchards near Skierniewice in central Poland found 13 species (Olszak & Niemczyk 1986).

In apple orchards in North America and elsewhere, there are normally <10 species. Eight species were found in central Washington (Carroll & Hoyt 1984) and four species in Indiana (Goonewardene & Bogyo 1988). Brown et al. (1988) reported that 12 species were found as adults in surveys conducted over 2 yr in 15 orchards in four

Table 4. Composition and characteristics of the assemblage of coccinellid adults on apple trees in the Juliannamajor orchard, 1980–1982

Species	Treated block				Insecticide-free block			
	1980	1981	1982	Total	1980	1981	1982	Total
Adalia bipunctata	6	12	55	73	94	105	69	268
A. decempunctata	1	1	5	7	15	38	3	56
Adonia variegata	43	90	9	142	89	69	6	164
Anatis ocellata	0	0	0	0	0	1	2	3
Calvia quatuordecimguttata	1	0	3	4	18	21	4	43
Coccinella septempunctata	94	254	67	415	333	303	210	846
Coccinula quatuordecimpustulata	0	6	0	6	0	1	1	2
Exochomus quadripustulatus	14	12	4	30	57	61	51	169
Harmonia quadripunctata	0	0	0	0	2	0	0	2
Hippodamia tredecimpunctata	3	1	0	4	7	0	0	7
Propylea quatuordecimpunctata	0	3	6	9	2	0	2	4
Scymnus apetzi	0	0	0	0	1	0	1	1
S. frontalis	0	0	0	0	0	2	0	2
S. rubromaculatus	0	0	0	0	0	1	0	1
S. subvillosus	0	0	0	0	0	1	3	4
Semiadalia undecimnotata	0	0	0	0	1	1	1	3
Stethorus punctillum	0	118	35	153	0	10	6	16
S. conglobata	0	0	0	0	1	0	0	1
S. lyrcea	0	1	0	1	0	0	0	0
Thea vigintiduopunctata	0	0	1	1	0	0	3	3
Total	162	498	185	845	620	614	361	1,595
Species number	7	10	9	12	12	13	13	19
Dominance	0.58	0.51	0.36	—	0.54	0.49	0.58	—
Q diversity	1.47	1.78	2.33	—	2.16	2.24	2.88	—

Yearly totals observed on 50 branches.

mid-Atlantic states. Individual orchards probably had fewer species. In Ontario, Canada, Hagley (1974, 1978) found 3–17 species. Apple orchards in Jammu and Kashmir, India, support a similar number of ladybird species (12 species reported by Bhagat et al. 1988). Most of these studies indicate the presence of adults only.

The most common species in this study (*C. septempunctata*, *A. bipunctata*, *A. variegata*, *E. quadripustulatus*, and *S. punctillum*) have all been reported from elsewhere in Europe, although their importance varies (Hodek 1973).

Although no eggs and only a few larvae of *A. variegata* were found, this species was common as adults and probably immigrated from the neighboring forest. The *Adalia* and *Calvia* species are typically arboreal, whereas *C. septempunctata* and *A. bipunctata* are eurytopic species with wide tolerance spectra (Jablokoff-Khnzorian 1982, Honek 1985).

Coccinellid assemblages in this orchard were dominated by aphidophagous species. From the species found as adults, only the four *Scymnus* species, *S. punctillum* (which are acarophages) and *Thea vigintiduopunctata* L. (mycetophage) belonged to a nonaphidophagous guild (Table 4). Observations on the other developmental stages showed assemblages even more dominated by aphidophagous species (Tables 1 and 3). These species had to share the aphid food resource with several other members of the aphidophagous guild, including heteropterans, lacewings, hoverflies, earwigs, spiders, staphylinids, and carabids (Mészáros 1984).

Of the nonaphidophagous species, only *S. punctillum* was common in both blocks, especially in the treated block in 1981. In this year, mites were abundant and the insecticide treatment was not effective against them (Kozár, unpublished observations).

Differences in species richness, diversity, and similarity in the insecticide-free versus treated block all pointed to a less stable coccinellid assemblage in the treated block. The species composition as well as the relative importance of the species varied among years more in the treated block than in the insecticide-free block. Similar but more pronounced differences in insecticide-free versus treated orchards were reported from an Ontario orchard by Hagley (1978) and from Japan by Hukushima (cited in Hodek 1973).

Two ways in which insecticide treatments probably influenced the coccinellid assemblages are the direct toxic effect of insecticide sprays and the indirect effect through changes in prey abundance. The number of sprays per season was low (a max-

Table 5. Renkonen similarities of the adult assemblages on the apple trees, Juliannamajor, 1980–1982

	TR 1981	TR 1982	IF 1980	IF 1981	IF 1982
TR 1980	0.743	0.482	0.828	0.742	0.733
TR 1981		0.654	0.709	0.674	0.602
TR 1982			0.628	0.663	0.638
IF 1980				0.904	0.821
IF 1981					0.823

TR, treated block; IF, insecticide-free block.

Table 6. Presence of coccinellid developmental stages in apple orchard in three consecutive years (1980–1982) at Juliannamajor, Hungary

Species	Block	Eggs	Larvae	Pupae	Adults	Reproduction (attempted/ successful)
Adalia bipunctata	TR	+++	+++	+++	+++	3/3
	IF	+++	+++	+++	+++	3/3
A. decempunctata	TR	−++	−++	−−+	+++	2/1
	IF	+++	+++	+++	+++	3/3
Anatis ocellata	TR	−−−	−−−	−−−	−−−	0/0
	IF	−++	−++	−++	−++	2/2
Calvia quatuordecimguttata	TR	−−+	−−+	−−+	+−+	1/1
	IF	+++	+++	+++	+++	3/3
Coccinella septempunctata	TR	−++	−++	−−+	+++	2/1
	IF	+++	+++	−++	+++	3/2
Exochomus quadripustulatus	TR	++−	+++	−−+	+++	3/1
	IF	+++	+++	+++	+++	3/3
Propylea quatuordecimpunctata	TR	−+−	−++	−++	−++	2/2
	IF	−++	−−+	−−−	+−+	2/0
Scymnus subvillosus	TR	−−−	−−−	−−−	−−−	0/0
	IF	−−+	−−+	−−+	−++	1/1
Semiadalia undecimnotata	TR	−−+	−−+	−−−	−−−	1/0
	IF	−−−	−+−	−−−	+++	1/0
Stethorus punctillum	TR	−++	−++	−+−	−++	2/1
	IF	−+−	−−−	−−−	−++	1/0
Adonia variegata	TR	−−−	−−+	−−+	+++	1/1
	IF	−−−	−−+	−−+	+++	1/1

TR, insecticide-treated block; IF, insecticide-free (untreated) block. +/−: developmental stage observed/not observed in a given year.

imum of three) and only one of these was at a time when it could have interfered with egg-laying or larval development. Of potential prey organisms, the aphids *Dysaphis devecta* Walker and *Dysaphis plantaginea* Pass. showed consistently higher densities in the insecticide-free block during egg laying; the density of *Aphis pomi* Deg., a species suitable for many coccinellids (Jablokoff-Khnzorian 1982), was much lower in both blocks (Kozár, unpublished data). Therefore, we think that the effect of direct toxicity was limited and the differences in observed patterns were caused by the indirect effect of changes to prey availability.

Observations of the developmental stages are open to criticism as to whether they actually detect reproduction. Our observations receive additional support from rearings in the laboratory where we found that several of the 11 species for which all developmental stages were observed were able to develop into fertile adults on the aphids present in the orchard (Radwan & Lövei 1983, Radwan 1984). Furthermore, observations of pupal eclosion and the presence of teneral adults indicate that we have detected reproduction, rather than new immigrants from neighboring areas. The observations are largely free from artifacts: of 66 potential observation series of eggs–larvae–pupae (11 species, 2 blocks, 3 yr), there is only one occasion (*Anatis ocellata* in the insecticide-free block, 1982) when pupae but no larvae were found. In addition, there were five more occasions when larvae were found but no egg batches were identified—*E. quadripustulatus*, *P. quatuordecimpunctata*, *A. variegata* (both blocks) in 1982, and *S. undecimnotata* in 1981 (Table 6).

Differences in the reproductive success of species in the two blocks shows that beetles not only attempted reproduction less often in the treated block, but also had reduced success even if this difference in reproductive 'investment' is taken into account.

Of the 20 species observed as adults, ten were able to complete reproduction in at least 1 yr and one block in the orchard. Of six possible opportunities (3 yr, two blocks), only five species managed to reproduce three or more times (Table 6).

To establish the relative importance of 'standard' members of the coccinellid assemblage, the following evaluation was performed. Species that failed to reproduce successfully in the orchard at least twice during the 3-yr study (no attempt to reproduce and unsuccessful reproduction were regarded as equal) were categorized as 'temporary' members of the assemblage. Next, we calculated the number of adults of these temporary species found in the three years. In the insecticide-free block, 210 of 1,595 individuals were temporary; in the treated block, there were 763 such individuals from a total of 845. This indicates that temporary members can be numerically very important in an insect community (Stork 1987).

Because coccinellid larvae are much less mobile and stress tolerant than adults, the choice of egg-laying site by the female has a profound effect on the survival chances of its progeny. Several lines of evidence suggest that egg-laying females make assessments and decisions about where and how to lay eggs. Syrphid females, with larvae that are even less mobile, assess the future resource potential of an aphid colony before deciding to oviposit nearby (Kan 1989). A female ladybird beetle might be expected to lay eggs in response to the estimated future resource availability, probably based on the overall density of aphids within the activity radius of the larvae (Kan 1989). The choice of a qualitatively appropriate food source is all-important because larvae indiscriminately eat even toxic prey (Hodek 1973). In *Hippodamia* spp., 1 mg of aphids per alfalfa stem were required to keep adults in the field and begin reproduction (Hagen & Sluss 1966). *A. bipunctata* females lay eggs close to aphid colonies in the early stages of population growth but egg laying is inhibited if larvae of the same species are present (Hemptinne & Dixon 1990). Species-specific differences are therefore expected in the relative success of these decisions.

Only a few species (*A. bipunctata*, *A. ocellata*, *C. quatuordecimpunctata*, *S. subvillosus*, and *A. variegata*) were efficient reproducers. When eggs were laid, both pupae and adults of these species were always found. In *E. quadripustulatus*, *P. quatuordecimpunctata*, *S. undecimnotata* and *S. punctillum*, the failure rate (percentage of cases when eggs or larvae but no pupae were observed) was 50–100% (Table 6). The high failure rate of *E. quadripustulatus* is unexpected because it was among the most common species of adult beetles (Table 4) and was able to develop on several species of aphids as well as coccids in the laboratory (Radwan & Lövei 1983). Larvae in the field either do not take aphid prey, or females do not lay eggs near aphid colonies, themselves being more prolific egg layers when fed on coccids (Radwan & Lövei 1983).

Further studies of early season activity and the effect of egg size, larval size, and searching ability on development may help explain the differences in developmental success in the field. Studies confined to adults are of limited value in assessing the biocontrol potential of coccinellids, or for understanding the patterns of their abundance.

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