

Aphid-mediated coexistence of ladybirds (Coleoptera: Coccinellidae) and the wood ant *Formica rufa*: seasonal effects, interspecific variability and the evolution of a coccinellid myrmecophile.

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It is generally believed that most homopteran-eating insects avoid ant-tended colonies of Homoptera, due to the ant aggression they encounter there. However, because homopteran colonies which are ant-tended often persist for longer than untended colonies, some homopteran-eaters may utilise ant-tended Homoptera when untended colonies are scarce. Furthermore, a few homopteran-eaters are myrmecophilous, habitually coexisting with ants. To investigate these phenomena, a study was made of aphids and aphidophagous coccinellids (ladybirds) on Scots pine, *Pinus sylvestris*, growing in areas foraged and unforaged by the wood ant *Formica rufa*. The non-tended aphid *Schizolachnus pineti* exhibited a marked population decline in late summer but persisted in both areas at very low density. Facultatively tended *Cinara* aphids exhibited higher population densities when associated with *F. rufa*, and remaining colonies of these aphids were only found associated with ants in late summer. Coccinellids exhibited considerable interspecific variability in their level of association with *F. rufa*, and there was some evidence of an increase in certain species' frequencies of occurrence with the ant when *Cinara* aphids were all ant-tended, in late summer. Coexistence with ants appears to be associated with either an intolerance of low aphid densities, in *Coccinella septempunctata* and *Harmonia quadripunctata*, or with extreme dietary specialisation, in *Myzia oblongoguttata*. Similar factors to those which bring *C. septempunctata* into contact with ants were probably of importance in the initial stages of the evolution of myrmecophily of its congener, *Coccinella magnifica*.

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The mutualism between ants and Homoptera has a marked effect on the distribution of homopteran-eating insects. In return for honeydew, Homoptera tended by ants gain a number of benefits, which often include protection from predators and parasites (Way 1963, Buckley 1987). The likelihood of ant attack on colonies of tended Homoptera makes such a resource risky to obtain and, as a result, many homopteran-eaters are generally believed to avoid ant-tended colonies.

In reality the situation is not so simple. Factors intrinsic to the mutualism such as the ant and homopteran species involved, homopteran colony distance from the ants' nest or even the weather, can exert complex effects on ant attendance and consequently on the distribution of homopteran enemies relative to ants (Way 1963, Addicott 1979). Other factors, related to the host plant, may also potentially modify distribution of homopteran-eaters relative to ants (Buckley 1987,

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Bristow 1991). No less important are factors intrinsic to the homopteran-eaters themselves which, in large part, remain poorly characterised.

Coexistence of homopteran enemies with ants can be divided into two types, depending on the permanence of the relationship. Some homopteran-eaters facultatively coexist with ants: in such cases coexistence is mediated by prey patch profitability. For much of the time, most parasites and predators probably avoid patches of ant-tended Homoptera, preferring untended Homoptera which constitute a less costly resource to obtain. Under certain conditions, however, feeding upon tended Homoptera might be favoured: if untended colonies of Homoptera are scarce, the relative value of tended Homoptera will increase. Since tended colonies of Homoptera may persist for longer than untended colonies (Bristow 1984, Mahdi and Whittaker 1993), such a situation is likely to occur in the field. For example, in temperate regions aphids are often scarce in late summer, due to the production of dispersive alates, and to predation and parasitism earlier in the year. Untended aphid colonies are particularly scarce, although ant-tended aphids remain more abundant (e.g. Mahdi and Whittaker 1993). At this time the value of ant-tended aphids to aphidophages will be much greater, and predators and parasitoids may risk ant attack to gain access to tended Homoptera.

The second type of coexistence is a more permanent, obligate or near obligate relationship. Some homopteran-eating species are myrmecophilous, invariably occurring with one or more ant species for part or all of their life cycle (Pontin 1959, Völkl 1997, Sloggett 1998). In such cases ants form an essential part of the predator's or parasitoid's habitat, and prey patch location typically occurs in the vicinity of the ant. A variety of studies related to myrmecophily in homopteran-eaters have been carried out (e.g. Pontin 1959, Tauber et al. 1993, Völkl 1995, 1997). In some cases benefits to the myrmecophile have been suggested or demonstrated, in the form of either a resource advantage or acquisition of enemy free space (Majerus 1989, Völkl 1992, 1995).

The possibility that coexistence between non-myrmecophilous homopteran-eaters and ants might be more than incidental has rarely been considered. Facultative coexistence between homopteran-eaters and ants, mediated by untended prey scarcity, has been a hitherto untested phenomenon. Its occurrence could explain much of the conflict evident in the literature concerning the effectiveness of ants in eliminating predators and parasitoids from the vicinity of their tended Homoptera. Avoidance of periods of prey scarcity by facultatively feeding on ant-tended Homoptera could also provide a starting point for the evolution of myrmecophily in homopteran-eaters.

A considerable body of work exists on the foraging behaviour and feeding ecology of aphidophagous coc-

cinellids (Hodek 1996a, Dixon 1997), many of which are large and brightly coloured, making them easy to identify and study in the field. During aphid scarcity coccinellid aphidophages are known to feed in non-ideal habitats (Iperti 1965, Majerus 1994), and on atypical foods such as pollen, nectar, sap, non-homopteran invertebrates and even conspecifics (Clausen 1940, Majerus 1994, Hodek 1996a). It has hitherto been unclear whether coccinellids frequently also attempt to feed on ant-tended aphids, and, if so, how this strategy is related to other foraging tactics adopted by coccinellids under conditions of aphid scarcity. This field study examines the role which untended aphid scarcity has on coccinellid coexistence with ants, and considers which aspects of coccinellid feeding ecology affect a species' requirement for ant-tended aphids. The role which the ant-tended resource has played in the evolution of a coccinellid myrmecophile is also considered within this framework.

The study system

The wood ants, *Formica rufa* group, obtain most of their carbohydrate in the form of honeydew from colonies of tended aphids (Wellenstein 1952, Jensen 1978, Skinner 1980). *Formica rufa*-group ants will prey upon some non-tended aphids, and even include tended species in their diet in subalpine habitats (Skinner 1980, Cherix 1987, Rosengren and Sundström 1991). In the vicinity of the ants, aphid numbers may be higher than elsewhere, although the situation is complicated by simultaneous ant predation of non-tended species (Müller 1958, Skinner and Whittaker 1981, Mahdi and Whittaker 1993). Tended aphid colonies can persist for longer (Scheurer 1971), and in the later part of summer, aphids associated with *Formica rufa* L. may outnumber comparable ant-free populations of aphids, which can dwindle to low levels (Mahdi and Whittaker 1993).

Formica rufa group ants are generally considered effective defenders of tended aphids (Adlung 1966, Fosset 1972, Majerus 1989). Although Wellenstein (1952) suggested that they were poor defenders of aphids against adult coccinellids, this appears to have been based upon the ants' inability to catch coccinellids rather than repulse them. Other authors report the Palaearctic *F. rufa* and the Nearctic *Formica obscuripes* to both be highly effective at defending Homoptera against non-myrmecophilous coccinellids (Bradley 1973, Majerus 1989). Members of the *F. rufa* group often attack coccinellids in the absence of Homoptera and *F. rufa* workers have been observed carrying coccinellid victims back to their nests. This suggests that sometimes coccinellids are even attacked as potential prey (Sloggett et al. 1999).

Scheurer (1971) observed coccinellids of several species in the presence and absence of ants, including *Formica pratensis*, but does not comment further on relative abundance. This study is noteworthy, since the system used (*Cinara* aphids on pine trees) is very similar to that considered here. Other authors have found numbers of most coccinellids, both adults and larvae, to increase in areas where ants are naturally absent or experimentally excluded, or with increasing distance from the nest (Schmutterer 1956, Bradley 1973, Majerus 1989, Völkl and Vohland 1996). Occasionally, aphid-tending *F. rufa*-group ants are overwhelmed by swarms of, probably hungry, coccinellids (Gösswald 1941, Bhatkar 1982; see also Hodek et al. 1993, Majerus and Majerus 1996).

The distribution of *F. rufa*-group ants throughout their large territories appears to be, in great part, a consequence of their tending aphids (Sudd 1983, Whittaker 1991) and it is thus relatively easy to quantify the consequent effects of ant-attendance, through comparison of ant foraged and unforaged areas. This study examines aphidophagous coccinellid associations with *F. rufa*, on *Pinus sylvestris* L., Scots pine, over a season, in southern England. A number of aphid species occur on *P. sylvestris*, some being tended by ants (Carter and Maslen 1982, Blackman and Eastop 1994).

Two distinguishable groupings of aphids occurred in this study. The first comprised the species *Schizolachnus pineti* (Fabricius), a small waxy aphid which lives on the needles. This aphid is not tended by ants; nor is it apparently predated by *F. rufa*, probably because its waxy covering makes it unpalatable (J. J. Sloggett pers. obs.). The second group comprised larger aphids of the genus *Cinara* [*Cinara pilosa* (Zetterstedt) (= *C. pinea* (Mordwilko) of most British authors) and *Cinara pini* (L.) (C. I. Carter pers. comm.)]. These large aphids occur on the shoots and branches and are often tended by ants, including members of the *F. rufa* group (Scheurer 1971, Sudd 1983).

Aphidophagous coccinellid species are also abundant on *P. sylvestris*, and four of the six coccinellid species considered in this study, *Myrrha octodecimguttata* (L.), *Harmonia quadripunctata* (Pontoppidan), *Anatis ocellata* (L.) and *Myzia* (= *Neomyzia*) *oblongoguttata* (L.), are conifer specialists, typically breeding on these trees (Klausnitzer 1966, 1967, Majerus 1994). The fifth coccinellid species, *Coccinella magnifica* Redtenbacher (= *C. distincta* Faldermann, *C. divaricata* Olivier), is an obligate associate of *F. rufa*-group ants, and possibly a few other *Formica* species: all stages of its life history are found associated with these ants in north-western Europe, although its associations are less well known in the south and east of its range, and may possibly differ (Donisthorpe 1919–1920, Schmidt 1936, Pontin 1959, Wiśniewski 1963, Majerus 1989, Sloggett 1998). Myrmecophilous species occur scattered throughout the family Coccinellidae, but *C. magnifica* is noteworthy,

being the only known myrmecophile in the intensively researched tribe Coccinellini, to which all of the six coccinellid species in this study belong (Sloggett 1998). *Coccinella magnifica* may have evolved myrmecophily to avoid periods of aphid scarcity, by feeding upon ant-tended aphids (Donisthorpe 1900, 1919–1920, Majerus 1989, 1994). An alternative, non-exclusive explanation is that *C. magnifica* may have adopted an association with ants under selection for enemy free space, because ant aggression limits the numbers of coccinellid parasitoids in their environs (Majerus 1989).

With the exception of myrmecophily, *C. magnifica* shares many biological features with its congener *Coccinella septempunctata* L., the sixth study species (Sloggett et al. 1998). *Coccinella magnifica* and *C. septempunctata* are alike in size and colour pattern, and both eat a similarly broad range of aphid species from a variety of plants (Donisthorpe 1919–1920, Iablokoff-Khnzorian 1982, Majerus 1994, Sloggett 1998). Without doubt, many biological characters are present in both species through common descent. The close relatedness of *C. magnifica* and *C. septempunctata* and their shared characteristics make *C. septempunctata* an ideal model for the non-myrmecophilous ancestor of *C. magnifica*. Comparison of *C. magnifica* with *C. septempunctata* has already been used to elucidate adaptations which have occurred in the *C. magnifica* lineage during the evolution of myrmecophily (Sloggett et al. 1998).

In a similar manner, comparison of *C. septempunctata* with species less closely related to *C. magnifica* can be used to reveal any traits predisposing the *Coccinella* genus towards the evolution of myrmecophily, such as facultative feeding on ant-tended aphids. In this study, the pattern of the *C. septempunctata* association with *F. rufa* is compared to that of the four non-*Coccinella* species, which are more distantly related to *C. magnifica*. Thus, the role which ant-tended aphids have played in the evolution of *C. magnifica* myrmecophily is elucidated.

Materials and methods

The study site

The study site was a south-facing slope at Longy Down, Esher Common, Surrey, England (Ordnance Survey grid reference TQ134625). In 1995, *P. sylvestris* was the dominant tree at Longy Down, although since that time most pine trees have been cleared from the site. *Pinus sylvestris* stands were approximately 30 yr old, estimated from tree-ring counts after the later tree-felling. A sparse understorey consisted of *Betula*, birch, and *Quercus*, oak saplings. Ground cover, where present, was primarily *Erica cinerea* L., ling.

The study site was divided into two areas. The western part of the site, of approximately 3500 m², was

designated the *F. rufa* area. This contained some five *F. rufa* mounds, although some of these mounds may have been interconnected, forming larger colonies of ants. Additional very small *F. rufa* mounds were observed in the *F. rufa* area later in the year. These presumably arose as a result of new colony foundation.

The eastern part of the study site, some 4500 m², was free of *F. rufa* and was designated the control area. There was some evidence that *F. rufa* were colonising the part of the control area nearest the *F. rufa* area, after the end of this study in 1996, before tree-clearing commenced. This suggests that there were no intrinsic microclimatic differences between the two areas, at least with respect to their potential for colonisation by *F. rufa*.

Some observations of *C. septempunctata* were also made in a bed of *Urtica dioica* L., stinging nettles, infested with the non-tended aphid species *Microlophium carnosum* Buckton. This nettlebed was some 600 m east of the main study site, forming a 7-m eastern verge of the A244 road, where it meets the A3 (Ordnance Survey grid reference TQ141625).

Method

Three branches, on individual pine trees, were marked in each area using coloured Tipp-Ex[®], in March 1995. Trees were dispersed throughout each area and initially chosen at random, although only trees with three branches less than 3 m from the ground were used, for ease of observation. At approximately two week intervals, from early April until early November, the marked branches were examined. All *F. rufa* workers, aphids of the two groupings (*S. pineti* and *Cinara* spp.) and coccinellids on these branches were recorded during this period. To control for differing branch size, insects were recorded from twigs and shoots within 1 m of the distal tip of the branch.

The sample size of trees was reduced after the start of the study, as several pines on the periphery of the ant foraging area were found to be rarely visited by ants. A similar reduction in sample size was made in the control area, leaving five pines in each area. During the course of observations, one branch on one of the five pines in the *F. rufa* area was broken and one in the control area died. Data from these branches were thus excluded from the final analysis, as were data from the abandoned trees.

Numbers of *S. pineti* and *Cinara* aphids were estimated separately for each branch, into the following classes: no aphids, one to 25 individuals, 26 to 50 individuals, 51 to 100 individuals, 101 to 200 individuals, 201 to 400 individuals, 401 to 800 individuals and 801 to 1600 individuals. The two *Cinara* species, *C. pilosa* and *C. pini*, were not differentiated in counts, since they are both facultatively tended by ants and are,

without doubt, predated by the same coccinellid species.

The numbers of adults and immature stages of all coccinellid species were recorded from the marked branches. A further 20 randomly selected branches, on unmarked trees in each area, were beaten and numbers of adults and larvae collected from these were also recorded. When possible, branches which had been beaten in the previous two weeks were not beaten in the following observational period in order to allow populations of aphids and coccinellids to recover. Some eggs, larvae and pupae were reared to adulthood in the laboratory, to confirm species identity.

Coccinella septempunctata density was assessed in the nettlebed between early April and mid-July. The number of adult *C. septempunctata* visible to the observer in five minutes of searching were recorded for each sampling date. The occurrence of *C. septempunctata* eggs, larvae and pupae was also recorded. Some rearing of eggs was carried out, again to confirm species identity. From the end of May *M. carnosum* populations declined. In June and July the nettlebed became overgrown, and was eventually cut down. Consequently observations were discontinued at this site after mid-July.

Statistical analysis

The recorded categorical data on aphid numbers per branch were converted into continuous data by treating each class as its median value (e.g. one to 25 individuals = 13 aphids; 101 to 200 individuals = 150.5 aphids). This continuous data was then log transformed ($\log_{10}(a + 1)$, where a = number of aphids) (Sokal and Rohlf 1981). The use of the log transformation eliminates statistical effects due to the breadth of the original categorical classes increasing with rising aphid number, such as an association between higher means and larger variances. $\log(a + 1)$ was used in preference to $\log(a)$ due to the presence of zero values in the data (i.e. branches from which no aphids were recorded). In order to avoid pseudoreplication, mean log values were calculated for each tree, from the recorded data from the three, or two, tree branches. These tree means were used for statistical analysis: the *F. rufa* and control areas were compared using repeated measures ANOVA (Minitab 8.21), with individual trees as a nested factor within the two areas.

Data on coccinellid numbers from counts on marked branches and beating of unmarked branches were pooled, since equal numbers of visual counts and beats were carried out in both areas on each date, and both methods are good predictors of coccinellid density, being well correlated with each other (Michels and Behle 1992). In order to test for interspecific differences in adult coccinellid association with ants, data for each

species obtained on all dates whilst the ants were considered active were pooled. Although there is a risk, in doing this, of counting a few coccinellids more than once (individuals which remained aestivating on the same marked branch for greater than two weeks in summer, for example), any resulting error is likely to be small, particularly since on each sample date, over half the data collected on coccinellids came from random beating of unmarked branches. Heterogeneity χ^2 -tests were applied to this data, followed by partitioning (Siegel and Castellan 1988), which was carried out twice, by sequentially including coccinellid species exhibiting increased frequency occurrence with *F. rufa* and vice versa. Only if groupings of species differed under both partitioning procedures, was a difference considered significant. Two analyses were carried out, either including or excluding the myrmecophile *C. magnifica*. Inclusion of this myrmecophile led to extremely high X^2 values and reduced the sensitivity of analysis to differences in frequencies of occurrence with *F. rufa* between the other, non-myrmecophilous species.

Heterogeneity χ^2 -tests and partitioning were also used to determine seasonal differences in the abundance of individual coccinellid species in the two areas. The data collected on *F. rufa* and aphid abundance in the two areas were used to determine when untended aphids became scarce and when *F. rufa* ceased to be active. Thus, the study period was divided into three periods: the period of aphid abundance, the period of aphid scarcity and the period of ant absence. For an individual coccinellid species, frequency data were pooled within each of these three periods and compared using a heterogeneity χ^2 -test. Partitioning was then carried out comparing, first the period of aphid abundance with the period of aphid scarcity, and then both together with the period of ant absence. In cases where a coccinellid species was restricted to a single area during both aphid abundance and aphid scarcity, data for both periods were pooled and tested against frequency data for the period of ant absence, using a χ^2 -test incorporating a continuity correction for 2×2 tables (Siegel and Castellan 1988).

Some clutches of coccinellid eggs from *P. sylvestris* proved difficult to breed to adulthood and many coccinellid pupae collected were found to be parasitised by phorid Diptera, *Phalacrotophora* spp. (Disney et al. 1994) and failed to emerge. These factors made identification of some egg clutches and pupae tentative and thus the only data analysed relating to immature coccinellid stages were larval data. Larval data were pooled for the entire season (larvae were only present when *F. rufa* was active), and for all instars. Interspecific differences in coccinellid larval occurrence with *F. rufa* were tested for using heterogeneity χ^2 -test and partitioning, as was used for the data for adult coccinellids. Only the more conservative test, including *C. magnifica*, was carried out, as the contingency table not

including *C. magnifica* exhibited unacceptably low expected values (three of eight expected values were less than five; one value was less than one).

In a few cases encountered during analysis, $2 \times n$ contingency tables contained 20% or more of expected values less than five. Although conventionally some classes in such tables are combined (Siegel and Castellan 1988), it was considered that this approach would markedly reduce the value of the analysis. Since this approach to low expected values is an extremely cautious one, as the χ^2 -test remains conservative even with values even as low as unity (Lewontin and Felsenstein 1965), except in the one case noted above where no χ^2 -test was carried out, the test has been applied without combining data. Attention is drawn to such cases in the Results section.

Results

Formica rufa

Formica rufa workers were found on marked branches in the *F. rufa* foraging area continuously from early April until early September (Fig. 1). Numbers remained approximately constant until July, except for a decrease in mid-May attributable to poor weather. From early July ant numbers increased, reaching a peak in late July. From late July onwards the majority of ants occurred associated with colonies of *Cinara* aphids. Only a single ant was found on the marked branches after early September.

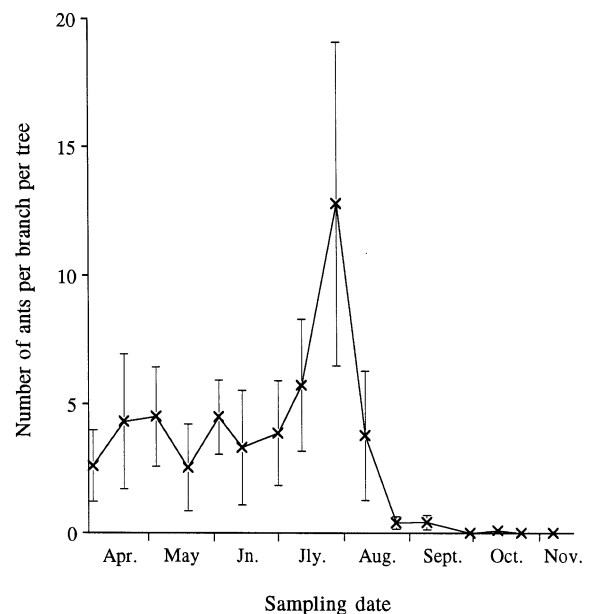


Fig. 1. Mean (\pm SE) number of ants occurring on branches in the *F. rufa* area during the study period. Means and SEs are calculated from branch means for each individual tree.

Single *F. rufa* workers were occasionally found during beating in the control area, though none were found on the control marked branches. Thus it is concluded that numbers were sufficiently low that *F. rufa* had no significant impact upon the coccinellid fauna in the control area.

Aphids

Schizolachnus pineti

Schizolachnus pineti were present throughout the study period and were abundant in both areas until late July (Fig. 2a). From late July until the end of the study, *S. pineti* was typically present in both areas, but at very low levels. No significant difference in *S. pineti* density was found between the two areas, either over entire study period, or for the period when *F. rufa* were active in the ant foraging area (Table 1). There was some indication that *S. pineti* might have declined later in the ant foraging area (Fig. 2a). Interestingly, *S. pineti* infestation varied strongly between trees (Table 1).

Cinara spp.

Throughout the period of their occurrence, *Cinara* aphids occurred at significantly higher density associated with *F. rufa* (Table 1, Fig. 2b). This difference was just significant for the period when *Cinara* density was increasing, but was highly significant as these aphids declined in number (Table 1, Fig. 2b).

Cinara spp. aphids were present on marked branches in the *F. rufa* foraging area until late September and in the control area until early August (Fig. 2b). During August and early September, when *Cinara* spp. were only found on marked branches in the ant foraging area, unmarked branches in both areas were checked thoroughly for other colonies, in order to deduce whether all *Cinara* colonies at this time were indeed ant tended. This further searching revealed several large well-tended colonies associated with *F. rufa* workers, as well as one colony, tended by another ant species, in the control area. Although *C. pilosa* was of common occurrence on the marked branches earlier in the year, all of the *Cinara* colonies observed at this time were *C. pini*, both on marked and unmarked branches. It can therefore be assumed that all *Cinara* colonies on *P. sylvestris* were *C. pini* tended by ants from August onwards.

When would feeding on ant-tended aphids be beneficial to coccinellids?

Large numbers of untended aphids, of both types, were available for feeding coccinellids in the absence of *F. rufa* throughout spring and early summer. Only when these untended aphids, in the control area, became

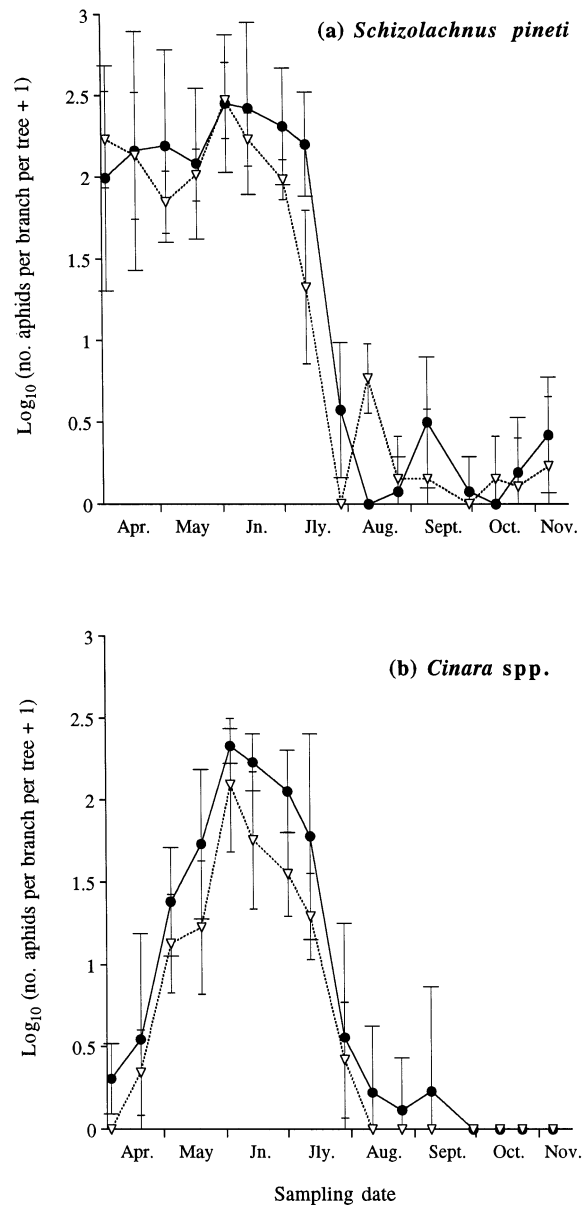


Fig. 2. Mean (\pm 95% CI) estimates of the number of aphids occurring on branches in the *F. rufa* and control areas during the study. Data are log-transformed (see text for details). Means and 95% CIs are calculated from branch means for each individual tree. (a) the untended *S. pineti*; (b) *Cinara* spp., which are often tended by ants.

scarce or absent, would feeding on ant-tended aphids be likely to be beneficial to coccinellids.

Schizolachnus pineti was present in both areas, albeit at low density, even after aphid populations declined in June and July. However, *Cinara* aphids were only found in the *F. rufa* area from early August onwards. The period of untended aphid scarcity, when non-

myrmecophilous coccinellids were most likely to facultatively feed on ant-tended aphids, is thus defined as the period when *Cinara* aphids were absent from marked branches in the control area, but *F. rufa* remained active. This extends from early August to early September, inclusive. After early September only a single *F. rufa* worker was observed on the marked branches in the ant foraging area, and it is unlikely that *F. rufa* would have exerted any effect upon coccinellids at this time.

In analysing results for coccinellid species the season was thus divided into three periods. The first extended from April to the end of July, when ants were present in the *F. rufa* area but untended *Cinara* aphids were present in the control area. Henceforth this is referred to as the period of aphid abundance. In the second period, August and early September, ants were present but untended *Cinara* aphids were not observed. This is designated the period of aphid scarcity. In the final period, from late September, few or no ants were observed on the marked branches in the *F. rufa* area. During this, henceforth referred to as the period of ant absence, the effect of *F. rufa* is considered negligible.

Table 1. Analysis of variance of the study data for aphid occurrence. Differences between the *F. rufa* and control areas are in bold. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	<i>F</i>	df	<i>P</i>
<i>Schizolachnus pineti</i>			
Over entire season (early April-early November)			
area	1.70	1	0.229
tree	12.00	8	<0.001***
sampling date	210.57	15	<0.001***
area × sampling date	4.06	15	<0.001***
When ants present (early April-early September)			
area	1.84	1	0.212
tree	13.12	8	<0.001***
sampling date	197.98	11	<0.001***
area × sampling date	5.21	11	<0.001***
<i>Cinara</i> spp.			
Entire period when <i>Cinara</i> aphids present (early April-early September: ants also present)			
area	18.01	1	0.003**
tree	1.85	8	0.078
sampling date	80.19	11	<0.001***
area × sampling date	0.64	11	0.793
Early season: aphid numbers increasing (early April-early June)			
area	6.27	1	0.037*
tree	3.13	8	0.010*
time	118.30	4	<0.001***
area × sampling date	0.63	4	0.646
Late season: aphid numbers decreasing (mid-June-early September)			
area	14.55	1	0.005**
tree	1.24	8	0.295
time	81.58	6	<0.001***
area × sampling date	0.80	6	0.575

Coccinellids

Adults

Thirteen species of adult coccinellid were found during the course of the study. Only the six most common species, mentioned in the introduction, are considered here: the four conifer specialist species, *M. octodecimguttata*, *H. quadripunctata*, *A. ocellata* and *M. oblongoguttata*, the myrmecophilous generalist aphidophage *C. magnifica*, and its non-myrmecophilous generalist congener *C. septempunctata*. The other species, which were either too scarce for meaningful analysis, or were not of the tribe Coccinellini and thus inappropriate to include, were *Adalia bipunctata* (L.), *Adalia decempunctata* (L.), *Propylea quatuordecimpunctata* (L.), *Aphidecta oblitterata* (L.), *Exochomus quadripustulatus* (L.), *Chilocorus renipustulatus* (Scriba) and *Scymnus suturalis* Thunberg. Some observations arising from this study, relating to these species and *F. rufa* will be published elsewhere.

All of the six common species showed a similar pattern of total abundance (Fig. 3). A limited number of individuals of the overwintered breeding generation were recorded before June or July. In addition to winter mortality, which was probably responsible for the reduced numbers of breeding coccinellids at this time, *C. septempunctata* were also reduced in number before July, because most individuals were breeding, away from *P. sylvestris* and *F. rufa*, on herbaceous vegetation, such as the nettlebed (Fig. 4; J. J. Sloggett pers. obs.). Numbers of all species increased in June and July, as the new generation of adult coccinellids emerged from pupae. In addition new generation *C. septempunctata* migrated onto *P. sylvestris* at this time. Thereafter numbers of coccinellids tended to decline, due to migration away from *P. sylvestris*, mortality and, later, dispersal to overwintering sites.

Interspecific variability in adult coccinellid association with *F. rufa*

There were considerable interspecific differences in the observed patterns of association of coccinellids with *F. rufa* (Figs 3, 4). Whilst the ants were active (April to early September) no *M. octodecimguttata* or *A. ocellata* adults were found in the *F. rufa* area (Fig. 3a, b). The first individuals of these species were found in the *F. rufa* area, after the ants ceased to be active, in late September. *Harmonia quadripunctata* occurred with ants at very low levels (14 of 265 occurrences, 5.3%, whilst the ants were active; Fig. 3c). *Coccinella septempunctata* occurred at much higher levels associated with *F. rufa* on pines (11 of a total of 50, 22.0%; Fig 3d), and of the five non-myrmecophilous species, *M. oblongoguttata* was most frequent in its occurrence with the ants (20 of 61, 32.8%; Fig. 3e). Whilst the ants were active, the myrmecophilous *C. magnifica* was found exclusively in the *F. rufa* area (Fig. 3f). The χ^2 -test of heterogeneity

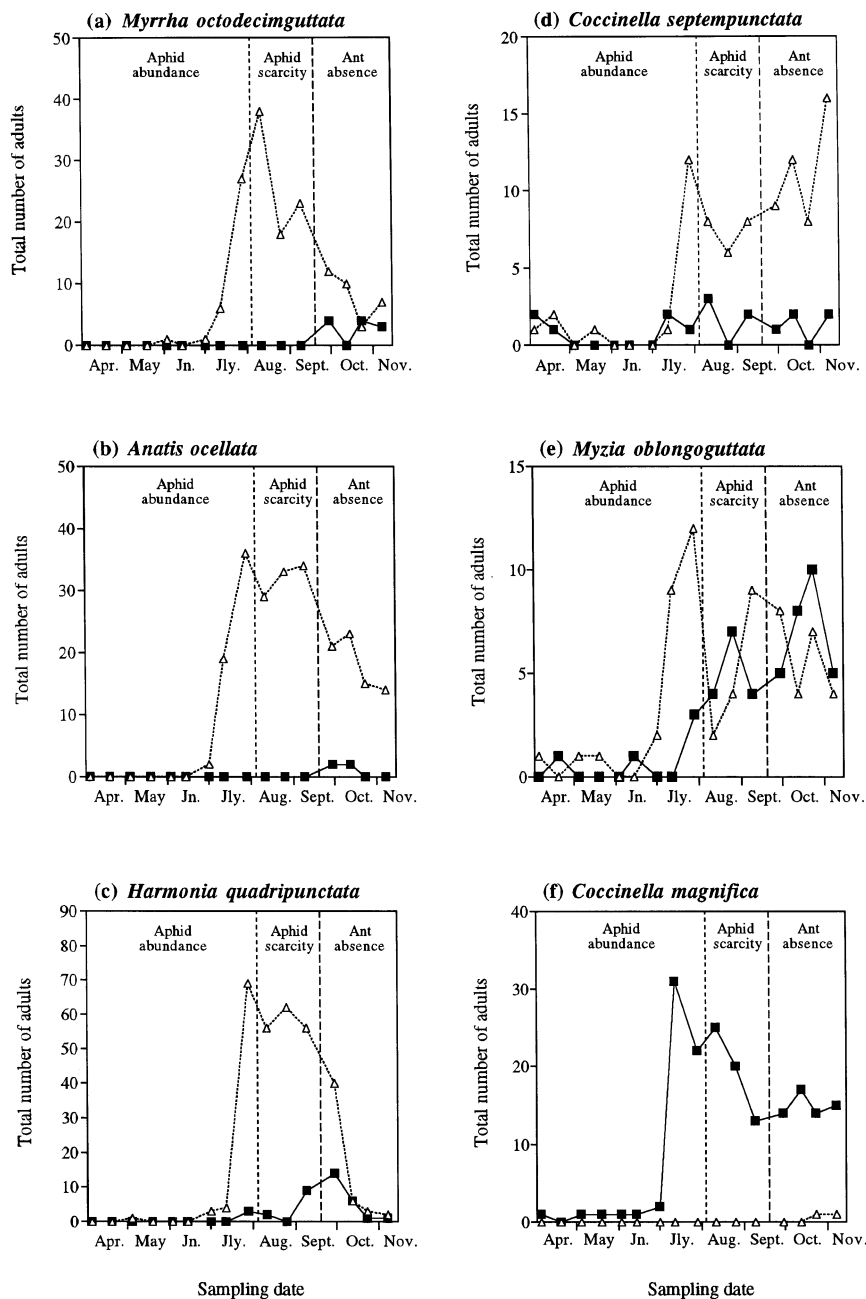


Fig. 3. Total numbers of the six coccinellid species found on marked and beaten branches in the *F. rufa* area —■— and the control area△ during the study period. Coccinellid species are ordered from the lowest (a and b) to the highest (f) levels of observed coexistence with *F. rufa* on *P. sylvestris*.

indicated that the differences in frequency of occurrence of the six species with ants was highly significant ($X^2 = 551.4$, 5 df, $P < 0.001$), the test remaining highly significant even if the myrmecophilous *C. magnifica* was excluded from the comparison ($X^2 = 100.9$, 4 df, $P < 0.001$: two of ten expected values less than five, but greater than three). Partitioning of all six species' frequencies of occurrence with ants supported four distinct groupings, with increasing frequency of occurrence with *F. rufa* (*M. octodecimguttata* + *A. ocellata* + *H. quadripunctata* vs *C. septempunctata* vs *M. oblongogut-*

tata vs *C. magnifica*). If *C. magnifica* was excluded from partition analysis, *H. quadripunctata* formed an additional group, distinct from *M. octodecimguttata* and *A. ocellata*. Although this difference is less supported than the others, it is concluded that *H. quadripunctata* typically occurs at very low frequencies with ants (Fig. 3c; see also Discussion, on this species and non-*F. rufa* ants), unlike *A. ocellata* and *M. octodecimguttata* (Fig. 3a, b; see also results for larvae and discussion thereof).

During aphid scarcity, the pattern of frequency of occurrence of the different coccinellid species in the *F.*

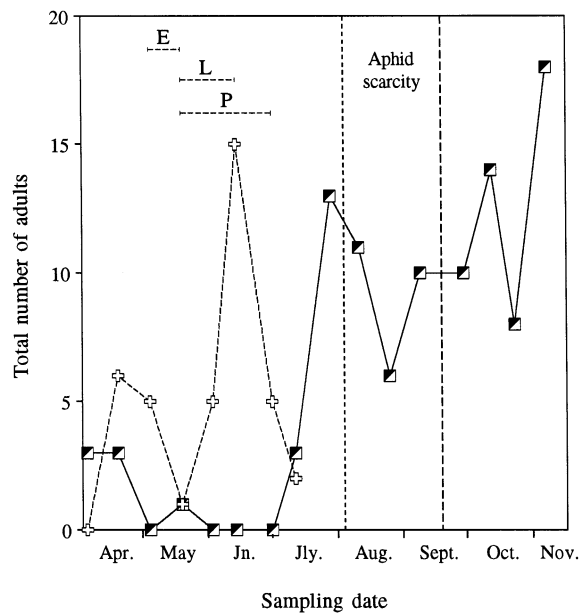


Fig. 4. Relative abundance of adult *C. septempunctata* on *U. dioica*, in the nettlebed (---□---), and on pines, summed for the control and *F. rufa* areas (—■—). Methods of counting coccinellids in the two areas differed (see Materials and Methods), thus numbers for the two areas are not directly comparable to each other. Counting in the nettlebed ceased after mid-July. Although no *C. septempunctata* were observed on *U. dioica* plants in early April, some individuals were observed emerging from overwintering in leaf litter and low herbage at the base of the plants. The lines E, L and P indicate the periods when *C. septempunctata* eggs, larvae and pupae respectively were found in the nettlebed. Two egg clutches, found in early May, were the only indication of *C. septempunctata* breeding on the pines.

rufa area was identical to that for the entire period whilst the ants were active, analysed above (i.e. *M. octodecimguttata* + *A. ocellata* < *H. quadripunctata* < *C. septempunctata* < *M. oblongoguttata* < *C. magnifica*). A similar pattern was observed earlier in the season, during aphid abundance, except that *C. septempunctata* exhibited a higher frequency of occurrence with *F. rufa* (26.1%) than *M. oblongoguttata* (16.1%).

Seasonal changes in coccinellid association with ants

Myzia oblongoguttata exhibited a significant increase in frequency in the *F. rufa* area during the period of aphid scarcity (50.0%, $n = 30$) compared to that during the period of aphid abundance (16.1%, $n = 31$; Table 2). *Harmonia quadripunctata* also slightly increased in frequency in samples from the *F. rufa* area during the period of aphid scarcity (from 3.7%, $n = 80$, to 5.9%, $n = 185$), although this did not approach significance (Table 2).

Adult *M. octodecimguttata* and *A. ocellata* were both found in the *F. rufa* area during the period of ant absence, although they had not been found there previously. In both cases the increase is statistically significant (Table 2). The frequency of *M. oblongoguttata* and *H. quadripunctata* also increased significantly in the *F. rufa* foraging area at this time, although the numbers of *H. quadripunctata* declined markedly on the final three sampling dates, in both areas (Fig. 3d). A non-significant opposite trend was observed in *C. magnifica*: in this species two individuals were found outside the *F. rufa* area after the ants became inactive, although, until this time, all *C. magnifica* had been found within the *F. rufa* area.

Coccinella septempunctata did not exhibit any significant changes in frequency of occurrence with *F. rufa* on the pines throughout the study (Table 2). Overall a slight decline was observed in the study samples, from 26.1%, $n = 23$ during the period of aphid abundance to 18.5%, $n = 27$ during aphid scarcity and 10.0%, $n = 50$ during ant absence.

Immature stages

Coccinellid larvae were only found during the period of aphid abundance and, with the exception of *C. magnifica*, those occurring with the ants appeared to be concentrated on pines at the edge of the *F. rufa* area, which were perhaps visited less by ants. Immature stages of *C. septempunctata* were common in the nettlebed (Fig. 4), with larvae reaching a maximum of 128 individuals counted in five minutes in mid-June. However, two clutches of *C. septempunctata* eggs, collected

Table 2. χ^2 analysis of seasonal differences in the distribution of individual species across the *F. rufa* and control areas, related to untended aphid scarcity and whether *F. rufa* was present on *P. sylvestris* or not. NS = not significant. +For *C. septempunctata*, two of six expected values were less than five, but greater than three.

Coccinellid species	Heterogeneity χ^2 -test		Aphid abundance (E. Apr.–L. Jly.) vs Aphid scarcity (E. Aug.–E. Sept.)		Ant presence (E. Apr.–E. Sept.) vs. ant absence (L. Sept.–E. Nov.)	
	X^2 (2 df)	<i>P</i>	X^2 (1 df)	<i>P</i>	X^2 (1 df)	<i>P</i>
<i>Myrrha octodecimguttata</i>	–	–	–	–	27.56	<0.001
<i>Anatis ocellata</i>	–	–	–	–	5.37	<0.05
<i>Harmonia quadripunctata</i>	37.43	<0.001	0.28	NS	37.15	<0.001
<i>Coccinella septempunctata</i>	3.21+	NS	–	–	–	–
<i>Myzia oblongoguttata</i>	12.69	<0.002	7.14	<0.01	5.55	<0.02
<i>Coccinella magnifica</i>	–	–	–	–	1.47	NS

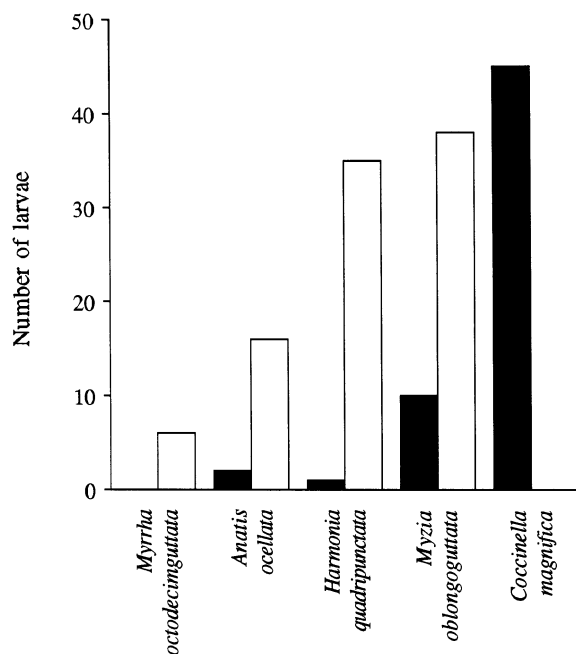


Fig. 5. Occurrence of larvae in the *F. rufa* area (■) and the control area (□). Data are pooled for the entire season: larvae were all recorded during the period of aphid abundance.

from the control area, were the only indication of breeding by this species on pines, which, it is concluded, was rare.

Larval coexistence with *F. rufa* exhibited a pattern similar to that for coccinellid adults, although two of 18 *A. ocellata* larvae were collected in the *F. rufa* area, despite a complete absence of recorded *A. ocellata* adults there during ant activity (Fig. 5). All *C. magnifica* larvae were recorded within the *F. rufa* foraging area. A heterogeneity χ^2 -test suggested significant interspecific variability in frequency of occurrence of larvae in the *F. rufa* area ($X^2 = 107.7$, 4 df, $P < 0.001$). However, partition analysis only discriminated between the myrmecophile *C. magnifica* and the other coccinellid species as a group.

Discussion

It is clear that the presence of *F. rufa* substantially modifies the coccinellid fauna on *P. sylvestris*. Not only were consistent differences observed in the abundance of different coccinellid species in the presence and absence of *F. rufa*, but after the cessation of ant activity in autumn, increases in relative abundance were observed for most coccinellid species in the *F. rufa* area. Seasonal changes in the relative abundance of *M. oblongoguttata*, and probably other species (see below), earlier in the season in the vicinity of active *F. rufa* appear to be related to the presence of ant-tended *Cinara* aphids.

Additionally, considerable interspecific variation in coccinellid coexistence with the ant was observed in this study. Rather than a clear-cut dichotomy between the myrmecophilous *C. magnifica* and the five “non-myrmecophilous” species, there appears to be a pattern more akin to continuum of coexistence, from such species as *M. octodecimguttata* and *A. ocellata* which virtually never occur with *F. rufa* through to the obligate *Formica* associate *C. magnifica*. These differences in coexistence with *F. rufa* are consistent with data on the behaviour of the six coccinellid species on colonies of *F. rufa*-tended *C. pini* (Sloggett 1998; J. J. Sloggett unpubl.).

Aphid food is almost certainly the reason why *M. oblongoguttata*, *C. septempunctata* and *H. quadripunctata* were found associated with ants in this study. A significant increase in the proportion of *M. oblongoguttata* associated with *F. rufa* was observed during the period of aphid scarcity, and the sampled frequency of *H. quadripunctata* associated with *F. rufa* also rose during this period, although this rise was not statistically significant.

Because *C. septempunctata* is a widespread generalist, and did not breed to any great extent on *P. sylvestris*, the interpretation of data for this species is necessarily complex. There was a slight, non-significant decrease in the frequency of *C. septempunctata* associated with *F. rufa* during aphid scarcity. However, in spring, *C. septempunctata* adults which had overwintered on *P. sylvestris* and at other sites (Banks 1954, Majerus 1994), migrated to nettle beds (Fig. 4) and other herbaceous plants to breed. In summer and autumn, some adults of the new generation returned to the pine trees. The sampling of *C. septempunctata* on *P. sylvestris* during aphid abundance is likely to be a biased estimator of *C. septempunctata* coexistence with ants at this time, as a result of this migratory activity.

Coccinella septempunctata collected from *P. sylvestris* during the period of aphid abundance were either late-departing overwintering individuals or early arrivals of the new generation. Those associated with *F. rufa* in the spring were possibly less well resourced, as might be expected had they needed to feed on tended aphids the previous year and remained in the *F. rufa* area until spring. These underresourced individuals might migrate to breeding sites later than well-provisioned *C. septempunctata* from the control area. Similarly, immigrants to *P. sylvestris* in summer might already be hungry and feed on the first aphids they encounter, ant-tended or not. Both factors could lead to overrepresentation of *C. septempunctata* in the *F. rufa* area during the period of aphid abundance, at a time when the majority of *C. septempunctata* were breeding on colonies of untended or non-tended aphids, like *M. carnosum*, and were consequently not associated with ants. The stability of *C. septempunctata* populations on *P. sylvestris* during aphid scarcity argue that data on coexistence with *F.*

rufa during this period are of greater reliability than those obtained earlier in the season, including migratory periods. However, even during aphid scarcity, pine-dwelling *C. septempunctata* do not necessarily reflect this species' total occurrence with ants summed over all habitats: this species is observed in wide variety of situations during aphid scarcity, late in the year (Honěk and Hodek 1996, Barron and Wilson 1998, J. J. Sloggett pers. obs.).

A case can, however, be made for all three species occurring in the presence and absence of *F. rufa* increasing their coexistence with ants during aphid scarcity. This trend is significant in *M. oblongoguttata*, a dietary specialist entirely restricted to conifers (Majerus 1993, 1994). A very small, non-significant, sampled increase is observed in the relative abundance of *H. quadripunctata* with ants during aphid scarcity. *Harmonia quadripunctata*'s overall cooccurrence with ants is so low that differences between the periods of aphid abundance and aphid scarcity, if they exist, are unlikely to be detected at significant levels, unless much larger samples were collected than were obtained in this study. *Coccinella septempunctata* coexistence with ants also probably increases during aphid scarcity, but this is difficult to ascertain with certainty as this generalist species, recorded on over 250 native plants in Britain alone (Majerus 1994), typically migrates between habitats over a season.

There are two non-exclusive explanations for this presumed late summer increase in coccinellid abundance associated with *F. rufa*. The first is that hungry coccinellids are risking ant-attack to feed on ant-tended *C. pini*, because untended prey is scarce. This seems probable in the light of the observations made on aphid abundance in the *F. rufa* and control areas during the period of aphid scarcity. In late summer in temperate regions, coccinellids must acquire sufficient resources to survive a period of overwintering (Hodek 1996b). Individual hungry coccinellids may be forced to feed upon ant-tended aphids because failure to obtain aphid food would mean death in the winter: they thus trade off risk of injury in feeding on ant-tended aphids against risk of death overwinter, which presumably rises with increasing starvation (see Barron and Wilson 1998).

Second, ant attendance of aphids ultimately declines as the end of the season draws near, notably as the ants become inactive. As ant attendance declines, it may be easier for coccinellids to obtain access to the dwindling aphid supply, causing an increase in coccinellid abundance near ant-tended aphid colonies (Banks and Macaulay 1967). In this study, however, *F. rufa* abandonment of aphids appeared to be of limited importance for most of the period of aphid scarcity. In the earlier part of the season many colonies of *Cinara* aphids were only sporadically tended by *F. rufa*, partly because aphid numbers were so high (see Wellenstein 1952, Way 1963) and partly because *C. pilosa*, which

predominated at this time, is invariably less well tended than *C. pini* (see Völkl and Kroupa 1997 on *C. pini* and *C. pinea*, a close relative of *C. pilosa*). In the closing stages of ant activity, ants were densely distributed on colonies of the more intensively tended *C. pini*. Behavioural experiments indicate that coccinellids meet greater resistance from *F. rufa* which are tending *C. pini* later in the season (Sloggett 1998, Sloggett et al. 1998, J. J. Sloggett unpubl.). The presence of sporadically tended *Cinara* aphids in the *F. rufa* area during aphid abundance also accounts for the occurrence of some non-myrmecophilous coccinellid adults and larvae associated with the ant at this time, when they might not be expected to occur there.

Only three coccinellid species, of the six in this study, appear to feed on ant-tended aphids when untended aphids are scarce, and even these exhibit marked variation in their frequencies of occurrence with *F. rufa*. Of the remaining three coccinellid species, two, *A. ocellata* and *M. octodecimguttata*, are very rarely, if ever, associated with ants and the third, *C. magnifica*, is an obligate myrmecophile. Ultimate explanations for this interspecific variability in coccinellid coexistence with ants can be found by examining these species' feeding ecologies, notably how specialised they are in their dietary requirements and the densities of aphids on which they can survive.

Myzia oblongoguttata is the most specialised in its diet. Unlike the other coccinellid species in this study, this species fails to copulate or oviposit and exhibits high larval mortality if aphids other than conifer dwellers are provided as food in the laboratory (Majerus and Kearns 1989, Majerus 1993, 1994). On the other hand, *C. septempunctata* and *A. ocellata* include a variety of non-aphid food in their diets (Kesten 1969, Triltsch 1997). In the latter species, this non-aphid diet has been linked to unavailability of aphid food (Kesten 1969). Some *A. ocellata* and *H. quadripunctata* migrate from conifers to deciduous trees to feed, when aphids become scarce on conifers (Majerus 1994); indeed *A. ocellata*, *H. quadripunctata* and the generalist *C. septempunctata* have all been collected from oak and birch at Esher Common in late summer.

The remaining four non-myrmecophilous coccinellids can be further separated on the basis of their preferred aphid densities, which, it is assumed, provide some indication of their ability to survive starvation conditions. In a Canadian study of coccinellids occurring on *Pinus resinosa*, red pine, Gagné and Martin (1968) observed that *Coccinella transversoguttata* predominated on young trees whereas *Anatis mali* was the dominant species in older stands. These differences were related to the density of aphid prey, which decreases in older *P. resinosa* plantations (Martin 1966). Although the data on Palaearctic coccinellids is more scattered, the findings of European workers are consistent with those of Gagné and Martin. *Coccinella sep-*

tempunctata and *H. quadripunctata* prefer younger trees and are thus probably less tolerant of low aphid densities than *A. ocellata* and *M. octodecimguttata*, which prefer older trees (Gumoś and Wiśniewski 1960, Klausnitzer 1968, Bastian 1982, Honěk 1985). It should be noted that in this study, all the trees in both areas were of approximately the same age: clearly the species can coexist in certain stands, as described here.

The small size of *M. octodecimguttata* suggests that this species primarily feeds on the diminutive, untended *S. pineti*, which persists on *P. sylvestris* into autumn irrespective of the presence of ants. Despite the very low densities of this aphid occurring on trees during aphid scarcity, hungry *M. octodecimguttata* probably continue to feed on *S. pineti*, although perhaps outside their optimal habitat. *Myrrha octodecimguttata* characteristically occur in the crowns of pine trees (Klausnitzer 1968, Majerus 1988) and the large numbers of this coccinellid recorded in this study on low branches during late summer are indicative of some migration away from this preferred habitat. Ant-tended *Cinara* aphids are of little benefit to *M. octodecimguttata* as the small size of this species renders it particularly vulnerable to ant attack and it is likely to have problems overwhelming such a large prey as *Cinara*. *Myrrha octodecimguttata* therefore does not coexist with ants, remaining exclusively on ant-free trees.

Although *A. ocellata* is largely restricted to breeding on conifers, feeding on both *Cinara* spp. and *S. pineti* (Klausnitzer 1967, Kesten 1969), this species' potential dietary range is relatively broad. Through a combination of migration to deciduous trees, consumption of non-aphid foods and, perhaps in part linked to the latter, resistance to low aphid densities, *A. ocellata* avoid the need to consume ant-tended aphids during aphid scarcity. Whilst there is no evidence that *H. quadripunctata* possess a narrower dietary range than *A. ocellata*, and *C. septempunctata*'s dietary range is considerably broader, both *H. quadripunctata* and *C. septempunctata* are apparently both less resistant to low aphid densities. Thus, although *H. quadripunctata*, like *A. ocellata*, migrates to deciduous trees and *C. septempunctata* feed in diverse habitats during aphid scarcity, some individuals of both species, perhaps the least well-provisioned, risk ant-aggression to feed on ant-tended aphids, and occur coexisting with ants.

Myzia oblongoguttata is so highly specialised in its conifer aphid diet that alternative food sources are unavailable to this species, in contrast to coccinellids such as *A. ocellata* and *H. quadripunctata*. During aphid scarcity, all *M. oblongoguttata* remain on conifers feeding on the dwindling conifer aphid supply. The few available *S. pineti* alone do not constitute an adequate food source for this large coccinellid, however, and since this meagre diet cannot be supplemented with alternative, non-conifer aphid food, hungry *M. oblongoguttata* seek ant-tended *Cinara* aphids on which to

feed. The high level of association between *M. oblongoguttata* and ants is thus a correlate of this coccinellid's extreme dietary specialisation.

Coccinella magnifica differs from the other species in that it is entirely restricted to the environs of *Formica* ants, notably the *F. rufa* group. Its obligate association and high specificity are in contrast to *M. oblongoguttata*, *C. septempunctata* and *H. quadripunctata*, which are facultative in their association with ants and which, during prey scarcity, can occur with a variety of aphid-tending ant species (J. J. Sloggett pers. obs.). *Coccinella magnifica*'s mode of life poses two related questions: why did this species evolve such a close association with ants and why is this association primarily with the *F. rufa* group?

Coccinella magnifica's close relative, *C. septempunctata*, coexists with *F. rufa* at moderate levels, probably in order to feed on ant-tended aphids during prey scarcity. Donisthorpe (1919–1920), also spoke of this species "experimenting in a myrmecophilous existence". Bhatkar (1982) observed large aggregations of *C. septempunctata* near nests of the wood ant *Formica polyctena*, and even claimed that this coccinellid could follow *F. polyctena* odour trails, to locate tended aphid colonies. *Coccinella undecimpunctata*, *C. transversoguttata* and *Coccinella trifasciata* have also been recorded with ants, the latter two notably in late summer (Bradley and Hinks 1968, Bhatkar 1982). Thus, the data from this study and other observations argue that members of the genus *Coccinella* often facultatively coexist with ants. This is probably due the continued occurrence of ant-tended aphids, when aphid food is scarce elsewhere, and is thus ultimately related to many *Coccinella* species not apparently being particularly tolerant of low aphid densities. It is probable that *C. magnifica*'s non-myrmecophilous ancestors also sought ant-tended aphids during prey scarcity, and this behaviour acted as a predisposing factor in the evolution of myrmecophily in the *C. magnifica* lineage.

Although resource acquisition initially brought *C. magnifica*'s ancestors into contact with ants, a variety of other factors could have led to the enhancement of this trait over evolutionary time. There may have been selective pressure for more efficient utilisation of the ant-tended resource through specialisation. This would eliminate most energetic costs related to migration between a variety of aphid sources in different habitats. Such costs must be substantial in a generalist such as *C. septempunctata*, which can migrate between habitats several times in a season (Iperti 1965, Honěk 1989). Generalist species perhaps also incur physiological costs associated with frequent prey switching (see Hattingh and Samways 1992 on coccidophagous *Chilocorus* species): myrmecophily might minimise these costs because one prey type persists for longer, although *C. magnifica*, like *C. septempunctata*, naturally consumes a broad range of different aphid species (Sloggett 1998). Alter-

natively, *C. magnifica*'s association with ants may have become obligate under selection for enemy free space, although there is little support for this hypothesis at present. *Coccinella magnifica* are rarely successfully parasitised by the hymenopteran *Dinocampus coccinellae*, an important parasitoid of *C. septempunctata* and numerous other coccinellids (Majerus 1989, 1997, Sloggett 1998). However, this, in part at least, results from some intrinsic property of the coccinellid, as much as any protective effect provided by the ant (Sloggett 1998). On the other hand, the pupa-parasitising Diptera *Phalacrotophora* spp., which also include *C. septempunctata* amongst their coccinellid hosts, often successfully parasitise *C. magnifica* pupae undisturbed by ants (J. J. Sloggett pers. obs.).

Avoidance of costly migration can also explain why *C. magnifica* coexists primarily with *F. rufa* group ants. Enough aphid food will occur in the large foraging territories of an ant such as *F. rufa* to support *C. magnifica* over an entire season. The smaller colony sizes and limited tended aphid populations of many other ant species would not be adequate for the coccinellid. Furthermore, the nests of *F. rufa* group ants are long-lived and their environs constitute an environment which is highly persistent over ecological time. *Coccinella magnifica* is thus freed from the need to migrate, except during dispersal.

It is clear from this study that there is as much ecological complexity associated with interactions between homopteran-tending ants and their potential competitors as exists in the ant-homopteran mutualism itself (Addicott 1979) and at the level of host plant (Buckley 1987). Further work is required to elucidate the role which ant-attendance of Homoptera plays in the biology of competitor taxa. The *F. rufa*-*P. sylvestris*-coccinellid system, described here, is a good model with which to examine how ant-attendance interacts with and affects other biological parameters. Broad correlations can be established between levels of coexistence with ants and factors such as diet (see above), investment in chemical defence (Holloway et al. 1991, de Jong et al. 1991, Marples 1993), population biology and genetics (Majerus 1994, Hodek and Honěk 1996) and life-history characteristics (Stewart et al. 1991). Through such studies, on this and other ant-competitor systems, it should ultimately be possible to more fully assess the impact which ant-attendance has had on homopteran-eaters over ecological and evolutionary time.

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References

- Addicott, J. F. 1979. A multispecies aphid-ant association: density dependence and species-specific effects. – *Can. J. Zool.* 57: 558–569.
- Adlung, K. G. 1966. A critical evaluation of the European research on use of red wood ants (*Formica rufa* Group) for the protection of forests against harmful insects. – *Z. Angew. Entomol.* 57: 167–189.
- Banks, C. J. 1954. Random and non-random distributions of Coccinellidae. – *J. Soc. Br. Entomol.* 4: 211–215.
- Banks, C. J. and Macaulay, E. D. M. 1967. Effects of *Aphis fabae* Scop. and of its attendant ants and insect predators on yields of field beans (*Vicia faba* L.). – *Ann. Appl. Biol.* 60: 445–453.
- Barron, A. and Wilson, K. 1998. Overwintering survival in the seven spot ladybird, *Coccinella septempunctata* (Coleoptera: Coccinellidae). – *Eur. J. Entomol.* 95: 639–642.
- Bastian, O. 1982. Die Coccinellidenfauna einiger Koniferenjungwüchse des Tharandter Waldes. – *Faun. Abhandl. Staatl. Mus. Tierk. Dresden* 9: 211–223 (in German with English summary).
- Bhatkar, A. P. 1982. Orientation and defense of ladybeetles (Coleoptera, Coccinellidae). Following ant trail in search of aphids. – *Folia Entomol. Mexicana* 53: 75–85.
- Blackman, R. L. and Eastop, V. F. 1994. Aphids on the world's trees: an identification and information guide. – CAB International, Wallingford.
- Bradley, G. A. 1973. Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator-prey relationship between *Hyperaspis congressis* (Coleoptera: Coccinellidae) and *Toumeyella numismaticum* (Homoptera: Coccidae). – *Can. Entomol.* 105: 1113–1118.
- Bradley, G. A. and Hinks, J. D. 1968. Ants, aphids and jack pine in Manitoba. – *Can. Entomol.* 100: 40–50.
- Bristow, C. M. 1984. Differential benefits from ant attendance to two species of Homoptera on New York ironweed. – *J. Anim. Ecol.* 53: 715–726.
- Bristow, C. M. 1991. Are ant-aphid associations a tritrophic interaction? Oleander aphids and Argentine ants. – *Oecologia* 87: 514–521.
- Buckley, R. 1987. Interactions involving plants, Homoptera and ants. – *Annu. Rev. Ecol. Syst.* 18: 111–135.
- Carter, C. I. and Maslen, N. R. 1982. Conifer lachnids. – *Forestry Comm. Bull.* 58.
- Cherix, D. 1987. Relation between diet and polythism in *Formica* colonies. – *Experientia Suppl.* 54: 93–115.
- Clausen, C. P. 1940. Entomophagous insects. – McGraw-Hill, New York.
- Disney, R. H. L., Majerus, M. E. N. and Walpole, M. J. 1994. Phoridae (Diptera) parasitising Coccinellidae (Coleoptera). – *Entomologist* 113: 28–42.
- Dixon, A. F. G. 1997. Patch quality and fitness in predatory ladybirds. – In: Dettner, K., Bauer, G. and Völkl, W. (eds), Vertical food web interactions – evolutionary patterns and driving forces. *Ecol. Stud.* 130: 205–223.
- Donisthorpe, H. St. J. K. 1900. A few notes on myrmecophilous Coleoptera. – *Entomol. Rec. J. Var.* 12: 172–176.
- Donisthorpe, H. St. J. K. 1919–1920. The myrmecophilous Lady-Bird, *Coccinella distincta*, Fald., its life history and association with ants. – *Entomol. Rec. J. Var.* 31: 214–222; 32: 1–3.
- Fossel, A. 1972. Die Populationsdichte einiger Honigtauerzeuger und ihre Abhängigkeit von der Betreuung durch Ameisen. – *Waldhygiene* 9: 185–191 (In German).

- Gagné, W. C. and Martin, J. L. 1968. The insect ecology of red pine plantations in central Ontario. V. The Coccinellidae (Coleoptera). – *Can. Entomol.* 100: 835–846.
- Gösswald, K. 1941. Rassenstudien an der roten Waldameise *Formica rufa* L. auf systematischer, ökologischer, physiologischer und biologischer Grundlage. – *Z. Angew. Entomol.* 28: 62–124. (In German.)
- Gumoś, H. and Wiśniewski, J. 1960. Nasilenie występowania biedronkowatych (*Col.*, *Coccinellidae*) w drzewostanach sosnowych. – *Polskie Pismo Entomol.* (B) 19-20: 217–223 (in Polish with English summary).
- Hattingh, V. and Samways, M. J. 1992. Prey choice and substitution in *Chilocorus* spp. (Coleoptera: Coccinellidae). – *Bull. Entomol. Res.* 82: 327–334.
- Hodek, I. 1996a. Food Relationships. – In: Hodek, I. and Honěk, A. (eds), *Ecology of Coccinellidae*. Kluwer, Dordrecht, pp. 143–238.
- Hodek, I. 1996b. Dormancy. – In: Hodek, I. and Honěk, A. (eds), *Ecology of Coccinellidae*. Kluwer, Dordrecht, pp. 239–318.
- Hodek, I. and Honěk, A. 1996. Effectiveness and utilization. – In: Hodek, I. and Honěk, A. (eds), *Ecology of Coccinellidae*. Kluwer, Dordrecht, pp. 351–389.
- Hodek, I., Ipert, G. and Hodková, M. 1993. Long-distance flights in Coccinellidae (Coleoptera). – *Eur. J. Entomol.* 90: 403–414.
- Holloway, G. J., de Jong, P. W., Brakefield, P. M. and de Vos, H. 1991. Chemical defence in ladybird beetles (Coccinellidae). I. Distribution of coccinelline and individual variation in defence in 7-spot ladybirds (*Coccinella septempunctata*). – *Chemoecology* 2: 7–14.
- Honěk, A. 1985. Habitat preferences of aphidophagous coccinellids [Coleoptera]. – *Entomophaga* 30: 253–264.
- Honěk, A. 1989. Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). – *Acta Entomol. Bohemoslov.* 86: 179–192.
- Honěk, A. and Hodek I. 1996. Distribution in habitats. – In: Hodek, I. and Honěk, A. (eds), *Ecology of Coccinellidae*. Kluwer, Dordrecht, pp. 95–141.
- Iablokoff-Khznorian, S. M. 1982. Les Coccinelles. Coléoptères–Coccinellidae. Tribu Coccinellini des régions Palearctique et Orientale. – Société Nouvelle des Éditions Boubée (in French).
- Ipert, G. 1965. Contribution à l'étude de la spécificité chez les principales coccinelles aphidiphages des Alpes-Maritimes et des Basses-Alpes. – *Entomophaga* 10: 159–178 (in French with English summary).
- Jensen, T. F. 1978. An energy budget for a field population of *Formica pratensis* Retz. (Hymenoptera: Formicidae). – *Nat. Jutl.* 20: 203–226.
- de Jong, P. W., Holloway, G. J., Brakefield, P. M. and de Vos, H. 1991. Chemical defence in ladybird beetles (Coccinellidae). II. Amount of reflex fluid, the alkaloid adaline and individual variation in defence in 2-spot ladybirds (*Adalia bipunctata*). – *Chemoecology* 2: 15–19.
- Kesten, U. 1969. Zur Morphologie und Biologie von *Anatis ocellata* (L.) (Coleoptera, Coccinellidae). – *Z. Angew. Entomol.* 63: 412–445.
- Klausnitzer, B. 1966. Relation of different species of Coccinellidae to the habitat of fir-forests. – In: Hodek, I. (ed.), *Ecology of aphidophagous insects*. Junk, Dordrecht, pp. 165–166.
- Klausnitzer, B. 1967. Zur Kenntnis der Beziehungen der Coccinellidae zu Kiefernwäldern (*Pinus silvestris* L.). – *Acta Entomol. Bohemoslov.* 64: 62–68 (in German).
- Klausnitzer, B. 1968. Zur Biologie von *Myrrha octodecimguttata* (L.) (*Col.*, *Coccinellidae*). – *Entomol. Nachr.* 12: 102–104 (in German).
- Lewontin, R. C. and Felsenstein, J. 1965. The robustness of homogeneity tests in 2 × N tables. – *Biometrics* 21: 19–33.
- Mahdi, T. and Whittaker, J. B. 1993. Do birch trees (*Betula pendula*) grow better if foraged by wood ants? – *J. Anim. Ecol.* 62: 101–116.
- Majerus, M. E. N. 1988. Some notes on the 18-spot ladybird (*Myrrha 18-guttata* L.) (Coleoptera: Coccinellidae). – *Br. J. Entomol. Nat. Hist.* 1: 11–13.
- Majerus, M. E. N. 1989. *Coccinella magnifica* (Redtenbacher): a myrmecophilous ladybird. – *Br. J. Entomol. Nat. Hist.* 2: 97–106.
- Majerus, M. E. N. 1993. Notes on the inheritance of a scarce form of the striped ladybird, *Myzia oblongoguttata* Linnaeus (Coleoptera: Coccinellidae). – *Entomol. Rec. J. Var.* 105: 271–277.
- Majerus, M. E. N. 1994. Ladybirds (New Naturalist series 81). – HarperCollins, London.
- Majerus, M. E. N. 1997. Parasitization of British ladybirds by *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae). – *Br. J. Entomol. Nat. Hist.* 10: 15–24.
- Majerus, M. E. N. and Kearns, P. W. E. 1989. Ladybirds (Naturalists' Handbooks 10). – Richmond Publ., Slough.
- Majerus, M. E. N. and Majerus, T. M. O. 1996. Ladybird population explosions. – *Br. J. Entomol. Nat. Hist.* 9: 65–76.
- Marples, N. M. 1993. Is the alkaloid in 2spot ladybirds (*Adalia bipunctata*) a defence against ant predation? – *Chemoecology* 4: 29–32.
- Martin, J. L. 1966. The insect ecology of red pine plantations in central Ontario. IV. The crown fauna. – *Can. Entomol.* 98: 10–27.
- Michels, G. J. and Behle, R. W. 1992. Evaluation of sampling methods for lady beetles (Coleoptera: Coccinellidae) in grain sorghum. – *J. Econ. Entomol.* 85: 2251–2257.
- Müller, H. 1958. Zur Kenntnis der Schäden, die Lachniden an ihren Wirtsbäumen hervorrufen können. – *Z. Angew. Entomol.* 42: 284–291 (in German with English summary).
- Pontin, A. J. 1959. Some records of predators and parasites adapted to attack aphids attended by ants. – *Entomol. Mon. Mag.* 95: 154–155.
- Rosengren, R. and Sundström, L. 1991. The interactions between red wood ants, *Cinara* aphids, and pines. A ghost of mutualism past? – In: Huxley, C. R. and Cutler, D. F. (eds), *Ant-plant interactions*. Oxford Univ. Press, Oxford, pp. 80–91.
- Scheurer, S. 1971. Der Einfluß der Ameisen und der natürlichen Feinde auf einige an *Pinus silvestris* L. lebende Cinarinen in der Dübener-Heide (DDR). – *Polskie Pismo Entomol.* 41: 197–229 (in German).
- Schmidt, G. 1936. Berichtigungen und Ergänzungen zur Pommerschen Fauna insonderheit der Coleopterenfauna. – *Dohrniana* 15: 53–59 (in German).
- Schmutterer, H. 1956. Saugschäden an Eichen und Buchen durch Lachniden in Abhängigkeit von Ameisen-Trophobie. – *Z. Angew. Entomol.* 39: 178–185 (in German with English summary).
- Siegel, S. and Castellan, N. J. 1988. Nonparametric statistics for the behavioural sciences. – McGraw-Hill, New York.
- Skinner, G. J. 1980. The feeding habits of the wood-ant *Formica rufa* (Hymenoptera: Formicidae), in limestone woodland in north-west England. – *J. Anim. Ecol.* 49: 417–433.
- Skinner, G. J. and Whittaker, J. B. 1981. An experimental investigation of inter-relationships between the wood-ant (*Formica rufa*) and some tree-canopy herbivores. – *J. Anim. Ecol.* 50: 313–326.
- Sloggett, J. J. 1998. Interactions between coccinellids (Coleoptera) and ants (Hymenoptera: Formicidae) and the evolution of myrmecophily in *Coccinella magnifica* Redtenbacher. – Ph.D. thesis, Univ. of Cambridge, Cambridge.
- Sloggett, J. J., Wood, R. A. and Majerus, M. E. N. 1998. Adaptations of *Coccinella magnifica* Redtenbacher, a myrmecophilous coccinellid, to aggression by wood ants (*Formica rufa* Group). I. Adult behavioral adaptation, its ecological context and evolution. – *J. Insect Behav.* 11: 889–904.

- Sloggett, J. J., Manica, A., Day, M. J. and Majerus, M. E. N. 1999. Predation of ladybirds (Coleoptera: Coccinellidae) by wood ants, *Formica rufa* L. (Hymenoptera: Formicidae). – Entomol. Gaz. 50: 217–221.
- Sokal, R. R. and Rohlf, F. J. 1981. Biometry – the principles and practice of statistics in biological research, 2nd ed. – Freeman, San Francisco.
- Stewart, L. A., Hemptinne, J.-L. and Dixon, A. F. G. 1991. Reproductive tactics of ladybird beetles: relationships between egg size, ovariole number and developmental time. – Funct. Ecol. 5: 380–385.
- Sudd, J. H. 1983. The distribution of foraging wood-ants (*Formica lugubris* Zett.) in relation to the distribution of aphids. – Insectes Soc. 30: 298–307.
- Tauber, M. J., Tauber, C. A., Ruberson, J. R. et al. 1993. Evolution of prey specificity via three steps. – Experientia 49: 1113–1117.
- Triltsch, H. 1997. Gut contents in field sampled adults of *Coccinella septempunctata* (Col.: Coccinellidae). – Entomophaga 42: 125–131.
- Völkl, W. 1992. Aphids or their parasitoids: Who actually benefits from ant-attendance? – J. Anim. Ecol. 64: 273–281.
- Völkl, W. 1995. Behavioural and morphological adaptations of the coccinellid, *Platynaspis luteorubra* for exploiting ant-attended resources (Coleoptera: Coccinellidae). – J. Insect Behav. 8: 653–670.
- Völkl, W. 1997. Interactions between ants and aphid parasitoids: patterns and consequences for resource utilization. – In: Dettner, K., Bauer, G. and Völkl, W. (eds), Vertical food web interactions – evolutionary patterns and driving forces. Ecol. Stud. 130: 225–240.
- Völkl, W. and Kroupa, A. S. 1997. Effects of adult mortality risks on parasitoid foraging tactics. – Anim. Behav. 54: 349–359.
- Völkl, W. and Vohland, K. 1996. Wax covers in larvae of two *Scymnus* species: do they enhance coccinellid larval survival? – Oecologia 107: 498–503.
- Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. – Annu. Rev. Entomol. 8: 307–344.
- Wellenstein, G. 1952. Zur Ernährung der Roten Waldameise (*Formica rufa* L.). – Z. Pflanzenkr. Pflanzenschutz 59: 430–451 (in German with English summary).
- Whittaker, J. B. 1991. Effects of ants on temperate woodland trees. – In: Huxley, C. R. and Cutler, D. F. (eds), Ant-plant interactions. Oxford Univ. Press, Oxford, pp. 67–79.
- Wiśniewski, J. 1963. Występowanie myrmekofilnej biedronki, *Coccinella divaricata* Oliv. (Col., Coccinellidae) w Polsce. – Przegl. zool. 7: 143–146 (in Polish with English summary).