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# Apparent competition between two aphid species

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## Summary

1. The population dynamics of colonies of nettle aphids (*Microlophium carnosum* Buckton) were studied on potted nettle plants placed beside plots of grass on some of which outbreaks of grass aphids (*Rhopalosiphum padi* L.) had been induced by fertilizer application.
2. Nettle aphid colonies adjacent to grass aphid concentration suffered an earlier population decline, and produced fewer alate dispersers, than control colonies.
3. The reduced performance of nettle aphids in the vicinity of grass aphid was due to increased predation by Coccinellidae, attracted into the area by the large concentrations of grass aphids. The indirect interaction between the two species of aphids is an example of apparent competition.
4. Because predators pre-emptively exploited nettle aphids on plants in the grass aphid treatment, the numbers of nettle aphids attacked by parasitoid wasps was greatly reduced in these sites compared to the controls.

**Key-words:** apparent competition, indirect effects, population dynamics, aphids, Coccinellidae

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## Introduction

Two species of animal that consume different resources and that do not interact directly can still influence each other's population growth rates if they share natural enemies such as predators, parasites or pathogens. If one species increases in abundance, the density of the shared natural enemy may also increase in density and in consequence the second species will suffer higher mortality. Because each species suffers a reduction in population growth rate as the other increases in abundance, exactly as is found in competitive situations, Holt (1977) has called such interactions apparent competition. The potential importance of such indirect interactions in community ecology has been frequently discussed (see Holt & Lawton 1994 and included references). In particular, a number of authors have suggested that communities of herbivorous arthropods might be structured by apparent competition mediated by shared predators and parasitoids (e.g. Jeffries & Lawton 1984; Lawton 1986; Godfray 1994). Both short-term and long-term apparent competition (Holt & Kotler 1987) may influence herbivore population densities. Short-term apparent competition occurs when an increase in the numbers of one species leads to heavier predation or parasitism of a second species due to, for example, a fast aggregative behavioural response by the natural

enemy. Short-term apparent competition need not always occur if two species are linked by a natural enemy: if the latter becomes satiated, per capita mortality may drop giving rise to 'short-term apparent mutualism' (Holt 1977; Abrams 1987). Long-term apparent competition occurs when the two species influence each other over a number of generations, normally involving population growth and reproduction by the natural enemy.

Many studies have found patterns in communities that are consistent with apparent competition (reviewed by Holt & Lawton 1994) and there is good experimental evidence of apparent competition from littoral and freshwater communities (Schmitt 1987; Huang & Sih 1990; Menge 1995), and from studies of terrestrial isopod species that share pathogens (Grosholz 1992). However, evidence that herbivorous arthropods interact through apparent competition is sparse. Settle & Wilson (1990a, b) studied two species of leafhopper that feed on the leaves of cultivated grape in California. During their study, one species (*Erythroneura variabilis* Beamer) invaded the San Joaquin Valley, an extension of range that was associated with a marked decline in the abundance of a second species, *Erythroneura elegantula* (Osborn). The two insects did compete, but intra- and inter-specific competition were of similar magnitude and Settle & Wilson argued that competition was unlikely to

explain the drop in numbers of *E. elegantula*. Instead, they suggested that *E. elegantula* declined because of attack by a shared mymarid egg parasitoid, *Anagrus epops* (Girault). *E. variabilis* eggs are better protected from attack by the parasitoid which gives this species an advantage in comparison with *E. elegantula*. Karban, Houghton-Eitzmann & English-Loeb (1994), also studied herbivores of cultivated grape in California, in their case two species of herbivorous mites. One species (*Eotetranychus willamettei* McGregor) tends to attack earlier in the season than the commercially important *Tetranychus pacificus* (McGregor). The artificial release into vineyards of *E. willamettei* and a shared natural enemy, the predatory mite *Metaseiulus occidentalis* (Nesbitt), led to lower populations of *T. pacificus*, at least on some occasions. Karban *et al.* interpret the reduction in *T. pacificus* as due to apparent competition mediated by the predacious mite.

We report here an experimental study of short-term apparent competition between two species of aphids mediated by shared predators. We show that the population dynamics of the common nettle aphid *Microlophium carnosum* (Aphididae) is influenced by the density of the bird cherry-oat aphid (referred to below as grass aphid), *Rhopalosiphum padi* (Aphididae) on adjacent grasses. *M. carnosum* suffers from the presence of *R. padi* as the latter acts as a source of shared predators, particularly Coccinellidae.

## Methods

The experiment was conducted at Silwood Park, Berkshire, in southern England, in spring 1995. We made use of an ongoing plant ecology experiment, as part of which, six experimental plots within a large field, each 19 × 16 m in size, consisting chiefly of grass with some low forbs, had been fenced to give protection from rabbit grazing. No nettle (*Urtica dioica* L.) grew naturally in the field. On 10–14 April, three of the sites were treated with NPK fertilizer (Growmore®) at a rate of 150 kg ha<sup>-1</sup> N, leaving the other sites untouched. The sites had been fertilized in the same way in the previous two Aprils. The fertilizer treatment led to rapid grass growth and large natural populations of *R. padi*, which were largely absent in the untreated sites (see Results). *R. padi* is a normally host-alternating aphid that migrates from bird cherry (*Prunus padus* L.) in early spring to feed on a variety of grass species, although some clones overwinter anholocyclically on grass (Dixon 1971). The most important grass species in the sites were *Alopecurus pratensis* (L.), *Arrhenathrum elatius* (L.), *Holcus lanatus* (L.), *Agrostis capillaris* (L.) and *Festuca rubra* (L.).

On 21 April, we placed eight nettles in large pots at regular intervals around the perimeter of each of the six experimental plots. The nettles had all been potted and fertilized the previous March and were approxi-

mately 40 cm in height when placed in the field. We collected *M. carnosum*, a common aphid that feeds only on *Urtica*, from natural populations in Silwood Park and placed them on the potted nettles so that all nettles had as similar densities as possible. We finished seeding the nettles with aphids on 5 May (designated the beginning of the experiment) and thereafter aphid numbers were allowed to vary naturally. Nettles were watered regularly throughout the experiment.

The number of aphids per nettle plant was counted every week from the beginning of the experiment until 7 July, when all densities had dropped to near zero. There was some variation in nettle size, chiefly related to the number of vertical stems per plant, which was also recorded. The number and identity of aphid predators on each nettle plant was recorded at the same time. Once a week we counted the number of parasitized aphids (aphid mummies) on each nettle. Mummies were collected from half the nettles at each site and reared in the laboratory to determine the identity of the parasitoid, and the fraction of parasitoids that were hyperparasitized.

The density of grass aphids was estimated on weeks 1–6 and 8. The numbers of aphids on 10 grass stems were counted at 1 m intervals around the perimeter of the six experimental sites. The density of grass stems per square metre was also measured. The numbers of aphid predators and aphid mummies were counted during each aphid survey and the mummies collected for rearing.

## STATISTICAL ANALYSIS

The data were analysed using one-way analysis of variance with repeated measures. Because the number of repeated measure (9) is greater than the total number of replicates (6), multivariate methods cannot be applied and all analyses used univariate techniques (we followed the guidance of Crowder & Hand 1990; see especially their Chapter 3). The assumption of sphericity was always violated and hence the degrees of freedom have to be adjusted. We calculated both Greenhouse–Geisser (GG) and Huynh–Feldt (HF) adjustments but, unless otherwise stated, used the former as it was the most conservative (note, the resultant degrees of freedom are non-integer). A dagger (†) after the probability value indicates that the lower bound adjustment was also significant at  $P = 0.05$ . Where statistical differences were found between treatments, we used a Scheffé test (with critical  $P = 0.05$ ) to identify the times at which the population densities in the two treatments were most divergent, but treat this as an informal indicator of differences rather than a formal statistical test. In some graphs we plot the mean numbers of aphids per nettle plant in each site with a bar representing the standard error of the mean. However, in analysing the differences between treatments, we avoid pseudoreplication by working only with the means for each site.

## Results

Figure 1 shows the density of *R. padi* on grass over the course of the experiment. At the beginning of the experiment, aphid densities were high in the fertilized plots but they declined rapidly over the first half of the experiment. In the unfertilized plots, *R. padi* remained very rare throughout the course of the experiment. There was a significant time/treatment interaction (GG:  $F_{1,7,6,9} = 8.56$ ,  $P = 0.013$ †) and the Scheffé test showed that the major differences between treatments occurred in weeks 1–3. In week 1, we estimate that there were approximately 224 000 aphids (including nymphs) in each fertilized plot and less than 5000 in the unfertilized plots. We found a few individuals of two other grass aphids, *Sitobion avenae* and *S. fragariae*, but these always remained at substantially lower densities than *R. padi*.

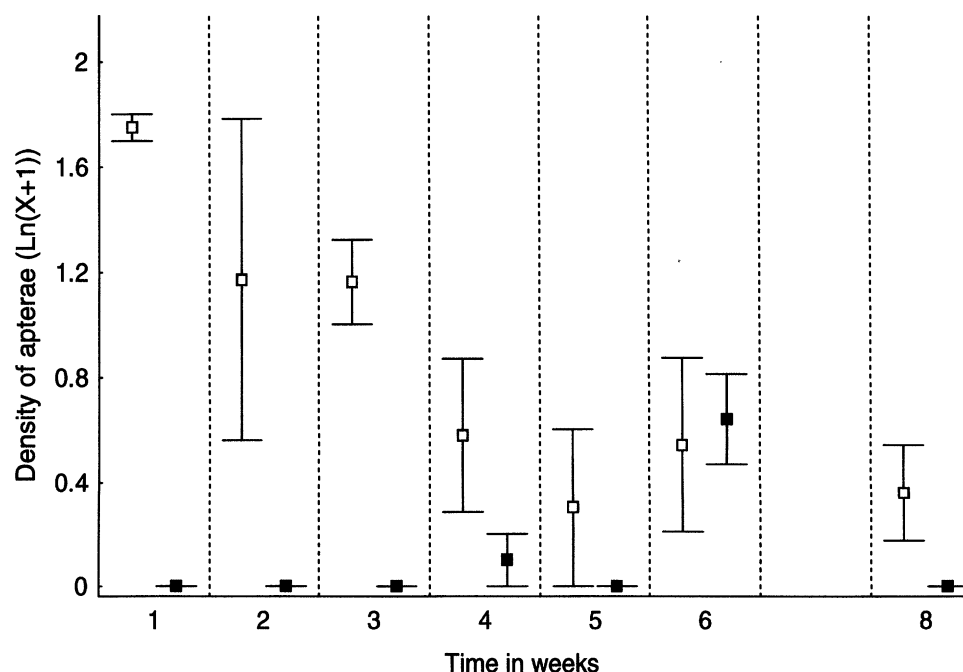
The major diurnal predator recorded attacking the grass aphid was *Coccinella septempunctata* (L.) (Coccinellidae). Small numbers of other Coccinellidae as well as Syrphidae, Chrysopidae, and Anthocoris (Anthocoridae) were also observed. *C. septempunctata* was found at high but variable densities on the fertilized plots but was largely absent from the unfertilized plots (Table 1). The peak of larval abundance occurred in weeks 3 and 4. We recorded no species of parasitoids from the scarce aphids in the unfertilized sites. In the fertilized sites we found some mummies (parasitized aphids) but they were too rare to be sampled quantitatively. The primary parasitoid responsible for the mummies was *Aphidius rhopalosiphi* (De Stefani-Perez) (Braconidae) and we also reared the hyperparasitoids *Asaphes vulgaris* (Walker), *Asaphes suspensus* (Nees) (Pteromalidae), *Alloxysta* sp. nr. *vic-*

**Table 1.** The number of larval, pupal and adult *C. septempunctata* recorded in the six grass plots (fertilized: F1, F2, F3; unfertilized U1, U2, U3) on the seven sampling occasions

	Week	1	2	3	4	5	6	8
<b>Larvae</b>								
F1	2	39	49	33	3	11	0	
F2	0	6	27	37	9	0	0	
F3	1	2	13	10	3	3	0	
U1	0	0	0	1	0	0	0	
U2	0	0	0	0	0	0	0	
U3	0	0	0	0	0	0	0	
<b>Pupae</b>								
F1	0	0	0	18	10	18	0	
F2	0	0	0	5	5	1	0	
F3	0	0	0	1	2	4	0	
U1	0	0	0	0	0	0	0	
U2	0	0	0	0	0	0	0	
U3	0	0	0	0	0	0	0	
<b>Adults</b>								
F1	1	2	3	4	2	45	0	
F2	6	9	7	4	3	0	3	
F3	5	3	3	0	0	1	2	
U1	0	0	0	0	1	0	2	
U2	0	0	0	0	0	0	1	
U3	0	0	0	0	0	0	2	

*trix* (Westwood) and *Phaenoglyphis villosa* (Hartig) (Charipidae).

The population densities of adult apterous *M. carnosum* on nettles over the course of the experiment are shown in Fig. 2. In the first 3 weeks of the experiment, densities were high and not significantly different on



**Fig. 1.** The densities of *R. padi* on grass over the course of the experiment. Means and standard errors of the density ( $\log_e + 1$ ) of adult apterous aphids per grass tiller on fertilized (open squares) and unfertilized sites (closed squares).

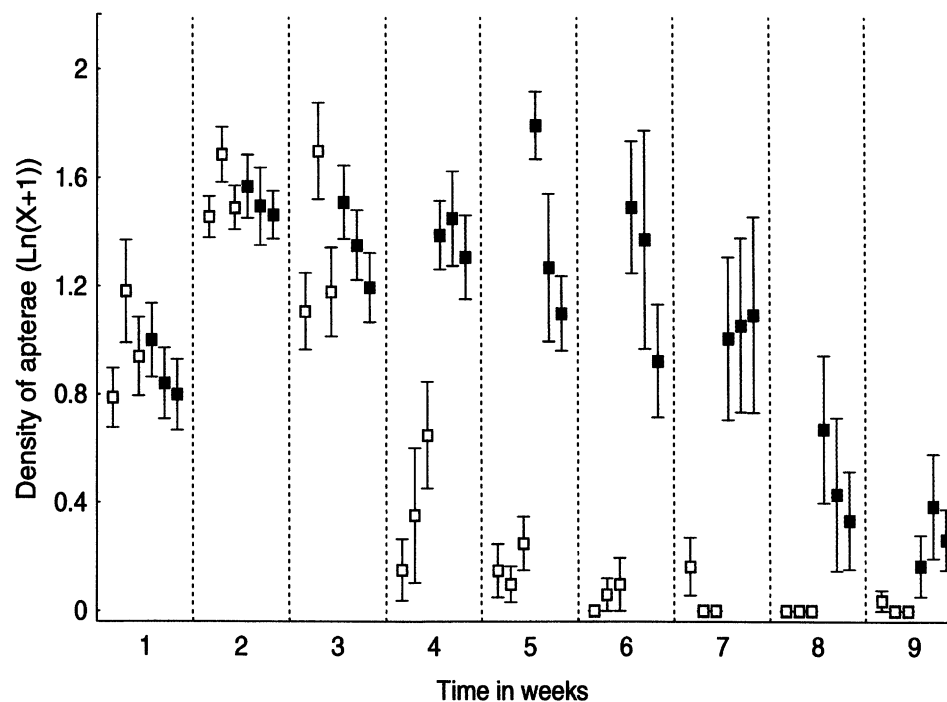


Fig. 2. The densities of *M. carnosum* on nettle over the course of the experiment. For each week, we show means and standard errors of the number ( $\log_e + 1$ ) of adult apterous aphids on the eight nettles placed around each of the three fertilized (open squares) and three unfertilized sites (closed squares). Further statistical analysis is performed on the mean densities of aphids per plot.

nettles surrounding fertilized and unfertilized plots. However, between week 3 and 4, aphid densities dropped dramatically on nettles surrounding all three fertilized sites, decreasing almost to zero in the following week, and remaining low throughout the rest of the experiment. In contrast, densities of aphids on nettles surrounding the unfertilized sites remained high until about week 7 and then declined in the remaining 2 weeks of the experiment. The time  $\times$  treatment interaction was highly significant (GG:  $F_{3,7,14,8} = 18.95$ ,  $P = 8 \times 10^{-5} \dagger$ ) with a Scheffé test showing the most important differences between treatment in weeks 4–7. A similar analysis performed on total aphids (nymphs, apterae and alates) gave very similar results. Figure 3 shows the densities of alate aphids over the course of the experiment. In both treatments, alate densities were low until week 4. On nettles adjacent to unfertilized sites, alates are then produced in large numbers in weeks 5–7, their numbers falling towards the end of the experiment with the decline of the aphid colonies. However, on nettles adjacent to fertilized sites this pulse of alates does not occur because of the dramatic decline in aphid numbers after week 4. The interaction between time and treatment was significant (GG:  $F_{2,6,10,4} = 8.48$ ,  $P = 0.004 \dagger$ ) with major differences between treatments in weeks 5 and 6 (Scheffé test). Some of the alates we recorded on the nettle plants are likely to have immigrated into the site, which explains why alate densities do not fall as low as the density of apterae towards the end of the experiment.

The same spectrum of aphid predators was recorded on nettle as on grass and again *C. septempunctata* was

the most important (Table 2). Figure 4 shows the mean numbers of coccinellid larvae on nettles in the two treatments. The number of larvae built up on nettles adjacent to the fertilized treatment reaching a peak in week 4 just prior to the dramatic crash in aphid numbers. There was also a build up of larvae on nettles adjacent to the unfertilized treatments which reaches a peak in week 5, despite the fact that aphid densities on these plots continued to rise. Based on observations of coccinellid movements in the field, we suspect that many adult *C. septempunctata* were attracted into the area by the concentration of grass aphids, first moving onto the adjacent nettles, but subsequently dispersing to the aphid colonies on nettles around the unfertilized treatments (practical constraints forced us to place both treatments in the same large field). This source of *C. septempunctata* eggs and larvae on the nettles in the unfertilized treatment ended by about week 3 when the grass aphid numbers declined. However, coccinellid numbers are very variable and the time  $\times$  treatment interaction is not significant (GG:  $F_{2,4,9,8} = 2.66$ ,  $P = 0.12$ ).

Parasitized aphids were more common on nettle than on grass. We reared four primary parasitoids (all Braconidae): *Aphidius urticae* (Haliday), *Aphidius microlophii* (Pennacchio & Trembley) (both common), *Aphidius picipes* (Nees) and *Praon dorsale* (Haliday) (only a few specimens), and the hyperparasitoids *Dendrocerus carpenteri* (Curtis), *Dendrocerus aphidum* (Rondani) (Ceraphronidae), *Asaphes vulgaris* (Walker) (Pteromalidae), *Syrphophagus* sp. (Encyrtidae), and *Alloxysta* sp. nr. *macrophadna* (Hartig)



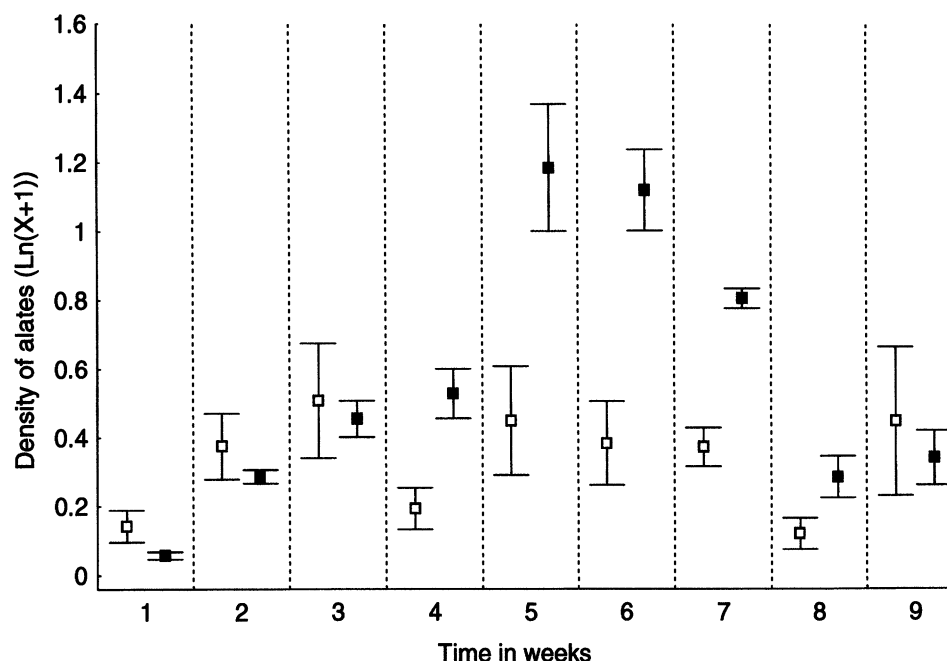


Fig. 3. The numbers ( $\log_e + 1$ ) of alate *M. carnosum* on nettle over the course of the experiment. Means and standard errors of densities across the three fertilized (open squares) and three unfertilized sites (closed squares).

(Charipidae). On the unfertilized sites, the numbers of parasitized aphids increased over the first 6 weeks of the experiment and then suffered a decline in the last 3 weeks concomitant with the decline in aphid numbers (Fig. 5). In the fertilized plots, mummy densities also increased in the first few weeks of the experiment but declined greatly when aphid densities crashed in week

4. Statistical analysis of the mummy data shows that the time  $\times$  treatment interaction is on the border of significance (GG:  $F_{1,1,4,5} = 5.96$ ,  $P = 0.064$ ; HF:  $F_{1,7,6,7} = 5.96$ ,  $P = 0.035$ ) with the major difference between the treatments occurring in week 6.

## Discussion

We have shown that the fate of a population of *Microrhopalum carnosum* on nettles depends critically on whether it develops in close proximity to populations of *Rhopalosiphum padi*, a grass aphid with which it never directly competes, but with which it shares natural enemies. We believe that this is an example of short-term, apparent competition.

## CRITICISM OF THE EXPERIMENT

We manipulated populations of *R. padi* by selective fertilization. One criticism of the experiment is that the differences in *M. carnosum* population dynamics might be due to an effect of the fertilization other than through an increase in *R. padi* densities. A direct effect of the fertilizer on the nettle plants can be ruled out as all nettles were maintained in pots under identical watering and fertilizer treatment. However, the grass in the fertilized plots was taller and denser than in the unfertilized plots. If predators are attracted or retained to a greater degree in areas of denser vegetation, then aphids on nettles adjacent to such areas might suffer heavier predation. Although we cannot rule out this explanation, we think it is highly unlikely. The most common predators were coccinellids which show strong recruitment to con-

Table 2. The number of larval, pupal and adult *C. septempunctata* recorded on nettles around the six grass plots (fertilized: F1, F2, F3; unfertilized U1, U2, U3) on the nine sampling occasions

Week	1	2	3	4	5	6	7	8	9
Larvae									
F1	1	8	25	18	3	0	0	0	1
F2	3	2	18	17	20	2	1	0	4
F3	5	2	3	22	10	0	2	0	0
U1	16	0	0	9	34	17	9	3	0
U2	0	1	0	4	8	0	3	0	0
U3	7	0	2	0	1	1	0	0	0
Pupae									
F1	0	0	4	8	10	5	0	1	0
F2	0	0	0	1	5	8	4	1	0
F3	0	0	0	0	2	5	1	0	0
U1	0	0	0	0	0	0	0	0	0
U2	0	0	0	0	0	0	0	0	1
U3	0	0	0	0	0	0	0	0	0
Adults									
F1	3	1	3	2	8	9	11	6	0
F2	6	4	2	0	5	20	14	12	2
F3	4	7	2	2	0	2	4	8	2
U1	1	0	1	2	7	16	20	17	4
U2	2	3	4	15	8	23	12	8	8
U3	1	2	6	5	3	5	11	14	2

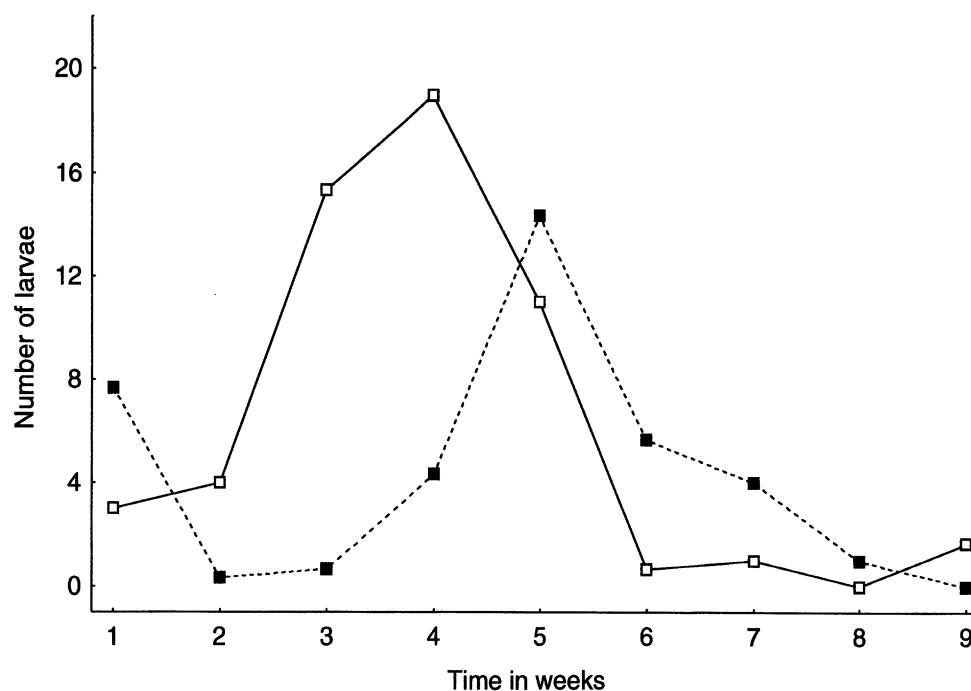


Fig. 4. The mean number of *C. septempunctata* larvae on nettles in fertilized (open squares) and unfertilized (closed squares) sites.

centrations of aphids (Dixon 1959; Carter & Dixon 1982; Kareiva and Odell 1987; Majerus 1994), and which oviposit in the vicinity of aphid colonies. Coccinellid activity in the fertilized grass plots was clearly concentrated on infested tillers and they were almost certainly attracted by the presence of their prey. Unfortunately, the natural control—fertilization plus aphid exclusion—is difficult to perform as the only

practical means of aphid exclusion is chemical and this would risk influencing predator mortality.

For logistic reasons we were only able to sample diurnal predators. We were thus unable to say whether nocturnal predators, for example Carabidae (ground beetles) (Scheller 1984), contributed to the different population dynamics of nettle aphids in the two treatments. A final caveat is that the strength of apparent

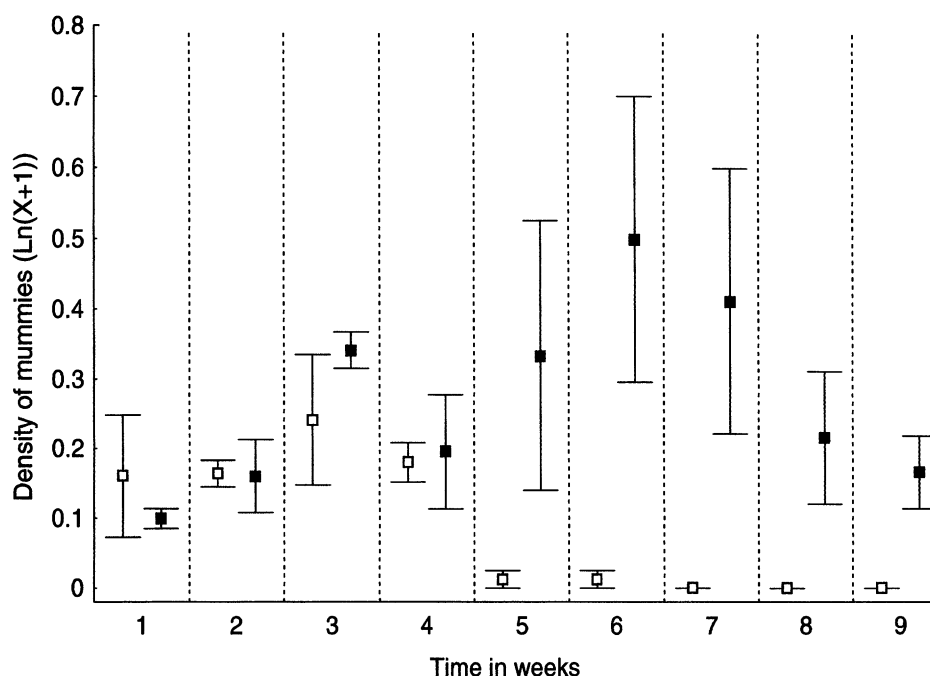


Fig. 5. The number ( $\log_e + 1$ ) of parasitized *M. carnosum* (mummies) on nettle over the course of the experiment. Means and standard errors of densities across the three fertilized (open squares) and three unfertilized (closed squares) sites.

competition is clearly scale-dependent and our experiment was limited to a single spatial scale. Extrapolation of our results to other scales must be made with care.

#### M. CARNOSUM POPULATION DYNAMICS

*M. carnosum* is a common aphid species on nettle which reaches high population densities in late spring. Population densities drop to very low levels in mid to late summer, sometimes rising slightly in the early autumn. The species is monophagous (no host alternation) and parthenogenetic throughout the spring and summer. At the study site, the aphid appears to overwinter chiefly as parthenogenetic females (Perrin 1976) but overwintering also occurs as eggs produced by sexual females that occur in the autumn. During the spring, colonies produce winged females that disperse to colonize new plants.

The main effect of the proximity of *R. padi* is to cause a premature drop in aphid densities, before the normal summer decline. The consequences of this for *M. carnosum* population growth rates are two-fold. First, local populations are reduced in size and risk extinction, and fewer individuals will survive through the summer and subsequent winter, either as parthenogenetic adults or as overwintering eggs. Secondly, there is a reduction in the number of dispersing aphids (See Fig. 3) and hence a drop in the number of secondary colonies founded by the clone. More information about the local and meta-population structure of *M. carnosum* is required to evaluate the relative importance of the two factors.

Parasitoids caused relatively little mortality in this experiment. This is partly explained by the experiment being conducted in early spring before the bulk of parasitoids had become active. However, other studies of nettle aphids have found little effect of parasitoids on population dynamics, possibly because the parasitoids themselves are heavily attacked by hyper-parasitoids (Mackauer & Völkl 1993) and often killed by aphid predators. In general, predators tend to be more important than parasitoids as aphid natural enemies (Dixon 1985).

#### TYPE OF INDIRECT INTERACTION

As discussed in the introduction, apparent competition mediated by natural enemies can be both short-term or long-term depending on whether the interaction is transient or whether a new three (or more) species equilibrium is attained. Our experiment only ran for part of one season and thus could only detect short-term apparent competition. Part of the reduction in nettle aphid density on plants adjacent to fertilized grass plots was due to adult coccinellids (and possibly other nocturnal predators) attracted into the area by the high densities of grass aphids, and which moved onto the nettle aphids, especially after

*R. padi* numbers had crashed. This component of the apparent competition is purely mediated by the behaviour of the predator. However, we believe that most damage to the nettle aphid populations was done by the coccinellid larvae, the progeny of the adults attracted into the area, and this component of the apparent competition is thus mediated by increased predator reproduction.

The way the experiment was set up, with large manipulated populations of *R. padi* and small initially constant populations of *M. carnosum*, meant that we could study only apparent competitive effects of *R. padi* on *M. carnosum* and not vice versa. The polyphagous nature of *C. septempunctata* suggests, however, that *M. carnosum* would in other circumstances influence the dynamics of *R. padi*, and indeed that many other pairs of aphid species may interact indirectly through shared polyphagous predators. It is interesting that forty years ago Banks (1955) suggested that *M. carnosum* might act as a source of predatory coccinellids that later attack the black bean aphid, *Aphis fabae*, a major pest. Banks surveyed *A. fabae* in three bean fields including one adjacent to a large area of nettles. This site suffered greater predation from coccinellids (the most important of which was *Adalia bipunctata*) which he suggested was due to a transfer of beetles from large populations attacking *M. carnosum* on nettles. More generally, it is widely believed that control of aphids on crops can be enhanced if other plants, especially non-cultivated plants, are grown nearby where they can act as host plants for alternative prey (e.g. van Emden 1965; van Emden & Willams 1974; Russell 1989; Hassall *et al.* 1992; Thomas, Wratten & Sotherton 1991, 1992; Dennis, Thomas & Sotherton 1994; Evans 1994; Zhou, Carter & Powell 1994). Such effects—which might be called diffuse apparent competition—are significant both in pest management and in understanding the community structure of terrestrial arthropods.

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