Cursorial spiders retard initial aphid population growth at low densities in winter wheat

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Abstract

Generalist predators contribute to pest suppression in agroecosystems. Spider communities, which form a substantial fraction of the generalist predator fauna in arable land, are characterized by two functional groups: web-building and cursorial (non-web-building) species. We investigated the relative impact of these two functional groups on a common pest (*Sitobion avenae*, Aphididae) in wheat by combining a molecular technique that revealed species-specific aphid consumption rates with a factorial field experiment that analyzed the impact, separately and together, of equal densities of these two spider functional groups on aphid population growth. Only cursorial spiders retarded aphid population growth in our cage experiment, but this effect was limited to the initial aphid-population growth period and low-to-intermediate aphid densities. The molecular analysis, which used aphid-specific primers to detect aphid DNA in predator species, detected the highest proportion of aphid-consuming individuals in two cursorial spiders: the foliage-dwelling *Xysticus cristatus* (Thomisidae) and the ground-active *Pardosa palustris* (Lycosidae). The results suggest that manipulating the community composition in favour of pest-consuming functional groups may be more important for improving biological control than fostering predator biodiversity *per se*. Agricultural management practices that specifically foster effective species or functional groups (e.g. mulching for cursorial spiders) should receive more attention in low-pesticide farming systems.

Keywords: aphids, Araneae, biological control, generalist predators, functional group diversity, DNA-based gut content analysis, natural enemies, *Sitobion avenae*

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Table 1. Number of immature (*Philodromus* sp.) and adult (all other species) individuals per species in spider functional-group treatments per cage.

Species	Family/subfamily	%	Web-builders		Cursorial		Assemblage	
			♂	♀	♂	♀	♂	♀
Diplostyla concolor	Linyphiinae	27	1	3	0	0	1	1
Meioneta rurestris	Linyphiinae	20	1	3	0	0	1	1
Erigone atra/dentipalpis	Erigoninae	27	1	2	0	0	1	1
Mangora acalypha	Araneidae	87	0	4	0	0	0	2
Xysticus cristatus	Thomisidae	71	0	0	0	1	0	1
Philodromus sp.	Philodromidae	100	0	0	0	1	0	1
Pardosa palustris	Lycosidae	62	0	0	4	8	1	3
Pachygnatha degeeri	Tetragnathidae	50	0	0	0	1	0	1

The number of removed individuals per species is given as a proportion (%) of the total number of spiders removed from the same family/subfamily.

Introduction

Aphids cause substantial economic loss to farmers in Europe and the US, with estimated annual yield losses ranging from 10 to 250 million US$ in North America (Brewer & Elliott, 2004). Generalist predators contribute to aphid suppression (Symondson *et al.*, 2002), a conclusion supported by several negative correlations between pest numbers and predator abundance in field surveys (Chambers *et al.*, 1986; Winder, 1990; Östman *et al.*, 2003). The impact of generalist predators may be critically important in systems under organic farming (Zehnder *et al.*, 2007), where reduced pesticide application may enhance densities of generalist predators, thereby potentially strengthening their contribution to pest control (Thorbek & Bilde, 2004; Hole *et al.*, 2005; Schmidt *et al.*, 2005). Early in the growing season aphids occur at low abundance within relatively distinct patches in arable fields (Östman, 2002; Birkhofer *et al.*, 2007). It has been suggested that generalist predators are most efficient in suppressing aphids during those early colonization stages (Edwards *et al.*, 1979; Chiverton, 1986).

Spiders are among the most abundant arthropod predators in temperate agroecosystems (Wise, 1993; Nyffeler & Sunderland, 2003). Laboratory experiments provided evidence that aphids can be low-quality or even toxic prey for spiders (Toft, 2005). In contrast, immunological and molecular techniques suggest that web-building (Harwood *et al.*, 2004) and cursorial (Harwood *et al.*, 2005) spiders consume aphids in the field. Reducing generalist-predator abundance (including spiders) in field experiments caused higher aphid numbers in some studies (Holland & Thomas, 1997a; Lang, 2003; Schmidt *et al.*, 2004) but not in others (Holland & Thomas, 1997b; Lang *et al.*, 1999).

We combined a factorial field experiment that analyzed the impact, separately and together, of two spider functional groups (web-building and non-web-building (cursorial) spiders) on aphid population growth, with a molecular approach to determine species-specific aphid consumption rates. With these two complementary approaches, we determined the effectiveness of the two functional groups, alone and together, in suppressing aphid population growth. We hypothesized that: (i) web-building and non-web-building spiders are each less effective in suppressing aphid numbers than when together in an assemblage; (ii) spider assemblages prevent aphid outbreaks during early stages of aphid colonization; and (iii) foliage-dwelling, non-web spiders consume aphids at higher rates than web-building or ground-active cursorial species.

Methods

Experimental design

In a winter wheat field close to Darmstadt, Germany, we conducted a 2×2 randomized-block experiment using 36 closed cages placed in groups of four (nine blocks, each cage 3 m apart within a block and 12 m from the field edge), which were installed March 29, 2006. The 0.7 m² cages consisted of a 50-cm high, round, plastic barrier that was inserted 10 cm in the soil (cage diameter, 95 cm). The cage sides were extended an additional 90 cm with gauze (mesh width < 1 mm) that was held by three upright wooden poles and was closed on top by tying the gauze in a knot. The interface between plastic barrier and gauze was sealed with duct tape. All cages were closed March 29 and only opened for predator removal, introduction of aphids and spider functional groups and tiller counts.

Between April 2 and 17, spiders were removed from the enclosures by means of two pitfall traps without preservative (emptied daily) and six visual searches per cage, each lasting six minutes. Other predaceous arthropods trapped by pitfall traps were released daily outside the cages (primarily carabid and staphylinid beetles). No naturally occurring aphids were found in cages during predator removal. All removed spiders ($N = 493$) were kept in the laboratory at 20°C, 10-h photoperiod, and were fed two *Drosophila melanogaster* (curly, b.t.b.e. Insektenzucht GmbH, Germany) every two days. On 18 April, 24 laboratory-reared, immature aphids (*Sitobion avenae*, Katz Biotech AG, Germany) were introduced in groups of 12 on two opposing tillers per cage. One day later, spider functional-group treatments were established in a 2×2 factorial design: two single-functional group treatments (web-building or cursorial spiders), an assemblage treatment (both functional groups) and a spider-free treatment (control). The choice of species for the functional-group treatments was based on guild definitions (Uetz *et al.*, 1999) and relative species abundances of spiders removed from the cages by pitfalls and visual inspection. Table 1 shows the species frequency within the family/subfamily as estimated from spider-removal and the functional-group assignment. Spiders needed in excess of the number removed from the cages were captured in the same

wheat field. The standardized number of spiders used for the functional-group treatments was estimated from the mean number of spiders removed from each cage and the upper 95% confidence interval (15 individuals) as a proxy for natural high abundance of spiders early in the season ($N \geq 15$, sampled from 17 cages). Because our goal was to uncover the impact of realistic spider densities on aphid populations, we established all treatments, including the assemblage, with identical numbers of individuals.

After five weeks (May 16, first interval), we estimated total aphid abundance in each enclosure non-destructively by visually inspecting all tillers for four minutes per cage. One week later, all cages were sampled by removing 12 tillers per cage to obtain counts of aphids on individual tillers (second interval); densities were too high for a total count of all aphids at this date. Total aphid numbers for the last count (second interval) were estimated by multiplying the average aphid number per 12 tillers with the number of tillers per cage. Both counts, therefore, provide a reliable estimate of aphid numbers per cage. Aphid growth rates were calculated by dividing the cage specific aphid numbers from the first estimate by the initial density of aphids ($N = 24$) for the first interval and by dividing aphid numbers from the second estimate by cage specific estimates from the first estimate for the second interval. After the final tiller count, pitfall traps were opened for one week and emptied daily to trap surface-active spiders. An estimate of web-building spider abundance was made by visually inspecting all cages twice (two minutes each search) during the final week. The number of spiders removed by pitfall traps and during the visual inspection provided an estimate of treatment effects over time. To estimate effects of caging on air temperature at the soil level, temperature loggers (Tinytag Talk 2, Tinytag, UK) were placed in three randomly chosen cages and three nearby, unenclosed spots. The experiment lasted nine weeks.

No pesticides were applied to the wheat field in 2006 prior to, or during, the experiment. In Darmstadt, the average monthly rainfall between April and May 2006 was 72.9 mm with an average air temperature of 12.7°C (long-term averages for April–May 1999–2004 were rainfall: 46.9 mm and air temperature, 12.5°C).

Molecular analysis

After the final tiller count, we removed individuals of three spider species from different functional groups by hand searching all cages to avoid contamination with DNA from potential prey species. The spiders were individually stored in cooling boxes (approximately 14°C) and transferred to the laboratory shortly after collection. A minimum of ten individuals of each species was stored at $-24°$. We analyzed females of the orb-weaver (Araneidae) *Mangora acalypha* (Walckenaer, 1802) as a common web-building species, females of the crab spider (Thomisidae) *Xysticus cristatus* (Clerck, 1757) as a foliage-dwelling cursorial spider, and females of the wolf spider (Lycosidae) *Pardosa palustris* (Linnaeus, 1758) as a representative ground-dwelling cursorial species (Nyffeler & Breene, 1992; Bogya & Marko, 1999). Additionally, five individuals of each species were starved for seven days before freezing at $-24°$C to test the primer's reactivity to starved spiders. We did not test a linyphiid species, as we were not able to sample the minimum of 15 adult individuals of one species with the

required hand-searching technique. DNA of all spiders, including the starved controls, was extracted using a DNeasy Tissue Kit (QIAGEN) by following the manufacturer's instructions with slight modifications. After an incubation step at 56°C, 10 µl RNAse A (100 µg µl^{-1}; QIAGEN) were added to the samples, which were then incubated at room temperature for 5 min. For further extraction steps, 50 µl (*Mangora acalypha*), 70 µl (*Pardosa palustris*) and 100 µl (*Xysticus cristatus*) were used.

The primer pairs S102 and A103 were used to amplify a 316-bp fragment of the mitochondrial cytochrome oxidase subunit I (COI) gene of *Sitobion avenae*. Both primers were developed and tested in a laboratory feeding trial (von Berg *et al.*, 2008); further cross-reactivity tests under field conditions could improve the applicability to field experiments (Admassu *et al.*, 2006). The PCR was carried out in 10 µl containing 0.25 mM dNTP (fermentas), 1 µM of each primer, 1 µl 10× buffer, 3 mM MgCl$_2$, 2.5 µg bovine serum albumin (BSA), 0.5 µl DMSO, 1.5 U *Taq* DNA polymerase (invitrogen) and 4.45 µl of DNA extract. Distilled water samples were included in each PCR reaction as a negative control to check for contamination. PCRs were carried out in a master cycler gradient (Eppendorf) with initial denaturation at 94°C for 2 min, followed by 40 cycles of 94°C for 15 s, 63°C for 45 s, 72°C for 45 s, and a final extension step at 72°C for 2 min. PCR products were checked on an agarose gel stained with ethidium bromide. To test the ability of the primer pair to amplify the DNA of *S. avenae* in the presence of predator DNA, we diluted aphid DNA with DNA of the three spiders in ratios 1 : 20.

Data analysis

Treatment effects on spider numbers at the end of the experiment, and on aphid population growth rates during the experiment, were analyzed by permutational analysis of variance (PERMANOVA (v. 1.6): Anderson, 2001; McArdle & Anderson, 2001). The Bray-Curtis dissimilarity distance measure was used to calculate distances among observations in similar treatment groups versus those in different groups. Permutation runs ($N = 4999$) of the observed data were used to generate probability values for the null hypothesis of no difference between groups. Effectiveness of the manipulations in altering the spider community was evaluated by permutational two-way MANOVA, with numbers of web-builders and non-web-builders sampled from cages at the end of the experimental period as the two response variables and the two manipulated spider functional groups as fixed factors. Permutational MANOVA was also used to evaluate spider treatment effects on aphid population growth rates. To further differentiate between effects of treatments on aphid population growth rates during the first and second part of the experiment, separate permutational one-way ANOVAs were performed on aphid growth rates from the 1st to 2nd and the 2nd to 3rd dates. Permutational one-way ANOVA was further used to estimate treatment effects on absolute aphid numbers. Differences in mean, minimum and maximum air temperature between cages and unenclosed field areas were analyzed by permutational one-way MANOVA. The species-specific detection rate for aphid DNA was compared between subsets by performing Fisher's exact test for comparison of proportions. Permutational ANOVAs were performed using PERMANOVA v. 1.6, and
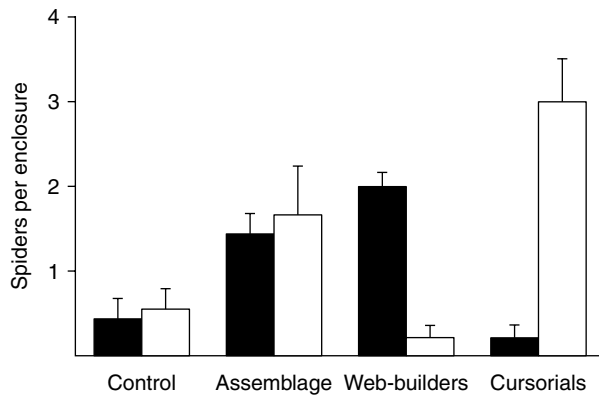
Fig. 1. Persistence of differences in spider numbers in the four spider functional-group treatments. Shown is the number of hand-collected (black bars) web-building and (white bars) cursorial spiders in the specific treatments after the last estimate of aphid numbers (May 23); means are given with SE.

all other analyses were performed using Statistica 7.1 (StatSoft, Germany); means are given with SE.

Results

Mean, minimum and maximum air temperatures at the soil level did not differ significantly between cages and surrounding, unenclosed areas in the wheat field (permutational MANOVA, $F_{1,5} = 1.74$, $P = 0.252$). We removed an average of 13.7 ± 0.6 spiders per cage ($N = 493$ spiders) prior to introducing aphids and establishing the functional-group treatments. Linyphiids comprised 65% of all removed spiders (Linyphiinae, 50%; Erigoninae, 15%) and only wolf spiders had comparably high densities (18%). All other families were represented by less than 10% of the total number of spiders (Araneidae, 6%; Thomisidae, 3%; Philodromidae, 2%; Tetragnathidae, 2%; and five other families together, 4%).

The manipulation of functional groups altered the abundances of cursorial and web-building functional groups at the end of the experiment (permutational MANOVA, effect of web-building species: $F_{1,35} = 15.70$, $P < 0.001$; permutational MANOVA, effect of cursorial species: $F_{1,35} = 11.49$, $P < 0.001$). Both functional groups responded to the experimental manipulation. Web-building spiders were 5.3 times more abundant in the web-building and assemblage treatments compared to the cursorial and spider-free treatments (fig. 1; permutational ANOVA: $F_{1,35} = 20.10$, $P < 0.001$). In a similar fashion, surface-active spiders were six times more abundant in the cursorial-spider and assemblage treatments compared to the web-builder and spider-free treatments (fig. 1; permutational ANOVA: $F_{1,35} = 13.53$, $P < 0.001$). Removal of one functional group did not affect the abundance of the other group (interaction term (cursorial × web-builders), permutational MANOVA: $F_{1,35} = 1.67$, $P = 0.183$).

Functional groups affected aphid growth rates differently during the first and second half of the experiment (permutational MANOVA: $F_{3,35} = 3.02$, $P = 0.020$). Cursorial spider presence had a negative impact on aphid population growth during the first five weeks (fig. 2a; permuta-
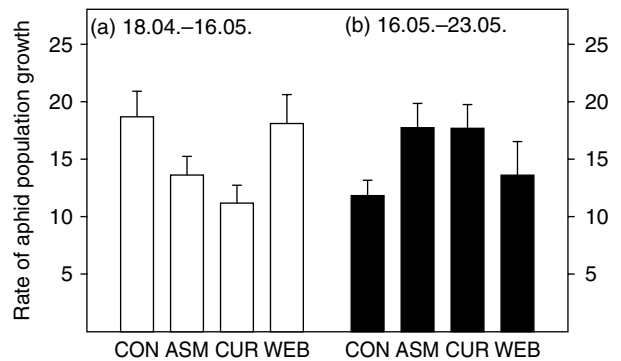

Fig. 2. Rate of aphid population growth between (a) April 18 and May 16 and (b) May 16 and May 23 in different spider functional-group treatments. CON, spider-free control; ASM, Assemblage (both functional groups); WEB, Web-builders only; CUR, cursorial spiders only; means are given with SE.
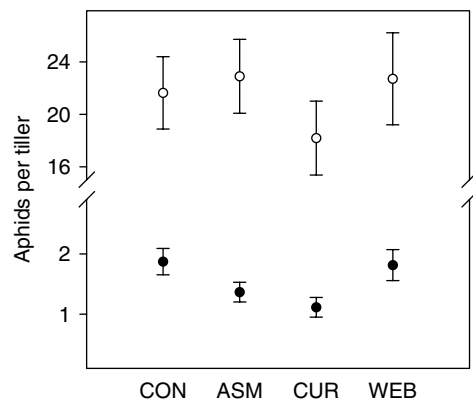

Fig. 3. Aphid density per tiller in different spider functional-group treatments on (●) May 16 and (○) May 23. For abbreviations see legend of fig. 2; means are given with SE.

ANOVA: $F_{3,35} = 1.88$, $P = 0.036$). During the last week in May, there was no negative effect of cursorial spiders on aphid growth rate; in fact, rates of aphid population growth were marginally higher in the presence of cursorial spiders (fig. 2b; permutational ANOVA: $F_{3,35} = 2.76$, $P = 0.060$). This response of aphid populations to spider functional-group treatments resulted in aphid densities that differed significantly after the first four weeks (fig. 3; permutational ANOVA: $F_{3,35} = 2.20$, $P = 0.045$) but not at the end of the experiment (permutational ANOVA: $F_{3,35} = 0.47$, $P = 0.784$).

Xysticus cristatus was the species with the highest proportion of individuals that tested positive for *S. avenae* DNA (fig. 4). Significantly more individuals of this species contained aphid remains compared to *M. acalypha* (Fisher's exact test: $P = 0.014$), with no significant difference between other combinations of species. The primer pair showed no amplifications when tested on the three spider species that had been starved for one week. DNA of *S. avenae* was amplified in the presence of spider DNA.

Discussion

At equal densities, surface-active cursorial spiders, but not web-builders, reduced the initial growth of aphid
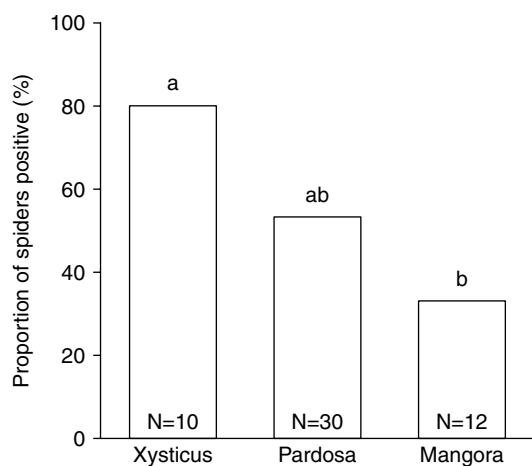
Fig. 4. Proportion of analyzed individuals (*Xysticus cristatus*, *Pardosa palustris* and *Mangora acalypha*) that tested positive for *Sitobion avenae* DNA. Different letters indicate significant differences (Fisher's exact test).

populations. Holland and Thomas (1997a, b) suggested that generalist predators may control aphids during early stages of crop colonization, when pests occur at low densities. Therefore, a generalist predator population that is already established early in the season may be an important prerequisite for successful aphid suppression (Scheu, 2001). In the present experiment, an initial aphid density of 0.1 aphids per tiller was established early in the growing season, a density well below the suggested thresholds at which aphids may cause economic damage in Germany (1–6 per tiller: Larsson, 2005). Our standardized spider densities were within the range of estimates of the number of spiders in wheat early in the growing season (Nyffeler & Sunderland, 2003). Our results, therefore, support the hypothesis that cursorial spiders retard the growth of aphid populations when aphid densities are low. As a single component of the natural-enemy community, however, cursorial spiders may not be sufficient to prevent aphid outbreaks under all conditions, particularly since their effect is most pronounced during the early stages of crop colonization (fig. 3). Larsson (2005) estimated peak densities of *Sitobion avenae* of 3–40 individuals per tiller during a seven year study in wheat. Aphids reached comparably high densities in our study with a mean of 21 aphids per tiller, independent of treatment. In fact, it appears that the reduced aphid growth rate in the cursorial-spider treatment during the first part of our experiment may have led to a higher growth rate in this treatment during the second part (fig. 2a, b), possibly due to reduced competition or density-dependent predation.

Earlier manipulations of overall spider numbers (web-building and cursorial spiders combined) in experimental plots in wheat did not uncover any significant effect of spider removal on aphid numbers (Lang, 2003). Spider activity-density and aphid densities were higher in our enclosures than in Lang's experiment, perhaps because the cages in his experiment were not closed and emigration was possible. An additional explanation for generally higher aphid numbers in closed cages may be the altered

microclimate. *Sitobion avenae* populations grow faster at higher temperature (Acreman & Dixon, 1989), but differences between cages and unenclosed areas were small in our study. However, we cannot exclude a positive impact of closed cages on aphid population growth, as *Sitobion avenae* populations suffer considerable mortality by rainfall (Mann *et al.*, 1996), and closed cages may weaken this effect. Open cages may further allow parasitoids to attack aphids inside cages, a condition that may have contributed to the fact that aphid numbers in Lang's study never reached densities comparable to those in our field experiment. Indeed, Schmidt *et al.* (2003) demonstrated that parasitoids may be more effective in aphid suppression than generalist predators. Thus, parasitoids may either mask effects of aphid predation by generalist predators, or the exclusion of parasitoids may artificially enhance the impact of cursorial spiders.

Web-building spiders consume aphids, with both orb-weavers (Araneidae: Nyffeler & Benz, 1979) and sheet-web-weavers (Linyphiidae: Sunderland *et al.*, 1986) potentially reducing aphid numbers. However, in our experiment, the web-building spider community did not affect aphid population growth, suggesting limited predation by this functional group. Further support is given by the lower proportion of web-building spiders that contained aphid remains, as compared to non-web-building species (*Xysticus cristatus* and *Pardosa palustris*). Web-building spiders (primarily linyphiids) in European cereal fields usually have a lower body mass than common cursorial species (primarily lycosids) but occur at higher densities and may, therefore, still contribute to aphid suppression even at a lower per capita aphid feeding rate.

As intraguild predation between spiders is frequent (Wise, 2006), secondary predation might have inflated rates of detecting aphid DNA (Sheppard *et al.*, 2005). Scavenging, although not common among spiders, may have further affected detection rates (Juen & Traugott, 2005). However, our results and previous studies (Nyffeler & Benz, 1988; Nyffeler & Breene, 1990) indicate that *Xysticus cristatus* and *Pardosa* species consume a considerable amount of aphids. Attracting these species to edge areas of arable fields before aphids arrive may significantly improve aphid control, with different factors affecting the strength of this interaction (e.g. alternative prey: Birkhofer *et al.*, in press). We conclude that during early stages of aphid colonization in wheat, cursorial spiders contribute more to aphid suppression than do web-building spiders. Management practices that specifically support cursorial species (e.g. mulching: Rypstra *et al.*, 1999; organic fertilization: Birkhofer *et al.*, submitted) may, therefore, be particularly useful in enhancing pest suppression by generalist predators.

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