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Intraguild predation in winter wheat: prey choice by a common epigeal carabid consuming spiders

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Summary

1. Predators can provide a valuable ecosystem service by suppressing crop pests. However, intraguild predation, where predators compete for the same prey resource whilst consuming each other, may destabilize population dynamics and increase the risk of pest outbreaks. Very little is known about intraguild predation in open fields or the strengths of trophic links between predators which may negatively affect pest control.

2. We tested the null hypothesis that predation by the epigeal predator *Pterostichus melanarius* (Coleoptera: Carabidae) on different spiders is species-independent (proportional to density). A combination of population monitoring in winter wheat, molecular identification of juvenile spiders, molecular analysis of predator gut contents and a Monte Carlo simulation model were used to analyse prey choice.

3. *Pterostichus melanarius* were pitfall-trapped over three months, and 622 individuals were screened for the remains of four spider species. Predation rates on spiders were 43.6% in June and 33.3% in August and showed clear evidence of prey choice.

4. Predation on the web-dependent *Tenuiphantes tenuis* (Linyphiidae) was significantly greater than predicted from a random choice model, while predation on *Bathypantes gracilis* (Linyphiidae) was significantly lower. The beetles may be selecting the most abundant species disproportionately (switching) or responding in some cases to spatial niche separation (*T. tenuis* locate their webs marginally lower than *B. gracilis*). However, two itinerant hunters, *Erigone* spp. (Linyphiidae) and *Pachygnatha degeeri* (Tetragnathidae), were consumed in proportion to their density.

5. *Synthesis and applications.* High levels of intraguild predation were revealed using molecular diagnostics. The gut analysis approach provided invaluable data that will inform the future design of appropriate pest management and integrated farming strategies that encourage these predators. The data showed strong evidence of prey choice. Managers can, however, probably encourage high densities of all these known aphid predators (spiders and carabids) because disproportionately high rates of predation on the most common spiders at our field sites (*T. tenuis*) were not sufficient to prevent strong growth in the density of this species between June and August (adults increased $\times 1.6$ and juveniles $\times 8.6$). Such work is essential if we are to reveal the processes behind functional biodiversity in crops.

Key-words: carabid beetles, food webs, functional biodiversity, linyphiid spiders, molecular gut content analysis, Monte Carlo simulations, prey choice, vertical separation

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Introduction

Conservation biological control seeks to maximize the economic and environmental benefits that can arise from optimizing natural regulatory systems. However, increased numbers and diversity of natural enemies does not

necessarily translate into improved pest suppression. While polyphagous arthropods can perform a valuable role as beneficial predators in agroecosystems (Symondson, Sunderland & Greenstone 2002) and may act in synergy to effectively suppress pests (e.g. Losey & Denno 1998, 1999), they also have the potential to disrupt biological control by interfering with and consuming one another (Polis & Strong 1996; Daugherty, Harmon & Briggs 2007; Holt & Huxel 2007). Intraguild predation (IGP) is predicted (Bohan *et al.* 2011a) or observed widely across food webs (Polis, Myers & Holt 1989; Polis & Holt 1992; Arim & Marquet 2004) and can be particularly significant among aphidophagous terrestrial arthropods, due to the tendency of predators and prey to aggregate both in time and in space (Snyder & Wise 1999; Winder *et al.* 2001; Holland *et al.* 2004). A diverse community of predators can theoretically lead to reduced herbivore suppression (Rosenheim, Wilhoit & Armer 1993; Finke & Denno 2004), especially where intraguild predators constitute a greater proportion of the predators (Finke & Denno 2005).

Our aim here was, for the first time, to measure the extent of intraguild predation directly in the field using a combination of molecular diagnostics and prey choice models to track predation by epigeal carabid beetles on spiders in winter wheat. Aphids, such as the grain aphid *Sitobion avenae* Fabricius, are major pests of wheat, affecting crop yield directly as phloem feeders and transmitters of major diseases such as barley yellow dwarf virus. Generalist predator assemblages, sustained on alternative prey (Symondson *et al.* 2000; Agustí *et al.* 2003; Sigsgaard 2007), possess the potential to attack nascent aphid populations early in the season (Harwood, Sunderland & Symondson 2004), causing delays or reductions in population peaks (Edwards, Sunderland & George 1979; Chiverton 1987; Chang & Kareiva 1999; Birkhofer *et al.* 2008). In much of Europe, linyphiids numerically dominate the arachnofauna in arable crops, especially *Bathypantes gracilis* Blackwall, *Tenuiphantes tenuis* Blackwall, *Erigone atra* Blackwall and *E. dentipalpis* Wider (Cocquempot & Chambon 1990; Feber *et al.* 1998; Schmidt & Tscharrntke 2005). These spiders feed primarily on Diptera, Collembola and aphids (Sunderland *et al.* 1987; Harwood, Sunderland & Symondson 2001, 2003, 2004). *Pachygnatha degeeri* Sundevall (Araneae; Tetragnathidae) is less abundant, but displays high rates of aphid predation (Harwood, Sunderland & Symondson 2005). The spatial niches of these species are vertically stratified, which is thought to be an evolutionary response to competition (Sunderland, Fraser & Dixon 1986; Herberstein 1998). *Erigone* spp. prefer to build their webs in small depressions in the ground, while *B. gracilis* and *T. tenuis* attach their webs to the vegetation c. 45 and 36 mm above the ground, respectively (Sunderland, Fraser & Dixon 1986). Adult *P. degeeri* do not spin webs, but are found in the foliage during the night (Madsen, Terkildsen & Toft 2004) and on the ground during the day (Roberts 1996).

The median heights of webs above the soil can, however, vary according to spider age and crop growth stage (Sunderland, Fraser & Dixon 1986). All five spider species are known to consume *S. avenae* (Sunderland *et al.* 1987; Harwood, Sunderland & Symondson 2004, 2005).

The carabid beetle *Pterostichus melanarius* Illiger is a common generalist predator in Europe and North America, known to feed on a wide range of prey, including insects, molluscs, and earthworms (Sunderland *et al.* 1987; Symondson *et al.* 2000, 2002; Sunderland 2002; Symondson, Sunderland & Greenstone 2002; Harper *et al.* 2005) as well as weed seeds (Bohan *et al.* 2011b). Much of its life cycle is subterranean (Sunderland *et al.* 1987; Thomas, Glen & Symondson 2008), where, as larvae, it hunts invertebrates such as slugs (Thomas *et al.* 2009), but as adults they hunt and scavenge mainly on the surface (but see Snyder & Ives 2001). The beetle is known to be a predator of aphids (Sunderland *et al.* 1987; Harper *et al.* 2005; Winder *et al.* 2005). Semi-field experiments investigating the influence of beetle banks on pest control (Prasad & Snyder 2004, 2006) suggest that *P. melanarius* is also an intraguild predator of smaller carabids and staphylinids. Adult *P. melanarius* are outside the prey size range of spiders, while the subterranean larvae are inaccessible to them. Intraguild predation by the beetles on the spiders is therefore entirely unidirectional (asymmetrical) (Polis, Myers & Holt 1989).

Our aim therefore was to identify whether *P. melanarius* is a significant intraguild predator of aphidophagous spiders in the field. Post-mortem gut analysis, using polymerase chain reaction (PCR), is revolutionizing our ability to track predator–prey relationships in the field. It provides a practical means of analysing, with minimal disturbance and to a high taxonomic resolution, trophic interactions amongst invertebrate communities that are difficult or impossible to study by direct observation (Symondson 2002; King *et al.* 2008). Molecular diagnostics can also, in parallel, be used to identify morphologically cryptic juvenile spiders (Hosseini *et al.* 2007), ensuring correct identification of the intraguild prey. We tested the null hypothesis that different species within spider communities would be consumed at random. We explored, *a priori*, two possible scenarios that might help explain deviation from random feeding (although other factors that may have affected deviations from expectations are discussed). As the predator *P. melanarius* is considered to be strictly epigeal, and would only be expected to encounter spiders on the ground, disproportionately higher numbers of beetles should test positive for those spider species whose spatial niche (the soil surface) overlapped the most with that of the beetles. Secondly, predators frequently switch to feeding on more abundant prey (Murdoch 1969; Sherratt & Harvey 1993); thus, predation on such species should not simply be greater but disproportionately so. We aimed to measure the extent of such negative interactions and provide recommendations for crop managers.

Materials and methods

FIELD SAMPLING

Ground beetles, spiders and aphids were collected, in 2006, from a field of winter wheat at Rothamsted Research, UK. Carabid beetles, *Pterostichus melanarius*, were collected using small (9 cm diameter) pitfall traps laid for 12 h overnight. Beetles were stored on ice in the field and transferred to separate micro-centrifuge tubes before being frozen at -80°C within 2 h of collection. Small arthropods, including spiders, were collected by Vortis sampler (Burkhard Ltd, Rickmansworth, UK) followed by hand-searching from a sampling area of c. 0.18 m^2 . At each point, samples were taken at three stages: flowering (week beginning 12 June: Zadoks scale 69–70); milky or mealy ripe ears (week beginning 10 July: Zadoks scale 73–85) and at pre-harvest (week beginning 31 July: Zadoks scale 90–92). There were 80 sample points (10×8), 16 m apart, but for the purposes of this paper, data were pooled for each invertebrate species on each date. This was in part because the number of spiders of each species at each sample point on each date was in most cases zero.

DNA EXTRACTION, PCR AMPLIFICATION, SEQUENCING AND PRIMER DESIGN

Full details of these procedures can be found in Appendix S1, Supporting information.

FEEDING TRIALS

Controlled feeding experiments were used to test the ability of each primer pair to detect semi-digested prey DNA in predators over time. *Pterostichus melanarius* and spiders were collected from Burdon's Farm, Wenvoe, Vale of Glamorgan, UK, between July 2007 and August 2008. Beetles were captured in small (9 cm diameter) pitfall traps and maintained individually in 12×6 cm clear plastic tubs containing c. 50 g of moist peat. The beetles were fed one *Calliphora* sp. maggot on the day of capture, then subsequently one maggot per week for 3–4 weeks. Spiders were collected by either pitfall trapping or suction sampler and maintained in 5-cm petri dishes filled to a depth of c. 1 cm with saturated plaster of Paris mixed with charcoal to maintain humidity. Beetles and spiders were maintained on a 16 : 8 light : dark cycle at $16 \pm 1^{\circ}\text{C}$. Beetles were starved for 14 days prior to the feeding trials, and spiders were starved for seven days. Both were subsequently killed by freezing at -80°C .

For each feeding trial, 106 *P. melanarius* were presented with a single starved spider in a 90-mm petri dish lined with a sheet of damp 85-mm filter paper c. 1 h after the onset of the dark phase of their day : night cycle, reflecting the time of day they are likely to begin to feed. Five beetles were killed after the 14-day starvation period as unfed controls. Prey items were presented for a 2-h period, the midpoint of which was designated as T_0 (the mean point at which consumption occurred). During this 2-h feeding period, prey consumption was monitored every 15–20 min. Once the beetles had fed, filter paper was removed from the petri dish. Those beetles which fed were divided into cohorts and allowed to digest their spider prey for 1, 3, 6, 12, 18, 24, 36 and 48 h following T_0 at a temperature of $16 \pm 1^{\circ}\text{C}$ (for the *Erigone* spp. feeding trial the 3-h digestion period was replaced with a 62-h sample). Beetles which did not feed were discarded. Each beetle

was killed by freezing at -80°C after being placed head first in a 1.5-mL micro-centrifuge tube (Fisher Scientific, Loughborough, UK). Ten beetles per time period were analysed for *Erigone* spp., *T. tenuis* and *P. degeeri* and eight per time period for *B. gracilis*. More males were caught in pitfall traps than females; therefore, only 2–3 female beetles were used for each time cohort.

IDENTIFICATION OF SPIDERS

Adult spiders were identified morphologically following the key of Roberts (1996). However, it is not usually possible to identify juvenile spiders to species level based on morphology. We took the novel approach of identifying juveniles with the same species-specific primers used to screen predators. Full details of the extraction of DNA from juveniles, and identification of them using multiplex PCR, may be found in Appendix S2, Supporting information.

STATISTICAL ANALYSIS

Median detection times (MDT, King *et al.* 2008) (the points at which the target fragment is amplified from 50% of the predators tested) were estimated by fitting data from the laboratory-feeding trials to Generalized Linear Models (GLM) with a logit link function and binomial error distribution (logistic regression) for each primer pair/spider species. Stepwise model simplification was used to assess the influence of time post-feeding, species and fragment size and their interactions on detection probability. Generalized Linear Models were also used to investigate the effects of time post-feeding and fragment size on detection probability.

We assessed whether the predator *P. melanarius* consumed spider species at random, in proportion to their abundance in the field, or exercised prey choice. Positive or negative prey choice was defined as any significant deviation, from whatever cause, from random feeding based upon numerical ratios. The Monte Carlo approach of Agustí *et al.* (2003) and King *et al.* (2010) was used, in which the structure of the original data is retained (number of beetles and primer positive results per beetle), but the identities of the detections within each beetle are allocated randomly: the probability of a particular prey being 'eaten' is proportional to its abundance in the field. The relative field abundances of the different prey items were drawn from Poisson distributions fitted to the raw count data from the 80 sample points in each month. Following 20 000 iterations, the model produced frequency distributions of expected consumption rates against which the observed values could be compared: observed numbers falling outside the central 95% of simulated values indicated that predation deviated significantly from the null, random-foraging model (Manly 1997). Simulations were run in R 2.8 (R Development Core Team 2008).

Results

PRIMER SPECIFICITY AND MULTIPLEXING

Primers designed to detect predation upon *Erigone* spp., *T. tenuis*, *B. gracilis* and *P. degeeri* (Table S1, Supporting information) each successfully amplified fragments of the predicted size in the presence of predator (*Pterostichus melanarius*) DNA. Cross-amplification testing produced no PCR products (Table S2, Supporting information),

showing that the primers were highly specific. Calibration tests of the multiplex PCRs, subsequently applied to the screening of juvenile spiders captured in the field and using all combinations of primers, are shown in Fig. S1, Supporting information. All target species were successfully identified with bands of the predicted sizes.

JUVENILE IDENTIFICATION

Overall, juvenile linyphiid spiders, identified by barcoding, were far more numerous than adults (72% juveniles), although this applied only to July and August. The linyphiid community was dominated by *T. tenuis* (67% of all linyphiids), and 76% of all *T. tenuis* were juveniles (see Table 1 for a breakdown). Barcoding of a small number of juvenile spiders (15 out of 1455) resulted in the simultaneous amplification of more than one species-specific band, probably due to low levels of IGP among juvenile spiders, and these were classified as Unknown.

DECAY RATES FROM FEEDING TRIALS

The MDT (\pm SE) (Fig. 1) for *P. melanarius*-eating spiders were 29.0 (\pm 5.91) h for the 271-bp fragment of *B. gracilis* DNA, 42.6 (\pm 9.47) h for a 145-bp fragment of *T. tenuis*, 19.7 (\pm 4.26) h for a 244-bp fragment of *Erigone* spp. and

29.6 (\pm 4.42) h for a 318-bp fragment of *P. degeeri* (Fig. 1). The resulting minimal model (after stepwise deletion of non-significant factors) showed that time post-feeding alone was sufficient to explain detection probability (GLM, $T = 6.77_{29}$, $P < 0.001$). Inclusion of fragment size, therefore, had no significant effect on the model's explanatory power in terms the amount of residual deviance explained.

ANALYSIS OF PREDATION IN THE FIELD

DNA from every spider species for which we had primers was found in the guts of *P. melanarius* during every month of sampling. Overall, predation on spiders was lowest in June, when beetle and spider numbers were low. However, the proportion of beetles testing positive for spider DNA was highest in June, when 44% (61 of 140 beetles) were positive, compared with 35% in July (96 out of 272) and 33% in August (70 of 210). Figure 2 shows the number of beetles testing positive for each spider species in the form of single predator food webs. The topology of the webs is very similar over the three months, suggesting predation was mainly on *T. tenuis*, with little consumption of other species. The number of beetles testing positive for more than one target spider species simultaneously was low, with 6 (4.2%) in June (one of which scored positive for three species), 5 (1.8%) in July and 2 (2.9%) in August. Given that predation on spider species other than *T. tenuis* was low, this is not surprising.

Monte Carlo simulations showed that, in all months, the levels of consumption of *Erigone* spp. and *P. degeeri* by *P. melanarius* were as would be expected where no prey choice was exercised. However, consumption of *B. gracilis* was significantly lower than expected in all months (Fig. 3). The number of beetles testing positive for *T. tenuis* was significantly greater than predicted from abundance in all months.

Discussion

Analysis of 622 *P. melanarius* showed consumption of all four species of the most numerous aphidophagous spiders at our field site. Rates of predation by *P. melanarius* on spiders were remarkably high (44% positive in June), and spiders appear to be a major component of the beetle's diet. Comparable DNA-based analyses of predation by this beetle on a range of prey have only recorded earthworms as being more frequently consumed (up to 56% positive) (Harper *et al.* 2005; King *et al.* 2010).

Natural pest control is thought to be most likely where seasonal and diel co-occurrence of predators occupying different spatial niches is high, but levels of IGP among these predators are low (Losey & Denno 1999). *Pterostichus melanarius* consumed the two web-dependent linyphiid species disproportionately, with *T. tenuis* eaten the most frequently (33% of beetles tested positive), and

Table 1. Total number of adult and juvenile spiders collected across the 80 sampling points on each date

Species		June	July	August ^a	Total
<i>Tenuiphantes tenuis</i>	Adult	80	95	129	304
	Juvenile	57	432	491	980
	Total	137	527	620	1284
<i>Bathyphantes gracilis</i>	Adult	49	91	36	176
	Juvenile	30	197	71	298
	Total	79	288	107	474
<i>Erigone atra</i> plus <i>E. dentipalpis</i>	Adult	12	31	7	50
	Juvenile	11	53	44	108
	Total	23	84	51	158
<i>Pachygnatha degeeri</i>	Adult	5	9	13	27
	Juvenile	17	46	6	69
	Total	22	55	19	96
<i>Oedothorax</i> spp.		4	12	10	26
Other tetragrathids		4	5	18	27
<i>Xysticus</i> spp.		3	21	37	61
Lycosidae		5	8	81	94
Others/Unknown ^b		51	229	187	467
Mixed		0	7	8	15
Grand total		328	1236	1138	2702

^aDNA extraction was impossible for c. 10% of the juvenile spiders sampled in August (samples dried up in storage tubes), and so total numbers for these were extrapolated in proportion to successfully identified juveniles (August only).

^bThe 'Others/Unknown' (17% of the total) comprised mainly juveniles that could not be identified morphologically and/or for which we did not have primers.

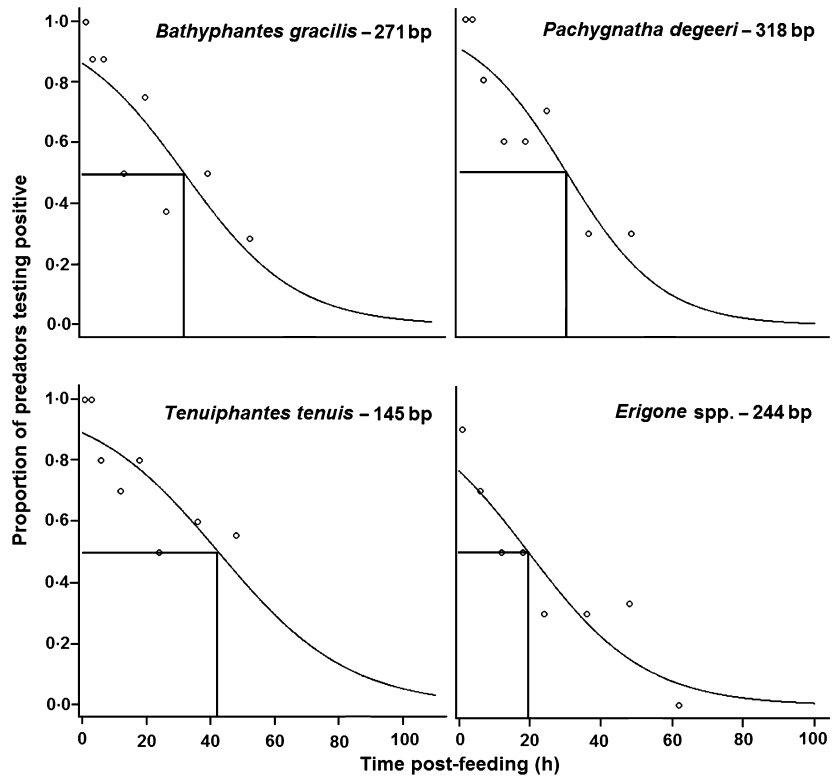


Fig. 1. Decay rates of target fragments of COI mtDNA from spiders in the guts of *Pterostichus melanarius*. The MDT (median detection time, right-angled solid line) was estimated by fitting data from the feeding trials to a binomial regression model. [Correction added after online publication 6 December 2012: Fig. 1 replaced with correct version.]

B. gracilis being consumed the least (1.3%) (Figs 2 and 3). The beetles tested positive for *T. tenuis* significantly more frequently in all months than predicted from the Monte Carlo simulations. By contrast, predation on *B. gracilis*, which builds its webs further from the ground than *T. tenuis* (c. 45 mm as opposed to c. 36 mm, Sunderland, Fraser & Dixon 1986), was significantly less than predicted in all months (Fig. 3). Apart from a record of *P. melanarius* climbing under artificial conditions (Snyder & Ives 2001), there appear to be no reports of this species climbing plants, and they are normally found on the soil surface. With a body length of 13–17 mm, *P. melanarius* may have found it easier to reach *T. tenuis* in their webs than *B. gracilis*, even though the latter were on average only 9 mm higher above the ground. Alternatively, the higher density of *T. tenuis*, which dominated the spider community, may have led to ‘switching’ behaviour, in which predators concentrate, and feed disproportionately, on the most common prey. However, this does not explain why rates of predation on *B. gracilis* were so low, as this was the second most common species at the field site but the least frequently eaten. The evidence suggests that vertical separation is a more likely explanation, especially given that predation on *B. gracilis* (as a proportion of surveyed prey consumed) decreased monotonically through time, perhaps reflecting the species’ tendency to be found further from the ground as the growing season progresses (Sunderland, Fraser & Dixon 1986). Alternatively, *B. gracilis* may simply have better escape strategies than *T. tenuis*.

Rates of consumption of the itinerant *Erigone* spp. and *P. degeeri* fell consistently within the expected range

predicted by both models in all months, showing no evidence of prey choice. Predation on these species was therefore independent of their vertical spatial niche overlap with the predator. This is perhaps surprising, especially for *Erigone* spp. which build their webs on the ground and would appear vulnerable to high rates of predation. Predation pressure may have led to the evolution of behaviours that help them to avoid these predators (Magalhaes *et al.* 2005). More behavioural work is needed, but it is possible that their dense flat webs, over soil depressions, provide refugia from hunting beetles. Adult *P. degeeri* forage in the foliage at night (Madsen, Terkildsen & Toft 2004), the time when *P. melanarius* are most active on the ground (Chapman, Armstrong & McKinlay 1999), but juveniles, which outnumbered adults (Table 1, Fig. 2), may have been vulnerable at this time.

We have shown that it is possible to construct food webs with a high degree of taxonomic resolution using species-specific primers. They provide a measure of trophic interaction strength taking into account prey availability, through the application of Monte Carlo models. Improving empirical estimates of per capita consumption rates relies, in part, on knowledge of the age structure of the prey population (Bascompte, Melian & Sala 2005). Our method of high-throughput identification of cryptic juveniles using multiplex PCR can facilitate such estimates. As in all such molecular analyses of the gut contents of invertebrates, we cannot be sure whether scavenging was occurring (Foltan *et al.* 2005). A discussion of technical issues relating to the molecular analyses and Monte Carlo models can be found in Appendix S3, Supporting information.

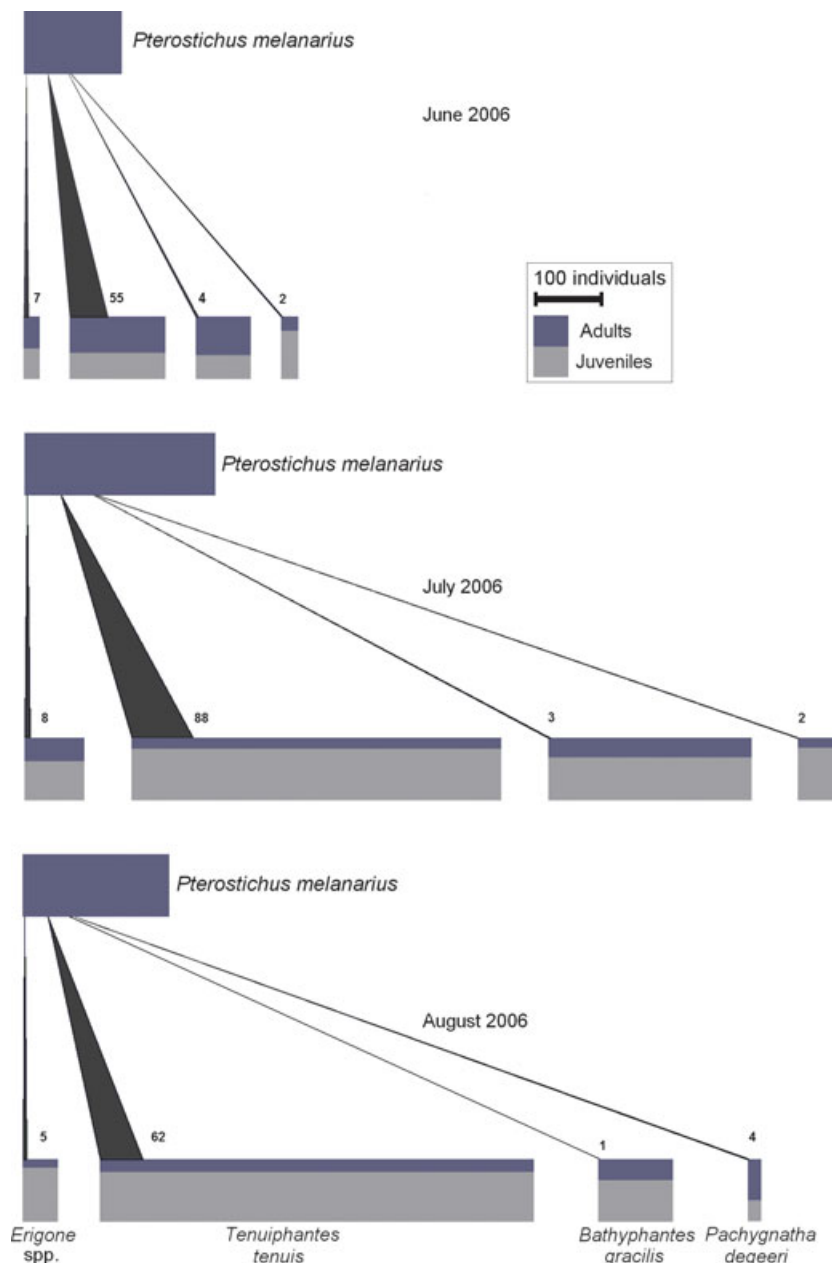


Fig. 2. Bipartite food webs created in R (R Development Core Team 2008) showing the numbers of *Pterostichus melanarius* testing positive for each spider species or group in each month. The width of each block represents the numbers of each species and the width of the arrows the number of beetles testing positive for each species of spider. The bars for spiders are split to show proportions of adults and juveniles. All beetles were adults. [Correction added after online publication 6 December 2012: Fig. 2 replaced with correct version.]

Disproportionately high rates of predation by carabids on *T. tenuis* (Fig. 3), the most common of the four species, may have the potential to release aphids from control by these spiders. Female (but not male) Linyphiinae, including *T. tenuis*, have been shown to eat a greater aphid biomass in the field than Erigoninae and might therefore be considered to be more valuable as biocontrol agents (Harwood, Sunderland & Symondson 2004). However, high rates of predation on *T. tenuis* did not prevent strong growth in the density of this species (between June and August adult increased $\times 1.6$ and juveniles $\times 8.6$) (Table 1). The degree to which *T. tenuis* numbers may be limited by *P. melanarius* will depend upon their relative densities and availability of alternative (non-spider) prey. For example, although in August predation on *T. tenuis* was still significantly greater than the expected value, it was much less than in other

months, possibly because other prey were diverting the predators. It is unlikely to be related to spider growth stage as juveniles were equally dominant in July when predation on this spider was disproportionately high. The spiders were also free to immigrate throughout the season, buffering any potential by the beetles to control their numbers. This species makes its web close to the ground and relies on aphids falling from above (Harwood, Sunderland & Symondson 2003, 2004), often in response to foliar predators (Losey & Denno 1998) and parasitoids (Gowling & van Emden 1994). Many of these aphids will not return to the growing points at the top of the crop in any case, succumbing to predation by a range of epigeal predators and desiccation (Winder 1990).

Although these results come from a single field of winter wheat, the data suggest nothing that might dissuade

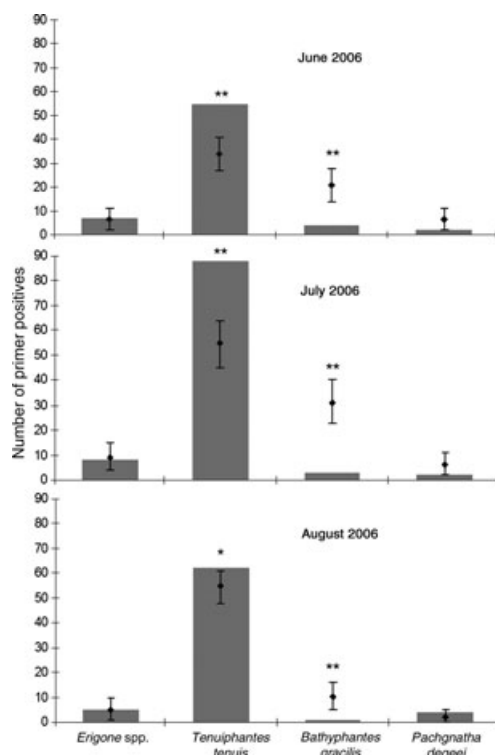


Fig. 3. Results from the Monte Carlo simulations, comparing the observed numbers of *Pterostichus melanarius* testing positive for spider prey (grey bars) with the range of values enclosing 95% of the simulated predation rates (vertical bars). Asterisks indicate levels of statistical significance (* = $P < 0.05$, ** $P < 0.01$). [Correction added after online publication 6 December 2012: Fig. 3 replaced with correct version.]

managers from encouraging high densities of both carabids and spiders in arable crops (Bell *et al.* 2002). Both groups are known to eat aphids and, acting in concert, are able to exploit aphids in all spatial niches from the ground to the top of the crop. Simple management changes, such as inclusion of beetle banks (e.g. Collins *et al.* 2002) or adjustment of the timing or type of cultivation (Symondson *et al.* 1996; Purvis & Fadl 2002), can locally increase carabid densities within the crop and reduce pest numbers. Providing holes in the soil, suitable as spider web sites, can significantly increase densities of spiders such as *T. tenuis* (Alderweireldt 1994, Samu *et al.* 1996). A review of habitat manipulation measures to increase predator densities can be found in Symondson, Sunderland & Greenstone (2002), providing a range of measures the practicability of which will depend upon the farming system employed. Employment of integrated farming systems (e.g. Glen, Greaves & Anderson 1995) that avoid non-selective agrochemicals harmful to these predators, especially at times of year when the predators are most active, should be encouraged. Further work is needed to address the variation in spatial co-occurrence of spiders and their prey at the microhabitat scale (Harwood, Sunderland & Symondson 2001, 2003, 2004) and to examine spider behaviours that make them more or less vulnerable to capture by carabids. Predators and

prey are known to be non-randomly spatially distributed on the horizontal spatial plane, even in relatively homogeneous fields, and this too is likely to be a major factor governing patterns of predation at local scales (Bohan *et al.* 2000; Winder *et al.* 2001, 2005; Bell *et al.* 2010).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Molecular methods.

Appendix S2. Molecular identification of juvenile spiders.

Appendix S3. Discussion of molecular techniques and modelling.

Table S1. Primer information.

Table S2. Taxa tested with the primers.

Fig. S1. Results of multiplexing primers for spider identification.