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Monoclonal antibodies reveal the potential of the tetragnathid spider *Pachygnatha degeeri* (Araneae: Tetragnathidae) as an aphid predator

J.D. Harwood[1]*, K.D. Sunderland[2] and W.O.C. Symondson[1]

[1]School of Biosciences, Cardiff University, PO Box 915, Cardiff, CF10 3TL, UK: [2]Warwick HRI, Wellesbourne, Warwick, CV35 9EF, UK

Abstract

The drive towards a more sustainable and integrated approach to pest management has engendered a renewed interest in conservation biological control, the role of natural enemy communities and their interactions with prey. Monoclonal antibodies have provided significant advances in enhancing our knowledge of trophic interactions and can be employed to help quantify predation on target species. The tetragnathid spider *Pachygnatha degeeri* Sundevall was collected from fields of winter wheat in the UK and assayed by ELISA for aphid proteins. It was demonstrated that this spider did not simply consume greater quantities of aphids because it was bigger. In addition, *P. degeeri* contained significantly greater concentrations of aphid in their guts than other spiders, showing that aphids comprised a greater proportion of their diet. Although *P. degeeri* constituted only 6% of the spider population numerically, females and males respectively contained 16% and 37% of total aphid proteins within all spiders screened, significantly more than their density would predict. These spiders also preyed upon aphids at a disproportionately high rate in June, during the aphid establishment phase, theoretically the best time for limiting growth in the aphid population. Although less abundant than other generalist predators, the capability of these hunting spiders to consume large numbers of aphids highlights them as a more significant component of the predator complex than had previously been realized. Limitation of aphid numbers early in the year by generalist predators provides more time for the specialist aphid predators and parasitoids to move in.

Introduction

Aphids damage crops throughout the world, both directly through phloem feeding (Vickerman & Wratten, 1979; Oakley *et al*., 1993) and indirectly by the transmission of viruses (e.g. Oswald & Houston, 1951, 1953; Araya *et al*., 1996). While specialist natural enemies can restrict growth in aphid numbers in the field, the effects of generalist predators, as part of a complex of natural enemies, can be additive or synergistic and provide significant levels of biological control (Losey & Denno, 1999; Symondson *et al*., 2002). In theory, suppression of pests by a combination of generalist and specialist natural enemies may reduce or eliminate the need for pesticide applications (DeBach & Rosen, 1991; Gurr *et al*., 2000). Such natural regulation should be particularly evident early in the season when generalists, subsisting on alternative prey (Murdoch *et al*., 1985; Chang & Kareiva, 1999) and whose populations dynamics are largely independent of those of the aphids, may be present in crops at the onset of pest colonization (Chiverton, 1986). The effectiveness of generalists at controlling pests has been attributed to

*Address for correspondence: Department of Entomology, University of Kentucky, S-225 Agricultural Science Center North, Lexington, KY 40546-0091, USA
Fax: 859-323-1120
E-mail: James.Harwood@uky.edu

high levels of predation during this early phase of pest colonization (Settle *et al*., 1996; Landis & Van der Werf, 1997; Chang & Kareiva, 1999), in part because more time is provided for specialist aphid predators and parasitoids to move in.

The ideal natural enemy would be a generalist with a significant preference for the target pests (aphids), but which can subsist on alternative prey when pest numbers are low or absent. Gut content analysis using antibodies has shown that aphids constitute a significant proportion of the diet of many species of spider in the field (Sunderland *et al*., 1987; Winder *et al*., 1994; Harwood *et al*., 2004). Among these spiders, the tetragnathid *Pachygnatha degeeri* Sundevall (Araneae: Tetragnathidae) is known to feed on aphids (Sunderland *et al*., 1985, 1987). However, the low abundance of these predators, which usually represent less than 5% of all spiders present within agricultural systems (Topping & Sunderland, 1992, 1994; Sunderland & Topping, 1993), leads to the assumption that the more numerous Linyphiidae are likely to be of greater importance in restricting aphid numbers. Despite the relative scarcity of these tetragnathids, their greater size should enable them to consume significantly greater quantities of prey relative to the smaller Linyphiidae.

Pachygnatha degeeri are found throughout Europe (Nyffeler & Breene, 1990; Samu *et al*., 1996; Ratschker & Roth, 2000), but little is known about their behaviour and ecology. Their hunting strategies differ from most linyphiids in that they build no webs but actively search for prey. These are univoltine spiders, usually peaking in activity-density during spring when they breed (Alderweireldt & De Keer, 1990), thus they are present at greatest densities at a time when generalist predators are more likely to have a significant effect on aphid numbers. In the laboratory, rates of aphid consumption did not vary between sexes (Madsen *et al*., 2004).

Many spiders demonstrate low preference for aphids when presented with a choice, and aphids have been shown to be a poor quality food in terms of maintaining spider fitness (Toft, 1995, 1997; Sunderland *et al*., 1997; Bilde & Toft, 2001). However, microcosm experiments have suggested that *P. degeeri* are able to tolerate a high-aphid diet to a greater degree than many other species of spider (Madsen *et al*., 2004), enhancing their potential to control aphids. In the field, in the presence of alternative non-aphid prey, *P. degeeri* may switch to feeding on more profitable food items (Marcussen *et al*., 1999; Mayntz & Toft, 2001). The most probable scenario is that alternative prey help to balance the nutritional requirements of the spiders, enabling them to exploit aphids as a food resource while maintaining predator fitness.

An effective method for studying prey choice and predator–prey relationships in the field is to analyse predator gut contents using monoclonal antibodies (Symondson, 2002). Such antibodies have been developed for the study of aphid consumption by carabids and spiders (Symondson *et al*., 1999; Harwood *et al*., 2001a). The hypothesis that *P. degeeri*, which do not build webs, would consume aphids to proportionally the same degree as other species of spider was tested, but that the overall quantity of aphid material consumed by these spiders would be greater due to their larger size. This was achieved by measuring the concentration and quantity of antibody-recognizable aphid protein in the spiders as separate parameters (Symondson *et al*., 2000). It was expected that the relative importance of this less common species, as aphid predators, would be greater than that predicted from their population densities alone. Whilst the web-based Linyphiinae intercept aphids falling from the crop plants into their webs (Harwood *et al*., 2003), *P. degeeri*, which hunt for prey on the ground and within the crop canopy, may perform a complimentary role by preventing aphids from regaining the crop canopy.

A further hypothesis to be examined was that there would be no significant difference between the concentrations and quantities of aphid proteins within female and male *P. degeeri*. Harwood *et al*. (2004) found that the larger female Linyphiidae contained a greater quantity of aphid than the males. However, this was not entirely caused by their greater size, because females also contained a greater concentration of aphid proteins than males, indicating that aphids comprise a significantly more important component of their diet. Such differences between the sexes may relate to the greater web-dependence of the females (Alderweireldt, 1994). Such sex differences may not exist in a species that does not construct webs to catch their prey.

Materials and methods

Production of anti-aphid monoclonal antibody

A general anti-aphid monoclonal antibody MdW-7(1)G1 was used to quantify predation by *P. degeeri* on aphids in winter wheat. This antibody was developed by Symondson *et al*. (1999) and has been used to study carabid–aphid interactions by Winder *et al*. (2005). It was recently further characterized and used to analyse predation on aphids in the field by Linyphiidae (Harwood *et al*., 2004). Feeding trials with this antibody indicated detection periods in spiders of up to 193 h in female and 169 h in male spiders (Harwood *et al*., 2001a, 2004). The rates of decay of the aphid proteins targeted by a monoclonal antibody was not significantly different between six species of linyphiid spiders (Araneae: Linyphiidae) (*Erigone atra* (Blackwall), *E. dentipalpis* (Wider), *Tenuiphantes tenuis* (Blackwall), *Bathyphantes gracilis* (Blackwall), *Meioneta rurestris* (C.L. Koch) and *Oedothorax* spp.).

In order to compare aphid protein levels within *P. degeeri* to those recorded in other species of spider (Harwood *et al*., 2004), it was necessary to determine rates of antigenic decay across species given that different species can sometimes (Symondson & Liddell, 1993; Harwood *et al*., 2001a), but not always (Harwood *et al*., 2004), vary in rates of digestion of target antigens. *Pachygnatha degeeri* were collected from fields of winter wheat and maintained at 16°C on a 16:8 light:dark cycle in triple-vented Petri dishes (diameter 5.5 cm, height 1.5 cm) with a plaster of Paris and charcoal base to ensure high humidity was maintained. All spiders were fed for approximately one month on a diet of *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) followed by a two-week starvation period. Given that antigenic decay rates in spiders did not vary between males and females in earlier work (Harwood *et al*., 2001a, 2004), only females were used. Spiders were allowed to feed *ad libitum* on live *Sitobion avenae* (Fabricius) (Hemiptera: Aphididae) and any non-feeding individuals excluded. Eight individuals were frozen immediately after feeding (0 h), and after a further 24 h and 48 h. Antigenic decay rates were determined by indirect enzyme-linked immunosorbent assay (ELISA) (described below) and compared to data collected, in parallel, for the Linyphiidae (Harwood *et al*., 2004).

Collection of Pachygnatha degeeri *and monitoring of aphid densities*

Male and female spiders were collected, by pooter, at random from fields of winter wheat at Warwick HRI (formerly Horticulture Research International), Wellesbourne, Warwickshire, UK (52° 12 18′ N, 1° 30 00′ W) during May to July 1999. Following collection, each individual was placed in separate 1.5 ml microcentrifuge tubes which were kept on ice and transferred to a −20°C freezer within 1 h of collection.

The availability of prey (including aphids) to ground-active spiders such as *P. degeeri* was monitored at the time of spider collection using mini-sticky traps and mini-quadrats, described in detail by Harwood *et al*. (2001b, 2003). Both trapping systems monitor prey densities on the soil surface, where *P. degeeri* are usually found. Therefore, only those aphids falling from the crop to the ground (which can happen at very high rates (Sunderland *et al*., 1986; Losey & Denno, 1998)) are likely to become potential prey items for epigeal predators. Mini-sticky traps (7.5 cm^2) were placed on the ground and left *in situ* for 24 h in the area from which spiders were collected. These passive sampling traps were designed to measure the activity-density of all prey entering the spiders' hunting area over a defined time period. Mini-quadrats were larger sampling areas (78.5 cm^2), which provided an estimate of availability of prey at a single point in time. All invertebrates within the template were collected by pooter. The mini-quadrats enabled the sampling of less active prey (which are rarely caught on sticky traps) and those species under stones or loose earth, both of which could be actively sought out by hunting spiders.

Screening spiders for aphid consumption

All spiders were analysed by indirect ELISA using 96-well microtitration plates (Falcon Pro-bind Assay Plates, Becton Dickinson Labware, Oxford, UK) following a standardized protocol (Symondson & Liddell, 1996). All spiders were weighed, whole bodies macerated on a dilution ratio of 1:20 in phosphate buffered saline pH 7.4 (PBS) and the homogenate dispersed on a vortex mixer for 1 min. These samples were centrifuged at room temperature for 15 min at 8000 *g*, the supernatants transferred into clean 0.5 ml microcentrifuge tubes and the particulate matter discarded. These supernatants were stored at −20°C until assayed for aphid proteins by indirect ELISA.

All samples were screened separately against the anti-aphid monoclonal antibody MdW-7(1)G1 (Symondson *et al*., 1999) in duplicate. The homogenized spider supernatants were diluted 1:20,000 (w/v) in PBS and 200 µl coated on two microtitration plate wells. In addition to coating microplates with field collected spiders, each plate was coated with a 1.5× dilution series of aphid (*S. avenae*) standards to provide spectrophotometric readings for known protein concentrations between 265.5 and 4.6 ng 200 μl^{-1}. These concentrations were calculated following a protein assay using the BioRad Protein Assay System (Bio-Rad Laboratories Ltd, GmbH, Munich, Germany). In order to keep protein concentrations constant throughout the dilution series (Symondson & Liddell, 1995), the aphid standards were diluted with heterologous protein extracted from starved spiders (also diluted 1:20,000). All plates also contained two negative and two positive controls.

The ELISA plates containing these samples were incubated overnight at room temperature and then washed three times in PBS-Tween (0.05% Tween 20) (Sigma-Aldrich, Poole, UK). 200 µl of the anti-aphid monoclonal antibody MdW-7(1)G1 (diluted 1:4000 in PBS-Tween) was added to alternate rows and incubated at room temperature for 2 h. No antibody was added to the duplicated wells, which were instead filled with 200 µl PBS-Tween. This enabled the potential effects of non-specific binding between the antigen and conjugate to be determined. These wells were incubated in parallel with the antibody-coated wells. Following incubation, all wells were washed three times in PBS-Tween and then coated with 200 µl of a 1:4000 dilution (in PBS-Tween) of ImmunoPure® goat anti-mouse IgG horseradish peroxidase conjugate (Pierce, Rockford, Illinois, USA) and left for 1 h at room temperature to enable binding between the anti-aphid mouse monoclonal antibody and the conjugate. As before, all wells were washed three times in PBS-Tween and the enzyme substrate, *o*-phenylenediamine in a citrate-phosphate buffer, added to all wells at 200 µl per well and placed in the dark for 30 min to allow colour development. The reaction was terminated by adding 50 µl of 2.5 M sulphuric acid and the absorbance recorded at 492 nm using an ELISA plate spectrophotometer (Thermomax Plate Reader, Molecular Devices, California, USA).

Absorbance readings for the duplicated wells, to which no antibody was added, were subtracted from those containing antibody, allowing the concentration of antibody-recognizable aphid protein within each sample to be calculated from the dilution series of aphid standards present on each microtitration plate. The quantity of aphid protein within each spider was calculated from the spider biomass and the concentration of antibody-recognizable aphid protein (Symondson *et al*., 2000).

Statistical analysis of data

Spiders that tested positive for aphid proteins were assumed to have preyed directly on these prey items. The importance of secondary predation is known to be negligible in spider–aphid systems and was assessed using the same monoclonal antibody by Harwood *et al*. (2001a). Although there was a low probability of scavenging on dead prey leading to false positives being recorded (Calder *et al*., 2005), hunting spiders tend to use visual movement and vibrational cues as the stimulus to attack prey (Barth, 1982; Persons & Uetz, 1997, 1998). Therefore, these predators were assumed to have consumed live aphids.

Data (both the concentration and quantity of antibody-recognizable aphid proteins within *P. degeeri*) were transformed log $(x+1)$ prior to analysis to stabilize variances and enable analyses by parametric tests (ANOVA).

Results

Decay of aphid remains within the guts of Pachygnatha degeeri

Two-way ANOVA, incorporating species and time, indicated that the mean aphid protein concentration equivalents for *P. degeeri* after 0 h ($204 \pm$ SE 7.3 ng 200 μl^{-1}), 24 h ($201 \pm$ SE 4.1 ng 200 μl^{-1}) and 48 h ($152 \pm$ SE 8.1 ng 200 μl^{-1}) were not significantly different to antigen concentrations in six linyphiids at the same time periods ($F_{6,147} = 0.27$, $P > 0.05$)

but, as expected, concentrations declined over time ($F_{2,147}$ = 68.03, $P < 0.001$). This lack of difference between spiders enabled direct comparisons to be made across species.

Pachygnatha degeeri *collected from winter wheat*

The tetragnathid *P. degeeri* was the most abundant non-linyphiid spider present within fields of winter wheat at the field site. This spider represented approximately 6% of the total spider population (and 63% of the non-linyphiid community). Importantly, in terms of the potential consumption rates of pest species, these spiders were significantly heavier than both sub-families of Linyphiidae, the Erigoninae (female, $F_{1,451} = 49.72$, $P < 0.001$; male, $F_{1,276} = 384.63$, $P < 0.001$) and Linyphiinae (female, $F_{1,724} = 36.39$, $P < 0.001$; male, $F_{1,288} = 342.71$, $P < 0.001$). The mean weight of female *P. degeeri* (0.293 ± SE 0.026 g) compared to female Linyphiidae was approximately 1.5 × greater whilst that of male *P. degeeri* (0.268 ± SE 0.017 g) was approximately 2.5 × greater than male linyphiids. There were no significant differences in weight of female versus male *P. degeeri* ($F_{1,101} = 0.24$, $P = 0.625$).

Aphid consumption by Pachygnatha degeeri

The three aphid species captured on mini-sticky traps and mini-quadrats (*S. avenae*, *Metopolophium dirhodum* (Walker) and *Rhopalosiphum padi* (Linnaeus) (Hemiptera: Aphididae)) were all detectable by the anti-aphid monoclonal antibody MdW-7(1)G1 used in the current study (Symondson *et al*., 1999).

The concentration and quantity of antibody-recognizable aphid protein within male (mean concentration = 1.13 ± SE 0.20 ng 200 μl^{-1}; mean quantity = 0.30 ± SE 0.07 ng) and female (mean concentration = 1.19 ± SE 0.09 ng 200 μl^{-1}; mean quantity = 0.26 ± SE 0.03 ng) spiders did not differ between gender (concentration, $F_{1,100} = 0.09$, $P = 0.771$; quantity, $F_{1,100} = 0.41$, $P = 0.525$) but did show significant temporal variation between months (concentration, $F_{2,99} = 6.78$, $P = 0.002$; quantity, $F_{2,99} = 4.18$, $P = 0.018$) (fig. 1). Interestingly, this temporal change in aphid consumption did not correlate with the availability of aphids to these spiders (fig. 1). During June, when aphids were just beginning to increase in number, these spiders were feeding disproportionately on aphids, a phenomenon reported previously by Harwood *et al*. (2004) for aphid feeding by Linyphiidae. Later the 11.7-fold increase in aphid abundance between June and July did not result in a significant increase in the consumption of aphids.

Comparison of levels of aphid consumption by *P. degeeri* with data obtained by Harwood *et al*. (2004) for linyphiid spiders indicated that the gut contents of the former contained a greater concentration of antibody-recognizable aphid protein (female, $F_{1,1098} = 39.0$, $P < 0.001$; male, $F_{1,543} = 29.1$, $P < 0.001$) and a considerably greater quantity of antibody-recognizable material (female, $F_{1,1098} = 39.8$, $P < 0.001$; male, $F_{1,543} = 369.2$, $P < 0.001$). The gut contents of both female and male *P. degeeri* were, due to their size, found to represent consumption of significantly more aphid protein than their population density would predict. Proportionally, the mean quantity of aphid protein as a proportion of total aphid protein detected within all spiders was 16% in females and 37% in males and this proportion varied temporally (figs 2,3). Interestingly, within males although both population size (fig. 3a) and spider biomass (fig. 3b) were

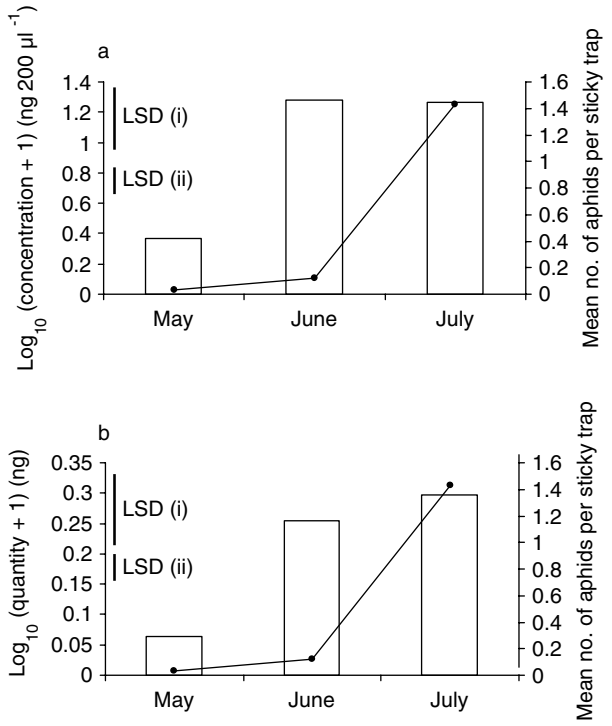

Fig. 1. Diffferences in the mean concentration (a) and quantity (b) of antibody-recognizable aphid protein within *Pachygnatha degeeri* during May, June and July 1999. Data for female and male spiders combined due to non-significant differences between the two sexes. Line with • represents mean number of aphids captured by sticky traps during sampling. Solid bars represent (i) LSD for monthly variation in concentration (fig. 1a) or quantity (fig. 1b) of aphid proteins and (ii) LSD for monthly variation in mean numbers of aphids per sticky trap.

considerably lower than linyphiids, during high aphid abundance in July, there was only a small difference in terms of total quantity of aphid protein present within the total population of *P. degeeri* and Linyphiidae (fig. 3c). Within females, although there is a gradual increase in their population (fig. 2a) and biomass (fig. 2b), parallel to similar population trends in the linyphiid females, the quantity of aphid protein within these females as a proportion of total aphid protein in the female population increased by 155% while that of the Linyphiidae actually declined by 15.7% (fig. 2c).

Aphid predation by other non-linyphiid spiders

With the exception of *P. degeeri*, all other non-linyphiid spiders were scarce in winter wheat fields at HRI Wellesbourne. Very few of these species (*Tetragnatha extensa* (Linnaeus) (Tetragnathidae), *Pardosa amentata* (Clerck) (Lycosidae), *Xysticus cristatus* (Clerck) (Thomisidae), *Meta segmentata* (Clerck) (Tetragnathidae), *Araneus cornutus* (Clerck) (Araneidae), *Araniella cucurbitina* (Clerck) (Araneidae) and *Pardosa* sub-adults) and the harvestman *Phalangium opilio* Linnaeus (Opiliones: Phalangiidae) screened positive for antibody-recognizable aphid protein within their guts (only a single *T. extensa*, *X. cristatus*, *M. segmentata* and *P. opilio* contained significant levels of aphid material).

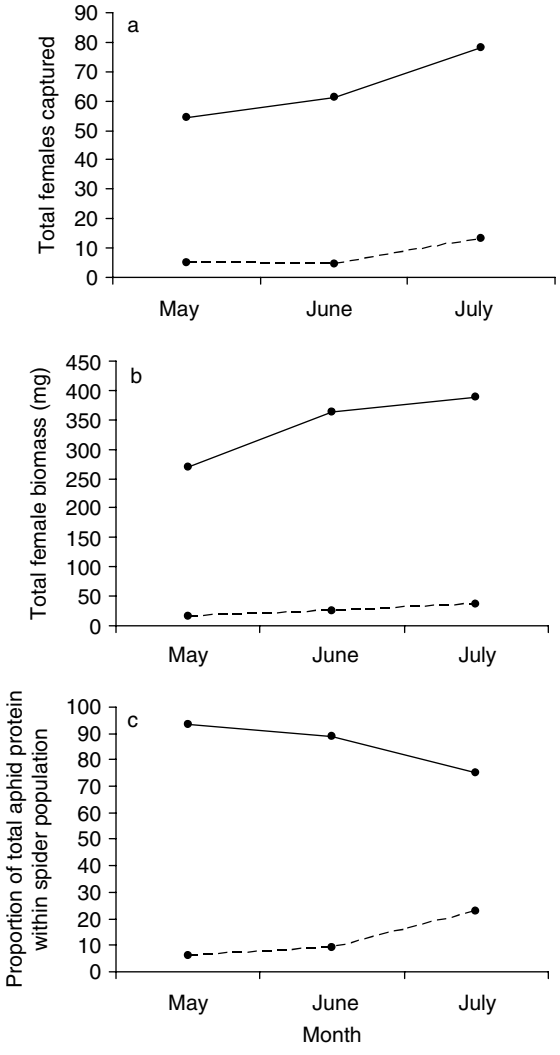

Fig. 2. Differences between Linyphiidae and *Pachygnatha degeeri* females captured during sticky-trap sampling (a), the total biomass of those captured (b) and proportion of total aphid protein within the two spider populations (c). Solid lines represent the Linyphiidae and dotted lines represent *P. degeeri*.

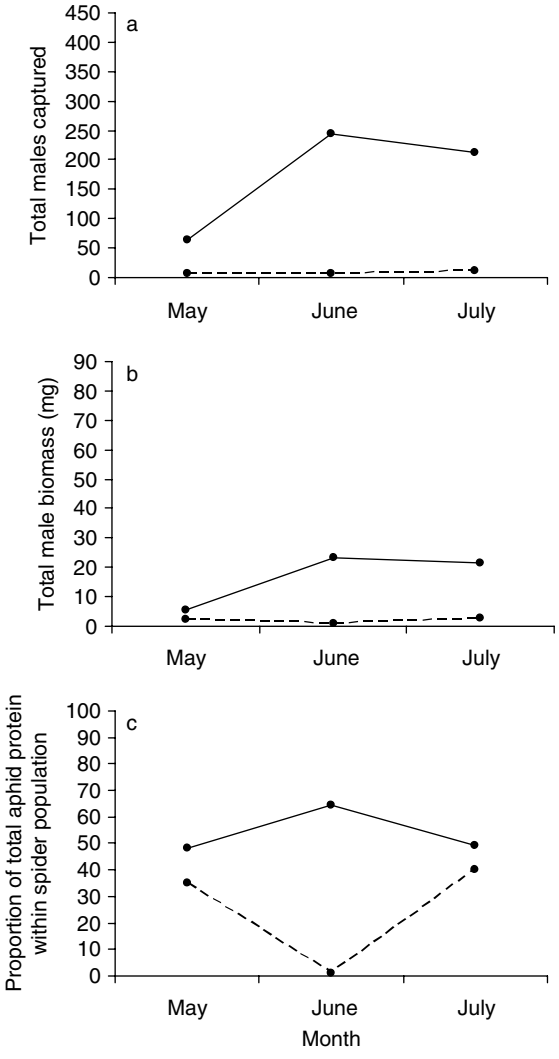

Fig. 3. Differences between Linyphiidae and *Pachygnatha degeeri* males captured during sticky-trap sampling (a), the total biomass of those captured (b) and proportion of total aphid protein within the two spider populations (c). Solid lines represent the Linyphiidae and dotted lines represent *P. degeeri*.

Discussion

Pachygnatha degeeri were, as in previous studies in British agroecosystems (Topping & Sunderland, 1992, 1994; Sunderland & Topping, 1993), captured in low numbers relative to the Linyphiidae. In the UK, spider communities in winter wheat tend to be dominated by the Linyphiidae (Topping & Sunderland, 1992, 1994; Sunderland & Topping, 1993; Harwood *et al*., 2001b, 2003; Nyffeler & Sunderland, 2003) although elsewhere in Europe *P. degeeri* can occur at higher densities within agricultural systems (Samu *et al*., 1996). Under certain environmental conditions, therefore, they may represent one of the dominant invertebrate predators of aphids and possibly other pests. Despite their relative low density in British cereals, these tetragnathids form an important part of the complex assemblage of predators and occupy a different niche to the web-based linyphiids.

In contrast to the consumption of aphids by Linyphiidae (Harwood *et al*., 2004), no significant differences were found in the quantities or concentration of antibody-recognizable aphid protein within the guts of male versus female *P. degeeri*. Unlike the female linyphiids, most of whom are relatively immobile and spend considerable periods of time within their webs (Alderweireldt, 1994), both male and female *P. degeeri* are active hunters, exposing both sexes to the same range of prey. This probably explained the lack of difference between the sexes.

Both female and male *P. degeeri* contained significantly greater concentrations of aphid material in their guts than linyphiid spiders captured at this site. Thus, in rejection of our original hypothesis, *P. degeeri* were not simply eating more aphids because they themselves were larger, but in addition aphids must have comprised a greater proportion of their diet. *Pachygnatha* sp. prevent aphids that have fallen

from above from regaining the plant and, by climbing the plant at night, selectively consume aphids within the crop canopy, and within this ecological niche are clearly eating a lot of aphids. Possible reasons why these spiders are consuming aphids as a larger part of their diet are complex. It could be that to this species of spider, aphids represent a better quality prey item than observed in other predators (Toft, 1995; Bilde & Toft, 2001). An interesting possibility might be that, like many coccinellid beetles that feed primarily on aphids, *P. degeeri* has evolved to cope with aphid toxins and can tolerate a higher proportion of aphids in their diet than most other species of spider. Alternatively, we cannot reject the possibility that there was simply a lack of suitable alternative prey at this field site for these larger hunting spiders and they were forced to eat them, despite any detrimental effects on fitness. Mini-sticky trap and mini-quadrat sampling (Harwood *et al*., 2001b, 2003) indicated that the primary potential prey on the ground were Collembola belonging to the families Isotomidae, Entomobryidae and Sminthuridae. Large, non-web based spiders such as *P. degeeri* are unlikely to consume significant numbers of these very small active invertebrates due to the difficulty of capture. Spiders would be reliant on their webs to aid in the trapping of such prey and therefore in the smaller web-based linyphiids, Collembola constitute a large proportion of their diet (Agustí *et al*., 2003). The larger, less mobile prey that these tetragnathids are likely to consume were scarce at this field site (Harwood *et al*., 2001b, 2003).

Although these spiders represented only 6% of all arachnids captured, the total quantity of aphid material within the guts of this spider population was high compared to other species. Female and male *P. degeeri* accounted for 16% and 37% respectively of the total quantity of antibody-recognizable aphid protein within all spiders during 1999. Although less than that for the linyphiid population, on a per-spider basis they consumed significantly more aphids and ultimately could prove more valuable (per spider) in biological control. This is most evident among male *P. degeeri* which, despite considerably lower densities, consumed non-significantly lower quantities of aphid material than the linyphiids during May and July. As with the Linyphiidae (Harwood *et al*., 2004), *P. degeeri* were also found to feed on aphids at a disproportionately higher rate when these pests were relatively scarce during the aphid establishment phase, the ideal scenario for an effective generalist predator of aphids. They failed to increase their feeding rate when availability increased during July, possibly as a result of satiation.

Other non-linyphiid spiders, which were even less common than *P. degeeri*, were found to feed vary rarely on aphids in the field. The use of an aphid-specific monoclonal antibody has shown that *P. degeeri*, a large tetragnathid spider, feeds extensively on aphid prey and could, if populations were enhanced, prove valuable in the biological control of aphids.

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