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Pollen interception by linyphiid spiders in a corn agroecosystem: implications for dietary diversification and risk-assessment

Julie A. Peterson · Susan A. Romero · James D. Harwood

Abstract Dietary diversification, including consumption of plant tissues such as pollen, can enhance the fecundity of generalist predators, resulting in improved control of pest prey. Supplemental pollen feeding has been observed in many natural enemies, including sheet-web spiders (Araneae: Linyphiidae), which represent a major component of food webs in agroecosystems. Their horizontal, ground-based webs have the potential to intercept pollen grains during anthesis of crop plants, providing the opportunity for consumption of pollen to occur. In laboratory feeding trials, *Frontinella communis* and *Tennesseellum formicum* (Araneae: Linyphiidae) readily fed on pollen grains dusted on their webs, with 82 and 92% of spiders consuming pollen within the 210 min trial. These results revealed a strong potential for dietary supplementation with pollen in ground-based sheet-web spiders, indicating that pollen feeding may be an important component of the feeding biology of linyphiids. To measure pollen and prey interception in simulated linyphiid webs, a 20 m × 20 m grid of miniature sticky traps was established within and downwind of a corn agroecosystem. Traps were exposed for 24 h, all intercepted material was transferred to the laboratory for subsequent identification, and replaced with additional traps for 28 consecutive days in July and August 2008, to encompass periods before, during and after anthesis. Over 150,000 corn pollen grains and 5,000 prey items (dominated by Collembola and Hemiptera) were intercepted at simulated web-sites. Dates of peak anthesis resulted in pollen counts as high as 4,000 grains per web-site in the interior of the cornfield. Spatial Analysis by Distance Indices (SADIE) indicated significant temporal and spatial variability in pollen interception within and outside the corn field, but interestingly there was no significant spatial association between pollen and prey. Furthermore, transgenic *Bacillus thuringiensis* corn expresses insecticidal proteins in pollen, posing an exposure risk to non-target arthropods. Consumption of corn pollen may be a route to transgenic protein exposure in this important taxon of generalist predators.

Keywords Linyphiidae · Dietary supplementation · Pollen · Spider webs · *Zea mays* · *Bacillus thuringiensis*

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Introduction

Habitat diversification can increase predator density and diversity through the provisioning of alternative food and enhanced habitat resources (Landis et al. 2000; Jonsson et al. 2008). These added nutritional inputs represent both prey and non-prey sources, such as floral and extra-floral nectar, pollen, seeds and fungi, all of which potentially increase the efficacy of predators in biological control (reviewed in Lundgren 2009a). It is becoming increasingly evident that the omnivorous tendencies displayed by many natural enemies can impact their feeding behavior and role in biological control (Hunter 2009). Dietary diversification via consumption of both prey and plant material by primarily predatory arthropods can be beneficial in multiple ways, including the provision of essential nutrients, sustainment of predators during periods of low prey availability, and reduction of interspecific competition (Coll and Guershon 2002). The ability of certain arthropod biological

control agents to feed on plant material during periods of prey scarcity can lead to improved survivorship and fecundity (Lundgren 2009a). In some predatory groups, such as the Heteroptera, plant feeding can not only sustain arthropods when prey is unavailable, but can also increase their fitness when supplementing a prey-based diet (Coll 1998). The addition of non-prey foods to the diets of ladybird beetles (Coleoptera: Coccinellidae) aid in their biological control efficacy by fueling immigration into crop systems, increasing survival during periods of low prey availability and diapause, and increasing their reproductive ability (Lundgren 2009b).

Pollen can be particularly valuable as a food resource to arthropod natural enemies (Lundgren 2009a). Corn pollen provides essential amino acids and vitamins, with proteins, carbohydrates, and lipids accounting for up to 27, 20, and 7% dry weight respectively (Goss 1968; Roulston and Buchmann 2000; Roulston and Cane 2000). Some important natural enemies whose omnivorous tendencies include consumption of pollen are ladybird beetles (Smith 1961), ground beetles (Mullin et al. 2005), green and brown lacewings (Canard 2001), hoverflies (Olesen and Warncke 1989), phytoseiid mites (Castagnoli and Simoni 1991; Van Rijn and Tanigoshi 1999; Vantornhout et al. 2004), crab spiders (Vogelei and Greissl 1989), and orb-weaving spiders (Smith and Mommsen 1984). The consumption of crop pollen in agroecosystems by predatory arthropods could therefore have important implications for biological control. In a corn Zea mays L. (Poales: Poaceae) field, anthesis typically occurs for 7–14 days during the VT (tasseling) and R1 (silking) life stages of the plant (Ritchie et al. 1997). Due to its large size and rapid rate of settling, most corn pollen released during anthesis remains close to the source, although it is possible for wind to carry pollen up to 30 m (Raynor et al. 1972) and the surface of plant leaves within corn fields may have pollen densities as high as 1,400 grains per cm^2 (Pleasants et al. 2001). Deposition of large amounts of corn pollen provides a resource that can be utilized by many natural enemies within cultivated fields. For example, the predatory hemipteran Orius insidiosus (Say) (Hemiptera: Anthocoridae) is found in abundance in corn agroecosystems during anthesis and it typically localizes at corn silks and leaf axils (which collect pollen during anthesis) (Isenhour and Marston 1981); these predators are found in higher abundance in those axils containing pollen (Coll and Bottrell 1991).

Spiders are typically considered predators of insect prey (Nyffeler et al. 1994) but are also of particular interest for examining pollen as a source of diet supplementation. The Araneae may engage in direct pollen feeding (Vogelei and Greissl 1989), as well as indirect pollen consumption through ingestion of pollen-dusted prey in the web and/or the web's silk itself (Smith and Mommsen 1984; Ludy and

Lang 2006). Spider webs are natural pollen traps; the abundance of pollen found on spider webs can even be used to analyze the deposition and dispersal of pollen grains by a given plant community (Bera et al. 2002; Song et al. 2007). Despite research on pollen-feeding with other groups of arachnids, there are few studies addressing this phenomenon in sheet-web weaving spiders (Araneae: Linyphiidae) (Sunderland et al. 1996; Carrel et al. 2000). Linyphiid spiders are known to selectively build their webs at micro-sites with high prey density and diversity (Harwood et al. 2001, 2003; Harwood and Obrycki 2007), but interception frequencies with non-prey food has not been documented. Their small, horizontal webs can be found on the surface of the ground or in leaf litter, where they catch and consume soft-bodied prey, such as Collembola and Diptera (Draney and Buckle 2005). These agrobiont (agriculturally dominant) spiders are adapted to the frequent disturbances in cropping systems by having an extended breeding season, higher eggsac production rates than species that frequent non-agricultural habitats (such as woodlands), and the ability to immigrate into annual crops from long distances via aerial ballooning (Bishop and Riechert 1990; Schmidt and Tscharntke 2005). Spiders are well adapted to life in agroecosystems; their low metabolic rates (Anderson 1970, 1996; Greenstone and Bennett 1980; Anderson and Prestwich 1982) allow for higher likelihood of survival during periods of food shortage (Nyffeler and Breene 1990) compared to other natural enemies. Indeed, spiders are frequently food-limited (Wise 1993; Bilde and Toft 1998) and intercept prey below thresholds required for successful growth and development (Romero and Harwood 2010). These life history traits allow linyphiids to make important contributions to biological control in certain agroecosystems (Riechert and Lockley 1984; Thorbek et al. 2004), typically as part of the assemblage of natural enemies present, as opposed to acting alone, to suppress pest populations (Sunderland et al. 1997).

Knowledge of the spatial and temporal distributions of species, as well as the causes and consequences of these patterns, are essential to understanding ecological processes (Levin 1992). For example, spatial dynamics between predator and prey populations in agricultural landscapes can affect the strength of trophic connections, altering a natural enemy's potential for biological control (Yasuda and Ishikawa 1999; Pearce and Zalucki 2006). To study such interactions, Spatial Analysis by Distance Indices (SADIE) methodology has been used to describe and quantify spatial patterns of arthropods (Holland et al. 1999, 2005; Sciarretta and Trematerra 2006), insect-vectored diseases (Jones et al. 2008) and soil nutrient deposition (Rodriguez et al. 2009). This tool for quantifying spatial data can be applied to a wide range of data sets that contain both location and count information (Perry 1995).

To study the impact of crop anthesis on linyphiid spiders, we used SADIE to examine the spatial pattern of pollen deposited inside and outside of a corn field during anthesis and, concurrently, to examine the distribution of prey available to linyphiid spiders in the same areas (after Perry et al. 1999; Perry and Dixon 2002). Additionally, we used SADIE to test for spatial association between pollen interception and prey availability (after Perry 1998). Using a microsite-specific sampling approach, this study examined the hypothesis that high amounts of corn pollen are intercepted at linyphiid web-sites to provide a potential supplemental food resource during crop anthesis. We also predict that prey of linyphiid spiders will be spatially associated with the distribution of corn pollen within an agroecosystem, as prey items will potentially utilize pollen as a nutritive resource.

Methods

Pollen consumption trial

Adult male and female linyphiid spiders of the species *Tennesseellum formicum* (Emerton) ($n = 37$) and *Frontinella communis* (Hentz) ($n = 44$) were collected by aspirator from agricultural fields at Spindletop Research Station, Lexington, Kentucky, USA. Spiders were placed separately into plastic Petri dishes (60×15 mm) with a moistened Plaster of Paris and charcoal base and maintained at 20°C with an 18:6 light:dark cycle. The spiders were starved for 1 week, but provided moisture daily. Non-Bt corn (Novartis hybrid NK4640) was grown under greenhouse conditions and pollen was harvested from mature corn plants and stored at −80°C. Prior to the feeding trials, pollen was removed from the freezer and allowed to thaw at 20°C for 30 m. Approximately 2.7 ± 0.45 mg of corn pollen was lightly dusted onto the web of each spider using a paint brush. Spiders were observed under a stereomicroscope every 15 m for 210 m following the introduction of pollen onto their webs. Initiation and cessation of feeding were recorded at each 15 m interval; time to initiate feeding and total duration of feeding for each spider was calculated, as well as total percent feeding for both species of linyphiid.

Field site

Fields of Roundup Ready®/YieldGard Corn Borer™ (Bt-hybrid 4842S) corn, grown under Monsanto Academic Research License/Stewardship Agreement #50290588 with the University of Kentucky, were planted at the Spindletop Research Station in Lexington, Kentucky, USA (GPS coordinates: 38°07.555 N, 84°30.901 W) on 6 May 2008 and maintained under standard agronomic practices with no insecticidal application. Herbicides (Lexar®, Syngenta Crop Protection, Greensboro, North Carolina, USA; Roundup®, Monsanto Company, St. Louis, Missouri, USA) were applied on 9 May 2008, followed by ammonium nitrate fertilization on 19 May 2008 (approximately 300 kg/ha). Southwesterly winds predominate at the field site during the summer months (personal communication, K. Thomas Priddy, University of Kentucky Agricultural Weather Station, http://wwwagwx.ca.uky.edu/cgi-public/hourly_www.ehtml) and an experimental plot was located at the center of the northeastern (downwind) field edge, in order to quantify the potential rate of pollen interception inside, and downwind of, the corn field. Adjacent field margins consisted of a mix of weedy grasses and forbs typical for the region, comprised mostly of tall fescue, crabgrass, foxtail, plantain, cocklebur and ragweed species, which were unmanaged throughout the duration of the study.

Sampling with miniature sticky traps

A 20×20 m grid consisting of 36 miniature sticky traps (after Harwood et al. 2001, 2003; Romero and Harwood 2010) was established in a 50×50 m cornfield, encompassing an area from 10 m within the cultivated field to 10 m exterior (field margin) (Fig. 1). The sticky traps consisted of a 7.5 cm^2 (5×1.5 cm) acetate sheet, comparable in size to common linyphiid (subfamily Erigoninae) spider webs (Sunderland et al. 1986; Alderweireldt 1994), coated with Tangle-Trap Insect Trap Coating Paste (The Tanglefoot Company, Grand Rapids, Michigan, USA). This acetate sheet was placed on a base consisting of a small plastic plant label painted with acrylic ''Burnt Umber'' paint (Cal-Western Paints Inc., Santa Fe, California, USA)
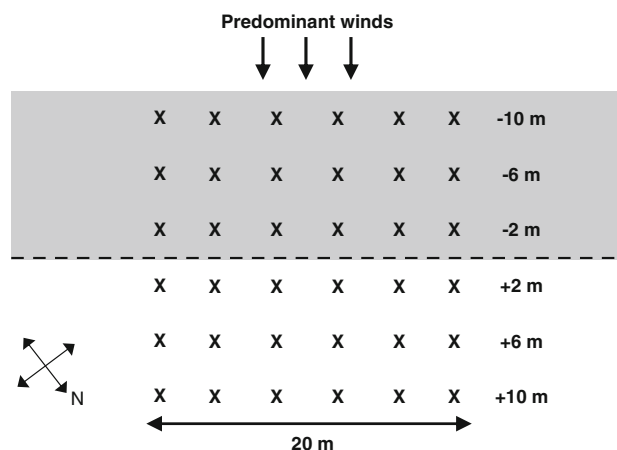

Fig. 1 Location of 36 miniature sticky traps (marked with an "X") used to quantify the interception frequencies of pollen and prey at simulated linyphiid spider web-sites. *Shaded area* indicates location of the corn field, with *dashed line* representing the edge of the field. Sticky traps were aligned in a 20×20 m grid from 10 m inside to 10 m outside the corn field

to match soil color and thereby avoid preferentially attracting certain prey due to color. Thirty-six miniature sticky traps were placed along the experimental grid and exposed in the field for 24 h, collected, and replaced with new traps every day from 12 July to 8 August 2008. This sampling period encompasses periods before, during and after anthesis.

Data analysis

In the pollen feeding study, data for total duration of feeding and time to initiate feeding (log $(x + 1)$ transformed to meet necessary assumptions of parametric analysis) were compared across the two linyphiid species using a t-test. Number of spiders feeding on pollen was also compared across species using a chi-square test (Minitab 14 Statistical Software 2003).

All potential prey items collected on miniature sticky traps were identified using a stereomicroscope and classified as prey or non-prey items. The distinction between categories was based on prior feeding trials and the inability of most linyphiid spiders to feed on arthropods larger than 5 mm, as reported in numerous published (Sunderland et al. 1986; De Keer and Maelfait 1987, 1988; Nyffeler and Benz 1988; Alderweireldt 1994; Jmhasly and Nentwig 1995; Toft 1995; Harwood and Obrycki 2007) and unpublished (Keith D. Sunderland; James D. Harwood, unpublished data) studies. In parallel, the number of corn pollen grains on each trap was counted.

Mean pollen and prey interception rates for inside versus outside the corn field traps on each date were compared using a non-parametric Mann–Whitney U test due to the absence of homogeneity of variance and normality in the data. Additionally, mean prey interception rates grouped by taxonomic order both inside and outside the field were compared using a Mann–Whitney U test (Minitab 14 Statistical Software 2003). SADIEShell (Conrad 2006) graphic user interface was used to identify and quantify clustering in the distributions of pollen and prey counts. During anthesis, pollen and prey counts were pooled into 3 sampling periods of 5 days each (period 1: July 12–16, period 2: July 17–21, and period 3: July 22–26). Within each sampling period, means were determined for pollen and prey counts at each trap location and then analyzed using SADIE. Given that linyphiid spiders remain within a localized area for many days, due to the high time and energy cost of web re-construction (Ford 1977), it is biologically relevant to analyze prey availability and pollen deposition in cumulative time periods.

SADIE analyses used spatially referenced point counts from sample locations to calculate a local clustering index which identifies clusters of units with either large or small counts. These clusters were differentiated by a randomization test which compared the actual counts with indeterminate (random) data. Clusters in SADIE were designated as patch clusters (high density) or gap clusters (low density). Patch clusters with counts higher than the mean were assigned a positive index value (v_i) and gap clusters were assigned a negative index value (v_j). A one-tailed clustering test determined significant clustering in the data when the proportion (P) of clustering in random data, compared to observed data, was <0.05. Surfer mapping software (version 9; Golden Software, Inc. 2009, Golden, Colorado, USA) was used to interpolate the index values into a contoured surface map of patches ($v_i > 1.5$) and gaps ($v_i < -1.5$). A spatial association test was also employed with SADIE methodology (after Perry 1998); this test was run to determine association (similarity) or disassociation (dissimilarity) between spatial patterns of pollen and prey for each of the sampling periods.

Results

Pollen consumption trial

Both species of linyphiid spider readily fed on pollen dusted on their webs. Spiders were observed consuming pollen that was intercepted in the silk strands of their webs by drawing the pollen grains into their mouths using alternating cheliceral movements, chewing with the endites, and periodic expulsion and retrieval of a bubble of salivary liquid from the oral cavity (Fig. 2). The percentage of spiders feeding on corn pollen during the 210 m trial did not vary significantly based on species for *F. communis* and *T. formicum*; however, *T. formicum* did show a significantly shorter mean time to initiate feeding on pollen grains when compared to *F. communis* (Table 1). Additionally, members of *T. formicum* also remained feeding on pollen for a longer period of time than did *F. communis*.

Pollen interception

A total of 156,881 corn pollen grains were intercepted on miniature sticky traps over the course of the study. Pollen shed began 12 July 2008 and peaked 1 day later, with a mean interception rate inside the corn field of 268 ± 29 pollen grains cm^{-2} 24 h^{-1}. Pollen shed continued for 14 days, but in declining numbers, until 26 July after which time no further pollen interception was recorded at simulated web-sites. As rates of anthesis declined, two dates resulted in pollen counts of zero for all miniature sticky traps (23 July and 25 July), as well as for the remainder of the study period (27 July–8 August). Mann–Whitney U tests comparing the rates of pollen deposition at simulated web-sites inside versus outside the field indicated that all dates from 14 July–22 July resulted in significantly
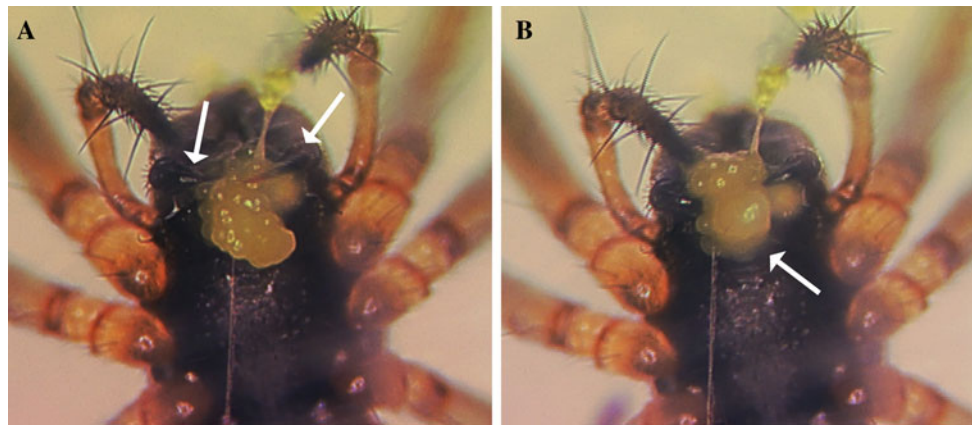
Fig. 2 *Frontinella communis* feeding on pollen in its web. **a** *Arrows* indicate chelicerae, which move pollen grains into the spider's mouth in concert with the endites; **b** *Arrow* indicates bubble of salivary liquid exuded from the spider's oral cavity, presumably for extraoral digestion of pollen grains

Table 1 Percent of spiders feeding on corn pollen grains, mean (±SE) time to initiate feeding, and mean (±SE) duration of feeding for linyphiid species *Frontinella communis* and *Tenneseellum formicum*

Species	Percent feeding on pollen	Time to initiate feeding (m)	Duration of feeding (m)
Frontinella communis	81.82%	34.64 ± 5.73	84.67 ± 6.07
Tennesseellum formicum	91.89%	14.18 ± 3.03	131.03 ± 9.53
Statistical comparison	$\chi^2 = 1.738$, $df = 1$, $P = 0.187$	$t_{64} = 2.31$, **$P = 0.024$**	$t_{59} = -3.98$, **$P < 0.001$**

Bold type indicates a significant *P*-value

higher numbers of pollen grains inside the field (at 99% confidence interval, $P < 0.01$). The dates when pollen interception frequencies did not vary significantly occurred at the initial onset of anthesis and on its final days (12–13 July and 23–26 July) (Fig. 3).

Prey interception

In total, 4,685 potential prey items were intercepted at miniature sticky traps over the course of the study. Additionally, 499 mites (Acari) and 17 spiders (Araneae) were identified on sticky traps, but were not categorized as potential prey due to the low likelihood of consumption by

Fig. 3 Mean (±SE) pollen grains per cm^2 intercepted in a 24 h period at miniature sticky traps located inside and outside a corn field, recorded from 12 July–8 August, 2008

linyphiid spiders. Intercepted prey were dominated by Collembola (74.74%), followed by Diptera (8.25%), Hemiptera (7.97%), Hymenoptera (4.22%), and Coleoptera (3.47%). Additional prey orders identified (Orthoptera, Thysanoptera, Lepidoptera, Psocoptera, and Neuroptera) combined to account for the remaining 1.35% of prey and therefore were not considered an influential part of the potential linyphiid prey community, but could be important in the context of dietary diversification (see "Discussion").

When comparing prey interception rates inside and outside the corn field, the rate was significantly higher outside the field on all but three dates (19 July, 3 August, and 4 August) (Fig. 4). Except for these three dates, prey interception rates outside the crop (0.08 cm^{-2} h^{-1}) were adequate for optimal growth and reproduction (De Keer and Maelfait 1988; Romero and Harwood 2010). For the three most abundant orders of prey (Collembola, Hemiptera, and Diptera), interception rate for inside versus outside the corn field was examined (Fig. 5). Collembola were found in higher numbers outside the corn field ($P < 0.0001$), as were Hemiptera ($P < 0.0001$), while interception frequencies of Diptera did not vary by location.
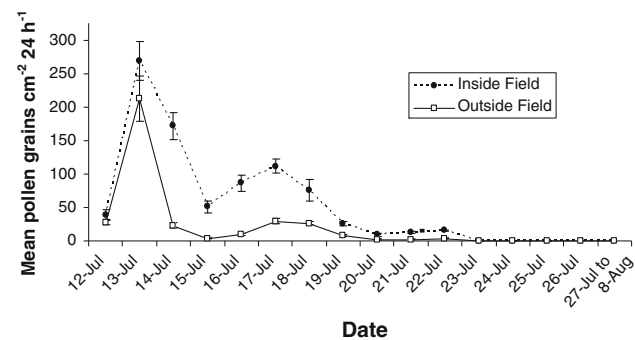
Pollen and prey distribution

SADIE analyses of pollen counts showed a significantly aggregated distribution over all three sampling periods

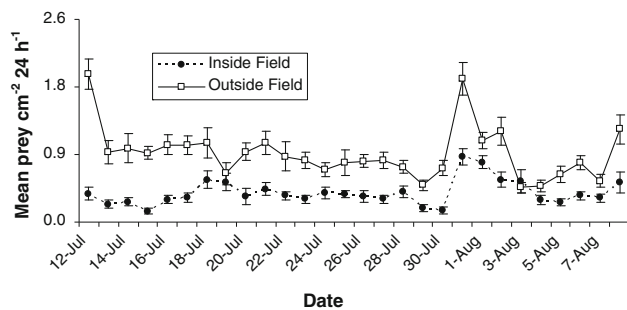**Fig. 4** Mean (±SE) prey interception frequencies (as prey items cm^{-2} 24 h^{-1}) for miniature sticky traps inside and outside the corn field, from 12 July–8 August, 2008

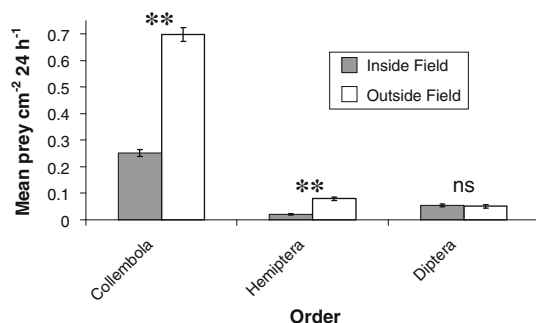**Fig. 5** Mean (±SE) interception frequencies (prey items cm^{-2} 24 h^{-1}) for miniature sticky traps inside and outside a corn field, for the three most abundant orders of prey: Collembola, Hemiptera, and Diptera

(Table 2). High values of the patch clustering index (v_i) within the corn (>1.5) indicate patches of strong pollen aggregation. The lowest values of the gap clustering index ($v_j < -1.5$), indicating gaps in the spatial pattern of pollen, occurred mainly outside the corn field in the old field area (Fig. 6a–c). In contrast, prey were significantly aggregated in patches outside of the corn field in the weedy margin area rather than inside the corn field (Table 2; Fig. 6d–f). In contrast to our hypothesis, pollen and prey were significantly disassociated at sampling periods 1: July 12–16 ($X = -0.6397$, $P = 0.999$), 2: July 17–21 ($X = -0.7341$, $P = 0.999$), and 3: July 22–26 ($X = -0.6033$, $P = 0.999$) (Table 3). This is an indication that prey were not aggregating to areas of higher pollen deposition within the corn field during periods of anthesis.

Discussion

The pollen feeding trial revealed that *Frontinella communis* and *Tennesseellum formicum* linyphiids will readily consume pollen that has been intercepted in their webs. These results indicated that a high percentage of linyphiids will feed on pollen (82 and 92% for *F. communis* and

T. formicum species, respectively) within a short period of time (mean time to feeding 35 and 14 m) and for an extended duration of time (mean 131 and 85 m). The palatability of corn pollen for linyphiid spiders is therefore validated, indicating that this plant-provided resource may play an important role in the feeding ecology of sheet-weaving spiders. Although pollen-feeding has been reported in other groups of spiders (e.g., Smith and Mommsen 1984; Vogelei and Greissl 1989), the significance of the present study is in the demonstration of pollen feeding by an agriculturally dominant species, therefore potentially impacting trophic linkages and biological control in agroecosystems.

The high levels of pollen interception recorded in this study (over 250 pollen grains cm^{-2} 24 h^{-1} during peak anthesis) indicate a high potential for corn pollen accumulation in the webs of linyphiid (and other) spiders. During peak anthesis, our recorded pollen deposition frequencies were higher than those reported on milkweed plants within corn fields for five of six localities measured (Pleasants et al. 2001) and two transgenic corn lines measured across 2 years (Jesse and Obrycki 2000). Differences in pollen interception are most likely due to the disparity in microclimatic conditions experienced at simulated linyphiid web-sites versus milkweed leaves, as well as specific corn variety used (Jesse and Obrycki (2000) examined Bt events 176 and Bt-11, while the current study utilizes the Bt event MON810) and methods of recording pollen deposition. Our study has also shown pollen aggregation within the corn field, with daily variation, which can be attributed to fine scale heterogeneity in plant structure, individual plant phenology, and abiotic factors such as wind and precipitation. High amounts of corn pollen were also intercepted up to 10 m from the edge of the cultivated field. It is unknown whether this high level of pollen interception in spider webs affects the efficacy of prey capture and/or the frequency that linyphiids abandon their webs. These results show that pollen grains are available as a potentially nutritive resource to the population of linyphiid spiders both within, and areas surrounding, corn cropping systems because both the interior and margin habitats are inundated periodically with this resource. As pollen has been reported to increase efficacy of many natural enemies when incorporated in dietary diversification (reviewed in Lundgren 2009a), the availability of this resource for linyphiid spiders during anthesis presents the opportunity for increased biological control by these abundant predators.

Prey interception rates were higher outside of the corn field, with the orders Collembola and Hemiptera caught in miniature sticky traps in higher frequency in field margins. The presence of a thatch layer and a diversity of weedy grasses and forbs in the field margins provided increased

Table 2 Summary data from SADIE analysis for pollen and prey miniature sticky trap catches recovered in three sampling periods (period 1, July 12–16; period 2, July 17–21; period 3, July 22–26) during anthesis in corn in July 2008

	Mean	Minimum	Maximum	Variance	I_a	P_a	Mean v_j	P (mean v_j)	Mean v_i	P (mean v_i)
Pollen										
Period 1	3,144.94	144	6,030	2,412,732	2.318	*0.0012*	−2.0	0.00	1.97	0.00
Period 2	1,137.89	243	3,663	726,946	2.284	*0.0012*	−1.99	0.00	2.11	0.00
Period 3	74.97	6	205	3,181	2.201	*0.0012*	−1.1	0.00	2.22	0.00
Prey										
Period 1	25.06	2	77	439	2.19	*0.0013*	−2.02	0.00	1.86	0.00
Period 2	25.28	6	80	202	1.82	*0.0013*	−1.57	0.0013	1.85	0.00
Period 3	20.75	5	60	173	1.47	*0.0103*	−1.325	0.037	1.59	0.00

I_a is an index of aggregation and P_a is the associated probability (significant values italicized). v_j and v_i are SADIE cluster indices and refer to gaps and patches, respectively
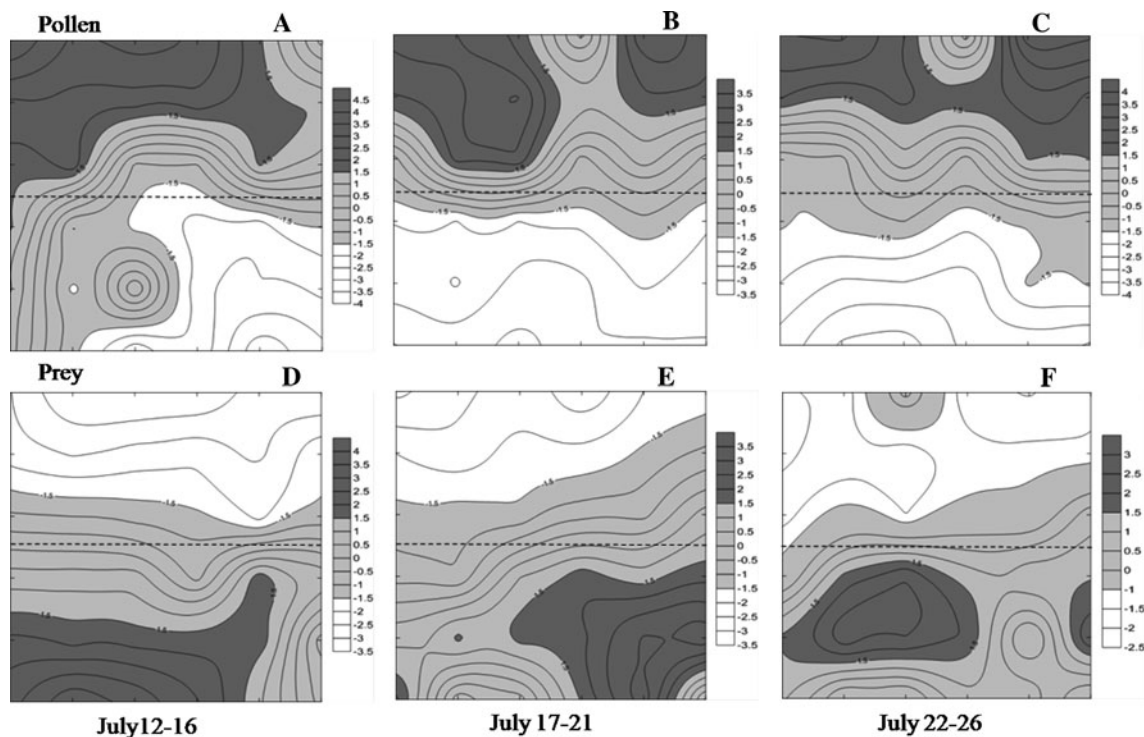

Fig. 6 Contour maps of count data for corn pollen (*top panel*, **a–c**) and prey (*bottom panel*, **d–f**) in a 20 × 20 m plot during three sampling periods of 5 days each. The *dashed line* across each map indicates the edge of the corn field with corn at the top and field margin at the *bottom*. Values on contour *lines* indicate areas of significant patch (+1.5, *dark gray area*) and gap (−1.5, *white area*) clustering

Table 3 Summary of association analysis of pollen and prey for three sampling periods (period 1, July 12–16; period 2, July 17–21; period 3, July 22–26) during anthesis of corn in July 2008

Sample period	X	P
1	−0.6397	*0.999*
2	−0.7341	*0.999*
3	−0.6033	*0.999*

X is the measure of degree of association and P is the probability level. Associations are significant when $P < 0.025$, and dissociations (italicized in the table) when $P > 0.975$

habitat complexity at the soil surface when compared to the tilled and bare soil of the cultivated field. A pattern of increasing biodiversity and abundance with increasing habitat complexity has long been observed (Southwood 1977). A similar comparison could be made to fields where the use of a cover crop increases arthropod abundance in comparison to bare soil (Fernandez et al. 2008). Prey was shown to be highly aggregated outside of the corn field. An aggregated distribution can be attributed to various mechanisms, including attraction and utilization of aggregated

resources, facilitation of mate-finding, common selection of optimal microclimatic conditions, and decreased risk of predation. Collembola show a non-random pattern of distribution, which can be correlated with conditions such as soil pH (Detsis 2009), presence of predator cues (Negri 2004), and moisture and food content (Verhoef and Nagelkerke 1977). However, in this study, prey interception was not correlated with pollen shed, despite the prediction that prey would aggregate to the areas where pollen deposition was highest. If prey are foraging on corn pollen, vertically mobile prey, namely hemipterans (e.g., leafhoppers) and dipterans, would not be restricted to those areas on the ground where higher amounts of pollen are intercepted, but rather could consume pollen directly from the anthers or where the grains have accumulated (e.g., leaf axils). Those prey items utilizing pollen as a nutritive resource, and that are not vertically mobile, particularly Collembola, would be more likely to demonstrate a pattern of spatial aggregation correlating with pollen deposition. Despite their vertical immobility and reports that Collembola will consume plant pollen (Kevan and Kevan 1970; Chen et al. 1996), we recorded no spatial association between prey items and pollen deposition in the corn agroecosystem during anthesis.

These data indicate that linyphiid web-sites located in the interior of a corn field will intercept higher quantities of corn pollen than those located in surrounding field margins during the period of anthesis. Additionally, ground-based webs inside the agricultural field will intercept fewer prey items from the orders Collembola and Hemiptera (which constitute a large portion of linyphiid spider diets). Daily prey interception rates varied widely from 0.14 prey items cm^{-2} 24 h^{-1} inside the corn field in mid-July to as high as 1.92 prey items cm^{-2} 24 h^{-1} outside the corn field a few days earlier. Based on the data of De Keer and Maelfait (1988), Romero and Harwood (2010) determined that linyphiid spiders would need to feed at a rate of 0.044 Collembola cm^{-2} h^{-1} to achieve optimal growth and reproduction. The low prey interception rate within the corn (0.006 cm^{-2} h^{-1}) indicates that spiders are food-limited within the crop. The combination of these two conditions, both lower prey availability (indicating food-limitation) and higher pollen interception, may facilitate supplemental feeding by linyphiid spiders on corn pollen. Prey interception rates, as reported herein, are inadequate for optimal growth and reproduction (De Keer and Maelfait 1988; Romero and Harwood 2010), therefore feeding on pollen in this agroecosystem could provide supplemental nutrition to linyphiid spiders. The addition of corn pollen to the diet of agrobiont linyphiid spiders has important implications related to dietary diversification, as well as to transgenic crop risk-assessment.

Pollen size and structure present two hurdles to consumption of pollen by spiders: pollen grain diameter is too large to pass through the cuticular platelets of a spider's pharynx (Foelix 1996) and the pollen grain possesses an exterior wall that impedes digestion (Roulston and Crane 2000). Smith and Mommsen (1984) hypothesized that spiders were able to dissolve the tough outer coating of a pollen grain via extraoral digestion, i.e., the method of feeding used by the Araneae (Foelix 1996). Alternatively, spiders may pierce the pollen wall with their mouthparts in order to access the nutritive center, similar to the method employed by several species of thrips (Kirk 1984). Observations of linyphiid spiders feeding on pollen grains in this study, particularly the appearance of a bubble of liquid in the oral cavity (Fig. 2b), support the idea that extraoral digestion plays a role in pollen consumption by these arachnids. Although this study, as well as Sunderland et al. (1996), have reported that linyphiids will consume pollen and yeast spores that are intercepted in their webs, the ability of these spiders to utilize the nutritive value of these resources, as well as the ability of a spider to develop and survive on a pollen and/or yeast diet, warrants further study.

Carrel et al. (2000) found that *Frontinella communis* (the same species used in our pollen consumption trials) lost mass when provided a pine pollen-only diet, performing similarly to those spiders given no nutritional input. Additionally, Sunderland et al. (1996) reported that *Leptyphantes tenuis* (Blackwall) (Araneae: Linyphiidae) spiderlings reared on a maceration of commercially prepared tablets of bee-collected pollen plus yeast showed a lower mean longevity than un-fed spiderlings. This seemingly toxic effect of a pollen and yeast diet is most likely attributed to the yeast, as consumption of fungal spores also had deleterious effects on juvenile orb-weavers (Smith and Mommsen 1984). These studies differ from our system in that pine pollen and commercially available bee-collected pollen was used, rather than corn pollen, which is a wind-pollinated monocotyledon. The pollen of wind-pollinated plants often have a higher water content than insect-pollinated grains (Stanley and Linskens 1974) and digestibility of pollen can vary significantly across plant phylogenies (Roulston and Cane 2000), indicating a variety of results can occur depending on the specific type of pollen and arthropods used in feeding trials. Beyond the family Linyphiidae, several studies have shown a positive effect of pollen consumption. Juvenile *Araneus diadematus* Clerck (Araneae: Araneidae) were able to persist almost twice as long and increase web-spinning frequency (a significant energetic output) on a birch pollen diet compared to no nutritional input (Smith and Mommsen 1984). Although juvenile spiders were unable to complete a molt on pollen alone, the addition of a single potato aphid to a pollen-only diet allowed for successful molting (Smith and Mommsen 1984). Additionally, when nectar was added to their diet,

cursorial spiders showed an increase in survival, growth, and fecundity; this plant-based resource allowed for greater fitness during periods of low prey availability or poor prey quality (Taylor and Pfannenstiel 2009). These results support the hypothesis that corn pollen may be able to sustain linyphiid spider populations during periods of lower prey availability, but that pollen alone would be an insufficient diet for development and reproduction.

Generalist predators, (e.g., spiders, carabids, some coccinellids) are often of value in biological control of pest populations because of their ability to persist in the environment during periods of prey scarcity (Symondson et al. 2002). Similarly, these generalists may be able to colonize a cropping system early in the season prior to the arrival and/or exponential growth phase of a pest, thereby providing additional pest suppression (Settle et al. 1996). Persistence by generalist predators during these periods is permitted by their ability to consume alternative prey and/or non-prey items (Symondson et al. 2002). The inclusion of non-prey resources, such as pollen, plant foliage, nectar and honeydew, in the feeding behavior of generalists can sustain predators during low prey availability, as well as improve fecundity (Lundgren 2009a), particularly when pollen is the added resource (Eubanks and Styrsky 2005). Dietary diversification in general can provide organisms with a more optimal mixture of nutrients. Predatory arthropods fed diets consisting of a mixture of prey species performed better in terms of growth rate and fecundity when compared to single-species prey diets [e.g., Lycosidae (Oelbermann and Scheu 2002) or Carabidae and Linyphiidae (Harwood et al. 2009)].

In addition to implications for dietary diversification, exposure to corn pollen should be examined in the context of risk-assessment of genetically modified crops. Transgenic *Bacillus thuringiensis* corn expresses insecticidal proteins targeting common lepidopterous and coleopterous corn pests. Currently employed Bt crops constitutively express endotoxins throughout the life of the plant in all tissues, including pollen (Fearing et al. 1996), creating the potential for a multitude of pathways to exposure of non-target arthropods. Natural enemies may feed on transgenic plant tissues in addition to prey (sometimes unexpectedly) (Moser et al. 2008). Studying these behaviors is essential in understanding Bt-endotoxin uptake by non-target organisms. In corn, pollen consumption represents a potential route for exposure of non-target organisms to transgenic Bt-endotoxins (Obrist et al. 2006a). Tritrophic movement of transgenic proteins (plant-herbivore-predator) may not be a major pathway for non-target spiders, as their primary prey, Collembola, often consume fungal hyphae growing on plant detritus, rather than engaging in direct plant feeding (Hopkin 1997; Rotheray et al. 2009). Some studies with non-target arachnids have shown negative effects of

transgenic pollen consumption: a 17% reduction in fertility and 9% increase in development time was reported in a phytoseiid mite fed Bt versus non-Bt corn pollen (Obrist et al. 2006b). However, Ludy and Lang (2006) reported no discernable effects on weight, survival, or web characteristics in juvenile *A. diadematus*, and Meissle and Romeis (2009) reported no negative effects on *Theridion impressum* Koch (Araneae: Theridiidae). The literature concerning the effects of transgenic pollen consumption on arachnids contains conflicting results and should be further studied, particularly for the family Linyphiidae, a numerically large yet rarely considered taxon of predators abundant in agricultural fields.

The temporal influx of corn pollen during periods of anthesis has resulted in high levels of pollen deposition in the webs of an abundant generalist predator. Both cultivated fields and field margins experience this nutritive addition annually, providing an additional component of the food web. By utilizing pollen resources to supplement a prey-based diet, linyphiid spiders may be able to increase their fecundity through dietary diversification or sustain themselves during periods of low prey availability, therefore providing greater ecosystem services as biological control agents.

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