

Feeding habits of lycosid spiders in field habitats

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Abstract Generalist arthropod predators are potential drivers of population dynamics in a wide variety of ecosystems but their feeding habits are often difficult to reveal as they are small, mobile, and live among dense vegetation or in soils. DNA-based gut-content analysis is a powerful tool that enables studies on arthropod predator–prey interactions. We studied lycosid spiders (*Pardosa* spp.) in agroecosystems to see if they consumed cereal aphids (*Rhopalosiphum padi*) and Collembolans at random, i.e., in proportion to their abundance in the field. We also tested if consumption of the target prey items was affected by the presence of alternative food. Spiders were captured in farmers' fields and their gut-contents screened by PCR with *R. padi* and Collembola primers. On all sampling occasions, concurrent assessments of total prey availability were carried out. Spider predation rates on *R. padi* always exceeded 50 %. Spiders also tested positive for Collembola but to a lower and more varying degree. In general, *Pardosa* did not consume *R. padi* and Collembolans in relation to their abundance in the field. Aphid predation was much higher than expected whereas consumption of Collembolans was considerably lower. The presence of alternative prey influenced consumption of the aphid. It was concluded that prey consumption by *Pardosa* spiders generally cannot be assumed to simply mirror prey availability. The spatial distribution of the target prey needs to

be considered as well as the abundance, composition, and nutritional content of potential alternative food items.

Keywords Predator–prey interactions · *Pardosa* · *Rhopalosiphum padi* · Collembola · Alternative prey · Gut-content analysis

Introduction

Detailed knowledge about the foraging behavior of predators is fundamental in food web ecology and necessary to make correct assumptions about the biological control potential of predators (Beckerman et al. 2006). In many cases, however, information about specific predator–prey interactions and how such pathways are affected by the presence of co-occurring species is limited (Schmitz 2007). In the case of arthropod predators, the lack of knowledge largely depends on difficulties associated with direct observation of small, mobile organisms that live under dense vegetation or below the soil surface. In addition, many arthropod predators are generalists and may include a wide range of prey items in their diet, which complicates studies on their feeding behavior in their natural habitats even further (Symondson et al. 2002).

One way to obtain specific information about the diet of arthropod predators, under a minimal level of disturbance, is to collect predators in their natural environment and analyze prey remains that are present in their gut-contents. Currently, detection of prey DNA using PCR-based techniques is the most commonly used approach (reviewed by Sheppard and Harwood 2005; King et al. 2008). If consumption data derived from such analyses are combined with assessments of prey availability new insights about a predator's feeding behavior or hunting strategy can be obtained.

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In agricultural habitats, generalist predators such as ground beetles and spiders feed on crop pests (Symondson et al. 2002; Kuusk et al. 2008; Tahir and Butt 2009; Öberg et al. 2011). Under certain conditions, they have the potential to maintain pest populations below economic thresholds and thus provide an important ecosystem service to the agricultural sector acting as biological control agents (Chiverton 1986; Östman et al. 2001, 2003). In addition to specific pests, generalist predators may consume alternative food items including other herbivores, decomposers such as earthworms and Collembola (Juen and Traugott 2007; King et al. 2010; Kuusk and Ekblom 2010), Dipterans (Harwood et al. 2007), and other natural enemies (Harwood et al. 2009). By comparing rates of predation derived from molecular gut-content assays with the observed proportion of the target prey in the field, the hypothesis that generalist predators are capturing prey at random can be tested. Such tests have been carried out but are so far restricted to only a few combinations of predators and prey; linyphiid spiders and Collembolans by Agusti et al. (2003), linyphiid spiders and aphids, dipterans, Collembolans (Harwood et al. 2004, 2007), carabid beetles and earthworms by King et al. (2010), coccinellid larvae and dipterans (Moser et al. 2011), carabid beetles and slugs (Hatteland et al. 2011). Therefore, there is a clear need for more data on other taxa.

Previously, we studied the foraging behavior of generalist spider predators from the genus *Pardosa* (Araneae: Lycosidae) in farmer's fields in central Sweden by combining DNA-based gut-content analysis and concurrent monitoring of prey availability (Kuusk et al. 2008; Kuusk and Ekblom 2010). *Pardosa* spiders are common ground-living predators in European agricultural habitats (Samu and Szinetár 2002; Schmidt et al. 2005; Öberg et al. 2007), they have good eyesight and some species are viewed as active hunters that localize their prey by visual cues (Foelix 1996). Others, which feed on highly mobile prey, hunt with a "sit-and-wait strategy," i.e., they lie in ambush and wait for a prey to come close enough to be overpowered (Edgar 1969). Samu et al. (2003) pointed out that sit-and-wait and actively foraging strategies represent two ends of a continuum and introduced another hunting category. Based on visual observations in alfalfa *Pardosa agrestis* (Westring) was classified as a "sit-and-move forager" that indeed spends most of the time sitting still but will frequently change their waiting positions.

We have focused on *Pardosa*'s consumption of the bird-cherry oat aphid, *Rhopalosiphum padi* (L.) (Homoptera: Aphididae) and springtails (Arthropoda: Collembola). The aphid is a major pest in spring-sown cereals in Northern Europe (Wikteliuss and Ekblom 1985; reviewed by Leather et al. 1989) whereas Collembolans are primarily detritivores that represent a substantial source of alternative prey to generalist arthropod predators worldwide (Hopkin 1997).

Our previous results were derived from DNA-based gut-content analyses of spiders collected in fields where *R. padi* densities were consistently very low. We demonstrated that *Pardosa* spiders did indeed feed on *R. padi* at such low pest densities, which is necessary if they are to suppress the aphid population below economic thresholds (Chiverton 1986; Östman et al. 2001). We also showed that *Pardosa* use Collembolans as alternative food and that there was a negative association between the probability of detecting aphid DNA in individual spiders and Collembola availability. This result was puzzling as we did not observe a positive relationship between Collembola consumption and Collembola availability. We suggested that the spiders changed their hunting strategy when ratios of sedentary and mobile prey changed. When the quick, jumping Collembolans were numerous, *Pardosa* hunted more passively with a "sit-and-wait" strategy and consequently did not encounter so many *R. padi* which are sedentary on plant stem bases when present in low densities. In contrast, when Collembolans were less abundant, *Pardosa* had to forage more actively to encounter more prey and consequently "ran into" more aphids.

The overall purpose of this study was to extend our knowledge about the foraging behavior and hunting strategy of *Pardosa* spiders. In line with previous studies, PCR-based gut-content analysis was used to screen field-collected predators for *R. padi* and Collembola consumption and at each sampling occasions concurrent assessments of prey availability were carried out. In contrast to previous studies, the collected spiders were exposed to both low and very high numbers of *R. padi* as well as varying abundances of different alternative prey.

The specific aims included to find out (1) if the probability of detecting *R. padi* and Collembolans in individual spiders was related to prey availability and (2) if *R. padi* predation was affected by the presence of alternative prey taxa.

Materials and methods

Collection of spiders in spring-sown cereals

Adult *Pardosa* spiders of both sexes, including *P. agrestis*, *P. palustris* (L.), *P. prativaga* (L. Koch), *P. fulviseps* (Collet), and *P. amentata* (Clerk), were randomly collected by hand from three organic farms in fields of spring-sown cereals around Uppsala, Sweden (59°51'N, 17°41'E). The shortest distance between farms was 19 km and the longest distance was 46 km. Each field was sampled on two occasions (Table 1); the first at the start of stem elongation of the crop and the second during booting. The collection area within each field measured 60 × 40 m² and was located 5–10 m from the field edge. All collections were carried out between

Table 1 Sampling scheme, mean numbers of available prey (with SE in parenthesis), sample sizes, and detection of *R. padi* and Collembola DNA in *Pardosa* spiders by PCR-based gut-content analysis

Location	Collection occasion	<i>R. padi</i> density on plants	<i>R. padi</i> density on traps	<i>R. padi</i> total density	Collembola density on traps	Diptera density on traps	Density of other prey	Number analyzed <i>Pardosa</i>	% <i>R. padi</i> positive <i>Pardosa</i>	% Collembola positive <i>Pardosa</i>	% <i>Pardosa</i> tested positive for both prey
Farm A	June 16	0.09 (0.03)	0.25 (0.13)	0.36	5.00 (0.89)	22.17 (3.89)	0.92 (0.36)	51	51	8	6
	June 26	0.96 (0.31)	1.5 (0.31)	2.70	58.33 (11.13)	49.92 (7.43)	3.50 (0.66)	35	66	14	14
Farm B	June 19	3.28 (0.53)	1.00 (0.17)	5.10	8.42 (1.23)	8.17 (1.69)	1.83 (0.39)	44	75	4.5	4.5
	June 29	41.34 (3.23)	10.83 (1.76)	62.45	55.42 (12.40)	3.25 (0.43)	0.92 (0.31)	31	87	3	3
Farm C	June 21	9.42 (1.39)	5.25 (1.55)	17.02	111.58 (23.93)	4.58 (0.72)	1.42 (0.15)	42	83	62	50
	June 30	38.62 (4.51)	11.08 (2.62)	59.33	16.17 (2.78)	8.42 (2.06)	3.25 (0.57)	28	71	21	14

Prey availability was monitored using ground-attached mini-sticky traps. Densities of the aphid pest, *R. padi*, were also assessed visually on the cereal plants. The combined measurement of *R. padi* availability was used in the chi-square goodness-of-fit test and the logistic regression analyses

0900 and 1400 h and captured predators were immediately transferred to individual Eppendorf tubes and frozen using dry ice. Spiders were stored at $-70\text{ }^{\circ}\text{C}$ prior to DNA extraction and PCR analysis described below. On one occasion during the storage period the predators were briefly handled to identify species and sexual category (males, females carrying an eggsac, females without an eggsac).

Assessments of natural prey abundances

An effective method of monitoring the availability of prey is the use of mini-sticky traps; Harwood et al. (2001, 2004) used such traps for studying the availability of prey to linyphiid spiders in agricultural habitats. We used a similar method to assess prey availability modified for wolf spiders, 12 mini-sticky traps ($10 \times 5\text{ cm}^2$) were randomly attached to the ground in each collection area. The catches represented a cumulative record of prey over 24 h starting in the afternoon 1 day prior to the collection of predators and ending when the capture session terminated (for more details about the traps see Kuusk and Ekbohm 2010). Captured arthropods were identified to the following taxa: Aphidoidea, Collembola, Diptera, Cicadoidea, Thysanoptera, Hymenoptera, Coleoptera, Araneae, and others. Mean prey abundances per trap and SE were calculated for each sampling occasion as well as the proportion of each taxa of the total prey community. Apart from assessing aphid densities on the ground with mini-sticky traps we also estimated the mean number of aphids per plant at each sampling occasion by randomly selecting 50–100 plants in the collection area; plants were gently removed from the soil so that both above and below ground aphids could be counted (Kuusk et al. 2008). Mini-sticky traps will most likely catch aphids that have fallen off plants and these aphids will be available to the wolf spiders. Bird cherry-oat aphids will often occur at the base of the plants (Wikteliuss 1987) and also be available to the wolf spiders. Therefore, the two measurements were finally combined to represent the total availability of aphids per 50 cm^2 (the surface covered by one trap) (Table 1). From the plant counts means per shoot were multiplied by 1.25 to convert them to means per 50 cm^2 area (we used a plant density of 250 plants per m^2 ; this is based on recommendations to sow to a density of 350 plants per m^2 and experience of an approximate establishment rate of 75 %) and then added to the means from the mini-sticky traps. The combined measurement of *R. padi* availability was then used in the chi-square goodness-of-fit test and the logistic regression analyses described below.

DNA extraction and PCR conditions

DNA was extracted from whole spiders using Qiagen’s DNeasy® Blood and Tissue Kit following the manufacturer’s

instructions for animal tissue. To ascertain that the DNA extractions were successful, the quality of all samples was checked using the universal invertebrate primers LR-J-12887 and LR-N-13398 (Simon et al. 1994). Two extracts did not yield any PCR product and were excluded from the study. Subsequently, the samples were screened for *R. padi* consumption using primers developed by Chen et al. (2000) and a protocol described in Kuusk et al. (2008). Collembola consumption was tracked using group-specific Collembola primers and the associated protocol developed by Kuusk and Agustí (2008). In each run, diluted prey DNA and water were used as positive and negative controls, respectively. As additional controls we used DNA extracts from starved spiders that had been fed with either a single *R. padi* or a Collembola. PCR products were separated by electrophoresis in agarose gels stained with ethidium bromide and visualized under UV light. A sample was scored as positive when a band of approximately 331 bp (*R. padi* product) or 272 bp (Collembola product) appeared on the gel. All negative samples were run a second time and if a band appeared on the gel they were scored positive.

Detection times can vary depending on the combination of predator and prey and it may be necessary to adjust field predation rates (Greenstone et al. 2010; Gagnon et al. 2011). Previous feeding trials with *Pardosa* spiders, *R. padi*, and Collembola, conducted at the same temperatures and using the same primers as those used here, showed that aphid detection success over time for 50 % of the predators was 3.7 h (Kuusk et al. 2008) and no springtail DNA could be detected after 24 h (Kuusk and Ekblom 2010). Although we cannot say that there is no significant difference in detection times for the two preys, the feeding trials indicate that the detection times are fairly close and adjustments would not change our conclusions.

Statistical analyses

To test the hypothesis that *Pardosa* spiders feed at random without any preference for a particular prey, the proportion of spiders that tested positive by PCR was compared with the observed proportions of *R. padi* and Collembolans in the field using a chi-square goodness-of-fit test. For each sampling occasion, the spiders were divided into four categories: (1) individuals positive for both aphid and Collembola DNA, (2) individuals positive for aphid but not Collembola DNA, (3) individuals positive for Collembola but not aphid DNA, and (4) individuals negative for both preys. We assumed for the purposes of the test that the probability that a spider would contain aphid or Collembola DNA was directly proportional to the observed proportion of prey at each sampling occasion and that the events “eating aphid” and “eating Collembola” were independent.

To investigate which factors may have affected *R. padi* and Collembola consumption, the PCR data were analyzed using logistic regression (Hosmer and Lemeshow 2000); the SAS LOGISTIC procedure with the model binary logit. To correct for possible overdispersion we used the “scale = deviance” option in SAS. The presence or the absence of *R. padi* and Collembola DNA were the dependent variables in two separate analyses. As *P. prativaga*, *P. fulviseps*, and *P. amentata* each represented <5 % of the total number of collected spiders, data for these species were not included in the analysis. We tested if consumption of aphids was affected by farm, *Pardosa* species (*P. agrestis* and *P. palustris*), sexual category (males, females with eggsac, females without eggsac), or prey availability in multiple logistic regressions (Table 2). The abundance of *R. padi* and the sum of all alternative prey (Collembola, Diptera, and other prey; Table 1) were used for prey availability in the analysis of *R. padi* consumption. The abundance of Collembola and the sum of all alternative prey (*R. padi*, Diptera and other prey; Table 1) were used in the analysis of Collembola consumption.

Results

Of all analyzed spiders ($n = 231$), 71 % tested positive for the presence of *R. padi* DNA and 19 % for the presence of Collembola DNA. We analyzed 28–51 spiders per collection occasion and the proportions that tested positive per field for *R. padi* and Collembola DNA varied between 51–87 % and 3–62 %, respectively (Table 1). Between 3 and 50 % of the tested individuals scored positive for both preys (Table 1).

The availability of *R. padi* varied considerably between collection occasions, ranging from approximately 0.1–41 individuals per plant and 0.25–11 individuals per trap (Table 1). The total amount of available *R. padi* per sampling occasion (aphids per plant and trap combined) varied between approximately 0.5 and 60 individuals per 50 cm². Mean abundances of Collembola, Diptera, and the pooled number of other potential prey varied between approximately 5 and 110, 3 and 50, and 1 and 3 per sampling occasion, respectively (Table 1). The proportions of *R. padi*, Collembola and other alternative prey of the total prey community are shown in Fig. 1.

The most common *Pardosa* species was *P. agrestis* (78 %), followed by *P. palustris* (16 %), *P. prativaga* (4 %), and others (2 %). Of the two most common species, 69 and 82 % tested positive for aphid predation whereas 13 and 39 % contained Collembola DNA. Of all collected spiders, 30 % were males, 56 % females carrying an eggsac, and 14 % were females without an eggsac. In each sexual category, 68, 71, and 76 % tested positive for

Table 2 Description and results of logistic regression models used to identify factors that influenced consumption on an aphid pest (*R. padi*) and springtails, Collembola, by spider predators from the genus *Pardosa*

Dependent variable	Independent variable	Likelihood-ratio test	Estimate (SE)	χ^2	df	P	Goodness-of-fit test
<i>R. padi</i> DNA detected/not detected in individual spiders	Farm	$\chi^2_7 = 16.49, P = 0.021$		6.76	2	0.034	$\chi^2_7 = 4.61, P = 0.71$
	<i>Pardosa</i> species			0.13	1	0.72	
	Sexual category			0.12	2	0.94	
	<i>R. padi</i> density			0.19	1	0.66	
	Alternative prey density		0.01 (0.005)	4.21	1	0.04	
Springtail DNA detected/not detected in individual spiders	Farm	$\chi^2_7 = 59.92, P < .0001$		8.33	2	0.02	$\chi^2_7 = 3.95, P = 0.86$
	<i>Pardosa</i> species			2.83	1	0.09	
	Sexual category			3.29	2	0.19	
	Collembola density		0.013 (0.007)	3.41	1	0.065	
	Alternative prey density			1.70	1	0.19	

The spiders were collected on three different farms in Central Sweden and analyzed by PCR-based gut-content analysis using *R. padi* and Collembola-specific primers. A significant Likelihood-ratio test means that at least one of the model’s predictors’ regression coefficients is not equal to zero. A non-significant Hosmer and Lemeshow Goodness-of-fit model indicates an adequate fit

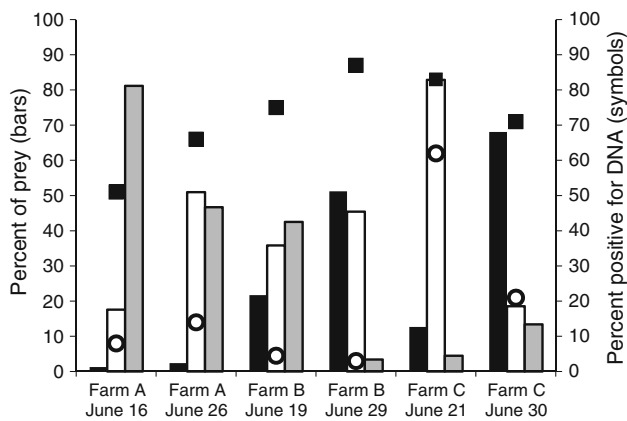


Fig. 1 Availability of *R. padi* (black bars), Collembola (white bars), and other alternative prey (gray bars) in three fields of spring-sown cereals at organic Farms A–C in central Sweden shown as percentages of the total prey community. Black squares and open circles show the proportion spiders tested positive for *R. padi* and Collembola DNA-remains, respectively, using PCR-based gut-content analysis

R. padi DNA, respectively. The corresponding data for Collembolans were 29, 18, and 3 %.

For five out of six collection occasions, the chi-square goodness-of-fit test clearly demonstrated that *Pardosa* spiders did not predate on *R. padi* and Collembolans in proportion to their abundances in the fields (Farm A June 16: $\chi^2_3 = 1030, P < .001$; Farm A June 26: $\chi^2_3 = 833, P < .001$; Farm B June 19: $\chi^2_3 = 120, P < .001$; Farm B June 29: $\chi^2_3 = 49, P < .001$; Farm C June 21: $\chi^2_3 = 276, P < .001$). Aphid predation was much higher than what would be

expected whereas the consumption of Collembolans was considerably lower (Fig. 1). For both prey types, the exception was Farm C June 30 (Fig. 1). On this collection occasion, the proportion of spiders that tested positive for *R. padi* and Collembola consumption corresponded to the availability of each prey ($\chi^2_3 = 0.4, P > 0.9$).

In the logistic regression analysis there was some overdispersion in the data and the covariance matrix for each model was multiplied by the heterogeneity factor (*R. padi* analysis = 1.44, Collembola analysis = 1.10). The models were significant and the fit was adequate (Table 2). The results showed that neither *Pardosa* species nor sexual category influenced the probability of detecting *R. padi* or Collembola DNA in individual spiders; but the probability was significantly affected by the farm where samples were collected (Table 2).

Considering the effect of the variation in prey abundance for the probability of detecting *R. padi* DNA, we found that there was no association between *R. padi* consumption and *R. padi* availability (Table 2). In contrast, alternative prey densities appeared to influence *R. padi* consumption ($P = 0.04$). The relationship with alternative prey availability was positive (Table 2).

The logistic regression analysis of the probability of detecting Collembola DNA and prey abundance showed that there was a weak, positive relationship between Collembola availability and Collembola consumption ($P = 0.065$, Table 2). There was, however, no influence of alternative prey (Table 2) on the probability of detecting Collembola DNA in spiders.

Discussion

This work has generated new information about the feeding habits and foraging behavior of lycosid spiders from the genus *Pardosa*. We tested if consumption of two types of prey, an aphid pest (*R. padi*) and detritivorous Collembolans corresponded to the ratios at which the food items were present in farmers' fields. In general, far more spiders contained *R. padi* DNA than expected while the reverse was true for Collembolans (Fig. 1). In total, 70 % of the analyzed specimens contained *R. padi* DNA and predation rates exceeded 50 % at all sampling occasions (Fig. 1). The results suggest that *Pardosa* spiders readily ate *R. padi* and that this aphid formed a substantial part of the predator's diet. The same trend was found in a previous study when aphid numbers were very low, far more spiders than expected tested positive for aphid DNA (Kuusk et al. 2008).

From one point of view this is surprising as laboratory studies have shown that a pure diet of *R. padi* is detrimental for cereal spiders with respect to various fitness parameters (Toft 1995; Oelbermann and Scheu 2002). In addition, it has been demonstrated that naïve *Pardosa* only have to consume a few *R. padi* individuals before developing an aversion against them (Toft 1997). On the other hand, ingestion of small amounts of *R. padi* together with other prey has proven superior to diets without any *R. padi* supplements indicating that the aphid contains essential nutrients (Toft 1995). Apart from nutritional aspects, another explanation to the disproportionately high predation rates of the aphid is that *R. padi* should be a fairly easy prey for the spiders to overpower. Aphids both on plants and on the ground were almost exclusively wingless individuals without any morphological characters that would impede a several times larger and faster predator from attacking.

Aphid predation rates for two subfamilies of Linyphiidae collected in winter wheat were found to be positively related to aphid densities (Harwood et al. 2004). Considering alternative prey, Harwood et al. (2004) found that Erigoninae spider aphid consumption was negatively influenced by Collembola densities but aphid predation rates by Linyphiinae were not affected by Collembola. The influence of hunting behavior by the two spider groups was explored by determining aphid consumption in web-based (sit-and wait) and non-web (active hunting) spiders. Harwood et al. (2004) suggested that higher densities of Collembola at Erigoninae web sites in contrast to non-web sites (Harwood et al. 2001) allowed the web-based Erigoninae to easily exploit Collembola while active hunters may be encountering aphids more often than web-based spiders. In the same study (Harwood et al. 2004), it was shown that Diptera abundance did not affect aphid consumption by either spider group. These findings with small,

generally web-based, spiders contrast somewhat with our results using larger wolf spider that actively hunt prey.

In our study, the probability of detecting *R. padi* DNA in individual spiders differed significantly among farms, but was not positively related to *R. padi* density (Table 2). Instead, it was observed that *R. padi* consumption was affected by the presence of alternative prey; there was a positive association with the availability of alternative prey. In a previous study, based on gut-content analysis of spiders collected in fields with consistently low aphid densities, we found a negative association between *R. padi* consumption and Collembola availability (Kuusk and Ekbohm 2010). As *Pardosa* spiders did not feed on Collembolans in relation to availability we suggested that the underlying mechanism was that the spiders changed their hunting behavior (from active to passive sit-and-wait) when mobile Collembolans became more numerous resulting in fewer encounters with sedentary aphids. To explain why approximately the same proportion of spiders tested positive for Collembola consumption at each sampling occasion irrespective of prey availability we suggested that the nutritional value of one or several species of the present Collembolans was of such importance that a fixed proportion of spiders regularly fed on them.

The positive relationship between *R. padi* consumption and alternative prey availability observed here contrasts with our previous findings. We suggest that the opposite relationships could be explained by the fact that in this study, densities of *R. padi* varied between sampling occasions and reached considerably higher levels than in the former, and because the spatial distribution of the prey was different. At high densities, aphids tend to leave the cereal plants and walk on the soil surface (Wikteliuss and Ekbohm 1985; Sopp et al. 1987). In our earlier study, when aphid densities were low in all fields, *R. padi* were exclusively observed on the plants and no aphids were caught on the ground-attached sticky-traps. In this study, *R. padi* were distributed both on plants and on the ground. Again, we suggest that an increased availability of mobile prey (Collembolans and Dipterans) made the spiders hunt more passively. However, while this change in foraging behavior caused decreased encounter rates with aphids on plants in the earlier study it had no negative effect on *R. padi* predation in the current as the prey items were available on the ground as well. Spiders may have consumed aphids more readily as they would be easier to catch than jumping springtails and flying Dipterans.

While spiders appeared to readily eat *R. padi*, fewer individuals than expected contained Collembola DNA with the exception of one sampling occasion Farm C June 30 (Fig. 1). In general, Collembola consumption was lower (~5–20 % positives) compared to *R. padi* consumption (~50–85 % positives) but on one sampling occasion

(Farm C June 21) as many as 62 % of the spiders tested positive for Collembola remains (Fig. 1). On this date, Collembola availability was clearly highest which in turn explains the observed positive relationship between Collembola detection and Collembola availability (Table 2). Collembolans have a wide global distribution and usually occur in high numbers in soils and leaf litter. Thus, they form a potential source of non-pest alternative food for generalist predators and indeed there are a growing number of DNA-based gut-content studies that confirm that generalist predators feed on Collembola in the field (Agustí et al. 2003; Chapman et al. 2010; King et al. 2011). We have previously demonstrated that *Pardosa* feed on Collembolans in agricultural fields. In the former study though, predation rates were less variable; ~15–30 % tested positive at each sampling occasion compared to ~5–60 % here. To explain why Collembola consumption was more variable and why Collembola predation was disproportionately low at five out of six sampling occasions we suggest that the current ratios of potential prey and/or the nutritional needs of the spiders “favored” a foraging behavior that generally increased predation on aphids and potentially Dipterans. Kruse et al. (2008) demonstrated that the flexible body, chelicerae and legs of lycosid spiders make them highly adapted to catch flying prey, such as Dipterans, compared to carabid beetles, which have stiff bodies and inflexible legs and mandibles. Carabid beetles were capable of catching *Drosophila melanogaster* (Meigen) only at low temperatures (5–10 °C) when the flies were able to fly just a few centimeters or not at all. In contrast, *P. prativaga* was observed to readily catch *D. melanogaster* also at high temperatures. Apart from having a suitable morphology for catching flies, Dipterans could be an important source of proteins for *Pardosa* spiders. Dipterans contain relatively high amounts of this macronutrient due to their flight musculature (Marden 1989; McLachlan and Neems 1996) and experimental studies have shown that *Pardosa* spiders can forage selectively for protein-rich food if previous diets had been protein poor (Mayntz et al. 2005).

When studying field predation rates using PCR-based gut-content analysis prey detection rates are important for comparisons between predators. For the aphid amplicon, we have demonstrated that the median detection period in *Pardosa* spiders is about 4 h (Kuusk et al. 2008). There is no precise estimate for the Collembola amplicon, but we carried out a feeding experiment where spiders were tested for Collembola DNA immediately and 24 h after ingestion of one *Isotoma* spp. (Kuusk and Ekblom 2010). The analysis showed that Collembola DNA could be detected in 11 out of 12 spiders (92 %) that were frozen immediately after prey ingestion. After 24 h, it was not possible to detect the remains in any of the 12 fed spiders. The reason for testing

the spiders after 24 h was that the sticky traps in the fields were exposed to prey for 24 h and we wanted to make sure that prey consumed before that period would not be detected. The feeding trials indicate that the detection times are similar and we argue that adjustments would not change the results in such a way that our conclusions would be different.

This study demonstrates that prey consumption by *Pardosa* spiders in agroecosystems cannot, in general, be assumed to simply mirror the ratio at which a particular food item is present in the field. When trying to obtain more knowledge about a predator’s foraging behavior other factors, such as the spatial distribution of the target prey and the abundance, composition, and nutritional content of potential alternative food items, need to be considered as well.

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