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Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters

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Abstract Structural features of habitat are known to affect the density of predators and prey, and it is generally accepted that complexity provides some protection from the environment and predators but may also reduce foraging success. A next step in understanding these interactions is to decouple the impacts of both spatial and trophic ingredients of complexity to explicitly explore the trade-offs between the habitat, its effects on foraging success, and the competition that ensues as predator densities increase. We quantified the accumulation of spiders and their prey in habitat islands with different habitat complexities created in the field using natural plants, plant debris and plastic plant mimics. Spiders were observed at higher densities in the complex habitat structure composed of both live plants and thatch. However, the numerically dominant predator in the system, the wolf spider *Pardosa milvina*, was observed at high densities in habitat islands containing plastic mimics of plants and thatch. In a laboratory experiment, we examined the interactive effects of conspecific density and habitat on the prey capture of *P. milvina*. Thatch, with or without vertical plant structure, reduced prey capture, but the plastic fiber did not. Pairwise interactions among spiders reduced prey capture, but this effect was moderated by thatch. Taken together, these experiments highlight the flexibility of one important predator in the food web, where multiple environmental cues intersect to explain the role of habitat complexity in determining generalist predator accumulation.

Keywords Density dependent · Generalist predators · Habitat structure · Refuge · Spiders

Introduction

Interactions between habitat heterogeneity and community dynamics have influenced ecological study for many years (Huffaker 1958; MacArthur and MacArthur 1961; Lawton 1983; Southwood 1996). Habitat structural complexity has substantial impacts on the abundance and diversity of animals in both aquatic (Heck and Crowder 1991; Hayse and Wissing 1996; Beck 2000; Stewart et al. 2003; Lepori et al. 2005) and terrestrial (Andow 1991; Uetz 1991; Rypstra et al. 1999; Langellotto and Denno 2004; Whittingham et al. 2006) ecosystems. Structurally diverse habitats provide a broad range of resources, insulate animals from physical disturbance, moderate environmental extremes, and provide cover for and protection from predators (Crowder and Cooper 1982; Rypstra et al. 1999; Langellotto and Denno 2004; Janssen et al. 2007). Particularly difficult to tease apart is the role of habitat complexity in interactions between predators and prey (Halaj and Wise 2002; Miyashita and Takada 2007; Birkhofer et al. 2008). In most habitats, the living and dead vegetation create complexity that are also resources for herbivores and detritivores fueling the rest of the food web (Price et al. 1980; Denno and McClure 1983; Wyman

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1998; Chen and Wise 1999). In addition, habitat complexity can influence the hiding, escape, and attack tactics of animals on both sides of the predator–prey equation (Crowder and Cooper 1982; Uetz 1991; Finke and Denno 2002; Legrand and Barbosa 2003; Warfe and Barmuta 2004).

For generalist predators, habitat structure can play a role in mediating any or all of the interactions occurring between individual animals, including their foraging success, risk of intraguild predation, and the outcome of competitive interactions (Warfe and Barmuta 2004; Finke and Denno 2004; Grabowski et al. 2008). Interestingly, interactions between arthropod predators seem to be more strongly affected by structure than the consumption of prey from a different trophic level (Roda et al. 2000; Finke and Denno 2002; Obermaier et al. 2008). A recent meta-analysis concluded that habitat structure should promote persistence of predators by reducing intraguild predation (Janssen et al. 2007), which can have important impacts on herbivore control (Finke and Denno 2006). Structure appears to dampen the impacts of interactions between generalist predators (Finke and Denno 2004), possibly by providing escape routes for intraguild prey (Janssen et al. 2007). It is less clear which aspects of structure the organisms are using, and how the various features of structure interact to determine the strength of interactions between foraging predators.

A recent synthesis of the information available for invertebrate natural enemies determined that the addition of detritus (e.g., leaf litter, thatch, mulch) in terrestrial systems has a more powerful effect on density than altering the plant community (Langellotto and Denno 2004). That same analysis did not uncover effects of habitat structure on the density of herbivorous prey, but not all types of potential prey were incorporated into the analysis and, as aptly noted, there are cases where arthropod predators accumulate in response to high densities of detritivores (Chen and Wise 1999; McNabb et al. 2001; Halaj and Wise 2002; Oelbermann et al. 2008). Indeed, other studies have shown that enhancing the decomposer community plays a role in the establishment of robust populations of predators living up in the vegetation (Scheu 2001; Rypstra and Marshall 2005). Thus, a complete understanding of the role that habitat complexity plays in food web interactions requires further studies that uncouple structure from its trophic contribution (Bultman and Uetz 1982; Warfe and Barmuta 2004; Miyashita and Takada 2007).

In this study, we examined the avenue by which habitat complexity affected the density of spiders and the prey capture of the wolf spider *Pardosa milvina* (Hentz) (Araneae, Lycosidae), which is one of the most abundant predators on the soil surfaces of agroecosystems in eastern North America (Young and Edwards 1990; Marshall and Rypstra 1999). We conducted an open field study that manipulated plant and soil habitat complexity using biologically based structure and physical artificial structure in a soybean agroecosystem to test the hypothesis that spiders accumulate in complex habitats independent of prey availability. In laboratory enclosures using the same biological and artificial structures, we explored the impact of habitat complexity and predator density on prey capture. We predicted that when predators reached high densities, increased interference and/or cannibalism would occur, reducing the advantages of selecting particular foraging sites. This approach enabled us to evaluate the separate and combined effects of spider density and habitat features on foraging and the frequency of cannibalism. This combination provides for a comprehensive perspective of environmental impacts on the performance of an important terrestrial generalist predator.

Materials and methods

Study species

Wolf spiders are among the most abundant arthropod predators in agricultural systems in the United States (Nyffeler and Sunderland 2003), and as predators they may have important impacts on the food web (Carter and Rypstra 1995; Halaj et al. 2000; Scheu 2001; Halaj and Wise 2002). In Southwestern Ohio, the wolf spider *P. milvina* (Hentz) (Araneae: Lycosidae) achieves densities of 5–100 spiders m^{-2} in soybean fields, making it the numerically dominant predator for much of the season (Marshall et al. 2002). *Pardosa milvina* is a relatively small (20 mg), vagabond species that actively pursues prey and moves between microhabitats, where it accumulates in areas containing higher levels of soil substrate complexity (Marshall and Rypstra 1999) and areas enhanced with composted material (Rypstra and Marshall 2005). An intraguild predator, the large wolf spider (100–300 mg), *Hogna helluo*, also occurs in this system and has been shown to alter the habitat preferences (Buddle 2002; Rypstra et al. 2007), vertical habitat use (Folz et al. 2006), foraging rate (Rypstra et al. 2007), and mating behavior (Hoefler et al. 2008) of *P. milvina*. To further understand the subtleties of this interaction, in a field experiment, we quantified the density of *P. milvina*, and other ground-dwelling spiders such as *H. helluo* that would be intraguild competitors for space and resources. In order to link predator density to some measure of performance, we conducted two laboratory experiments which explored the effects of habitat structure and spider density on the foraging success of *P. milvina*.

Spider abundance and habitat complexity

To determine the effects of habitat complexity on abundance of spiders and prey availability we established replicate sets of 2 × 2 m plots in five 0.42 ha soybean fields at Miami University's Ecology Research Center (ERC) (3 km north of Oxford, Butler County, OH, USA; see Online Resource 1). Each field measured 60 × 70 m and was separated from the surrounding habitats and one another by a 15 m border of mown grass (Kemp and Barrett 1989). The fields were tilled on 5 May 2005 and planted with rows (approximately 61 cm apart) of soybean plants (*Glycine max*, Fabaceae) on 10 May 2005. On 20 June 2005, when the soybean plants were 20–25 cm tall, the plots were tilled to eliminate weeds, raked to smooth the soil surface, and randomly assigned to one of six habitat complexity treatments. Four treatments ($n = 5$) were designed to contain habitat features spiders would typically encounter: (1) bare soil, (2) soybeans only: two rows of plants in each plot, (3) thatch: a 15–20 cm layer of wheat straw covered the soil surface, and (4) soybeans plants plus thatch: a combination of treatments (1) and (3). Two additional treatments ($n = 5$) were designed to provide a similar structural complexity of plants and thatch but to lack biologically based components that would encourage growth of the prey community: (5) fiber: a 15–20 cm layer of polypropylene fiber (Textraw® Synthetic Straw, St. Simons Island, GA, USA) covered the soil surface, and (6) polyvinyl plants plus fiber: two rows of polyvinyl plants similar in structure to soybean plants combined with a 15–20 cm layer of fiber on the soil surface. To account for the growth of the living soybean plants, polyvinyl stems and leaves were added to the artificial plants on 15 July 2005 to bring them to a height of 40–45 cm. On that same date, living soybean plants were trimmed so that their sizes matched the artificial plants.

Habitat complexity of each plot was quantified on 25 July 2005 at five regularly spaced sites in each plot: one in the middle and four others approximately 15 cm from each corner. Leaf area index (LAI) was used to indirectly estimate the amount of vertical vegetation in each plot by measuring the transmittance of light through the vegetation using the LAI-2000 plant canopy analyzer (LI-COR, Inc., Lincoln, NE, USA). In plots with substrate addition (thatch or fiber), the depth of these structures was measured; in plots with real or artificial plants, the height and width of the plants were measured. We expected thatch and fiber to effect temperature (°C) and humidity (absolute humidity g m^{-3}) at the soil surface. Therefore, using one HOBO® data-logger (Onset Computer Corporation, Bourne, MA, USA) which was centered in each plot and below any thatch or fiber, we measured the mean daily temperature and humidity by logging at 15-min intervals between 25 June 2005 and 12 July 2005 in three contrasting treatments: bare soil, soybeans plus thatch, and polyvinyl plants plus fiber.

To understand the bottom-up effects of structure on potential prey, the activity density of the prey was measured by placing two sticky traps on top of any soil surface structure in the plots for 3 days just prior to quantifying spider abundance (29 July 2005–2 August 2005). The traps were constructed from transparent acetate sheets measuring 8 × 24 cm. A 6.5 × 6.5 cm sampling area of the trap was coated with nontoxic adhesive (Harwood et al. 2003; Tangle Trap™, Grand Rapids, MI, USA). Upon collection, the traps were placed in a freezer to preserve the insects. We counted the most common spider prey, including Collembola, Diptera, Homoptera and Orthoptera (Nentwig 1986; Nyffeler et al. 1994).

Spider abundance was quantified on 2 August 2005 by destructively sampling using a restricted area search (Marshall et al. 2000). Two steel rings (each measuring 0.75 m^2 in diameter and 30 cm in height) were dropped simultaneously in each plot to delineate a search region of 1.5 m^2. One observer at each ring searched the enclosed area by systematically stirring any litter and digging up any cracks in the soil. Plant, thatch or fiber material was subsequently sifted using a 50 mm mesh litter reducer over a white bucket to recover less obvious spiders. All spiders collected were counted and identified.

Prey capture: conspecific density and habitat complexity

The *Pardosa milvina* individuals used in experiments were all penultimate or adult female spiders collected between June and October 2005 from agricultural fields at Miami University's Ecology Research Center. When not involved in experiments, the spiders were housed individually in plastic containers (6 cm in diameter and 4 cm in height) with a 1.5 cm layer of moist soil in an environmental chamber at 25°C, 50–58% RH and a 13:11 L:D cycle. To equalize hunger levels, we fed each spider two 0.32 cm *Acheta domesticus* (hereafter referred to as crickets) twice per week for at least two weeks prior to the experiment, and then starved them for 7 days immediately before their scheduled test. Twenty-four hours before the experiment commenced, individuals were marked with a drop of nontoxic paint on the dorsal surface of the abdomen to allow for identification. Just before the experiment, the carapace and abdomen width were measured to the nearest 0.1 mm using a microscope equipped with a digital micrometer. Body measurements are commonly used as indications of body condition (Anderson 1974; Jakob et al. 1996). Specifically, the carapace width is a measure of size, and the abdomen of the spider is flexible and widens as the spider feeds (Jakob et al. 1996). Spiders assigned to treatments were similar in size (one-way ANOVA carapace width: $F_{15,202} = 0.40$, $P = 0.96$) and condition (one-way ANCOVA of abdomen width using carapace as covariate: $F_{15,202} = 1.12$, $P = 0.32$) prior to introduction into arenas (for data, see Online Resource 2).

Using these laboratory-standardized spiders, we conducted two experiments in order to understand the influence of predator accumulation in patches with contrasting structural features on prey capture (number of crickets captured in a 24 h period). Experiments were conducted in cylindrical plastic arenas (20 cm in diameter and 30 cm in height) with a 4 cm layer of moist soil covering the base. The first experiment was designed to investigate the impacts of density and habitat structure on prey capture in all of the structural treatments used in the field study. Habitat treatments (bare soil, soybean plants, thatch, soybean plants + thatch, fiber, and plastic plants + fiber) were crossed with two spider densities (one spider, and five spiders equivalent to 159 spiders m^{-2}) for a minimum of ten replicates per treatment combination. Vertical plant structure was manipulated by adding either two live soybean plants, each measuring 20–24 cm in height with five leaves, or two polyvinyl plants fabricated to simulate soybean plants. To manipulate substrate structure, either a 4 cm layer of thatch or fiber covered the soil. We used 0.32 cm crickets, *A. domesticus*, to represent an easy to capture ground-dwelling prey species. We chose crickets because they are common prey for spiders and are easy to rear and recapture following experimental manipulation. To initiate the trials, 40 crickets were placed into each arena and allowed to disperse for 15 min before *P. milvina* were released into the arenas. After a 24-h period, the spiders were captured, and the number of crickets remaining was counted.

In the second experiment we examined the pairwise interference between conspecifics relative to habitat structure. We used one spider density, two spiders (field density equivalent to 64 spiders m^{-2}) and three representative habitat treatments (bare soil representing no structure, fiber representing artificial, and thatch representing natural structure). Habitat treatments and experimental protocols were administered in the same way as the first laboratory experiment. Prey capture from this experiment (observed prey capture when spiders forage together) was then compared to the predicted prey capture expected when spiders forage in isolation.

Statistical analyses

In the field experiment, we measured the effects of habitat structure on colonizing predators. This experiment was specifically designed to address the importance of natural (biologically based) structure as compared to artificial (physical structure), and secondly to assess the importance of different structural features. Models were generated to explain predator responses (*P. milvina* and other ground-dwelling spider abundance) to habitat treatments in the field using Schwarz's Bayesian information criterion (BIC, Burnham and Anderson 2002). Comparison of BIC between models permits the evaluation of different levels of support for the various components that could be incorporated into the model. Models are ranked according to change in BIC (ΔBIC), and less evidence is present to support models when $\Delta\text{BIC} > 2$ (Burnham and Anderson 2002). BIC was selected because it imposes a higher penalty for extra parameters and thus identifies less complex models (Murtaugh 2009). To initiate model selection, we built a model containing potential predictors that we measured in our habitat treatment plots, which included LAI and prey activity density of Collembola, Diptera, Homoptera, and Orthoptera. All variables were transformed using natural log to normalize the distributions and variance, except for the two categorical predictor variables of habitat treatment and field (which was included as a random variable). The upper scope of model complexity contained the two-way interactions between habitat and prey groups. Model selection was conducted in R (R Development Core Team2009) by implementing stepAIC {MASS} (Venables and Ripley 2002), which compared models using BIC [i.e., specifying $k = \log(n)$ where n is the number of cases] through a stepwise algorithm (Venables and Ripley 2002).

Since we were specifically interested in the impact of our habitat manipulations on spider abundance, we estimated the effect size for each of our habitat treatments on the abundance of *P. milvina* and other spiders. We calculated Hedge's unbiased g^* effect size by computing the mean difference and 95% confidence intervals between the natural log-transformed abundances observed in each of the habitat treatments and bare soil containing no additional habitat treatment (Nakagawa and Cuthill 2007). Because many of the bare soil plots contained few (if any) spiders, we used the standard deviation of the habitat treatment instead of the pooled standard deviation.

In the first laboratory experiment, we measured the effects of habitat complexity and predator density on prey capture (number of crickets captured in a 24 h period). Weighted least-squares two-way ANOVA was used to test for the main effects of habitat (all habitat treatments) and *P. milvina* density (one vs. five) on prey capture (number of crickets captured in a 24 h period). Significant main effects were compared using the post hoc Tukey (HSD) multiple comparisons test. Prior to analysis, prey capture was natural log transformed to normalize distributions and variance. Since *P. milvina* are cannibalistic (Buddle et al. 2003;

Rypstra and Samu 2005), logistic regression was used to test for the effect of habitat treatments on the frequency of cannibalism. Because sealed laboratory arenas were used, any spider missing at the end of the 24 h period was counted as one cannibalism event.

In a second experiment we measured the prey capture of two *P. milvina* in an arena to assess how interference between individuals is related to habitat type. To test for interference between individuals, we compared the observed total number of crickets captured over a 24 h period with predictions from a basic rule of probability (Soluk and Collins 1988; Sih et al. 1998). The probability that crickets (prey) were captured by two *P. milvina* foraging in isolation equals 1 minus the probability that crickets were not captured. Rearranging this expression, accounting for independence between each predator's capture, and multiplying this probability by the initial number of prey yields the predicted prey capture (C):

$$C = N_{\mathrm{p}}(P_{\mathrm{a}} + P_{\mathrm{b}} - P_{\mathrm{a}} \times P_{\mathrm{b}}).$$

Here N_{p} equals the initial prey density, P_{a} and P_{b} equal the probabilities of the crickets being captured by the two *P. milvina* foraging in isolation, and the $P \times P$ term equals the probability that prey are not captured by either of the spiders (Soluk and Collins 1988; Sih et al. 1998). To test the null hypothesis that observed equals predicted and is consistent across habitat type, we used a two-way ANOVA relating cricket capture to habitat type, and an indicator variable (state) to test for differences between predicted and observed at each habitat level. When observed is greater than predicted, this indicates synergistic prey capture or kill rates; when observed is less than predicted, this indicates that the predators interfere with each other, which would reduce capture rates. A significant interaction between the indicator and habitat would cause the rejection of the null hypothesis that the interference levels are equal in the habitat types tested. These analyses were conducted in JMP 8 (SAS Institute, Inc.).

Results

Spider abundance and habitat complexity

Although soil surface structure was equivalent between natural and artificial plots, there was more vertical vegetation (soybean plants) in the natural plots than the artificial plots (see Online Resource 3). The amount of surface structure—the depth of either thatch or fiber—was similar across treatments (ANOVA $F_{3,72} = 0.65$, $P = 0.59$), but by the end of the experiment the soybean plants (height = 72.65 ± 8.66 cm) were significantly larger than the polyvinyl plants (height = 39.2 ± 2.75 cm) (ANOVA $F_{1,34} = 464.73$, $P = 0.0001$), despite our efforts to equalize them. Correspondingly, LAIs were greater in plots containing soybeans than in those with polyvinyl plants ($F_{1,34} = 32.05$, $P = 0.0001$).

The microclimate was similar for the natural and artificially structured plots, but it was more variable in the plots lacking structure than in either of the structured plots (see Online Resource 3). Bare soil plots had the lowest absolute relative humidity (abs. humidity = 15.92 g m^{-3}; $F_{2,269} = 7.49$, $P = 0.0007$) and the highest mean daily temperature (25.26°C; $F_{2,269} = 7.69$, $P = 0.0006$). The fluctuations in temperature (CV = 10.13) and humidity (CV = 32.29) were highest in the no-structure plots. The artificial and naturally structured plots were similar in terms of mean daily humidity, but there was more variability in humidity in the artificial (CV = 23.99) as compared to the natural (CV = 16.13). Neither temperature nor fluctuation in temperature differed between the artificial and natural plots.

Total prey availability was highest in plots containing thatch or living soybean plants and thatch, and this pattern was largely driven by the abundance of Collembola, a common prey group for ground-dwelling spiders ($F_{5,29} = 10.77$, $P = 0.0001$, Fig. 1a). Contrastingly, the structure provided by the fiber with or without the polyvinyl plants did not enhance total prey availability as compared to bare soil or soybean plants alone.

Pardosa milvina was the numerically dominant spider in our community, comprising 68.3% of the 389 spiders captured. Clearly the ground-dwelling spider community (see the Online Resource 4) and *P. milvina* increased in density when habitat structure was present in the experimental plots (Fig. 1b). Model selection determined that models containing habitat structure and field provide the most evidence of support for predicting the abundance response of *P. milvina* (Table 1). All competing models containing prey availability covariates gave $\Delta\mathrm{BIC} > 2$ for *P. milvina*, which indicates that there was less evidence in the data supporting models containing prey covariates, and models with only prey availability were inferior by comparison, yielding substantial ΔBIC. Conversely, for the other ground-dwelling spiders, models containing a combination of habitat structure and prey availability were superior to models lacking prey availability covariates (Table 1; Fig. 1b). Specifically, the top competing models suggest that some combination of habitat structure and the abundance of Diptera, Homoptera and Collembola provide better insight into habitat associations for the rest of the ground-dwelling spider community as compared to habitat structure alone.

The effect of habitat treatments on all spiders was least when only soybean plants were added to bare soil, and the addition of soil substrate complexity had strong effects

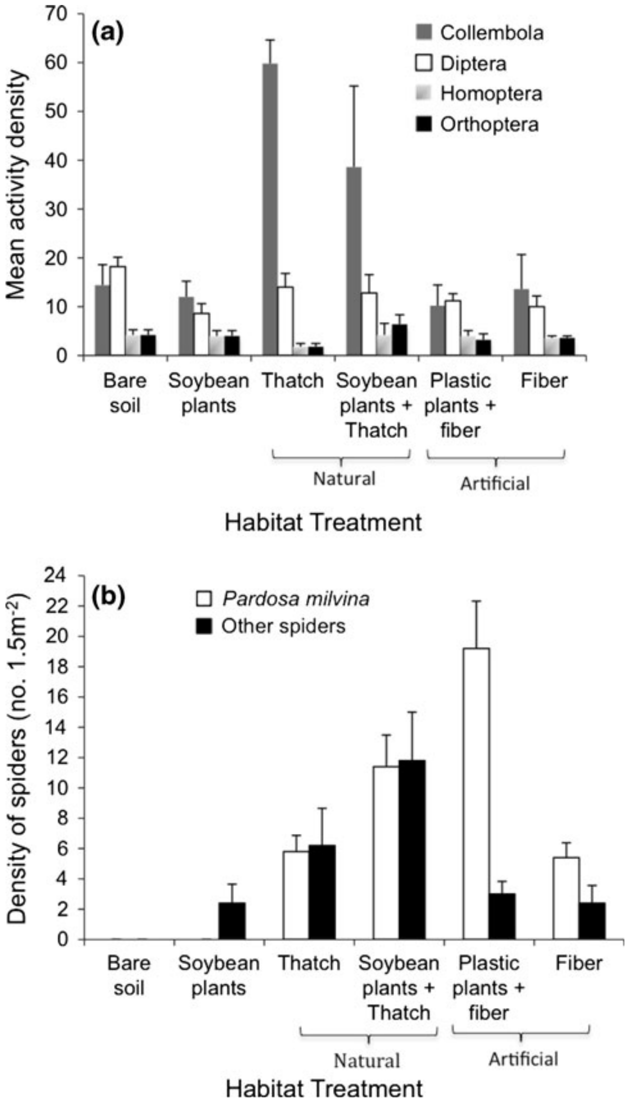

Fig. 1 Effect of habitat treatment on **a** prey activity density and **b** the densities of *P. milvina* and other spiders in a soybean agroecosystem ($n = 5$). *Natural* and *artificial* represent the complexity treatments compared in the analyses

where abundance was highest in treatments with vertical plants or plant-like structure added in combination with thatch (Table 2; Fig. 1b). *Pardosa milvina* responded differentially to both the position of the structure (plant-like or soil surface) and to the nature of the structure provided (natural or artificial). Natural and artificial structure had similar effects on the abundance of *P. milvina*. Interestingly, although no *P. milvina* were found in patches with soybeans alone, combining the vertical structure of soybean plants or plastic plants with thatch or fiber had the largest positive effect on abundance. Conversely, the other ground-dwelling spiders primarily responded positively to the natural habitat treatments (Table 2; Fig. 1b). These spiders were lowest in abundance in plots containing artificial structure, and the largest effects were observed when thatch was paired with soybean plants, which was also the treatment containing the highest overall prey abundance (Table 2; Fig.1).

Prey capture: conspecific density and habitat complexity

Prey capture was consistently higher at both densities in arenas containing no structure, soybean plants or artificial structure as compared to natural structure ($F_{16,179} = 60.57$, $P < 0.0001$; Fig. 2). The presence of thatch generally reduced prey capture with or without the addition of soybean plants. Cannibalism was only observed in the natural structure treatments for high-density treatments (Fig. 3). At high density, the likelihood that cannibalism occurred was significantly reduced by the presence of thatch (logistic regression $\chi^2 = 8.38$, $P = 0.0038$), and there was no interaction between the presence of plants and the presence of thatch on the occurrence of cannibalism (logistic regression $\chi^2 = 2.11$, $P = 0.15$; Fig. 3).

To assess interference between individual predators, we compared the observed prey capture when the spiders were combined to their predicted prey capture in isolation. The observed number of prey captured when the two *P.milvina* were foraging in bare soil or artificial fiber was significantly lower than the numbers predicted for each of these habitat types (Table 3; Fig. 4). This indicates that in bare soil or fiber, the presence of a conspecific lowered the combined capture rate. Conversely, prey capture in the thatch by two *P. milvina* was similar to the predicted consumption, which indicates that adding this form of structure reduced interactions between conspecifics. There was a significant interaction term which indicated that interference was not consistent across all habitat types, and this can be explained by a reduction in interference in the thatch habitat, leading to near equivalence between predicted and observed.

Discussion

Members of the genus *Pardosa* are highly successful in agroecosystems worldwide (Young and Edwards 1990; Vogel 2004; Nyffeler and Sutherland 2005; Ubick et al. 2005) and have direct consumptive effects in food webs (Gratton and Denno 2003; Wise 2004) as well as nonlethal effects (Hlivko and Rypstra 2003). Data from the current study suggest that these ubiquitous predators actively colonize novel unoccupied habitat patches based on prey capture and on avoidance of competitors or intraguild predators, providing insight into the success of these generalist predators in highly disturbed habitats.

Table 1 Comparison of models examining the influence of habitat structure plots (habitat), prey availability (*Coll* Collembola, *Dipt* Diptera, *Hom* Homoptera, *Orth* Orthoptera), leaf area index (*LAI*), and field (a random variable), on the abundance of *P. milvina* and other ground-dwelling spiders

Models	BIC	ΔBIC
Pardosa milvina		
Habitat + field	−62.40	0.00
Habitat + field + Orth	−60.31	2.09
Habitat + field + Orth + Hom	−57.46	4.94
Habitat + field + Orth + Hom + Dipt	−57.29	5.12
Habitat + field + Orth + Hom + Dipt + LAI	−54.35	8.05
Habitat + field + Coll + Dipt + Hom + Orth + LAI	−47.75	14.65
Habitat	−46.55	15.85
Orth	15.44	77.84
Field	15.79	78.19
Coll + Dipt + Orth + LAI	18.64	81.04
Coll + Dipt + Hom + Orth	25.25	87.65
Other spiders		
Habitat + Dipt + Hom	−27.40	0.00
Habitat + Dipt	−26.96	0.44
Habitat + Dipt + Coll	−26.78	0.62
Habitat + Dipt + Coll + LAI	−24.66	2.74
Habitat + Dipt + Coll + LAI + field	−24.56	2.84
Habitat + Dipt + Coll + Orth + LAI + field	−24.12	3.28
Habitat + Dipt + Orth	−23.74	3.66
Habitat + Dipt + Orth + field	−23.68	3.72
Habitat + Dipt + Orth + field + LAI	−23.43	3.97
Habitat	−21.45	5.95
Habitat + Dipt + field + LAI	−20.40	7.01
Habitat + Orth + field + LAI	−15.43	11.97
Orth + field + LAI	−6.21	21.19

Table 2 Analysis of the size of the effect of habitat treatment on the abundances of *P. milvina* and other ground-dwelling spiders

Habitat treatment	*Pardosa milvina*	Other spiders
Soybean plants	0.66 (0.74)	1.57 (1.58)
Thatch	4.85 (0.84)	3.96 (1.14)
Soybean plants + thatch	5.39 (0.88)	5.41 (1.12)
Fiber	5.27 (0.65)	2.23 (1.18)
Polyvinyl plants + fiber	9.69 (0.56)	2.63 (0.90)

Values for effect size represent Hedge's unbiased g^*, and values in parentheses represent 95% confidence intervals

Our study is one of only a few that have distinguished between habitat structure as a spatial resource (i.e., increased living space, Bell et al. 1991) and as a trophic resource (i.e., increased supplemental resources for predators and food provisions for potential prey, Miyashita and Takada 2007; Birkhofer et al. 2008). Our approach is also unique since it combines more than one habitat structural type (i.e., vertical plant structure and soil surface structure) and uses artificial representatives to distinguish spiders' response to structure from their response to biologically based resources encouraging the recruitment of potential prey. In addition, laboratory trials enabled us to comprehensively explore the effects of structure and the resultant increase in predator density on the foraging performance of the most common species in our system.

We anticipated that habitat structure would increase the density of arthropod predators, as many studies have documented such a correlation (Halaj et al. 2000; Langellotto and Denno 2004). However, the benefits of different habitat features to generalist predators remains poorly understood because multiple, possibly competing mechanisms help to explain abundance and diversity patterns (Denno et al. 2005; Janssen et al. 2007; Schmitz 2008). Here, by selecting structurally complex habitat patches, we show that the wolf spider *P. milvina* is able to capture prey and avoid intraguild predation. Surprisingly, even though the activity density of prey appeared to be important to other spider species in our field study, we found no evidence that the absolute availability of prey was important for this *Pardosa*. *Pardosa milvina* accumulated in plastic mulch in field plots with low prey abundance and low densities of other spiders. Prey capture in the laboratory was reduced in straw thatch that was structurally similar to the plastic fiber, but there was no evidence that the plastic fiber

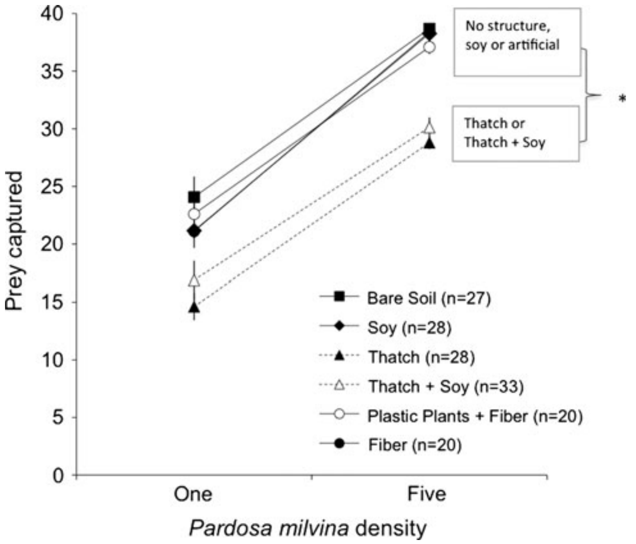

Fig. 2 Interaction plots showing the results from a laboratory predation experiment measuring the prey capture (crickets captured, mean ± SE, over a 24 h period) by *P. milvina*. A factorial experimental design containing the habitat treatments listed in the legend and two density levels (one spider per arena, five spiders per arena of field density of 159 spiders m^{-2}) was used. *Asterisk* indicates significant differences determined by post hoc tests (Tukey–Kramer, $P < 0.05$)

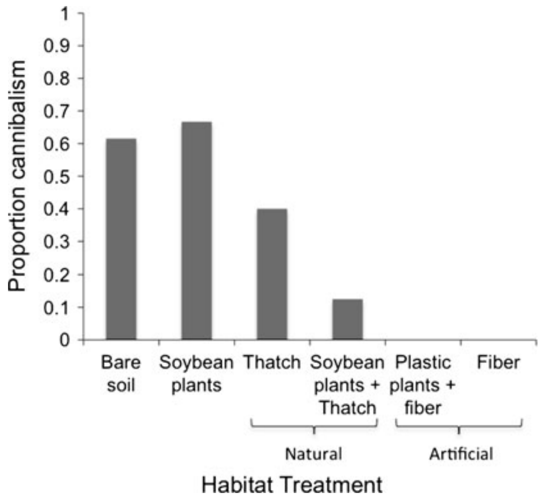

Fig. 3 Proportion of laboratory trials where cannibalism was observed. Cannibalism was only observed in the five-spider treatment (field density of 159 spiders m^{-2}). If cannibalism was observed, it was only observed once in an experimental trial

Table 3 Two-way ANOVA of the effects of habitat on prey capture by *P. milvina* (performed to assess interference in different habitats in a laboratory experiment)

Source	*df*	SS	*F*	*P*
State	1	460.93	58.46	<0.0001
Habitat treatment	2	958.51	60.79	<0.0001
Habitat treatment × state (interaction)	2	58.09	3.68	0.0316
Observed bare versus predicted bare	1	274.51	34.82	<0.0001
Observed fiber versus predicted fiber	1	204.64	25.96	<0.0001
Observed thatch versus predicted thatch	1	39.83	5.05	0.0287
Residual	54	425.74		

The prey capture of two spiders foraging together was compared to the predicted prey capture (Soluk and Collins 1988, Sih et al. 1998) of two spiders foraging in isolation within three different habitat types. *State* represents an indicator variable for either observed or predicted prey capture. Bonferroni adjusted orthogonal linear contrasts were used when testing the hypothesis of the interaction between habitat treatment and state ($\alpha = 0.05/3 = 0.017$)

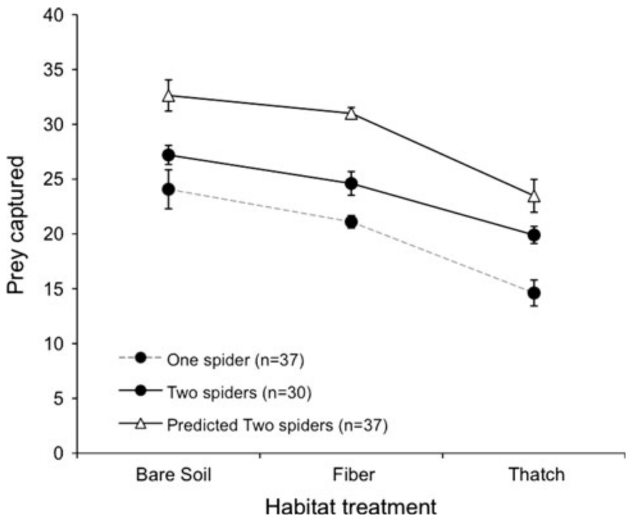

Fig. 4 Interaction plots comparing observed and predicted prey capture (crickets captured, mean ± SE, over a 24 h period) by *P. milvina* in isolation and when together. The one-spider data are for one spider foraging in isolation, and the two-spider data represent the observed prey capture when two *P. milvina* were foraging in a habitat together. The predicted two-spider values were obtained by combining the prey capture probabilities of the two *P. milvina* in isolation (see text and Soluk and Collins 1988; Sih et al. 1998)

interfered with prey capture efficiency. Although we found that the high spider densities reached in the plastic fiber would likely lead to higher levels of intraspecific competition than in the straw thatch habitat, cannibalism was eliminated.

Taken together, these experiments suggest that habitat selection in *P. milvina* is motivated by their ability to forage on and within certain substrate structures more than the prey available in a specific habitat patch. Of all the factors we measured, habitat complexity was the most important predictor of the overall spider density in our field plots. Interestingly, although prey availability was important in explaining the abundance of other spiders, the abundance of the most common spider species, *P. milvina*, was linked more closely to habitat structure. This result suggests that cues used by spiders to select foraging sites vary between species, and although the spider community in our agroecosystem appeared to respond to increases in their trophic resources, *P. milvina* did not. A synthesis of ecological studies on spiders indicates that, as a group, spiders are food limited in nature, and prey consumption and foraging site selection have strong effects on fitness (Wise 1993; Halaj and Wise 2002; Wise 2006). Therefore, we expected the impacts of structure and prey abundance to be linked, as they were for the non-*P. milvina* component of the spider community in this study. In fact, in a previous study of *P. milvina* conducted at the same field site, their densities increased in plots where prey availability was augmented through the addition of detritus on the soil surface (Marshall et al. 2000). Although the results of this study are consistent with the generalization that *P. milvina* is successful in highly disturbed agroecosystems because it is a good colonizer, these results also suggest that specific habitat selection mechanisms in this generalist predator are not as simple as they seemed based on previous work (Marshall et al. 2000, 2006; Buddle et al. 2003).

Pardosa milvina accumulated in areas where cannibalism was low (Fig. 3), the abundance of competitors or intraguild predators was low (Fig. 1), and their predation rate was high (Fig. 2). In our laboratory experiment, we found that even at high densities of *P. milvina*, increased habitat complexity reduced predation rate. High spider density led to prey depletion in experimental arenas, and the likelihood of cannibalism was reduced when thatch was present. However, interactions between *P. milvina* foraging together in the laboratory reduced predation rate (Fig. 4). Langellotto and Denno (2006) determined that thatch reduced cannibalism in *P. littoralis* when lower levels of prey were available. In our study, cannibalism only occurred in treatments containing high densities of *P. milvina*, and more frequently when no substrate structure was present. Notably, these were treatments where few prey remained at the end of the trial.

In an open field setting, intraspecific interference may be mitigated by the versatility of *P. milvina* in making broad use of the available habitat patches (Marshall and Rypstra 1999; Buddle et al. 2003), which is consistent with the idea that scaling of interaction strength is an important component of predator space use (Drapela et al. 2008). For instance, a congener occupying agroecosystems of eastern Europe has been characterized as a “sit and move” predator that changes foraging location frequently (Samu et al. 2003), which is likely the reason that populations of *P. milvina* are not sensitive to habitat fragmentation or to the destruction of neighboring patches of habitat (Marshall et al. 2006). Thus, the intraspecific interference and cannibalism we observed at increasing densities in laboratory experiments, where neither predator nor prey could escape, are probably artifacts of the experiment and an overestimate. In a more natural situation, they can more easily adjust to the presence of a conspecific by relocating.

Not surprisingly, the thatch and fiber mulches provided protection to the spiders from the microclimate fluctuations that occur in exposed plots of soil during an Ohio summer. Indeed, it has been demonstrated that the distributions and abundances of other spiders are influenced by their abilities to withstand temperature and humidity extremes (Henschel et al. 1992; DeVito et al. 2004). Our field study revealed that natural wheat straw with live soybean plants moderated microclimatic extremes to a greater degree than the plastic mimics, but *P. milvina* selected artificially structured patches anyway. Although temperature and humidity certainly would affect habitat selection in these small ectotherms, *P. milvina* seemed to compromise by selecting an environment that was more moderate than bare soil but where prey-capture efficiency was high and the threat of competitors or predators was low.

We initially assumed that additional habitat structure would hinder foraging ability, as such a connection has been documented in a wide variety of arthropod natural enemy taxa (Andow and Prokrym 1990; Lukianchuk and Smith 1997; Clark et al. 1999; Legrand and Barbosa 2003). In the field, the addition of either live or artificial plants increased the density of *P. milvina*, and in the laboratory, *P. milvina* frequently used plants as resting sites. However, the presence of plants had little impact on prey capture in the laboratory (Fig. 2). It is possible that, in the field, plants provided critical protection from temperature extremes, but temperature and humidity differences between plots with and without plants were not quantified. Nonetheless, the finding that *P. milvina* preferred the plastic patches with larger humidity fluctuations and slightly higher temperatures than the thatch and live soybean treatments indicates that subtle differences in microclimate provided by the plants were not driving this preference. Alternatively, *P. milvina* may have shifted its habitat use due to the presence of chemical information from the larger syntopic intraguild predator *H. helluo* (Araneae: Lycosidae) (Rypstra et al. 2007). Folz et al. (2006) documented that *P. milvina* climbs up onto vertical surfaces to avoid exposure to *H. helluo* chemical cues, placing them out of the predatory reach of this larger, slower wolf spider. Therefore, it is possible that *P. milvina* selects a habitat containing plants that provide escape routes for this small, agile spider. This response would account for the observed difference in *P. milvina* density between plots with natural or artificial mulch on the soil surface and those with mulch and live or artificial plants.

Foraging site selection appears to be dynamic in *P. milvina*; lower predation risk coupled with greater capture efficiency may explain why *P. milvina* chose novel habitats containing artificial structure over natural ones preferred by other spiders. We were surprised to discover that this spider was so effective at prey capture in plastic fiber habitats. Wolf spiders have scopulae, dense tufts of bristles under their tarsal claws, which enable them to climb burnished surfaces (Foelix 1996). These structures may have allowed *P. milvina* to gain more traction than the cricket prey on the plastic fiber, and thus enhanced their prey capture success. Whatever the reason, the habitat and foraging differences between *P. milvina* and the rest of the spider community offer one explanation for our failure to detect strong top-down effects by arthropod predators in terrestrial systems (Halaj and Wise 2001). Early work suggested that spider assemblages were more apt at providing effective biological control than a few species (Riechert and Lockley 1984). More recently, a meta-analysis showed that overall natural enemy diversity improves pest regulation (Letourneau et al. 2009); however, agricultural intensification that reduces both within-field and landscape complexity negatively impacts natural enemy abundance and diversity (Tscharntke et al. 2007). In our system, the numerically dominant arthropod predator responded differently to habitat structural features when compared to the rest of the spider community. As these predators sort themselves out in space, they may enhance their overall impact on plant production through niche partitioning (Finke and Snyder 2008), but a complex suite of direct and indirect behavioral responses to habitat, other predators, prey, and conspecifics make those effects more difficult to detect. Therefore, these results underscore the importance of continued efforts to characterize important resources that are required to promote and maintain high predator abundance and diversity in managed systems.

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