Spider Fauna of Semiarid Eastern Colorado Agroecosystems: Diversity, Abundance, and Effects of Crop Intensification

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ABSTRACT Spiders are critical predators in agroecosystems. Crop management practices can influence predator density and diversity, which, in turn, can influence pest management strategies. Crop intensification is a sustainable agricultural technique that can enhance crop production although optimizing soil moisture. To date, there is no information on how crop intensification affects natural enemy populations, particularly spiders. This study had two objectives: to characterize the abundance and diversity of spiders in eastern Colorado agroecosystems, and to test the hypothesis that spider diversity and density would be higher in wheat (*Triticum aestivum* L.) in crop-intensified rotations compared with wheat in conventional rotations. We collected spiders through pitfall, vacuum, and lookdown sampling from 2002 to 2007 to test these objectives. Over 11,000 spiders in 19 families from 119 species were captured from all sampling techniques. Interestingly, the hunting spider guild represented 89% of the spider fauna captured from all sites with the families Gnaphosidae and Lycosidae representing 75% of these spiders. Compared with European agroecosystems, these agroecosystems had greater diversity, which can be beneficial for the biological control of pests. Overall, spider densities were low in these semiarid cropping systems, and crop intensification effects on spider densities were not evident at this scale.

KEY WORDS Araneae, crop intensification, semiarid, diversity, dryland agroecosystems

Spiders can play a key role in suppressing agricultural pests (Chiverton 1986; Winder 1990; Symondson et al. 2002; Lang 2003; Schmidt et al. 2003, 2004). High spider species richness is associated with reduced pest densities (Riechert 1999, Schmidt et al. 2003). This is likely because of niche complementarity, such that species using different prey capturing strategies increase overall pest suppression (Marc and Canard 1997). Abundance of spiders also improves pest control through a simple numeric effect (Riechert and Lockley 1984). To achieve effective pest management, species evenness as well as species richness are important (Hillebrand et al. 2008). An increase in species evenness can decrease pests significantly (Crowder et al. 2010). Because of the effectiveness of spiders as predators and their ubiquity, enhancing their abundance and diversity is, thus, an important goal of conservation biological control.

Crop management practices directly influence predator density, including that of spiders (Luff 1987).

For example, in conventionally-farmed monocultures, growers often till their fields and eliminate vegetation (Nyffeler and Benz 1979), which can reduce predator densities and increase pest outbreaks (Pimentel 1961, Benton et al. 2003). In contrast, more heterogeneous agricultural landscapes provide refuges for predators and prey (Ryszkowski et al. 1993, Sunderland and Samu 2000), which generally reduces pest outbreaks (Altieri 1994).

A dominant crop in dryland agriculture in the western Great Plains is wheat, *Triticum aestivum* L. (Poales: Poaceae), and one of its most significant pests is the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae). Wheat production is dominated by a wheat-fallow rotation but more diverse rotations also are used. Given the production risks of dryland farming because of variable weather conditions (Dhuyvetter et al. 1996), wheat is only profitable if pest management costs are low or absent. Spiders are proven predators of aphids in wheat (Sunderland et al. 1986, Mansour and Heimbach 1993, Kerzicnik et al. 2012), yet to date, data regarding the spider fauna of eastern Colorado agroecosystems are entirely lacking, as is information on how crop rotations affect spider diversity and abundance.

The wheat-fallow rotation has dominated dryland agriculture in the Great Plains because of water conservation principles. For example, during the 14-mo fallow period, soil water is stored, which increases the

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Table 1. Description of field sites, plot sizes, and rotations at Akron, Briggsdale, and Lamar, Colorado, 2002–2007

Site	Annual precipitation[a] (mm)	Plot length	Conventional rotation	Crop-intensified rotation
Akron	405	27.4 by 54.9 m	Winter wheat–fallow	Winter wheat–corn–fallow
Briggsdale	350	27.4 by 125.0 m	Winter wheat–fallow	Winter wheat–millet–fallow[b]
Lamar	375	30.5 by 97.5 m	Winter wheat–fallow	Winter wheat–sorghum–fallow[c]

[a] 1961–1990 mean.
[b] Summer crop changed to millet in 2005–2006, 2006–2007 crop year.
[c] Summer crop changed from grain to field sorghum in 2005–2006, 2006–2007 crop year.

chances for a successful subsequent crop (Peterson et al. 1996). Water storage is maximized if fields are weed free (Peterson and Westfall 2004), but this barren environment could create an unsuitable habitat for natural enemies and their prey (Samu et al. 1999). The addition of other crops to the wheat-fallow rotation and a concordant reduction in the fallow period, also referred to as crop intensification, might enhance landscape heterogeneity (Farahani et al. 1998) and, thus, increase natural enemy densities.

With crop intensification, a multitude of crops can be grown asynchronously such that senescence occurs at different times and periods, which prevents vast acreage from being barren. This provides alternative prey sources and habitat for predators (Altieri 1994), so that they can move into the crop quickly after it is planted, improving predator to prey ratios (Chiverton 1986, Holland and Thomas 1997, Landis and van der Werf 1997, Birkhofer et al. 2008) and resulting in more effective biological control. Disturbance from crop sowing, cultivation, harvesting, and also a lack of prey, causes spiders to emigrate. Therefore, it is important to have consistent habitat (i.e., more crops in the rotation), to maintain the presence of spiders within agroecosystems. In addition, increased structural diversity created by the addition of more crops to the rotation could enhance the diversity of the predator fauna (Landis et al. 2000).

This study had two goals: First, we aimed to characterize the abundance and richness of the spider community of eastern Colorado dryland agroecosystems. Second, we tested the hypothesis that an intensified crop rotation would have greater spider diversity and density than a conventional wheat-fallow rotation.

Materials and Methods

Field Sites. The eastern Colorado dryland agroecosystem study sites were the following: Akron, located in Washington County (40.16° N, 103.21° W; elevation of 1,420 m); Briggsdale, located in Weld County (40.60° N, 104.34° W; elevation of 1,475 m); and Lamar, located in Prowers County (38.09° N, 102.62° W; elevation of 1,104 m). These sites are semiarid with precipitation and plot sizes varying at each location (Table 1). Each site included both a conventional wheat-fallow rotation and a crop-intensified rotation (for the purposes of this study, the crop-intensified rotation is defined as a winter wheat–summer crop–fallow rotation). In the conventional systems, wheat is planted

(August and September through June and July) followed by ≈14 mo of fallow. For the intensified cropping system, wheat is planted (August and September through June and July), a summer crop (site-defined, Table 1) is planted the next year (May through October), and then the field is in fallow for 14 mo after the harvesting of the summer crop. Each phase of the crop rotation was present in each repetition (wheat–summer crop–fallow-intensified rotation; wheat–fallow-conventional rotation), and there were four replications at each site for a total of 12 plots in the crop-intensified rotation and eight plots in the conventional rotation. The plot sizes varied with location (Table 1). To characterize the abundance and diversity of spiders in eastern Colorado agroecosystems (objective 1), we collected spiders from all wheat, fallow, and summer crops in both cropping systems, which totaled 20 plots per site. To test the hypothesis that an intensified crop rotation would have greater spider density and diversity (objective 2), only the abundance data for spiders collected from the wheat plots in the crop-intensified and conventional rotations were used for a total of eight plots. At each site, treatments were assigned randomly to plots within blocks (Peterson et al. 2004).

Site Management. Winter wheat was planted in the fall, 2001–2006, and well-adapted cultivars were chosen for each site (Supp Table S1) (Peterson et al. 2004). At Akron, the fallow plots in the conventional rotation were tilled once with a tandem disc in the spring and swept twice before planting. Fallow plots were not tilled at Briggsdale as herbicides were applied monthly during the spring and summer to control weeds. At Lamar, the fallow in the crop-intensified rotation was swept once during midsummer. Locally-adapted summer crop varieties were planted from May to July, 2002–2007 (Supp Table S2). At all sites, glyphosate was applied preplant, and another herbicide was applied postcrop emergence (Peterson et al. 2004). The summer crop (sorghum) was not planted in 2002 in Lamar because of drought conditions.

Spider Sampling. Sampling was conducted from 2002 to 2007 by using the following methods: pitfall (April–October, 2002–2006), vacuum (May–August, 2006–2007), and lookdown sampling (May–August, 2004–2006). All techniques (pitfall, vacuum, and lookdown) were used to characterize spider abundance and diversity. Vacuum and pitfall sampling were used to test treatment effects from crop intensification but were analyzed separately. There was significant vari-

ation between collectors with lookdown sampling, regardless of their level of experience.

Pitfall Trapping. Two pitfall traps (10 cm in diameter) (Miller 2000) were placed within the center of each plot ≈5 m apart. Once monthly they were filled with 165 ml of a 70:30 mixture of propylene glycol: water, which served as a killing agent and preservative. The spiders were collected after 7 d by sieving the contents with a strainer and paper towel, placing the paper towel in a plastic bag, and then into the freezer until further processing. Collection traps were covered when not in use. The spiders were transferred to vials in 75% ethanol.

Vacuum Sampling. A modified Stihl (Waiblingen, Germany) BG 55 leaf vacuum was used to capture spiders in the foliage (Stihl HomeScaper Series; 417 cfm). Vacuum samples were taken once monthly. Two areas were selected randomly within each plot at each site (Southwood 1978), and a circular toothed sheet-metal frame with an area of 0.55 m² was placed around the area to be sampled. The area then was searched for 5 min to collect any spiders present but not captured by the suction sampler. The contents of the suction sleeve were transferred to 2-liter plastic bags. Spiders were sorted live in the laboratory, collected with aspirators, and placed into vials with 75% ethanol.

Lookdown Sampling. Lookdown sampling involved the collection of spiders found by walking through plots and collecting spiders observed below knee level in the crop or at the soil surface. Collections were made once monthly between 2000 and 2400 hours for 30 min per plot with three repetitions by using headlamps as a light source. Spiders were hand-collected and placed in 125-ml Nalgene (Nalge Nunc International, Penfield, NY) cups filled with 75% ethanol and transferred to the laboratory for identification.

Adult spiders were identified to species under a microscope at 40–250× by the first author; adult Linyphiidae were identified by M. Draney at 20–250×. Several representative species were sent to specialists for verification; see Acknowledgments. Immature spiders cannot be identified to species and were not identified beyond the family level. Voucher specimens are deposited at the Denver Museum of Nature and Science in Denver, CO (Accession no: DMNS 2007-134).

Analyses

Characterizing the Abundance and Richness of the Spider Community in Eastern Colorado Agroecosystems. Several analyses were conducted to provide an indication of whether the sampling effort for this study was complete (Coddington et al. 2009). First, an inventory completion calculation was performed by dividing the observed species richness (total number of species collected) by the Chao 2 estimate. The Chao-2 estimator (Chao 1987, Colwell and Coddington 1994) is a nonparametric estimator that can be used for multiple samples combined within an area to estimate species richness as a whole using the following formula:

$$S_2 = S_{obs} + \frac{Q_1^2}{2Q_2}$$

where S_{obs} is the number of species observed, Q_1 being species occurring in only one sample (singletons), and Q_2 as the number of species appearing twice in a sample (doubletons). Then the number of singletons (a species represented by only one individual) and sampling intensities (number of individuals per number of species) also were recorded. These calculations can provide an indication of whether an area was undersampled, which might affect the interpretation of the diversity of the area (Coddington et al. 2009). Finally, species accumulation curves were calculated for all sites to address whether sampling effort was adequate to estimate the total number of species present (Colwell and Coddington 1994). The species richness estimators Chao I (Chao 1987) and ACE I (Chazdon et al. 1998, Chao et al. 2000) were calculated with Estimate S (Colwell 2005) to estimate the true number of species present at each site.

Effects of Crop-Intensified Rotations on Spider Diversity and Densities

Diversity. Diversity analyses were performed using adult spiders from pitfall sampling. Because immature spiders cannot be identified to species, they were not used in the diversity analyses.

The Shannon Index. The Shannon index was calculated for wheat plots in both rotations and years for each site for pitfall samples from 2002 to 2006, using the following formula (Krebs 1989):

$$H = -\sum_{i=1} p_i \log_e P_i$$

where p_i = the proportion of individuals in the *i*th species and S_T = the total number of species. The H index values were converted to the actual number of species rather than using the logarithmic values to facilitate interpretation of the data (Ricklefs 2007). Statistical computations using the calculated Shannon indices were performed using the "Mixed" procedure in SAS (SAS Institute 2008) with the REML estimation method and the Kenward–Roger approximation for degrees of freedom (Kenward and Roger 1997). Mean species diversity between wheat in the two rotations was pooled over months because of low spider densities and were compared for each year by repetition by using a two-factor, repeated measures analysis of variance (ANOVA). Wheat rotation and year were fixed effects, mean spider diversity was a dependent variable, and year was a (repeated measure) time effect. If any fixed effects within the model were significant ($P \leq 0.05$), pair wise comparisons were performed using the "lsmeans" statement in SAS.

Evenness. Pielou's evenness index can be used to measure the distribution of species within the community. Evenness was calculated for wheat in each of the rotations each year. Because spider densities were low, data for wheat in each rotation were pooled across all months, and evenness was calculated for

year and each wheat rotation by repetition by using the following formula:

$$E = e^H / s$$

where H = the value of the Shannon index, and s = the number of species within the sample. Statistical computations using the calculated evenness indices also were performed using the "Mixed" procedure in SAS (SAS Institute 2008) with the REML estimation method and the Kenward–Roger approximation for degrees of freedom (Kenward and Roger 1997). An "E" of "1" would indicate that for a certain number of individuals present, there would be an equal number of species. Therefore, "E" cannot exceed a value of "1." Mean species evenness between wheat in the two rotations was pooled over months because of low spider densities and was compared for each year by repetition using a two-factor, repeated measures ANOVA with wheat rotation and year as fixed effects, mean spider evenness was the dependent variable, and year was a (repeated measure) time effect. Similar to the methods used when calculating the Shannon index, fixed effects within the model that were significant ($P \leq 0.05$) were compared using pair wise comparisons.

Densities. Data were analyzed as a randomized complete block design with year and month as repeated measures. Sites were analyzed separately because of differences in plot sizes and environmental factors (i.e., precipitation, evapotranspiration rate). The effects of crop rotation type (wheat in a crop-intensified rotation and wheat in a conventional rotation); year (pitfalls: 2002–2006, vacuum: 2006–2007); month (pitfalls: April–October, vacuum: May–August); and their interactions were analyzed separately for pitfall and vacuum samples with the dependent response variable of spiders (both adult and immature spiders). Spider activity-densities and densities were square-root transformed ($x + 0.5$) to homogenize the variances. October was excluded from statistical analyses of Lamar pitfall captures because this month was missing in two of the five sampling years and interfered with the statistical analysis. Weekly pitfall and vacuum samples were averaged by dividing the total catch by two to avoid pseudoreplication (Hulbert 1984). Repeated measures models with autoregressive errors and unequal variances across years were measured and used when justified by Akaike's information criteria values (Burnham and Anderson 2002). Statistical computations were performed using the "Mixed" procedure in SAS (SAS Institute 2008) with the REML estimation method and the Kenward–Roger approximation for degrees of freedom (Kenward and Roger 1997). When significant effects were observed ($P \leq 0.05$), pair wise comparisons were performed using the "lsmeans" function in SAS (SAS Institute 2008). Untransformed means and standard errors are presented in tables and figures herein.

Results

Characterizing the Abundance and Richness of the Spider Community in Eastern Colorado Agroecosystems. In total, 11,207 spiders in 17 families and 119 species were collected from all sites (Table 2). For all sites, from 2002 to 2007, the families Lycosidae and Gnaphosidae dominated the adult spiders collected (29 and 46%, respectively). Six families—Gnaphosidae, Linyphiidae, Salticidae, Lycosidae, Thomisidae, and Philodromidae–represented over 75% of the total species for all sites. The most spiders were collected in Lamar (Table 3). The percentage of immature and mature spiders sampled was about equal in Akron and Briggsdale and dominated by immature spiders in Lamar. At all sites, the male to female ratio was at least 1 1/2 to double. Akron and Briggsdale represented a similar number of species, whereas Lamar was slightly lower. Several species were unique to each site. *Schizocosa mccooki* was dominant at all sites, and *Gnaphosa clara* (Gnaphosidae) was common to Akron and Briggsdale. The other dominant species varied between sites.

The inventory completion for all sites was as follows: Akron: 61.1, Briggsdale: 82.7, Lamar: 85.2%. The sampling intensities for Akron, Briggsdale, and Lamar were 18.6, 21.8, and 20.7%, respectively. On average, other arthropod surveys revealed an average sampling intensity of 17%, ranging from 1 to 83% (see review in Coddington et al., 2009). The percentage of singletons for the Akron, Briggsdale, and Lamar sites for 2002 through 2007 was 32.7, 28.9, and 34.0%, respectively.

The observed richness demonstrated in the species accumulation curves shows a slight rise at all sites (Fig. 1), which indicates that additional species beyond those sampled may be present. In addition, the richness estimators (Chao I and Ace) in this figure show that the estimated true number of species was higher than the actual number of species sampled (observed species).

Effects of Crop-Intensified Rotations on Spider Diversity and Densities

Diversity. At Akron, mean Shannon diversity indices ranged between 1.56 and 2.22 from 2002 to 2006, and there were no differences in diversity between years ($F = 2.22$; df = 4, 28; $P = 0.0927$) with diversity highest in 2005 (Fig. 2). There were no significant differences between diversity in the wheat in the conventional or crop-intensified rotations ($F = 0.02$; df = 1, 3; $P = 0.9058$). At Briggsdale, diversity indices ranged from 1.16 to 2.35 (Fig. 2). Like Akron, diversity was not influenced by wheat between the two crop rotations ($F = 0.37$; df = 1, 3; $P = 0.5860$), but diversity was influenced by year ($F = 12.13$; df = 4, 28; $P < 0.0001$). Diversity was highest in 2005 and 2006, and these years were different from all other years except for one another (for 2005, 2002: $t = -4.33$, df = 28, $P = 0.0002$; 2003: $t = -3.52$, df = 28, $P = 0.0015$; 2004: $t = -5.58$, df = 28, $P < 0.0001$) (for 2006, 2002: $t = -3.95$, df = 28, $P = 0.0005$; 2003: $t = -3.14$, df = 28, $P < 0.0001$; 2004: $t = -5.19$, df = 28, $P < 0.0001$). Also, diversity was lowest in 2004, which differed from 2003 ($t = 2.06$,

Table 2.　Species of Araneae collected at Akron (A), Briggsdale (B), and Lamar (L), Colorado, 2002–2007

Family	Species	A	B	L
Agelenidae	*Agelenopsis aleenae* Chamberlin & Ivie			4
	Agelenopsis oklahoma (Gertsch)	2	2	
Araneidae	*Larinia borealis* Banks	2	4	
Clubionidae	*Clubiona pikei* Gertsch[a]	1		
Corinnidae	*Castianeira alteranda* Gertsch	2		
	Castianeira amoena (Koch)			1
	Castianeira descripta (Hentz)	23	2	
	Phurotimpus certus Gertsch	4		
Dictynidae	*Cicurina* sp. 1[b]			94
	Cicurina sp. 2[b]	5	7	3
	Cicurina sp. 3[b]			1
	Cicurina sp. 4[b]		2	
	Dictyna coloradensis Chamberlin	2	3	
	Dictyna personata Gertsch & Mulaik		9	18
	Dictyna terrestris Emerton	10	33	1
	Dictyna sp.	1	2	
	Emblyna consulta (Gertsch & Ivie)	5	2	
	Emblyna reticulata (Gertsch & Ivie)	4		10
	Emblyna scotta Chamberlin		1	
	Iviella sp. 1[b]	16	1	9
	Iviella sp. 2[b]			8
	Phantyna bicornis (Emerton)	1	13	
	Tricholathys sp.	1		
Gnaphosidae	*Drassodes gosiutus* Chamberlin	1		12
	Drassodes neglectus (Keyserling)	1		
	Drassodes saccatus (Emerton)		1	5
	Drassyllus depressus (Emerton)	14	3	
	Drassyllus lamprus (Chamberlin)	2	3	
	Drassyllus lepidus (Banks)	5		13
	Drassyllus nannellus Chamberlin & Gertsch	137	92	8
	Drassyllus notonus Chamberlin	22	25	65
	Gnaphosa clara (Keyserling)	155	322	
	Gnaphosa parvula Banks	1		
	Gnaphosa saxosa Platnick & Shadab			399
	Gnaphosa sericata (Koch)	30	23	
	Haplodrassus chamberlini Platnick & Shadab	61	93	44
	Haplodrassus signifer (Koch)	8	21	7
	Micaria gertschi Barrows & Ivie	1		
	Micaria gosiuta Gertsch[a]		1	
	Micaria longipes Emerton		2	
	Micaria medica Platnick & Shadab		3	
	Zelotes anglo Gertsch & Riechert	59	36	9
	Zelotes gertschi Platnick & Shadab	33	39	1
	Zelotes hentzi Barrows	4		
	Zelotes lasalanus Chamberlin	23	57	1
	Zelotes nannodes Chamberlin[a]			2
	Zelotes puritanus Chamberlin	18	41	17
Linyphiidae	*Agyneta cf. unimaculata* (Banks)[a]	3		
	Agyneta uta (Chamberlin)[a]		1	
	Agyneta/Meioneta sp. 1[b]	26	15	41
	Agyneta/Meioneta sp. 2[b]		1	1
	Agyneta/Meioneta sp. 3[b]		6	
	Ceratinella brunnea Emerton	28	1	2
	Ceratinops latus (Emerton)[a]		1	
	Coloncus siou Chamberlin[a]	19	2	
	Erigone aletris Crosby & Bishop	1	40	
	Erigone barrowsi Crosby & Bishop[a]			2
	Grammonota suspiciosa Gertsch & Mulaik[a]			1
	Islandiana flaveola (Banks)	27	10	1
	Islandiana princeps Braendegaard[a]	2		1
	Mythoplastoides exiguus (Banks)[a]	14	1	
	Tennesseellum formicum (Emerton)[a]	38	75	21
	Walckenaeria maesta Millidge[a]			1
	Walckenaeria spiralis (Emerton)[a]	1		
Lycosidae	*Alopecosa kochi* (Keyserling)	50	18	7
	Arctosa rubicunda (Keyserling)	34	2	
	Geolycosa missouriensis (Banks)		1	4
	Geolycosa rafaelana (Chamberlin)			2
	Hogna antelucana (Montgomery)			31
	Hogna coloradensis (Banks)		28	180
	Hogna frondicola (Emerton)	1		
	Schizocosa crassipalpata Roewer	10		

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Table 2. Continued

Family	Species	A	B	L
	Schizocosa mccooki (Montgomery)	324	165	186
	Schizocosa minnesotensis (Gertsch)	15	4	
	Varacosa gosiuta (Chamberlin)	2	6	
Philodromidae	*Ebo iviei* Sauer & Platnick[a]		1	
	Ebo parabolis Schick		1	4
	Ebo pepinensis Gertsch		2	10
	Thanatus altimontis Gertsch	1	10	1
	Thanatus coloradensis Keyserling	1	6	
	Thanatus formicinus (Clerck)	21	39	7
	Thanatus rubicellus Mello-Leitão			1
	Tibellus chamberlini Gertsch	2		1
	Tibellus duttoni (Hentz)	33	11	2
	Tibellus oblongus (Walckenaer)	3	1	
Pholcidae	*Psilochorus imitatus* Gertsch & Mulaik	1	6	3
Salticidae	*Habronattus altanus* (Gertsch)	49	31	16
	Habronattus conjunctus (Banks)	15		
	Habronattus cuspidatus Griswold	19	2	1
	Habronattus klauseri (Peckham & Peckham)		53	20
	Pellenes crandalli Lowrie & Gertsch[a]			12
	Pellenes levii Lowrie & Gertsch			2
	Phidippus apacheanus Chamberlin & Gertsch	4	1	
	Phidippus ardens Peckham & Peckham		1	2
	Sassacus papenhoei Peckham & Peckham	2		
	Sitticus dorsatus (Banks)	3	4	
	Synageles occidentalis Cutler		2	
	Talavera minuta (Banks)	9	4	
Tetragnathidae	*Tetragnatha laboriosa* Hentz	1	1	1
Theridiidae	*Enoplognatha joshua* Chamberlin & Ivie	1	6	9
	Euryopis texana Banks	3	45	
	Latrodectus hesperus Chamberlin & Ivie		2	3
	Robertus sp[b]			2
	Steatoda albomaculata (De Geer)	19	8	24
	Steatoda americana (Emerton)	7	1	
	Steatoda medialis (Banks)			1
	Theridion petraeum Koch			1
	Theridion rabuni Chamberlin & Ivie	6	14	8
Thomisidae	*Mecaphesa celer* (Hentz)	3		
	Xysticus auctificus Keyserling			2
	Xysticus coloradensis Bryant		7	
	Xysticus cunctator Thorell	5	14	3
	Xysticus ferox (Hentz)	1		
	Xysticus lassanus Chamberlin	9	20	6
	Xysticus nigromaculatus Keyserling		1	
	Xysticus orizaba Banks	114	26	22
	Xysticus pellax O.P.-Cambridge	47	65	6
	Xysticus texanus Banks	17	29	13
Titanoecidae	*Titanoeca nigrella* (Chamberlin)	42	4	7

Only 15 of 17 families are shown because two families, Mimetidae and Miturgidae, were collected in the immature stages and could not be identified further than family.

[a] New state records for Colorado.

[b] Possible new species.

df = 28, $P = 0.0492$). Lamar had diversity indices that ranged from 1.04 and 2.04 (Fig. 2). Diversity was not influenced by wheat when comparing the crop-intensified and conventional rotations ($F = 0.01$; df = 1, 3; $P = 0.9105$), but was influenced by year ($F = 8.39$; df = 4, 28; $P = 0.0001$). Similar to Briggsdale, diversity was highest in 2005 and 2006, and these years differed from all other years except one another (for 2005, 2002: $t = -3.38$, df = 28, $P = 0.0022$; 2003: $t = -2.73$, df = 28, $P = 0.0108$; 2004: $t = -4.04$, df = 28, $P = 0.0004$) (for 2006, 2002: $t = -3.87$, df = 28, $P = 0.0006$; 2003: $t = -3.22$, df = 28, $P = 0.0032$; 2004: $t = -4.53$, df = 28, $P < 0.0001$).

Evenness. Evenness ranged from 0.680 to 0.872 at Akron (Fig. 3). Evenness did not vary between wheat treatments in the conventional fields and in the crop-intensified fields ($F = 1.01$; df = 1, 3; $P = 0.3887$) nor did it vary among years ($F = 1.85$; df = 4, 28; $P = 0.1465$). Averaged over years, Akron spider evenness was higher than Briggsdale and Lamar. At Briggsdale, evenness ranged from 0.469 to 0.812 (Fig. 3) and was similar between rotations ($F = -0.95$; df = 1, 3; $P = 0.4139$) but different among years ($F = 7.16$; df = 4, 28; $P = 0.0004$). Spider evenness was highest in 2006 and lowest in 2004 with 2004 being different than all other years. At Lamar, evenness ranged from 0.565 to 0.702 (Fig. 3). Like Briggsdale, there were no differences in evenness in wheat between crop rotation types ($F = 0.00$; df = 1, 3; $P = 0.9880$), but there was a difference among years ($F = 3.02$; df = 4, 28; $P = 0.0345$). Even-

Table 3.   Total number of Araneae, percentage matures, sex ratio, species collected, unique species at each site, and the dominant species at Akron (A), Briggsdale (B), and Lamar (L), CO, 2002–2007

	A	B	L
No. of spiders	3,255	3,381	4,571
% matures	50	48	31
Sex ratio for matures (male to female)	1.9:1	1.5:1	1.9:1
Species collected	77	78	67
Unique species to site	16	12	19
Dominant species			
Schizocosa mccooki (Montgomery)	x	x	x
Gnaphosa clara (Keyserling)	x	x	
Drassyllus nannellus Chamberlin and Gertsch	x		
Haplodrassus chamberlini Platnick and Shadab		x	
Gnaphosa saxosa Platnick and Shadab			x
Hogna coloradensis (Banks)			x

ness was highest in 2005, lowest in 2004 with 2004 differing from all other years except 2002.

Densities

Pitfall Sampling. At Akron, the activity-density of spiders varied between years ($F = 24.97$; df = 4, 232; $P < 0.0001$). Activity-densities were highest in 2005 and were different from all other years (Fig. 4). Also, spider activity-densities varied among months ($F = 5.94$; df = 6, 232; $P < 0.0001$) and were highest in June (Fig. 5). During specific years, spider activity-densities varied among months (year by month interaction, $F = 4.55$; df = 24, 232; $P < 0.0001$). Mean spider activity-densities typically declined from August to October (Fig. 5). However, in 2005, activity-densities were higher from June to September. Crop rotation type differed during particular months, averaged over years (rotation by month interaction, $F = 3.60$; df = 6, 232; $P = 0.0020$). In May, spider activity-densities in the crop-intensified rotations were higher than activity-densities in the conventional rotations ($t = -3.34$, df = 232, $P = 0.0010$). Conversely, in June, activity-densities were higher in the conventional rotations ($t = 2.94$, df = 232, $P = 0.0036$). Contrary to the hypothesis, spider activity-densities were not significantly higher in the crop-intensified wheat compared with the conventional wheat ($F = 1.76$; df = 1, 3; $P = 0.2764$).

Similarly, at Briggsdale, spider activity-densities varied among years ($F = 53.77$; df = 4, 238; $P < 0.0001$). Again, spider activity-densities were highest in 2005 and different than all other years (Fig. 4). Spider activity-densities also varied among months ($F = 9.30$; df = 6, 238; $P < 0.0001$) with July representing the highest spider activity-densities and August the lowest (Fig. 5). There was an interaction between year and month ($F = 2.11$; df = 24, 238; $P = 0.0025$). Activity-densities increased from April to July and decreased from August to October, except for 2004. In 2005, July spider activity-densities were almost double the densities of other months. Spider activity-densities were not higher in the crop-intensified
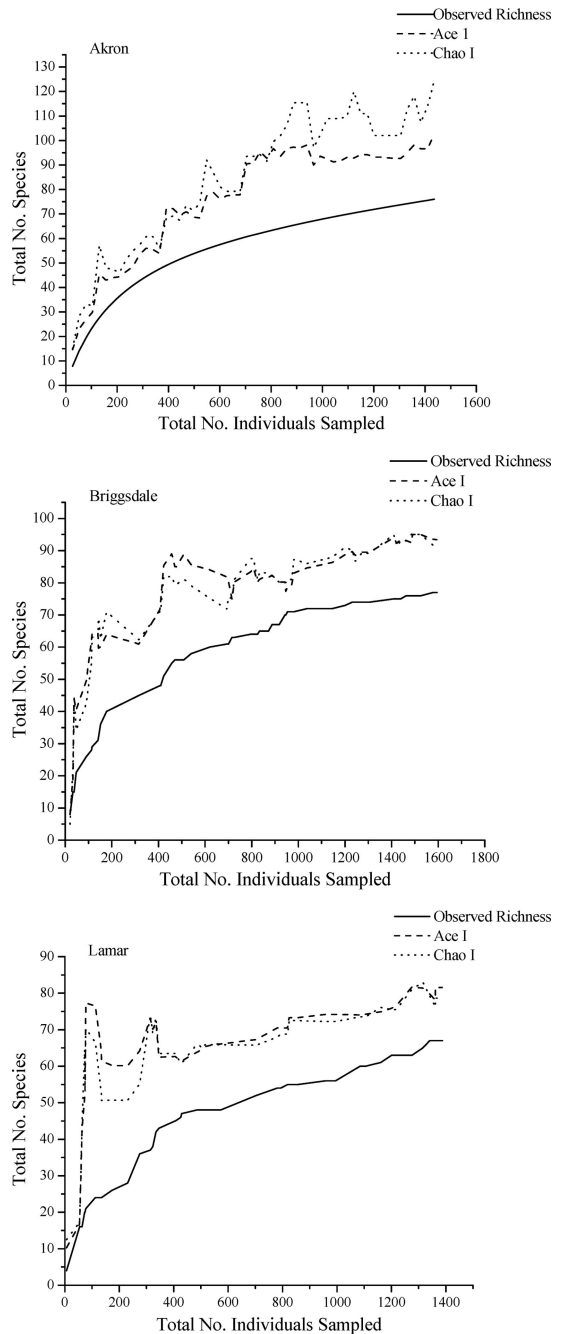

Fig. 1. Species accumulation curves for Akron, Briggsdale, and Lamar, CO, from all sampling techniques from 2002 to 2007 by using Chao I and ACE one species richness estimators graphed with the actual observed number of species (observed richness).

wheat compared with the conventional wheat ($F = 0.48$; df = 1, 3; $P = 0.5384$).

At Lamar, activity-densities differed among years ($F = 22.88$; df = 4, 203; $P < 0.0001$) (Fig. 4). Mean spider activity-densities in 2006 were higher than all
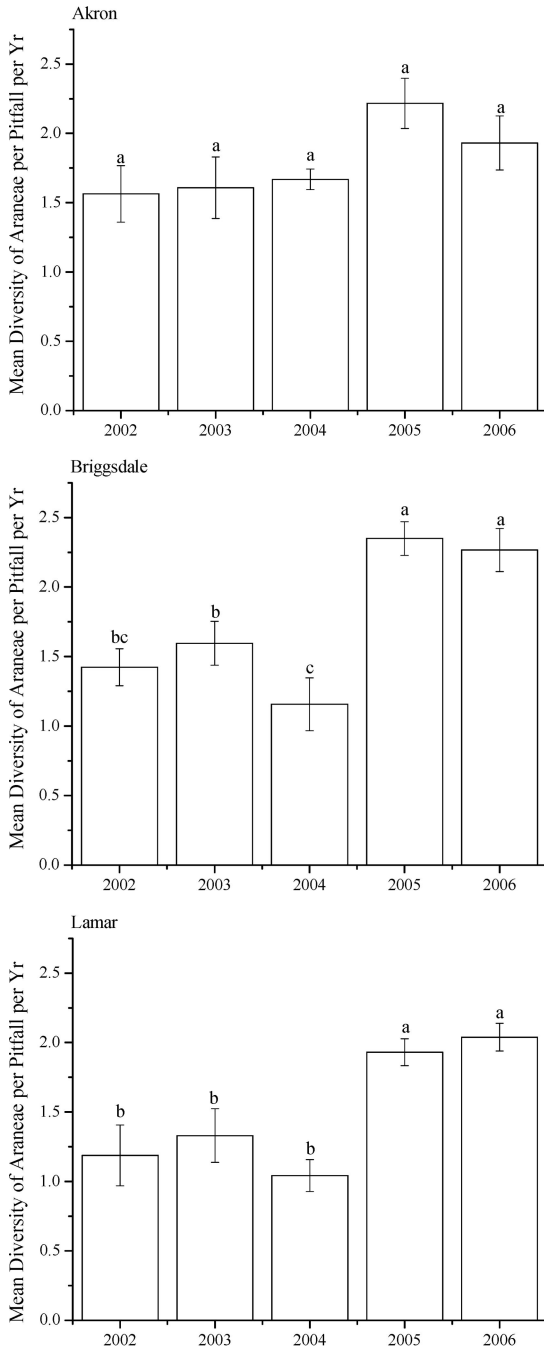
Fig. 2. Mean species diversity per year for Araneae collected from pitfall sampling at Akron, Briggsdale, and Lamar, CO, 2002–2006.

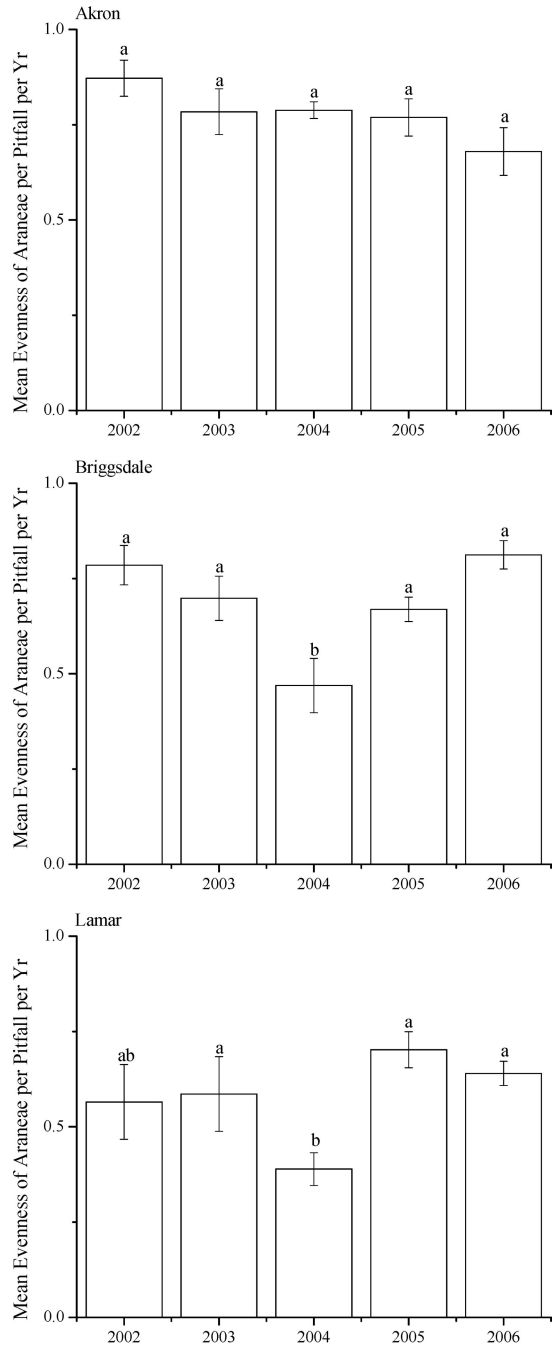**Fig. 3.** Mean species evenness per year for Araneae collected from pitfall sampling at Akron, Briggsdale, and Lamar, CO, 2002–2006.

other years. Spider activity-densities also varied among months ($F = 8.26$; df = 5, 203; $P < 0.0001$) (Fig. 5). April through July had the highest spider activity-densities, and August had the lowest. Months also varied in particular years (year by month interaction, $F = 8.57$; df = 20, 203; $P < 0.0001$). In 2002, activity-densities were highest in April and subsequently declined. In contrast,

in 2003, 2004, and 2006, activity-densities were lowest in April and highest in June, May, and September, respectively. Similar to the other two sites, spider activity-densities did not differ in the two wheat rotation systems ($F = 0.05$; df = 1, 3; $P = 0.8306$).

Vacuum Captures. Vacuum sampling predominantly captured immature spiders. At Akron, spider
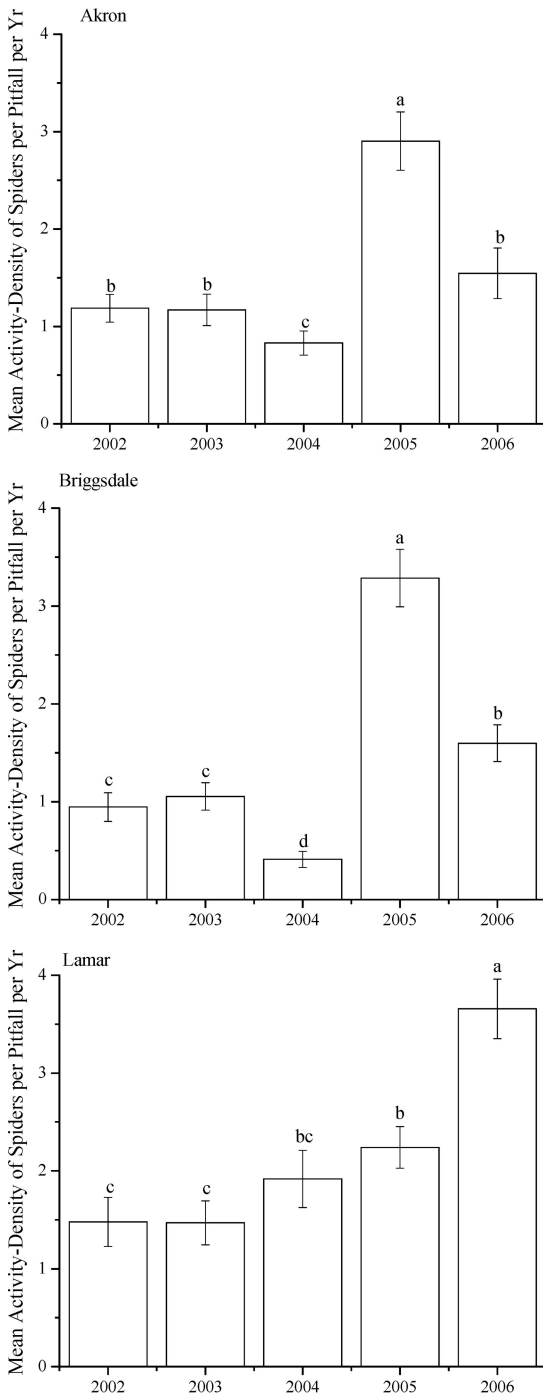
Fig. 4. Mean density of Araneae per pitfall per year for 2002–2006 at Akron, Briggsdale, and Lamar, CO.
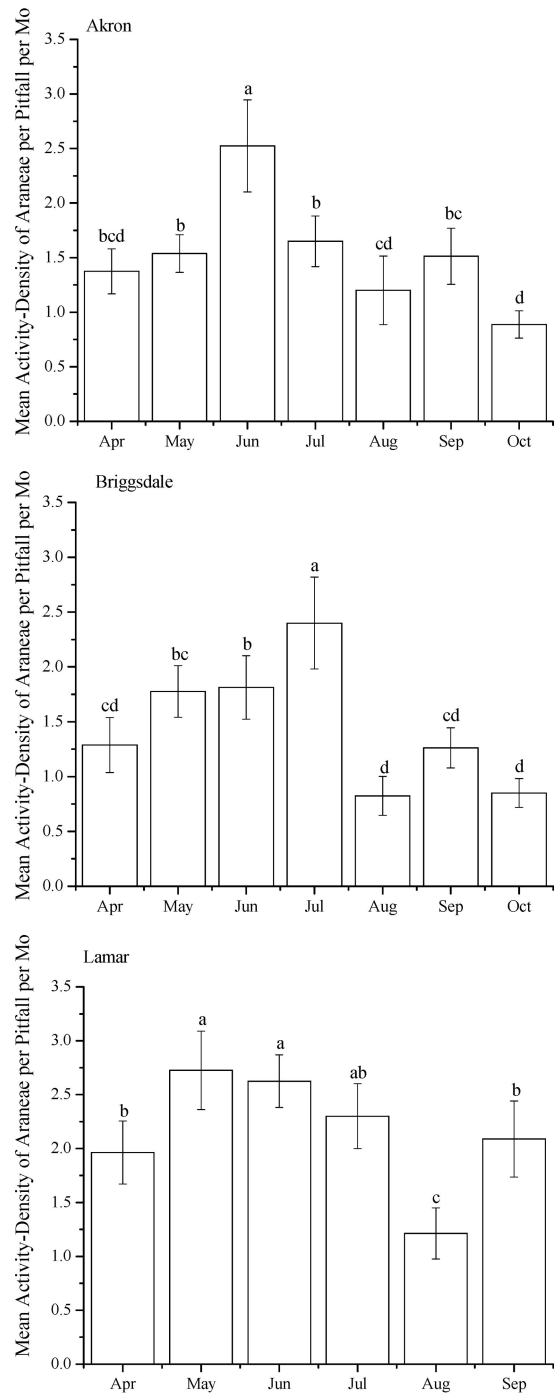

Fig. 5. Mean density of Araneae per month per pitfall at Akron, Briggsdale, and Lamar, CO.

densities varied among years ($F = 4.26$; df = 1, 35; $P = 0.0464$), with densities higher in 2007. There was also a difference among monthly spider densities ($F = 3.84$; df = 3, 35; $P = 0.0178$). Densities were highest in August. During particular months each year, there was a difference among spider densities ($F = 3.01$; df = 3, 35;

$P = 0.0430$). In 2006, spider densities were higher in June than in May ($t = -2.18$, df = 35, $P = 0.0359$) and July ($t = 2.52$, df = 35, $P = 0.0166$). August 2007 spider densities were higher than all other months that year (May: $t = -2.46$, df = 35, $P = 0.0188$; June: $t = -2.48$, df = 35, $P = 0.0181$; July: $t = -3.46$, df = 35, $P = 0.0015$). Spider

densities did not differ between wheat in either of the rotations ($F = 0.03$; df = 1, 2; $P = 0.8690$).

Contrary to Akron, spider densities did not vary among years at Briggsdale ($F = 0.98$; df = 1, 35; $P = 0.3284$). Densities did vary among months ($F = 13.58$; df = 3, 35; $P < 0.0001$) with densities higher in July than all other months (May: $t = -5.41$, df = 35, $P < 0.0001$; June: $t = -5.53$, df = 35, $P < 0.0001$; August: $t = -2.62$, df = 35, $P = 0.0130$). During each year, spider densities varied with particular treatments each month ($F = 4.44$; df = 3, 35; $P = 0.0095$). In 2007, in particular, densities in July were at least two and a half times higher than other months. Similar to Akron, spider densities did not differ between wheat in either of the rotations ($F = 1.86$; df = 1, 2; $P = 0.3056$).

Lamar spider densities varied among years ($F = 6.38$; df = 1, 25; $P = 0.0183$) with mean densities higher in 2007. Only 2 mo were sampled in 2007 because of inclement weather; however, mean spider densities in 2007 were higher than those sampled in 2006. Spider densities did not vary significantly between months ($F = 2.23$; df = 3, 25; $P = 0.1100$). Like Akron and Briggsdale, there were differences among particular months each year ($F = 9.00$; df = 1, 25; $P = 0.0060$). For 2006, densities were highest in July. In 2007, densities were over three times higher in June. There were no significant differences between spiders in the conventional wheat and crop-intensified rotations ($F = 2.45$; df = 1, 2; $P = 0.2582$).

Discussion

Although the species accumulation curves and the high percentage of singletons present (32.7, 28.9, and 34.0% for Akron, Briggsdale, and Lamar, respectively) indicate that not all species present were captured, this study is comparable to other intensive arthropod surveys (average of 31.6% singletons, reviewed in Coddington et al. 2009). Typically, the precision of species estimates increases as the sampling size increases.

The composition of spiders differed compared with other agricultural areas around the world. Western European agriculture and other agroecosystems generally are dominated numerically by spiders in the family Linyphiidae, which can comprise over 90% of the total spider fauna (Nyffeler and Sunderland 2003). In a desert agroecosystem in Isreal, wheat fields were dominated by the families Linyphiidae, Gnaphosidae, and Theridiidae, in order of their dominance (Gavish-Regev et al. 2008). Typically, cropping systems in the United States contain more diverse spider fauna with hunters (spiders that catch prey without a web) comprising over 50% of the total spiders and linyphiids only ≈17% (Nyffeler and Sunderland 2003). This study compliments literature describing species composition from cropping systems in the United States (Young and Edwards 1990, Nyffeler 1999); hunting spiders represented 89% of the total adult spiders collected (based on guilds described in Uetz et al. 1999), and the remaining spiders were representative of the web-building guild. Similarly, in Peru, 80–90% of the spiders found in cotton also were hunters (Aguilar

1977, 1979). This could be because of climatic differences, mainly in the form of higher temperatures in the southern United States, as spider fauna differ between climates (Bristowe 1939).

A diversity of natural enemies rather than dominance by a single web-building family such as Linyphiidae may be beneficial to the biological control of crop pests (Straub and Snyder 2008). Natural enemies that vary in their microhabitat use can have additive effects on reducing pest densities (Straub 2006). For this study, there was a diversity of spiders using several niches. The families Lycosidae, Gnaphosidae, Thomisidae, Linyphiidae, Philodromidae, and Salticidae represented the greatest density of spiders and species for this study. An increase in natural enemy diversity has decreased pest densities in several studies (Stiling and Cornelissen 2005, Cardinale et al. 2006, Letourneau et al. 2009), with a particularly strong connection between increased predator richness and herbivore suppression in agricultural systems (Letourneau et al. 2009).

Spider densities were low in these agroecosystems. Spider densities in European cereal agroecosystems can reach up to 600 m^{-2} and averaged 52 m^{-2} in several studies; however, in the United States, densities average a maximum of 12 m^{-2} in cropping systems (Nyffeler and Sunderland 2003). In a study of spider diversity and densities in Lamar, CO, (close to the Lamar site for this study) spider densities were estimated at 0.7 m^{-2} with a total of 14 species within 11 families (Greenstone 2001).

Of the spiders collected from all collection methods from 2002 to 2007, 75% were in the families Gnaphosidae and Lycosidae. Similarly, the Gnaphosidae and Lycosidae families represented over 85% of the spider fauna collected from pitfalls in a shortgrass steppe ecosystem in Weld County, CO, close to the Briggsdale site for this study (Weeks and Holtzer 2000). Five families contained 61% of the species identified in a field crop survey of spiders in North America (Young and Edwards 1990). In Hungary, 10% of the spider species made up 60–90% of the entire community in a 10-yr spider survey (Samu and Szinetár 2002). Likewise, in a New Mexico diversity study of spiders in alfalfa, four species within four families, *Pardosa sternalis* (Thorell) (Lycosidae), *Misumenops* sp. (Thomisidae), *Grammonota cf. pictilis* (O.P.-Cambridge) (Linyphiidae), and *Tetragnatha laboriosa* Hentz (Tetragnathidae) represented 95% of the collection (Richman et al. 1990). Thus, domination by a small number of families is common in agroecosystems.

In Akron, spider activity-densities were higher earlier in the season in the crop-intensified treatment compared with the conventional wheat treatment, suggesting an earlier peak of spider activity-densities. The early presence of generalist predators in the crop results in more efficient biological control of pests (Edwards et al. 1979, Chiverton 1986, Birkhofer et al. 2008). Furthermore, spiders were consistently present in April through June before average peak densities of pests such as *D. noxia* that typically peak in early to mid-June (Kerzicnik et al. 2012). Spider activity-den-

sites were highest from April to July at all sites and declined after this time, likely because of disturbances from wheat harvest. Spider activity-densities and densities were low except in 2005 in Akron and Briggsdale and in 2006 in Lamar. Crop rotation effects might not be apparent with such low spider densities. Diversity was highest in 2005 and 2006 at all sites. Spider evenness was highest when mean spider activity-densities were lowest in Akron and Briggsdale, and evenness was highest in Akron overall.

Crop intensification had little effect on spider activity-densities and densities, limited effects on diversity, and minimal effects on spider evenness. Additional crops within the rotation can provide a level of connectivity between habitats, which can be crucial for maintaining natural enemy populations (Duelli 1988). However, for this study and on this scale, diversity and density of spiders did not increase with crop intensification.

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