Habitat and Season in Structuring Ground-Dwelling Spider (Araneae) Communities in a Shortgrass Steppe Ecosystem

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ABSTRACT We assessed habitat differences in ground-dwelling spider communities that stem from fine-scale differences in plant cover types and height in a shortgrass steppe ecosystem. The number of spiders captured in pitfall traps was used to determine habitat and temporal dynamics in the spider communities. Two habitat types were sampled, grass and mixed-grass/shrub during May, June, July, and August 1995 and 1996. Spiders in the Lycosidae (56%) and Gnaphosidae (29%) were the numerically dominant spiders collected. The Lycosidae was represented by three species and significantly more abundant in grass habitats in 1995 only. The Gnaphosidae was the most speciose family collected (15 spp). The most abundant species of Gnaphosidae exhibited consistent habitat and seasonal patterns of species turnover and abundance during the 2-yr study. Results from detrended correspondence analysis revealed significant species-specific differences in the spider communities between the two habitats. Of the 10 most abundant species, *Schizocosa mccooki* (Montgomery), *S. mimula* (Gertsch), *Gnaphosa clara* (Keyserling), and *G. brumalis* (Thorell), were more abundant in grass sites. The most abundant spiders in the mixed-grass/shrub habitat were *Schizocosa* spp. (immatures), *Gnaphosa* spp. (immatures), *G. sericata* (Koch), *Haplodrassus signifer* (Koch), *Habronattus altanus* (Chamberlin), and *Xysticus nigromaculatus* (Keyserling). Overall, the spider communities differed between grass and mixed-grass/shrub habitats in their response to seasonal change, and these differences in community composition were similar both years of the study. Our results underscore the importance of habitat selection at fine-scales and patterns of seasonal activity that translate to population and community patterns at larger spatial and temporal scales.

KEY WORDS ground-dwelling spiders, community structure, shortgrass steppe, species diversity, habitat preferences, seasonal patterns

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IN GRASSLANDS, GROUND-DWELLING spiders are often considered the most diverse and numerically abundant group of predatory arthropods (Rushton and Eyre 1992). Improved understanding of the environmental factors influencing their distribution and abundance in natural and agricultural ecosystems may lead to habitat management practices that conserve and enhance the beneficial use of these generalist invertebrate predators. Investigations of spider community patterns in several specific grassland types have been used to develop and evaluate land-use practices, mostly in the United Kingdom (Rushton et al. 1987, Rushton et al. 1989). Rushton (1988) studied spiders in chalk grasslands, and Duffey (1962) examined spiders in limestone grasslands and in sand dunes (Duffey 1968). These studies have shown that spider communities are strongly and predictably influenced by habitat type and land-use patterns. Spider community organization and habitat architecture have been studied in sagebrush steppe in Utah (Hatley and MacMahon 1980, Robinson 1981, Abraham 1983), an arid-grassland in New Mexico (Muma 1980), calcareous fens in southern Missouri (Bultman 1992), and deciduous forest ecosystems (Uetz 1975, 1979). Results from these studies have shown that fine-scale habitat structure and seasonal variation influence the distribution and abundance of spider species in these ecosystems. However, with the exception of a limited spider survey conducted by Kumar et al. (1976) during the United States International Biome Project (U.S. IBP), there are no other studies examining the diversity, ecology, or community structure of spiders in shortgrass steppe.

North American grasslands are centrally located in the Great Plains and constitute one of the largest contiguous areas of grasslands worldwide (Lauenroth et al. 1999). The Great Plains are composed of several different grassland types (Singh et al. 1983). Of the central Great Plains, the shortgrass steppe encompasses some 280,000 km^2 (Lauenroth and Milchunas 1991), with ≈45% remaining as native grassland (Milchunas et al. 1998). The shortgrass steppe ranges from the Colorado–Wyoming border (41° N latitude) south into western Texas (32° N latitude). The western border of this biome runs along the foothills of the Rocky Mountains and the eastern edge lies at about the 100th meridian. Up to 90% of the arthropod fauna can be

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found inhabiting the soil and litter (Lauenroth and Milchunas 1991). The objectives of this study were to investigate habitat and seasonal patterns of abundance and species diversity of ground-dwelling spiders in grass and mixed-grass/shrub habitats in a shortgrass steppe ecosystem.

Ground-Dwelling Spider Community Definition. The spider fauna most commonly captured in pitfall traps may be considered primarily ground-dwelling (Uetz and Unzicker 1976). They are found in grasses, forest litter, meadows, under rocks and sticks, around the bases of shrubs, in abandoned rodent burrows, and in cracks and crevices in the soil. Ground-dwelling spiders are relatively small, abundant, and mobile arthropods that exhibit a high degree of species overlap among habitats (Syrek and Janusz 1977; Platnick 1995) yet are spatially segregated at fine scales (Greenquist and Rovner 1976, Robinson 1981, Cady 1984). These spiders are active, generalist predators that also demonstrate considerable overlap in food requirements (Kaston 1978, Wise 1993). With the exception of a few species, these spiders do not build webs for prey capture, but use various other foraging strategies for prey capture (e.g., ambush, pursuit and pouncing). Foraging strategies and guild structure of ground-dwelling spider species usually follow familial classification (Post and Riechert 1977, Uetz et al. 1999). The ground-dwelling spider community in this study was subdivided by family: Corrinidae (running spiders), Gnaphosidae (nocturnal running spiders), Lycosidae (diurnal running spiders), Philodromidae and Thomisidae (ambushing spiders), and Salticidae (stalking spiders). Web-building spiders captured were from Agelenidae, Dictynidae, and Theriididae.

Materials and Methods

Study Site. This study was conducted at the Central Plains Experimental Range (CPER) Shortgrass Steppe Long-term Ecological Research (SGS-LTER) site, which is administered by the U.S. Department of Agriculture (USDA) in cooperation with the National Science Foundation (NSF). The CPER (6,280-ha) site is ≈60 km northeast of Fort Collins in Weld County, CO, USA. The CPER is contiguous with the Pawnee National Grassland and is representative of the shortgrass steppe of the central Great Plains. The site is ≈1,650 m in elevation and averages ≈320 mm in annual precipitation, with mean monthly temperatures ranging from −5°C in January to 22°C in July (Milchunas et al. 1989). The site has been divided into fenced pastureland for cattle grazing since 1939 (Van Cleve and Martin 1991).

We chose two representative habitat types with similar domestic cattle grazing regimes for this study: grass and mixed-grass/shrub. We chose three sites (i.e., pastures) in each habitat type to conduct spider sampling. Grass sites are typified by rolling plains dominated by a mosaic of perennial shortgrasses *Bouteloua gracilis* (Humboldt, Bonpland, & Kunth) Lagasca, *Buchloë dactyloides* (Nuttall) Engelmann, with fringed sagewort (*Artemisia frigida* Willdenow) and cactus (*Opuntia polycantha* Haworth) interspersed with small patches of bare ground. Bare ground patches are the result of erosion and disturbances associated with domestic cattle, prairie dogs (*Cynomys ludovicianus* Ord), and western harvester ants (*Pogonomyrmex occidentalis* Cresson).

Mixed-grass/shrub areas consist of a mixture of shortgrasses, mid-grasses and shrubs along swales, and drainages. Typical shrub species include four-wing saltbrush *Atriplex canescens* (Pursh) Nuttall, fringed sagewort (*Artemisia frigida* Willdenow), broom snakeweed *Gutierrezia sarothrae* (Pursh) Britton & Rusby, and wildbuckwheat (*Eriogonum effusum* Nuttall). Typical mid-grass species include rabbitfoot grass *Polypogon monspeliensis* (L.) Desfontaines, needle-and-thread (*Stipa comata* Trinius & Ruprecht) and bottlebrush squirreltail *Sitanion hystrix* (Nuttall) J. G. Smith.

Habitat Measurements. To quantify the vegetation cover in each trapping area, we recorded cover types along two 29.25-m transects bisecting each trapping area in late June 1995 and again in early July 1996. Each of the transects were oriented in opposing directions, one in a north-south direction the other in an east-west direction. We recorded the extent of each dominant cover type that intercepted each transect line in centimeters. In July 1996 a vegetation height measurement was added, with vegetation height in centimeters measured at 10 randomly located points in each of the six study pastures where trapping was conducted. We separated the study sites into two habitat types with different vegetation structure (grass versus mixed-grass/shrub) so that we could evaluate differences between the ground-dwelling spider communities.

Spider Sampling Protocol. We collected ground-dwelling spiders with live (dry) pitfall traps in each of six pastures. We chose a live pitfall trapping technique based on comparative studies of live versus kill pitfall trapping techniques conducted by Weeks and McIntyre (1997) in the same system. Weeks and McIntyre (1997) showed that for 29 of 32 arthropod species that were collected by both live (checked daily) and kill (checked every sixth day) pitfall traps there was no significant difference in the average number of individuals per species collected in both trap types. These results suggest that within trap predation in live traps or better retention of animals by the kill traps were not significant collecting factors, when live traps were checked daily. Further, by using live pitfall traps, we attempted to reduce any confounding impacts on the spider communities being sampled through the intensive and indiscriminant removal of other arthropod taxa by kill pitfall trapping. The effects of kill pitfall trapping techniques on local communities are poorly known. Each pitfall trap was a Barber-style trap (Adis 1979; Weeks and McIntyre 1997), consisting of a 500-ml plastic cup buried in the ground with the lip of the cup flush with the soil surface. A 125-ml cup was placed inside the larger cup to allow for specimens to be removed easily without having to displace the entire trap. Small water-drainage slits were cut into the

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bottom edge of the cups. An opaque plastic funnel (after the design in Gist and Crossley 1973) placed in each cup provided shade, deterred escape, and discouraged predation from outside sources such as birds or rodents. All traps were covered with flush-fitting wooden lids when not in use.

We used a 0.0638-ha trapping web (Anderson et al. 1983, Parmenter et al. 1989) design to capture ground-dwelling spiders. This trap arrangement is used to estimate relative population densities. Each web consisted of eight trap lines (arms) of 10 traps per line (80 traps total) spaced apart by 45° radiating from a central point. The distance between traps within a line was 1.5 m except at the center, where traps were spaced adjacent to each other in a 0.5-m-diameter ring.

Sampling was conducted in 1995 and 1996 over a total of eight 6-d trapping sessions at 4-wk intervals (mid-May, mid-June, mid-July, and mid-August of each year). All spider specimens were collected daily for identification, resulting in 23,040 total trap nights (11,520 per year = 80 traps per web × six webs × six trapping days × four sampling periods). Spider captures over each 6-d trapping session were pooled by individual trap numbers for each month and trapping web. All specimens were identified to genus and most to species. Species identifications were provided or verified by David B. Richman (Department of Plant Pathology and Weed Science, New Mexico State University, Las Cruces, NM). Voucher specimens were deposited at the C. P. Gillette Museum of Arthropod Biodiversity, Department of Biological Sciences and Pest Management, Colorado State University, Fort Collins, CO.

Diversity and Multivariate Analyses. We used species richness because it is commonly used in entomological work and provides a relatively direct expression of diversity (Magurran 1988). Differences in mean species richness between the two habitats and among sampling periods were compared for each year separately using a two-factor repeated measures analysis of variance (ANOVA) with habitat and family effects on mean species richness as fixed effects and season as a (repeated measure) time effect.

The number of individual spiders collected by family type were compared between the two habitat types using a two-factor repeated measures ANOVA with habitat and spider family as fixed effects and season as a (repeated measure) time effect. If the analysis indicated significant differences then mean values were compared with the Tukey–Kramer least significant number procedure (Tukey 1953, Kramer 1956). Differences in the abundance of spiders between habitats and among sampling periods were compared for each year separately.

Spider species presence and abundance were compared between habitats using detrended correspondence analysis. We removed spider species from the detrended correspondence analysis if the number of individuals collected was less than two because we considered them to be too rare or less vagile, therefore less likely to be captured by pitfall traps, to include in the detrended correspondence analysis. Program PCORD (McCune and Mefford 1997) performs detrended correspondence analysis, which is an extension of correspondence analysis. Detrended correspondence analysis has been used to analyze grassland spider (Rushton et al. 1987) and ground-foraging ant communities (Bestelmeyer and Wiens 1996). Detrended correspondence analysis uses site/habitat-scores, which are the weighted averages of species abundances from a particular sampling web (site) and habitat, to generate joint plots of species and site/habitat scores. Site/habitat scores in the ordination diagram lie at the centroids of the positions of species that occur in them. Species scores that lie close to a particular site/habitat score are therefore likely to have a high abundance at that site and those farther away a lower abundance. Differences in site/habitat-score positions within the ordination space indicate the effects of habitat structure in structuring the spider community, whereas changes in site/habitat-score positions from one sampling period to the next reflects seasonal turnover in community composition (Jongman et al. 1995). Species scores on the edge of the diagram are either rare species or are species that prefer extreme environmental conditions (Jongman et al. 1995). The effects of habitat type on ground-dwelling spider community structure was assessed by comparing site/habitat-scores and species-scores in the first two detrended correspondence analysis dimension axes. The units of ordination length in detrended correspondence analysis are standardized and expressed as the average standard deviation (SD) of species turnover, where 1 SD indicates ≈50% turnover and sites >4 SD are expected to have no species in common. Site/habitat scores were plotted as minimum-space polygons including the three trapping webs in each habitat type for 1995 and 1996 superimposed with the positions of the 10 most abundant spider species.

We used the four sampling periods (May, June, July, August) each year to determine the seasonal composition of spider communities in grass and mixed-grass/shrub habitats. The degree of seasonal turnover in spider species distribution and abundance can therefore be measured by the change in site/habitat positions of the four sampling periods. In addition, by comparing the two years, we were able to evaluate the similarity in seasonal dynamics between the two years sampled.

Results

Habitat Measurements. Our measurements of the various cover types within each trapping web quantitatively support our division of the six trapping webs into one of two habitat types. Three of the six trapping webs (webs 1–3) were located in areas dominated by shortgrasses with very few mid-grasses and shrubs (i.e., grass sites), whereas the other three trapping webs (webs 4–6) were in areas with substantially higher percentages of mid-grasses and shrubs (mixed-grass/shrub sites) (Table 1). Trapping web 6 had the highest percentage of bare ground cover compared

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Table 1. Percentage of cover types measured in centimeters along two randomly placed 29.25-m transects bisecting each trapping web for each year at the Central Plains Experimental Range (CPER), Weld County, CO

Web / Pasture[a]	% cover types							
	G1	G2	S1	S2	BG	LT	CA	CP
				1995				
Grass								
1/22cs	81.8	—	2.7	—	11.0	—	4.5	—
2/22cn	89.4	0.5	2.0	—	6.3	—	1.8	—
3/15swe	89.9	6.1	—	—	2.0	—	1.7	0.3
Mixed-grass shrub								
4/24ne	30.8	38.2	5.4	5.4	11.1	—	5.1	—
5/13ses	47.3	19.5	15.2	1.6	9.6	4.1	2.5	0.2
6/30ne	27.7	34.4	0.8	9.7	26.5	—	0.6	0.3
				1996				
Grass								
1/22cs	77.1	3.3	1.3	—	9.3	2.2	6.8	—
2/22cn	87.1	3.5	1.9	—	3.2	1.2	3.1	—
3/15swe	94.8	2.0	0.7	1.1	0.3	—	1.1	—
Mixed-grass shrub								
4/24ne	23.9	38.6	12.6	5.5	10.9	6.1	2.4	—
5/13ses	34.6	8.2	13.3	12.9	11.7	15.7	3.3	0.3
6/30ne	23.3	38.0	2.3	6.6	28.1	1.6	0.1	—

The extent of one cover type that intersected a transect was recorded at a time, if more than one cover type was present the dominant type was recorded. G1, shortgrasses (≤5 cm); G2, mid-grasses (>5 cm); S1, small shrubs and forbs (≤20 cm); S2, mid-tall shrubs (>20 cm); BG, bare ground; LT, litter; CA, cactus; CP, cow pat.

[a] Pasture locations on CPER site map. Maps located at Central Plains Experimental Range (CPER), Shortgrass Steppe (SGS), and Long-term Ecological Research (LTER) headquarters in Weld County, CO.

with the other trapping webs. The range of average height of the vegetation measured in centimeters at 10 randomly located points within each trapping web was 4.65–8.70 cm in the grass sites and 17.65–20.55 cm in the mixed-grass/shrub sites (1996 data only).

Species Richness. We recorded a greater diversity of ground-dwelling spiders than previously reported for the shortgrass steppe (Kumar et al. 1976; Table 2). In the 2-yr study, we collected 3366 spiders belonging to nine families, 20 genera and 37 species (Table 2). There were five species collected in the grass habitat only, whereas nine were unique to the mixed-grass/shrub habitat. Total species richness in the grass and mixed-grass/shrub habitat was 31 and 32, respectively. Two spider families comprised 85% of the total sample, the Lycosidae (56%) with three species and the Gnaphosidae (29%) with 15 species.

Results of the species richness analysis by family and habitat, using a repeated measures ANOVA, shows that there was no significant difference in the mean number of species collected between the two habitats during both years ($P > 0.05$). However, there were significant differences in the mean number of species collected between families which were dependent upon sampling period (1995, $F = 3.0059$; df = 15, 61.13; $P = 0.0012$ and 1996, $F = 5.1847$; df = 15, 61.134; $P = 0.0000$). In May of 1995, there were significantly fewer species of Corinnidae (May, 0.00 ± 0.00; June, 0.50 ± 0.22; July, 0.50 ± 0.22; August, 0.83 ± 0.17 [±1 SEM]) and Lycosidae (May, 1.00 ± 0.25; June, 2.16 ± 0.17; July, 2.16 ± 0.17; August, 1.83 ± 0.31 [±1 SEM]) collected than in the other sampling periods. In May and June of 1996, there were significantly more species of Gnaphosidae collected than in July and August (May, 8.00 ± 0.44; June, 4.00 ± 0.73; July, 2.83 ± 0.54, August, 1.83 ± 0.17 (±1 SEM)]. Overall, Gnaphosidae was the most species rich group collected (15 spp.), although the numerically dominant species of Gnaphosidae changed from month to month (Table 3).

Abundance Analyses. Habitat and season had variable effects on the ground-dwelling spider community. Two-factor (repeated measures) ANOVA showed significant family and habitat effects in both 1995 and 1996 and significant interaction effects between habitat and family in 1995 only (Table 4). The analysis showed significant seasonal effects plus significant season and family interaction effects, whereas season and habitat type did not reveal any significant interaction effects (Table 4). The numerically dominant families and species varied among sampling periods (Table 3). Lycosid spiders were significantly more abundant than the other spiders in both habitat types, however there were significantly more spiders of Lycosidae collected in grass sites than in mixed-grass/shrub sites in 1995 only (Table 5). In 1995, Lycosid spiders were significantly more abundant in 3 of 4 mo (June, July, and August) and it was dominant in all of the 1996 samples (Table 3). *Schizocosa mccooki* (Montgomery) was the numerically dominant species of Lycosidae in June, July (1995 and 1996), and August (1995, Table 3). The order of species turnover in Gnaphosidae was similar for the two years. *Haplodrassus signifer* (C. L. Koch) and *Gnaphosa clara* (Keyserling) were numerically dominant in May and June, whereas *G. sericata* (L. Koch) and *G. brumalis* (Thorell) were more abundant later in the summer (Table 3). Theridiid spiders were collected significantly more in grass sites than mixed-grass/shrub sites in both 1995 and 1996 (Table 5). Theridiidae was the third most common family in May 1995 (18 adults, 15

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Table 2. Ground-dwelling spiders captured in each habitat type (grass versus mixed-grass/shrub) in 1995 and 1996 at the Central Plains Experimental Range, Weld County, CO

Family Species	Habitat	
	Grass	Mixed-grass
Agelenidae		
Agelenopsis longistylus (Banks)	2	0
Agelenopsis oklahoma (Gertsch)	2	0
Agelenopsis spp.–immatures	5	0
Corinnidae		
Castianeira alteranda (Gertsch)	4	8
Castianeira descripta (Hentz)	3	5
Castianeira spp.–immatures[a]	4	3
Dictynidae		
Dictyna personata (Gertsch & Mulaik)	1	0
Gnaphosidae		
Drassyllus lamprus (Chamberlin)	0	1
Drassyllus mumai (Gertsch & Riechert)	15	11
Drassyllus nannellus (Chamberlin & Gertsch)	3	3
Drassyllus sp. A[a]	0	1
Drassodes gosiutus (Chamberlin)	13	6
Drassodes succatus (Emerton)	1	1
Drassodes sp. A	4	4
Drassodes spp.–immatures	4	1
Gnaphosa antipola (Chamberlin)	1	3
Gnaphosa brumalis (Thorell)[a]	137	25
Gnaphosa clara (Keyserling)	159	30
Gnaphosa sericata (Koch)	11	182
Gnaphosa spp.–immatures[a]	110	64
Haplodrassus signifer (Koch)[a]	31	44
Micaria porta (Platnick & Shadab)	4	7
Micaria spp.–immatures[a]	1	2
Zelotes lasalanus (Chamberlin)	22	43
Zelotes puritanus (Chamberlin)[a]	1	2
Zelotes spp.–immatures[a]	4	10
Lycosidae		
Lycosa carolinensis (Walckenaer)[a]	0	1
Lycosa spp.–immatures[a]	2	19
Schizocosa mccooki (Montgomery)	723	314
Schizocosa mimula (Gertsch)	255	231
Schizocosa spp.–immatures	154	183
Salticidae		
Habronattus altanus (Chamberlin)	58	40
Habronattus texanus (Chamberlin)	0	2
Habronattus spp.–immatures[a]	3	5
Pellenes spp.–immatures[a]	1	1
Phiddipus apacheanus (Chamberlin and Gertsch)	0	5
Phiddipus ardens (Peckham & Peckham)	5	0
Phiddipus spp.–immatures	1	1
Salticus scenicus (Clerck)	0	1
Salticus spp.–immatures	0	1
Theridiidae		
Latrodectus hesperus (Chamberlin and Ivie)	8	0
Latrodectus mactans (Fabricius)	11	2
Latrodectus spp.–immatures	58	6
Steatoda albomaculata (De Geer)	51	21
Steatoda variata (Gertsch)	0	2
Steatoda spp.–immatures[a]	22	10
Philodromidae		
Thanatus altimontis (Gertsch)[a]	3	11
Tibellus chamberlini (Gertsch)	0	2
Thomisidae		
Xysticus aprilinus (Bryant)	24	8
Xysticus nigromaculatus (Keyserling)	28	53
Xysticus spp.–immatures[a]	15	17

Species identifications were aided by David Richman (Department of Plant Pathology and Weed Science, New Mexico State University, Las Cruces). Immatures were not distinguished to species. Voucher specimens were deposited at the C. P. Gillette Museum of Arthropod Biodiversity, Department of Biological Sciences and Pest Management, Colorado State University, Fort Collins, CO.

[a] Spider species reported by Kumar et al. (1976).

immatures) and in August 1995 (four adults, 32 immatures). The remaining families (Agelenidae, Corrinidae, Dictynidae, Thomisidae and Philodromidae, and Salticidae) were collected in relatively low numbers.

Species-Specific Responses. To analyze how the overall spider community was influenced by habitat type, we used detrended correspondence analysis to define multivariate axes describing the spider community. Detrended correspondence analysis of the grass and mixed-grass/shrub spider communities revealed site/habitat-score positions that did not overlap, indicating significant differences in the spider communities between the two habitats (Fig. 1). Axis 1 represents between habitat differences. Axis 2 represents yearly and within-habitat variation. There was relatively high similarity in species composition and abundance among trapping webs occurring in the grass sites, whereas trapping webs in the mixed-grass/shrub habitat appear more variable along axis 1 (Fig. 1). In the mixed-grass/shrub sites, one trapping web (web 6) is well separated from the other trapping webs along axis 1 in both 1995 and 1996. Eigenvalues obtained from the detrended correspondence analysis measure the proportion of total variation in ground-dwelling spider abundance explained by each axis (Jongman et al. 1995). The eigenvalues for axis 1 through 3 were 0.262, 0.0548, and 0.0263, respectively. The two-axes solution explains 71.49% of the variance. Axis 1 explains 59.12% of the species- (between) habitat relationship and axis 2 explains 12.36% of the species-within habitat relationship. Of the 10 most abundant spider species, several species clearly were associated more with a particular habitat type (Fig 1). *Schizocosa mccooki* (Montgomery), *S. mimula* (Gertsch), *Gnaphosa clara* (Keyserling), and *G. brumalis* (Thorell) were most abundant in the grass sites. In mixed-grass/shrub sites, *Schizocosa* spp. (immatures), *Gnaphosa* spp. (immatures), *G. sericata* (Koch), *Haplodrassus signifer* (Koch), *Habronattus altanus* (Chamberlin), and *Xysticus nigromaculatus* (Keyserling) were most abundant. *Gnaphosa sericata* had especially high counts in trapping web 6, hence its distant position on the ordination diagram.

Seasonal Responses. Detrended correspondence analysis also revealed consistent seasonal changes in the distribution and abundance of spider species between the two habitats (Fig. 2). Axis 1 and 2 represent monthly variation along both axes. The site/habitat scores for each early-season (May and June) sampling period occupied the same region of the detrended correspondence analysis space. Late-season communities differed between habitat types along both axes (Fig. 2). This shows that there were significant changes in the spider communities between the two habitats throughout the summer and that the seasonal dynamics influencing these changes were unique and consistent for each habitat type. The seasonal positions and trajectories of the site/habitat scores for the spider communities in both habitat types were the same in both years. Trapping web 6, a mixed-grass/shrub web, was less variable along the ordination axes

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Table 3. Family and species ranks of numerically dominant spiders collected by month in 1995 and 1996 at the Central Plains Experimental Range, Weld County, CO

Month	Family rank	Numerical dominants		Species rank
		Family	Species	
		1995		
May	1	Gnaphosidae	*Haplodrassus signifer*	2
	2	Lycosidae	*Schizosa* spp.–immatures	1
June	1	Lycosidae	*Schizocosa mccooki*	1
			Schizocosa mimula	2
	2	Gnaphosidae	*Gnaphosa clara*	3
July	1	Lycosidae	*Schizocosa mccooki*	1
	2	Gnaphosidae	*Gnaphosa sericata*	2
August	1	Lycosidae	*Schizocosa mccooki*	1
			Schizocosa spp.–immatures	2
	2	Gnaphosidae	*Gnaphosa brumalis*	4
	3	Theridiidae	*Latrodectus* spp.–immatures	3
		1996		
May	1	Lycosidae	*Schizocosa mimula*	1
	2	Gnaphosidae	*Gnaphosa clara*	2
June	1	Lycosidae	*Schizocosa mccooki*	1
			Schizocosa mimula	2
	2	Gnaphosidae	*Gnaphosa sericata*	3
July	1	Lycosidae	*Schizocosa mccooki*	1
			Schizosa spp.–immatures	2
	2	Gnaphosidae	*Gnaphosa brumalis*	3
August	1	Lycosidae	*Schizocosa* spp.–immatures	1
	2	Gnaphosidae	*Gnaphosa* spp.–immatures	2

than the other trapping webs, especially in June, July and August, for both years. Trapping web 6 is the same web that was more distant from the other mixed-grass/shrub trapping webs in the site by habitat ordination (Fig. 1). This suggests that trapping web 6 may be unique among the mixed-grass/shrub sites investigated. The eigenvalues for axis 1 through 3 were 0.3520, 0.2463, and 0.1598, respectively. The two-axes solution explains 78.92% of the variance. Axis 1 explains 46.43% of the species-across season relationship and axis 2 explains 32.48% of the species-within season relationship.

Table 4. Two-factor ANOVA with repeated measures (family and habitat as fixed effects and season as a repeated measure) on the mean number of spiders collected by family in 1995 and 1996 at the Central Plains Experimental Range, Weld County, CO

Factors	Wilks lambda	*F*	df	*P*
	1995			
Between subjects				
Family	0.1150	36.9318	5, 24	0.0000
Habitat	0.8188	5.3112	1, 24	0.0301
Habitat°Family	0.6381	2.7219	5, 24	0.0438
Within subjects				
Season	0.3860	11.6629	3, 22	0.0001
Season°Family	0.0672	6.7600	15, 61.1	0.0000
Season°Habitat	0.7692	2.2004	3, 22	0.1166
Season°Habitat°Family	0.4548	1.3460	15, 61.1	0.2041
	1996			
Between subjects				
Family	0.1417	29.0678	5, 24	0.0000
Habitat	0.9161	2.1970	1, 24	0.0000
Habitat°Family	0.8721	0.7037	5, 24	0.1513
Within subjects				
Season	0.3285	14.9885	3, 22	0.0000
Season°Family	0.1317	4.4174	15, 61.1	0.0000
Season°Habitat	0.9462	0.4165	3, 22	0.7429
Seaon°Habitat°Family	0.6474	0.6951	15, 61.1	0.7793

Table 5. Mean number of spiders collected by family pet trapping web in grass and mixed-grass/shrub habitats (±1 SEM) at the Central Plains Experimental Range, Weld County, CO

Spider family	Grass	Mixed-grass/shrub
	1995	
Corinnidae	0.42 ± 0.19aA	0.75 ± 0.22aA
Gnaphosidae	20.75 ± 2.80bA	17.67 ± 3.46bA
Lycosidae	52.83 ± 9.63cA	30.33 ± 8.23cB
Salticidae	3.75 ± 0.74abA	2.33 ± 0.68abA
Theridiidae	5.17 ± 1.42abA	1.91 ± 0.80abB
Thomisidae	3.00 ± 0.55aA	3.08 ± 0.84aA
	1996	
Corinnidae	0.50 ± 0.26aA	0.67 ± 0.19aA
Gnaphosidae	24.33 ± 4.35bA	18.33 ± 4.60bA
Lycosidae	41.67 ± 5.29cA	32.00 ± 6.36cA
Salticidae	2.08 ± 0.40aA	2.17 ± 0.70aA
Theridiidae	7.33 ± 1.68aA	1.50 ± 0.45aB
Thomisidae	2.83 ± 0.60aA	4.50 ± 1.10aA

Different lowercase letters denote statistical significance in column values within year at $P = 0.05$. Different capital letters denote statistical significance in row values at $P = 0.05$.

Discussion

We found significant differences in the ground-dwelling spider communities between grass and mixed-grass/shrub habitats and throughout the summer. Based on fine-scale habitat measurements we were able to detect broad scale differences in the ground-dwelling spider communities in grass and mixed-grass/shrub habitats in the shortgrass steppe. Overall species richness was not a good indicator of species-specific habitat differences. This may be a function of the relative mobile ability of ground-dwelling spiders to move among habitats, such as 'ballooning' or 'wandering.' However, there were clear habitat differences in the distribution and abundance of the 10 most common spider species that may reflect species-specific differences in habitat requirements. Grass sites were dominated by two families, Lycosidae and Gnaphosidae, whereas abundant spiders in the mixed-grass/shrub sites were from the families, Lycosidae, Gnaphosidae, Thomisidae (*Xysticus nigromaculatus*), and Salticidae (*Habronattus altanus*). Because Lycosidae and Gnaphosidae comprised 85% of the total captures we will focus most of our discussion on spiders in these two families.

Lycosids have been shown to demonstrate microhabitat preferences along forest litter gradients (Uetz 1975, 1977, 1979) and in agroecosystems (Marshall and Rypstra 1999). They may select microhabitats based on available moisture, leaf litter, and herbaceous vegetation (Cady 1984, Richman 1995). In our study,

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Schizocosa mccooki and *S. mimula* (Lycosidae) were the most abundant spider species collected. Overall, *S. mccooki* was the most abundant spider species captured and was more than twice as abundant in grass sites compared with mixed-grass/shrub sites (Table 2). However, at the family level, lycosids were significantly more abundant in grass sites in 1995 only. In 1996 there was a similar although not statistically significant difference. Also, in the genus *Schizocosa* there was habitat separation between adults and immatures, with adults being more abundant and highly associated with grass than mixed-grass/shrub sites (Fig 1). This pattern may reflect some spatial partitioning between habitats at a critical developmental stage in these spiders. It is possible that immature *Schizocosa* spp. may escape predatory pressures from adult spiders of the same species in mixed-grass/shrub habitats or that these spiders may be partitioning prey resources by reducing the spatial overlap of foraging activities (Uetz 1977, Kronk and Riechert 1979). An alternative hypothesis is that immature *Schizocosa* species were less mobile and less active in mixed-grass/shrub compared with grass sites, thereby decreasing their chances for capture. Local population distributions have been attributed to environmental effects on the mobility of organisms (Wiens et al. 1995). Therefore, habitat separation of adult and immature lycosid spiders may be a function of movement capabilities of adult compared with immature spiders or a consequence of some spatial partitioning of resources by the same or taxonomically similar species at different developmental stages.

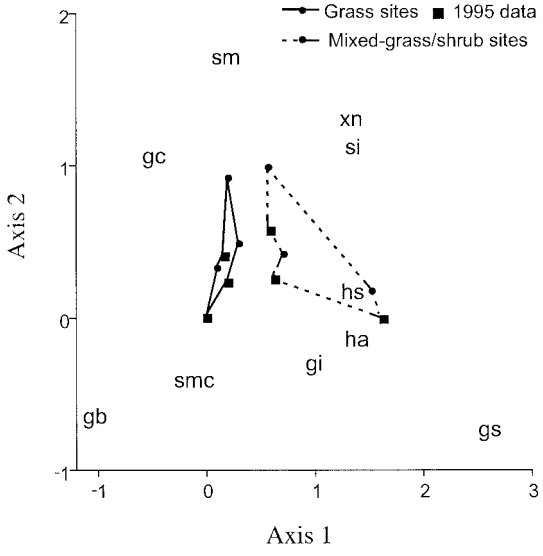

Fig. 1. Locations of grass and mixed-grass/shrub sites and species positions of the 10 most abundant spider groups in the space defined by a detrended correspondence analysis. smc, *Schizocosa mccooki;* sm, *Schizocosa mimula;* gb, *Gnaphosa brumalis;* gc, *Gnaphosa clara;* si, *Schizocosa* spp. (immatures); gs, *Gnaphosa sericata;* gi, *Gnaphosa* spp. (immatures); ha, *Habronattus altanus;* xn, *Xysticus nigromaculatus;* hs, *Haplodrassus signifer.*

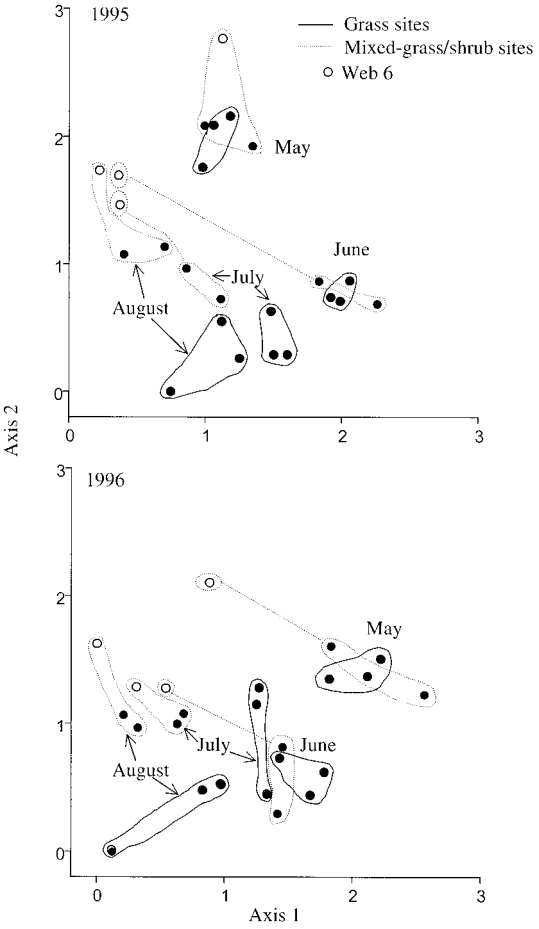

Fig. 2. Locations of site/habitat scores of grass and mixed-grass sites in the space defined by a detrended correspondence analysis of spider community composition and abundance at different sampling periods in May, June, July, and August of 1995 and 1996. The analysis was conducted on both 1995 and 1996 data together, however each year is graphed separately for presentation simplification.

The family Gnaphosidae had the greatest diversity in terms of species and demonstrated significant species-specific patterns of habitat and seasonal abundance. Species of Gnaphosidae can be found in a wide diversity of habitats. The southern Rocky Mountains, especially Colorado, has been considered the center of speciation of *Gnaphosa* in North America (Platnick and Shadab 1975). Most gnaphosids are nocturnal, which in part explains why they are among the least well-known of American spiders (Platnick and Shadab 1975, Platnick 1993). The hunting tactics of many species may resemble those used by lycosids. The high abundance and nocturnal habits of gnaphosids (sensu, Bishop and Riechert 1990) suggests that there may be some diel partitioning of resources between lycosids and gnaphosids (the two most abundant spider families collected). Habitat differences and seasonal turnover of species in Gnaphosidae was consistent in both years. *Haplodrassus signifer* (mixed-grass/shrub) and

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Gnaphosa clara (grass) may be considered early-season spiders, each with different habitat affinities. *Gnaphosa sericata* (mixed-grass/shrub) and *G. brumalis* (grass) were late-season spiders with different habitat affinities (Fig. 1; Table 3). This extreme turnover in species abundance and habitat segregation of the most abundant gnaphosids, both within and between habitat types, may represent some temporal and spatial partitioning of resources by the most abundant gnaphosid species. A similar pattern has been described in alpine tundra spiders (Schmoller 1970).

Some spiders may have been underrepresented in our samples, especially the Agelenidae, Dictynidae, and Theridiidae. Members of these families are probably best sampled with techniques other than pitfall trapping (e.g., sweepnets or vacuum extraction) due to their web-building habits (Comstock 1965, Kaston 1978) and may not be suitable for inclusion in our ground-dwelling community. Yet, several theridiid spider species were relatively abundant, significantly most abundant in grass sites, suggesting that they may be important members of the ground-dwelling community at certain times, especially during early stages in their development when they may be searching for web site locations.

There is evidence that trapping web 6 (a mixed-grass/shrub site) had a different influence on the mixed-grass/shrub spider community than the other mixed-grass/shrub sites. The uniqueness of site 6 may stem from a higher percentage of bare ground, fewer small shrubs and cactus, and a prevalence of sandy-loam soil (Table 1). Web 6 recorded the highest abundance of *G. sericata* (an abundant Gnaphosidae) than the other sites. It appears that the high percentage of bare ground patches in this area may have had a dampening effect on the microclimate in this site, thereby influencing ground-dwelling spider community structure. This is evident in the relatively similar seasonal positions of web 6 compared with the other grass and mixed-grass/shrub sites in the ordination diagram and the numerical dominance of *G. sericata* (Fig. 2). These results may underscore an additional habitat component or threshold in the amount of bare ground tolerable in an area before significant changes in the spider communities are evident.

Analysis of the spider community at the family level resulted in few significant differences and failed to elucidate many of the important ecological patterns in the data. By examining the spider community at the species level we show that there are complex species-specific requirements for the spatial and temporal heterogeneity of the shortgrass steppe environment. Other research conducted at the site has demonstrated species-specific responses by insects (beetles) and small mammals to mixed-grass/shrub and grass habitats (McIntyre 1997, Stapp 1997). Our results suggest that species-specific responses to variations in habitat structure are important in structuring the overall spider community and that this sort of species level knowledge is necessary to predict habitat and seasonal distributions of ground-dwelling spiders in grassland ecosystems. These results provide a foundation for future studies of ground-dwelling spider communities in grasslands and are relevant to literature and research on the population dynamics and community interactions of rangeland arthropods.

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