

## GROUND-LAYER SPIDERS (ARANEAE) OF A GEORGIA PIEDMONT FLOODPLAIN AGROECOSYSTEM: SPECIES LIST, PHENOLOGY AND HABITAT SELECTION

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**ABSTRACT.** Monthly pitfall trapping in 1990 and 1991 at Horseshoe Bend Experimental Area, Clarke County, Georgia, yielded 112 species of spiders belonging to 25 families. Examination of additional collections brings the site total to 145 species in 26 families, including southern or southeastern range extensions for *Agelenopsis kastoni*, *Sphodros atlanticus*, *Bathypantes pallidus*, *Eridantes erigonoides*, *Floricomus tallulae*, *Grammonota inornata*, and *Walckenaeria carolina*, and a northeastern range extension for *Paratheridula perniciosus*. *Ceraticelus emertoni* and *Neriene redacta* are also reported from Georgia for the first time. The proportional distribution of pitfall-trapped species within families does not differ significantly from that reported for Berry's (1966) pitfall trapping in the North Carolina Piedmont (about 450 km away), suggesting regional similarity of the Piedmont ground-layer spider fauna. Data on phenology and relative catch of species among the four habitats sampled (conventional and no-tillage agricultural fields, grassy field borders, and the surrounding deciduous riparian forest) are given for the most abundant species. Habitat selection of 15 abundant species was statistically analyzed; most of the species' populations displayed strong preferences for particular habitats. It is clear that species "spillover" from adjacent habitats contributes to the faunal richness of each habitat, and that maintenance of a mosaic of habitats within an agroecosystem landscape maximizes spider biodiversity.

Since Chamberlin & Ivie's (1944) seminal effort, little work has been conducted on the ground-layer spider fauna of the southeastern Piedmont Plateau region, the mid-elevation area located between the Appalachian Mountains and the Atlantic Coastal Plain. One notable exception is Berry's (1966, 1970) study of the old-field succession of the North Carolina Piedmont, which lists 331 species from the region, including 217 (66%) from over 10,000 pitfall trap/days. The present work reports on the spiders collected during ecological research conducted at Horseshoe Bend Experimental Area, a mosaic of agricultural plots and forest on the floodplain of the Oconee River on the Georgia Piedmont.

In order to better understand the distribution of spiders within the various habitats of this agroecosystem, systematic pitfall trapping was conducted in four distinct (but adjacent) habitats: (1) the natural floodplain forest, undisturbed by management practices, (2) con-

ventional tillage agricultural fields, (3) no-tillage agricultural fields, and (4) the grassy field borders that surround these habitats. Although the four habitat types at Horseshoe Bend are rather small and in close proximity (all within 10 m of each other), they are typical of the modern fragmented landscape of Georgia. Much of the cultivated land in the Georgia Piedmont consists of small plots with a high proportion of "edge" (Turner & Ruscher 1988).

The Horseshoe Bend agricultural fields are planted in grain sorghum in the summer and in winter-rye and crimson clover in the winter. Blumberg (1979) examined ground-layer spiders in these systems at Horseshoe Bend as part of an overall arthropod community characterization, but the low sampling intensity and broad scope of the study meant that the spider assemblages were not extensively characterized and analyzed. The only other study of spiders in grain sorghum is Bailey & Chada's (1968) work describing assemblages in Oklahoma. Blumberg (1979) and this study remain the only examinations of grain sor-

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ghum spider assemblages in the southeastern United States.

The Horseshoe Bend site might be expected to harbor a fairly high diversity of species. The floodplain on which the site is located is a mesic, highly productive site, and the fairly undisturbed floodplain forest is now a rather uncommon habitat in the Georgia Piedmont. The north-facing slopes of the Oconee River harbor a flora (e.g., beech, *Fagus grandifolia*) more characteristic of forests farther north (F.B. Golley pers. comm.). The various open field habitats increase the site's spatial heterogeneity and plant species diversity. Finally, riparian zones such as Horseshoe Bend's floodplain forest may serve as corridors, allowing organisms that are more eurytopic in the mountains or the coastal plain to extend their ranges into the Piedmont.

The objectives of this work are to list the spiders that occur in various habitats on a Georgia Piedmont floodplain; to compare the resultant data with Berry's (1966) list of North Carolina Piedmont fauna, and with other faunal lists compiled using similar collecting methods; and to present phenology and habitat selection data for some of the most abundantly trapped species at the site.

#### METHODS

**Study site and habitats.**—This study was conducted at the University of Georgia's Horseshoe Bend Experimental Area near Athens in Clarke County, Georgia (33°55'52"N, 83°21'04"W). It is located on the floodplain of the Oconee River (elevation 244 m) and much of the 14 ha site is occupied by a deciduous riparian forest. The 2 ha currently occupied by the agricultural plots were used as pasture prior to 1964. Between 1964–1978, studies of old-field succession occupied the site (Blumberg & Crossley 1983). The area is relatively flat (slopes < 3%) and the soil is a well-drained, moderately acidic sandy-clay loam (House & Parmelee 1985). The area is flooded in certain years; one corner of the study area was flooded during a week in the winter of 1990, several months before this study was conducted.

The four habitats sampled are as follows:

**Floodplain forest.** This habitat is a deciduous forest typical of southeastern Piedmont riparian zones. Some areas have not been logged for a considerable period, probably in

excess of 100 years, judging from the diameter of some of the trees (F. Golley pers. comm.), though some of the forest was logged as recently as 50 years ago (P. Hendrix pers. comm.). Dominant trees include sweetgum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), water oak (*Quercus nigra*), chestnut oak (*Quercus prinus*) and beech (*Fagus grandifolia*). The dominant understory tree is flowering dogwood (*Cornus florida*), and poison ivy (*Toxicodendron radicans*) is abundant in the herbaceous layer.

**Grassy field border:** The agricultural fields are separated from the forest by grassy field borders approximately 5 m wide. These consist mainly of fescue grass (*Festuca* sp.) interspersed with annuals. The field borders are contiguous with larger areas of meadow of up to 15 m width in other areas of the Horseshoe Bend clearing. All meadow areas are maintained by periodic mowing, usually four times during the growing season.

**No-tillage agroecosystem:** Four of the eight 32 × 32 m experimental sub-plots on the site have been maintained as no-tillage agricultural plots since 1978. Sorghum (*Sorghum bicolor*) is grown as a summer crop (approx. June–October), and winter rye (*Secale cereale*) and crimson clover (*Trifolium incarnatum*) are grown as cover crops in the winter (approx. November–May). Major weeds include pigweed (*Amaranthus retroflexus*), sicklepod (*Cassia obtusifolia*), and Johnson grass (*Sorghum halepense*) (Parmelee et al. 1989). At the end of both growing seasons the crop is harvested and the next crop is planted by drilling (summer crop) or by surface broadcasting (winter crop). Lack of disturbance to the soil allows a thick litter layer to build up, creating a very different ground-layer microclimate than in the conventional tillage plots (Hendrix et al. 1986).

**Conventional tillage agroecosystem:** The four conventional tillage plots are maintained under the same crop rotation as are the no-tillage plots. However, after the crops are harvested, the conventional tillage plots are moldboard plowed, disked, rotary tilled, and seeded. At the beginning of each growing season, the conventional tillage plots are essentially bare, exposed soil. Conventional tillage plots are thus the most highly disturbed of the four floodplain habitats, with the forest being

the least disturbed by management practices. No pesticides or irrigation are used on any habitat. For specific dates of plowing, planting, and mowing, see Draney (1992).

**Sampling.**—The ground-layer spider assemblages of the four habitats were sampled with 9.5 cm diameter plastic pitfall traps (Morrill 1975) containing 70% ethanol. Traps were run only during days without significant precipitation. Pitfall traps were run for one 24-hour period approximately once a month from August 1990 to August 1991. Twenty-four hour trapping periods sample fauna equally during all times of the day, avoiding the diel bias that can result in a distorted view of community structure (Costa & Crossley 1991). During the first five trapping periods (August 1990–January 1991), ten pitfall traps were placed in each habitat. To obtain a large enough sample to examine the patterns of spider diversity in the four habitats, the number of pitfall traps in each habitat was increased to 20, starting in February 1991 and continuing for the duration of sampling. Cumulative sampling effort was 760 trap-days, 190 days per habitat. For specific trapping dates, see Draney (1992).

Traps were placed in lines of five traps each, resulting in a stratified-random design. Traps within a line were separated by approximately 5 m. Lines were separated from each other by a randomly-selected distance between 5–15 m. In the agroecosystems and the forest, the first trap of each line was placed 5 m from the habitat boundary and lines continued perpendicular to the habitat boundary. In the grassy field margins, traps were placed approximately in the center of the field margin strips, which were 4–5 m wide. For purposes of data analyses, each five trap pitfall line was pooled as a sample unit.

**Processing of samples.**—All Arachnida (other than Acari) were removed from the samples by visual inspection under a dissecting microscope, and stored in clean 70% ethanol for subsequent identification. Initially, spiders in each sample were sexed (male, female, or immature) and identified to morpho-species. Subsequently, animals were identified to species. Errors in initial morphospecies assignment precluded analysis of phenology and habitat selection for species in certain genera, including *Drassyllus*, *Gnaphosa*, *Scotinella*, *Theridion*, *Meioneta*, and two species of

*Phrurotimpus* (*P. borealis* and *P. emertoni*). Since specimens in many of the original samples were removed for use as voucher material, accurate re-examination of the original samples was not possible.

**Other sources of material.**—In order to include as much of the site's spider fauna as possible, all available material collected from Horseshoe Bend was examined in compiling the species list, although only the above-mentioned pitfall data were used in analyses of phenology and habitat selection. The sources are listed in Table 1.

All material was determined by the author, 1992–1995, except as noted in the acknowledgments. Identifications were confirmed during visits to the National Museum of Natural History and the American Museum of Natural History, 1995–1996. Voucher specimens of all taxa have been deposited at the University of Georgia's Natural History Museum.

**Comparison of pitfall faunas.**—Barnes & Barnes (1955) remains the most comprehensive comparison of southeastern spider assemblages. Their work described the "abstract" spider community which occurs fairly constantly in the broomsedge successional habitats occurring on the southeastern Piedmont, and was the first paper to identify such a predictable spider assemblage (Turnbull 1973; Foelix 1982). Comparison of the pitfall fauna of the present study with that of Berry (1966) could indicate the degree of constancy in the ground-layer Piedmont fauna, at least between two widely separated sites (about 450 km apart) in the region.

Differences in sampling effort and nomenclatural changes in the years since Berry's (1966) work make a direct species-level comparison impossible. However, the faunas can be compared at the level of family by examining the proportion of total species found in each family (Table 2). Family richness (28 vs. 24) varies little between the lists. If forest and field assemblages are similar in structure, function, and biogeographic history throughout the Piedmont region (the abstract community *sensu* Barnes & Barnes 1955), then given families should likewise either be diverse and dominate assemblages in terms of species, or remain species-poor throughout the region. To test this, I compared the proportion of total species found in each family at Horseshoe Bend with the number of species ex-

Table 1.—Spiders of Horseshoe Bend Experimental Area, Clarke County, Georgia. All species were trapped in the trough-type or monthly cup-type pitfall traps run in 1990 and 1991 except those species marked with an \*, which are not considered "pitfall species" and not included in comparisons with other pitfall trap faunas. Sources of specimens are: 1, Collected by J. I. Richardson in 1967. Collection methods not known; 2, Collected by G. Bakelaar, 1975, via vacuum sampling and/or sweepnetting of herbaceous vegetation; 3, Hand collected or observed by M. Draney at various times in 1990 and 1991; 4, Large formalin-filled, trough-like directional pitfall traps (140 × 40 cm) placed at habitat boundaries and operated 26 May–8 July, 1991; 5, Monthly 24-hour cup-type pitfall traps in 1990 and 1991 (total effort = 918 trap/days). prob. = "probably;" adult specimens/male specimens needed to confirm identification. cf. = "near;" specimen may be an individual of that species, but differences from the descriptions indicate that it may belong to a closely related species. Genera within families and families within suborders are listed alphabetically. Nomenclature follows Platnick (1993).

	Source of specimens
<b>Mygalomorphae</b>	
<b>Atypidae</b>	
<i>Sphodros atlanticus</i> Gertsch & Platnick 1980	4
<b>Ctenizidae</b>	
<i>Ummidia audouini</i> (Lucas 1835)	4
<b>Cyrtachenidae</b>	
<i>Myrmekiaphila fluviatilis</i> (Hentz 1850)	3, 5
<b>Araneomorphae</b>	
<b>Agelenidae</b>	
<i>Agelenopsis kastoni</i> Chamberlin & Ivie 1941	2, 3, 5
<b>Amaurobiidae</b>	
<i>Coras medicinalis</i> (Hentz 1821)	4
<i>Coras</i> sp.	4
<i>Wadotes bimucronatus</i> (Simon 1898)	4, 5
<b>Anyphaenidae</b>	
* <i>Teudis mordax</i> (O. P.-Cambridge 1896)	2
* <i>Wulfila saltabunda</i> (Hentz 1847)	2
<b>Araneidae</b>	
<i>Acacesia hamata</i> (Hentz 1847)	2, 4, 5
* <i>Acanthepeira stellata</i> (Walckenaer 1805)	2, 3
* <i>Araneus bicentenarius</i> (McCook 1888)	3
* <i>Araneus</i> sp.	2
* <i>Araniella displicata</i> (Hentz 1847)	2
* <i>Argiope aurantia</i> Lucas 1833	2, 3
* <i>Cyclosa turbinata</i> (Walckenaer 1841)	1, 2, 3
<i>Gea heptagon</i> (Hentz 1850)	1, 4, 5
* <i>Larinia directa</i> (Hentz 1847)	2
* <i>Micrathena gracilis</i> (Walckenaer 1805)	3
<i>Micrathena mitrata</i> (Hentz 1850)	5
* <i>Micrathena sagittata</i> (Walckenaer 1841)	2
* <i>Neoscona arabesca</i> (Walckenaer 1841)	2, 3
<b>Clubionidae</b>	
<i>Cheiracanthium inclusum</i> (Hentz 1847)	2, 5
<i>Clubiona</i> sp. A	1, 2, 5
* <i>Clubiona</i> sp. B	2
<i>Elaver</i> prob. <i>exceptus</i> (L. Koch 1866)	4
<b>Corinnidae</b>	
<i>Castianeira cingulata</i> (C. L. Koch 1841)	3, 5
<i>Castianeira gertschi</i> Kaston 1945	4, 5
<i>Castianeira longipalpa</i> (Hentz 1847)	4, 5
<i>Castianeira trilineata</i> (Hentz 1847)	4
<i>Trachelas deceptus</i> (Banks 1895)	2, 4, 5

Table 1.—Continued.

	Source of specimens
<b>Ctenidae</b>	
<i>Anahita punctulata</i> (Hentz 1844)	5
<b>Dictynidae</b>	
<i>Dictyna volucripes</i> Keyserling 1881	2, 5
<b>Gnaphosidae</b>	
* <i>Callilepis</i> sp.	2
<i>Cesonia bilineata</i> (Hentz 1847)	2, 4
<i>Drassyllus covensis</i> Exline 1962	5
<i>Drassyllus dixinus</i> Chamberlin 1922	4, 5
<i>Drassyllus eremitus</i> Chamberlin 1922	4
<i>Drassyllus ellipes</i> Chamberlin & Gertsch 1940	4
<i>Drassyllus novus</i> (Banks 1895)	5
<i>Gnaphosa fontinalis</i> Keyserling 1887	4, 5
<i>Gnaphosa sericata</i> (L. Koch 1866)	3, 4, 5
<i>Sergiolus ocellatus</i> (Walckenaer 1837)	1, 4
<i>Zelotes aiken</i> Platnick & Shadab 1983	3, 4, 5
<i>Zelotes duplex</i> Chamberlin 1922	4
<b>Hahnidae</b>	
<i>Neoantistea agilis</i> (Keyserling 1887)	5
<i>Neoantistea riparia</i> (Keyserling 1887)	5
<b>Linyphiidae</b>	
<b>Erigoninae</b>	
<i>Ceraticelus emertoni</i> (O. P.-Cambridge 1874)	1, 5
<i>Ceratinella brunnea</i> Emerton 1882	5
<i>Ceratinops crenatus</i> Emerton 1882	5
<i>Eperigone fradeorum</i> (Berland 1932)	4, 5
<i>Eperigone inornata</i> Ivie & Barrows 1935	5
<i>Eridantes erigonoides</i> (Emerton 1882)	4, 5
<i>Erigone autumnalis</i> Emerton 1882	1, 4, 5
<i>Floricomus tallulae</i> Chamberlin & Ivie 1944	5
<i>Floricomus</i> sp.?	5
<i>Goneatara platyrhinus</i> (Crosby & Bishop 1927)	5
<i>Grammonota inornata</i> Emerton 1882	5
<i>Idionella sclerata</i> (Ivie & Barrows 1935)	5
<i>Walckenaeria carolina</i> Millidge 1983	5
<i>Walckenaeria spiralis</i> (Emerton 1882)	4, 5
<b>Linyphiinae</b>	
<i>Bathyphantes pallidus</i> (Banks 1892)	4, 5
<i>Centromerus latidens</i> (Emerton 1882)	5
<i>Florinda coccinea</i> (Hentz 1850)	1, 3, 4, 5
<i>Frontinella pyramitela</i> (Walckenaer 1841)	1, 3, 4, 5
<i>Lepthyphantes sabulosus</i> (Keyserling 1886)	5
<i>Meioneta angulata</i> (Emerton 1882)	5
<i>Meioneta barrowsi</i> Chamberlin & Ivie 1944	5
<i>Meioneta</i> cf. <i>leucophora</i> Chamberlin & Ivie 1944	5
<i>Meioneta</i> cf. <i>longipes</i> Chamberlin & Ivie 1944	5
<i>Meioneta micaria</i> (Emerton 1882)	5
<i>Meioneta</i> cf. <i>meridionalis</i> (Crosby & Bishop 1936)	5
<i>Meioneta serrata</i> (Emerton 1909)	5
<i>Neriere radiata</i> (Walckenaer 1841)	5
<i>Neriere redacta</i> Chamberlin 1925	1, 5
<i>Neriere variabilis</i> (Banks 1892)	5
<i>Tennesseeum formicum</i> (Emerton 1882)	4, 5

Table 1.—Continued.

	Source of specimens
<b>Liocranidae</b>	
<i>Agroeca</i> prob. <i>pratensis</i> Emerton 1890	5
<i>Phrurotimpus alarius</i> (Hentz 1847)	4, 5
<i>Phrurotimpus borealis</i> (Emerton 1911)	3, 4, 5
<i>Phrurotimpus emertoni</i> (Gertsch 1935)	4, 5
<i>Scotinella fratrella</i> (Gertsch 1935)	5
<i>Scotinella redempta</i> (Gertsch 1941)	5
<b>Lycosidae</b>	
<i>Allocosa funerea</i> (Hentz 1844)	3, 4, 5
<i>Gladicosa gulosa</i> (Walckenaer 1837)	1, 5
<i>Hogna lenta</i> (Hentz 1844)	2, 3, 5
<i>Hogna timuqua</i> (Wallace 1942)	3, 4, 5
<i>Pardosa atlantica</i> Emerton 1913	2, 3, 4, 5
<i>Pardosa milvina</i> (Hentz 1844)	4, 5
<i>Pardosa pauxilla</i> Montgomery 1904	4, 5
<i>Pirata iviei</i> Wallace & Exline 1978	1, 4, 5
<i>Rabidosa rabida</i> (Walckenaer 1837)	3, 4, 5
<i>Schizocosa ocreata</i> (Hentz 1844)	4, 5
<i>Schizocosa</i> prob. <i>bilineata</i> (Emerton 1885)	5
<b>Oxyopidae</b>	
* <i>Oxyopes aglossus</i> Chamberlin 1929	2
<i>Oxyopes salticus</i> Hentz 1845	1, 2, 3, 4, 5
<i>Peucetia viridans</i> (Hentz 1832)	2, 3, 4
<b>Philodromidae</b>	
* <i>Philodromus imbecillus</i> Keyserling 1880	2
* <i>Philodromus</i> sp. A	2
* <i>Thanatus formicinus</i> (Clerck 1757)	1
<i>Tibellus duttoni</i> (Hentz 1847)	1, 4
<b>Pisauridae</b>	
<i>Pisaurina mira</i> (Walckenaer 1837)	3, 5
<b>Salticidae</b>	
<i>Corythalia canosa</i> (Walckenaer 1837)	4, 5
<i>Habrocestum parvulum</i> (Banks 1895)	4, 5
<i>Habronattus coecadus</i> (Hentz 1846)	2, 5
* <i>Maevia inclemens</i> (Walckenaer 1837)	2
<i>Marpissa lineata</i> (C. L. Koch 1848)	4
* <i>Marpissa pikei</i> (Peckham & Peckham 1888)	2
* <i>Metaphidippus galathea</i> (Walckenaer 1837)	2
<i>Metaphidippus sexmaculatus</i> (Banks 1895)	2, 4, 5
<i>Phidippus audax</i> (Hentz 1845)	2, 3, 4
* <i>Phidippus princeps</i> (Peckham & Peckham 1883)	2
* <i>Phidippus rimator</i> (Walckenaer 1837)	1, 2
* <i>Sarinda hentzi</i> (Banks 1913)	1
<i>Sitticus cursor</i> Barrows 1919	4, 5
<i>Sitticus</i> prob. <i>magnus</i> Chamberlin & Ivie 1944	5
<i>Thiodina puerpura</i> (Hentz 1846)	2, 4
<i>Zygoballus sexpunctatus</i> (Hentz 1845)	2, 4
<b>Segestriidae</b>	
<i>Ariadna bicolor</i> (Hentz 1842)	5
<b>Tetragnathidae</b>	
<i>Glenognatha foxi</i> (McCook 1893)	3, 4, 5
<i>Pachygnatha tristriata</i> C. L. Koch 1845	4
<i>Tetragnatha laboriosa</i> Hentz 1850	2, 3, 4
<i>Tetragnatha straminea</i> Emerton 1884	2, 4

Table 1.—Continued.

	Source of specimens
<b>Theridiidae</b>	
<i>Argyrodes lacerta</i> (Walckenaer 1841)	5
<i>Dipoena nigra</i> (Emerton 1882)	5
<i>Latrodectus mactans</i> (Fabricius 1775)	3, 5
<i>Paratheridula pernicioso</i> (Keyserling 1886)	5
<i>Pholcomma hirsutum</i> Emerton 1882	5
<i>Phoroncidia americana</i> (Emerton 1882)	5
<i>Steatoda americana</i> (Emerton 1882)	5
<i>Stemmops ornatus</i> (Bryant 1933)	5
<i>Theridion</i> (2–3 spp.)	5
<i>Theridula opulenta</i> (Walckenaer 1841)	1, 2, 4
<b>Thomisidae</b>	
* <i>Misumena vatia</i> (Clerck 1757)	1, 2
* <i>Misumenoides formosipes</i> (Walckenaer 1837)	1, 2
* <i>Misumenops</i> (2 spp.)	2
* <i>Synema parvulum</i> (Hentz 1847)	1
* <i>Tmarus angulatus</i> (Walckenaer 1837)	2
<i>Xysticus ferox</i> (Hentz 1847)	1, 2, 3, 4, 5
<i>Xysticus triguttatus</i> Keyserling 1880	2, 4, 5
<i>Xysticus</i> sp.	4, 5
<b>Uloboridae</b>	
<i>Uloborus glomosus</i> (Walckenaer 1841)	3, 4
<b>Zoridae</b>	
<i>Zora pumila</i> (Hentz 1850)	4

pected in each family based on the proportional representation of the Berry (1966) data via a Chi-square test ( $\alpha = 0.05$ ; Table 3). For both lists, species identified only to genus were included only if no congener exists in the same list. Placement of species within families follows Platnick (1993) rather than Berry's (1966) original placement. In order to account for rare families that were not present in both lists, I lumped species from all families representing  $< 5\%$  of species richness of the Berry (1966) data into a single "other families" category.

If there is a similarity of ground-layer faunas throughout the Piedmont region, it is expected that the structure of the Horseshoe Bend fauna would be more similar to the Piedmont fauna of Berry (1966) than to pitfall fauna of other regions. I examined this by comparing the fauna of the present study to six other complete lists of pitfall spider species from outside the Piedmont Plateau region (Table 3) using the same chi-square test procedure.

**Data analysis.**—In comparing the Horseshoe Bend fauna with other faunas, only the pitfall samples are included, due to the un-

quantifiable and uneven collecting of vegetation-layer spiders. The 1990–91 pitfall collections (cup and trough traps) together represent a significant portion of the total spider diversity sampled at the site, including 112 species (77% of Horseshoe Bend total) belonging to 25 families, of which 71 species (63% of pitfall fauna) were sampled only with these methods.

For examining phenological patterns, data representative of the entire year without temporal bias are preferable. The phenology data set consists of 10 traps per habitat-date for all dates, August 1990–August 1991, and includes 960 adult spiders trapped over 480 trap/days.

To ensure taxonomic accuracy, only adult spiders were included in examining species' habitat preferences. In order to maximize sample size while avoiding temporal bias in sampling effort, only months with 20 pitfall traps (February–August 1991) were included in the data set from which habitat selection information was extracted. Each habitat was sampled with four 5-pitfall sample units on each of seven dates, giving 28 samples at each hab-

Table 2.—Comparison of Horseshoe Bend pitfall fauna with North Carolina Piedmont pitfall fauna listed in Berry (1966). Only species captured in pitfalls in the piedmont are recorded for Berry (1966). Taxa identified only to "sp." were included only if no congener was listed. Families are listed in descending order of species richness of the Horseshoe Bend fauna, with ties listed alphabetically.

Family	Number of species		% in this study	% in Berry 1966
	(this study)	(Berry 1966)		
Linyphiidae	29	47	25.89	21.66
Gnaphosidae	11	17	9.82	7.83
Lycosidae	11	34	9.82	15.67
Salticidae	10	23	8.93	10.60
Theridiidae	10	12	8.93	5.53
Liocranidae	6	6	5.36	2.76
Corinnidae	5	3	4.46	1.38
Tetragnathidae	4	4	3.57	1.84
Araneidae	3	16	2.68	7.37
Clubionidae	3	2	2.68	0.92
Thomisidae	3	11	2.68	5.07
Amaurobiidae	2	2	1.79	0.92
Hahniidae	2	4	1.79	1.84
Oxyopidae	2	4	1.79	1.84
Agelenidae	1	4	0.89	1.84
Atypidae	1	1	0.89	0.46
Ctenidae	1	0	0.89	0.00
Ctenizidae	1	1	0.89	0.46
Cyrtachenidiidae	1	1	0.89	0.46
Dictynidae	1	5	0.89	2.30
Philodromidae	1	5	0.89	2.30
Pisauridae	1	3	0.89	1.38
Segestriidae	1	1	0.89	0.46
Uloboridae	1	0	0.89	0.00
Zoridae	1	1	0.89	0.46
Anyphaenidae	0	5	0.00	2.30
Mimetidae	0	1	0.00	0.46
Mysmenidae	0	1	0.00	0.46
Nesticidae	0	1	0.00	0.46
Oonopidae	0	1	0.00	0.46
Titanoecidae	0	1	0.00	0.46
Total species	112	217	100.00	100.00
Total families	25	29		

itat. This data set consists of 1436 adult spiders trapped over 560 trap/days.

Data from each of 15 species in which at least 20 adults were trapped were analyzed separately by 2-Way ANOVA, with habitat as the major predictive variable and blocked by sample date. Data showing a significant among-habitat effect were subjected to a uni-

variate ANOVA and habitat means separation via Fisher's LSD.

## RESULTS AND DISCUSSION

**The Horseshoe Bend spider fauna.**—In all, 145 spider species belonging to 26 families have been collected at Horseshoe Bend (Table 1). This list represents the most extensive pitfall trapping survey yet conducted on the Georgia Piedmont. Note, however, that species collected only in 1967 and/or 1975 should be viewed with caution, as the collections were made in old field successional habitats that are largely absent from the site today.

A Chi-square test showed that the observed proportional distribution of species within families was not significantly different from the distribution predicted based on the Berry (1966) list (Table 3). Thus, the two faunas have similar family-level structure, which is consistent with the concept of an abstract Piedmont ground-layer assemblage.

In contrast to the Piedmont fauna comparison, the species-within-families distribution of the Horseshoe Bend fauna was significantly different ( $\alpha = 0.05$ ) from each of the six non-Piedmont faunas (Table 3). While the above does not constitute a rigorous test of the hypothesis that there exists an "abstract Piedmont ground-layer spider assemblage", it is at least consistent with such a hypothesis, and suggests some broad regional similarity of ground-layer spider faunas at the level of family.

**Range extensions.**—The pitfall data include records of new range extensions for eight species. Seven of these are southern or southeastern and one is a northeastern range extension. The predominance of southern over northern range extensions at this site is not surprising considering: 1) the site is located near the southeastern corner of the continent, so much more land occurs to the north and west of this site than to the south and east, and 2) much more spider collecting has been conducted to the north of this area, due to the historical distribution of arachnologists in the midwest and middle and northern Atlantic states.

*Agelenidae: Agelenopsis kastoni* Chamberlin & Ivie 1941: Two males were captured in the forest on 26–27 March and another male on 23–24 April 1991. Few collection localities of this spider have been published since

Table 3.—Results of Chi-square test ( $\alpha = 0.05$ ) of hypothesis that distribution of pitfall spider species richness between families is similar between present study and other faunas. Comparison studies are listed in descending order by number of families.

Study	Location	Habitats
Present study	Georgia Piedmont	Riparian fields and forest
Berry 1966	North Carolina Piedmont	Forests and old fields
Muma 1973	Central Florida	Pine, citrus, residential
Bailey & Chada 1968	Oklahoma	Grain sorghum
Muma 1975	New Mexico	Desert grassland, sand dunes
Maelfait & DeKeer 1990	Belgium	Grazed pasture, grassy edge
Muma & Muma 1949	Nebraska	Prairie, wooded ravine
Koponen 1992	Northwest Territories, Canada	Various low arctic habitats

Chamberlin & Ivie (1941) described the species from single male and females types from Haddam, Connecticut. It is known from Oconee and Pickens Counties, South Carolina (Gaddy & Morse 1985), and was listed in Berry (1966) as a North Carolina Piedmont pitfall spider, also collected in forest. The Horseshoe Bend records extend the known range of the species at least 50 km south. Recently, four males were trapped on the inner coastal plain as well, extending the known range even farther south (South Carolina: Barnwell County, Savannah River Site; Set-Aside #29, Scrub Oak Natural Area, 17 April–3 May 1996. Coll./Det. M. Draney).

*Atypidae: Sphodros atlanticus* Gertsch & Platnick 1980: One male was captured in a trough trap between the forest and the grassy field border during the last week of June 1991. Another male was trapped one week later at the edge of the sorghum field, about 75 m from the forest edge, where the spider presumably originated. Hall County, Georgia is the previous southernmost collection record; these specimens extend the known range of the species southward by about 40 km. Other localities reported for *S. atlanticus* are Jackson County, Illinois; Carteret and Jackson Counties, North Carolina; and Spotsylvania County, Virginia (Gertsch & Platnick 1980; Coyle et al. 1985). Berry's (1966, 1970) list does not include *S. atlanticus* but lists *Sphodros niger* (Emerton) (listed as *Atypus*); however, like many of the taxa on the present list, *Atypidae* was revised and *S. atlanticus* described since the publication of Berry's (1966, 1970) list (Gertsch & Platnick 1980).

*Linyphiidae: Bathyphantes pallidus* (Banks

1892): Seven adult individuals of this species were captured in the no-tillage and grassy field border habitats in March, May, June, July and September 1991. The species is widely distributed across the United States to about 34° N, with the southernmost localities at Highlands and Clingman's Dome, North Carolina (Ivie 1969). The Horseshoe Bend records extend the known range of the species southward by about 120 km. However, a single female was recently trapped even further south on the inner coastal plain (South Carolina: Aiken County; Jackson. Deciduous woods behind 110 Cowden St.; Pitfall, 12–16 March 1995. Coll./Det. M. Draney). These are the southernmost records for the genus, except that an undetermined species of *Bathyphantes* was reported from Florida (Anonymous 1986).

*Linyphiidae: Eridantes erigonoides* (Emerton 1882): This species is common in the no-tillage fields at Horseshoe Bend, where 31 of the 38 adults were captured (Table 4, Fig. 6). It has previously been collected in several states north of Georgia, including Maryland, Tennessee, Virginia, and the District of Columbia (Roth et al. 1988). It is absent from Berry's (1966, 1970) list. The Horseshoe Bend records are the southernmost known, except that a male and female were trapped further south on the upper coastal plain (South Carolina: Barnwell County; Savannah River Site. Pipeline cut with brambles and *Prunus*; Sifting litter, 28 October 1994. Coll./Det. M. Draney).

*Linyphiidae: Floricomus tallulae* Chamberlin & Ivie 1944: Two females were trapped in February and seven males in April 1991 in the

Table 3.—Extended.

Species	Families	Significantly different from present study?
112	25	
217	29	No
128	24	Yes
64	17	Yes
45	16	Yes
77	13	Yes
55	13	Yes
22	5	Yes

forest. Chamberlin & Ivie (1944) collected this species (then new to science) from Habersham, Hall, and Rabun Counties, Georgia, with the southernmost collection locality being Gainesville (about 40 km north of Horseshoe Bend). The species is absent from Berry's (1966, 1970) list, and seems not to have been collected since its description.

*Linyphiidae: Grammonota inornata* Emerton 1882: The species is quite common at Horseshoe Bend, where it thrives in the no-tillage fields (Table 4, Fig. 9). The species is

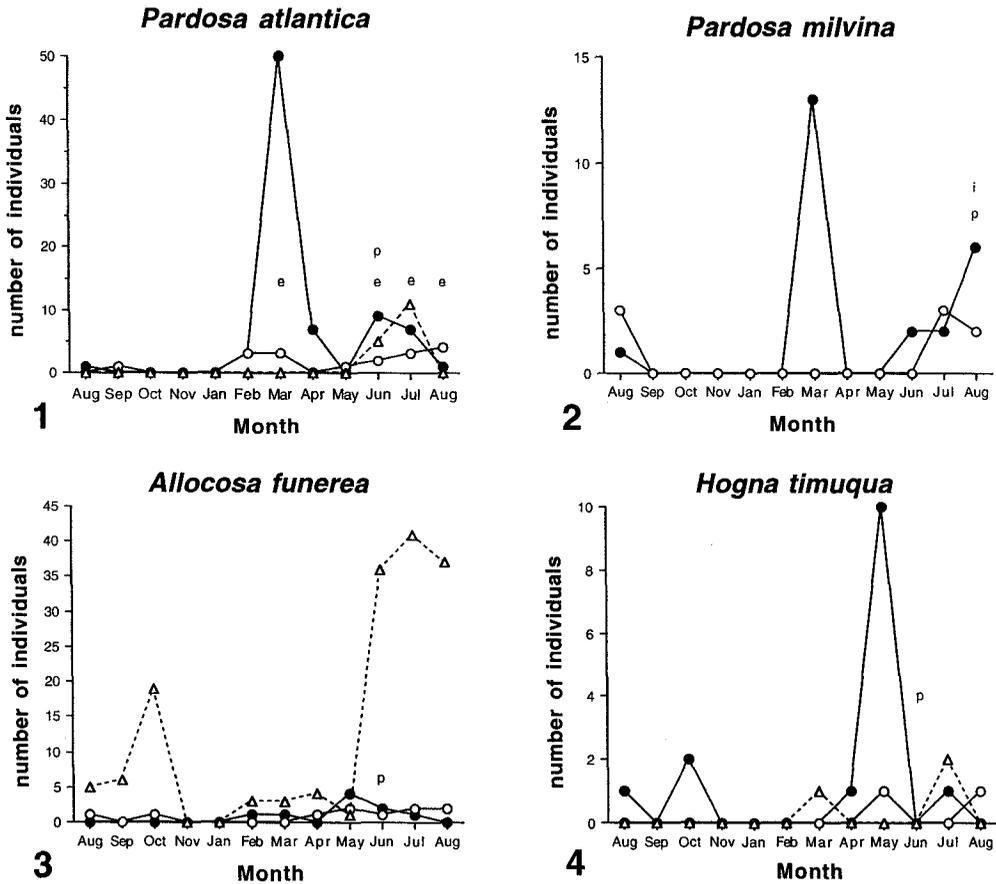
known from states north of Georgia, including North Carolina, Tennessee, and Virginia. The records at this site confirm that it thrives in Georgia, but the southern range extension is provided by a male found in the UGA Natural History Museum from the outer coastal plain (Georgia: Tift County; Tifton; Oatfield sweep, December 1963–January 1964. Coll. R. Davis, Det. H.E. Frizzell, examined).

*Linyphiidae: Walckenaeria carolina* Millidge 1983: A single male was trapped in conventional tillage winter rye/crimson clover in January 1991. Prior to my finds, it was known from only a few localities in Missouri, North Carolina and West Virginia. This species was described recently (Millidge 1983, holotype collected by J. Berry at Durham, North Carolina), so range extensions are not surprising. The species appears to be common on the inner coastal plain; over 60 individuals of this species were trapped in various habitats in Aiken, Barnwell, and Allendale Counties, South Carolina during 13 December 1995–21 February 1996 (Coll./Det. M. Draney).

*Theridiidae: Paratheridula perniciosus* (Keyserling 1886): Several specimens of both sexes were taken in June, July and August 1991 in the conventional tillage field ( $n = 4$ )

Table 4.—Habitat selection of 15 abundant pitfall species. Table includes all taxa in which at least 20 adults were trapped in 7 monthly 24-hour trap periods of 20 traps/habitat (total = 560 trap/days). Taxa are listed in descending order of number of adults trapped. Habitat abbreviations: C = Conventional tillage field; N = No-tillage field; G = Grassy field borders; F = Floodplain forest. Significance levels: \*  $P < 0.05$ ; \*\* =  $P < 0.01$ ; \*\*\* =  $P < 0.0001$ . ns = Not significant at alpha = 0.05.

Species	Total adults	Adults in each habitat				Habitat 1-way ANOVA means separation	2-Way ANOVA		
		C	N	G	F		Habitat	Month	M-H interaction
<i>Erigone autumnalis</i>	212	61	48	103	0	G > C, N > F	***	**	ns
<i>Pardosa atlantica</i>	175	78	67	30	0	C > G, F; N > F	***	***	***
<i>Glenognatha foxi</i>	137	65	66	6	0	C, N > G, F	***	***	***
<i>Grammonota inornata</i>	104	11	84	6	3	N > C, G, F	***	**	***
<i>Pardosa milvina</i>	55	38	5	12	0	C > N, G, F	***	***	***
<i>Idionella sclerata</i>	46	0	2	40	4	G > C, N, F	**	ns	ns
<i>Eridantes erigonoides</i>	38	1	31	6	0	N > C, G, F	***	ns	ns
<i>Phrurotimpus alarius</i>	34	0	3	0	31	F > C, N, G	***	***	***
<i>Allocosa funerea</i>	31	3	8	20	0	G > C, N, F; N > F	***	***	*
<i>Ceraticelus emertoni</i>	30	4	1	23	2	G > C, N, F	***	ns	*
<i>Eperigone fradeorum</i>	30	15	1	12	2	C > N, F; G > N	**	**	ns
<i>Hogna timuqua</i>	26	5	15	5	1	N > C, G, F	**	***	ns
<i>Neoantistea agilis</i>	26	0	3	8	15	F > C, N	**	***	ns
<i>Tennesseelum formicum</i>	23	12	2	6	3	C > N, F	**	ns	**
<i>Pirata iviei</i>	20	2	5	11	2	No differences	ns	*	ns



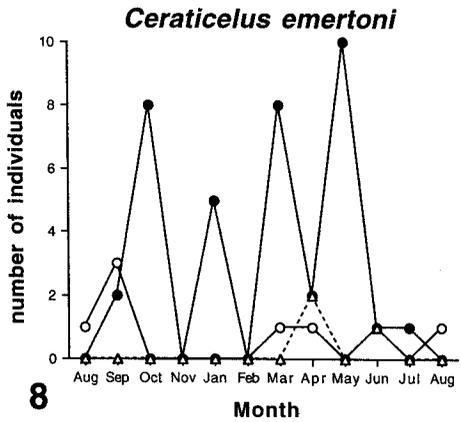
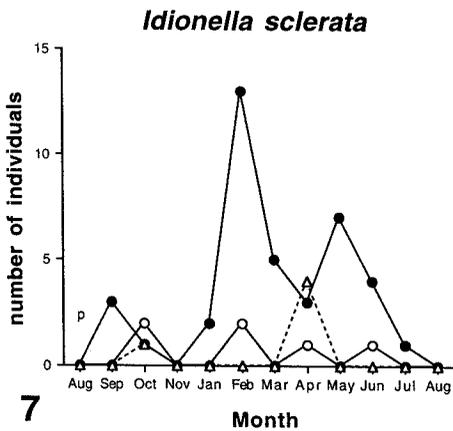
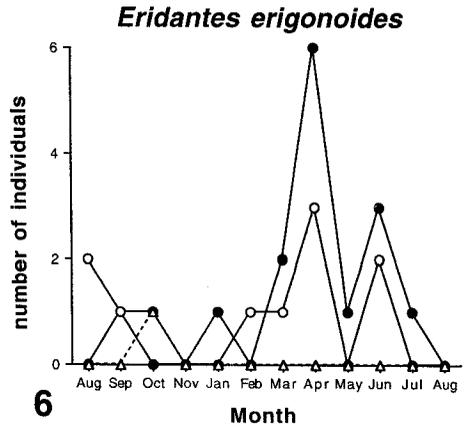
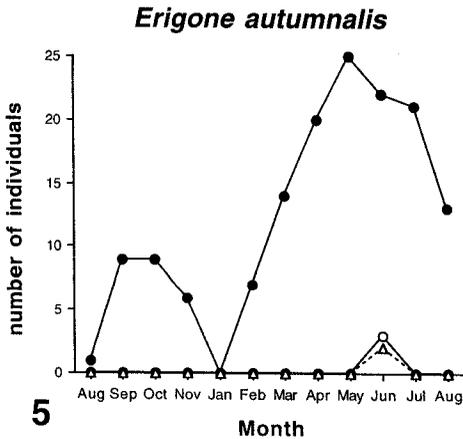
Figures 1-4.—Phenograms of four spider species, family Lycosidae. Graphs illustrate numbers of each stage trapped in 40 traps (10 in each of four habitats) during each of 12 monthly 24-hour trapping periods. Closed circles (●) = males; open circles (○) = females; triangles (Δ) = immatures; “p” = penultimate instar males; “e” = egg sac; “i” = immatures on female.

and the grassy field borders ( $n = 1$ ). This species is most commonly collected on the outer coastal plain of the gulf coast states, and has been found as far north as Tuscaloosa, Alabama (Levi 1957, as *P. quadrimaculata* (Banks)). The Horseshoe Bend records are a northeastern range extension for the species, which was not listed in Berry (1966, 1970).

Besides the three species noted above, several other Horseshoe Bend species were also missing from Berry’s (1966) list, including *Castianeira gertschi*, *Neriene redacta*, *Ceraticelus emertoni*, *Eperigone inornata*, and *Idionella sclerata*. Of these, *C. gertschi* and *I. sclerata* are recorded from North Carolina and *C. emertoni* probably occurs there, having been recorded from Virginia (Reiskind 1970; Roth et al. 1988). The remaining five species

not yet recorded from North Carolina represent less than 5% of the Horseshoe Bend pitfall fauna (Table 1), indicating the high degree of similarity of the Piedmont fauna of North Carolina and Georgia. Two of these species, *C. emertoni* and *N. redacta*, are also new records for the state of Georgia, although they have been collected in other southeastern states (Roth et al. 1988). Two female *N. redacta* were also collected at the site by J.I. Richardson on 5 September 1967.

**Phenology.**—Twelve spider species were trapped in large enough numbers to give some insight into their life cycles. Phenograms for these species are given in Figs. 1-12. Because pitfall catches reflect the level of activity of a population in addition to its density (Uetz & Unzicker 1976), the numbers trapped should

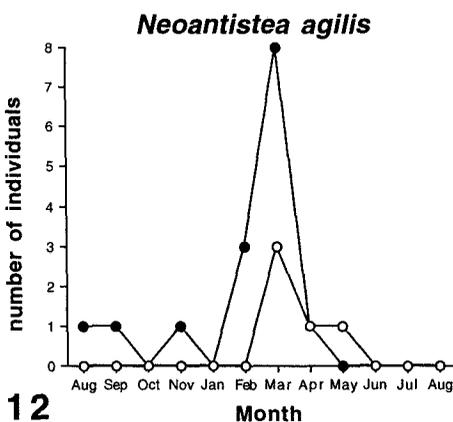
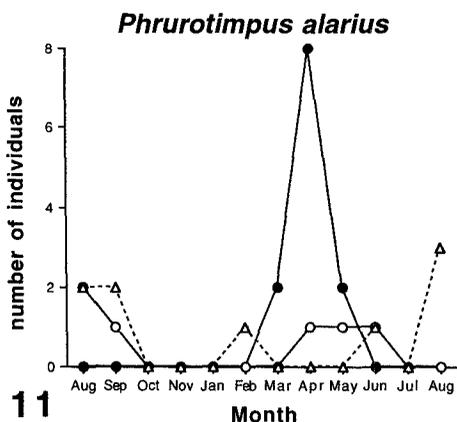
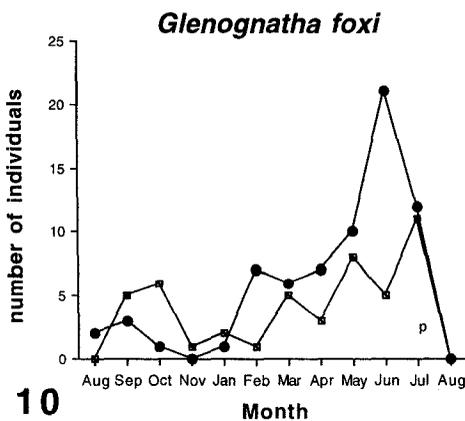
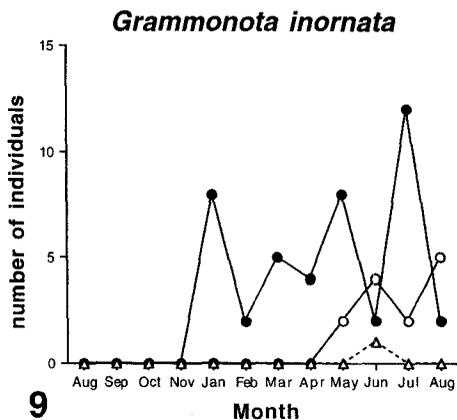


Figures 5–8.—Phenograms of four spider species, family Linyphiidae. Graphs illustrate numbers of each stage trapped in 40 traps (10 in each of four habitats) during each of 12 monthly 24-hour trapping periods. Closed circles (●) = males; open circles (○) = females; triangles (△) = immatures; “p” = penultimate instar males.

not be interpreted as directly reflecting population density during the trapping period. In general, male spiders are most active when searching for mates and female spiders are most active when foraging or searching for oviposition sites just prior to and during the period of egg production. Thus the peaks in pitfall catch can be roughly equated with the periods of copulation and egg production (DeKeer & Maelfait 1987). Assuming that immature spiders are often food limited (Wise 1993) and likely to be actively foraging, pitfall catch can be roughly equated with density of immatures. This is likely to be valid only during the warm season, when the immatures are not in diapause or otherwise inactive.

Phenograms for four abundant lycosid species are given in Figs. 1–4. Note the peak in

male abundance in March for both *Pardosa* species, *P. atlantica* and *P. milvina* (Figs. 1,2). Both species (the two most abundantly trapped lycosids) seem to have an identical “mating season” after which low numbers of adults continue to be captured until August or September and immatures are trapped until October or November. Berry (1971) documents the seasonal distribution of another *Pardosa* species, *P. parvula* Banks (as *P. saxatilis* (Hentz)). His pitfall catches show no adults present in March, followed by two peaks of adults. The first peak, in April, was dominated by males (28:1), but by the second, July, peak almost equal numbers of males and females were captured (76 and 65, respectively; J. Berry unpubl. data). This could indicate a spring “mating season” peak similar to the



Figures 9–12.—Phenograms of four spider species: 9, Linyphiidae; 10, Tetragnathidae; 11, Liocranidae; 12, Hahniidae. Graphs illustrate numbers of each stage trapped in 40 traps (10 in each of four habitats) during each of 12 monthly 24-hour trapping periods. Closed circles (●) = males; open circles (○) = females; triangles (△) = immatures; “p” = penultimate instar males. In Fig. 10, squares (■) represent females and immatures of *Glenognatha foxi*, which could not be reliably separated.

Horseshoe Bend *Pardosa* species, but delayed due to cooler weather than occurred at Horseshoe Bend in 1991 (a warmer than normal year). Berry (1971) states that the weather during his April collecting period was “very cold and wet.” Alternatively, the later peak of *P. parvula* could be due to life history properties intrinsic to the species.

*Allocosa funerea* showed a similar, but less pronounced spring peak of males, but in May instead of March (Fig. 3). A high proportion of *A. funerea* individuals was trapped as immatures, beginning in June. It is unclear whether this indicates that *A. funerea* adults had a particularly successful reproductive season relative to the *Pardosa* species, or whether juveniles of this species are relatively more active or the adults relatively less active than

is the case with the other lycosid species. These three species probably overwinter as large juveniles, then mature and mate in the spring. This pattern seems to be the rule among smaller lycosids in temperate regions (Doane & Dondale 1979).

The larger lycosid *Hogna timuqua* showed a distinct peak of males in May (Fig. 4). This species probably mates in the spring but most likely needs two years to mature instead of one, perhaps overwintering the second winter as adults, as is the case with other large temperate lycosids (Dondale 1977). Immatures of two distinct size classes can be found in the summer (Draney pers. obs.).

Adults of many species of erigonine Linyphiidae were trapped during all seasons of the year (Figs. 5–8). Males of the most commonly

trapped spider species, *Erigone autumnalis* were present in all months except January; the catch peaked in May. The few females and identifiable immatures of this species were trapped in June (Fig. 5). The very skewed sex ratio in the pitfall catch probably indicates that the females are not normally very active on the ground surface. Other erigonines which were trapped during most of the year include *Idionella sclerata* (Fig. 7), *Eridantes erigonoides* (Fig. 6), and *Ceraticelus emertoni* (Fig. 8). The mainly year-round presence of adults and the erratic occurrence of both males and females (no clearly defined peak indicating a "mating season") suggests that these species are probably multivoltine with overlapping generations. This may be the case with *E. autumnalis* as well. Other erigonine species from the southeast are capable of completing their life cycle (egg to egg) in under four months in the lab (Draney unpubl. data), so more than one generation per year is a possibility for these species. One erigonine which seems to display an annual life cycle at Horseshoe Bend is *Grammonota inornata* (Fig. 9). The sequential appearance of males in January, females in May, and identifiable immatures in June, and the absence of any identifiable individuals in the autumn suggests a strong seasonal cycle for this species.

The tetragnathid *Glenognatha foxi* was trapped in all months of the year, with catch increasing from a low in November to a peak in June (Fig. 10). This pattern probably indicates an annual reproductive cycle with mating in the early summer. Alternatively, these small tetragnathids may reproduce throughout the year, with population levels and/or dispersal behavior (thus trap vulnerability) highest in the early summer. Knowing when immature *G. foxi* exist at the site should resolve the question, but I was unable to confidently separate females from immatures in this species, so females and immatures are lumped in the data. Berry (1971) graphed the seasonal distribution of *G. foxi* (as *Mimognatha foxi*) in his pitfalls. His data show low numbers (< 5 individuals/sample date) of adults (males and females pooled) trapped throughout the year, and low numbers of immatures trapped during June through September. The two sets of data together indicate an annual reproductive cycle for this species in the Piedmont region.

Most males of the liocranid *Phrurotimpus alarius* were trapped in April, with immatures and females found at low levels from February to September (Fig. 11). If the hypothesis of an annual cycle with spring mating is correct, then I expect that immatures captured in late winter/early spring would be large sub-adult specimens, whereas those captured in the summer would be smaller immatures that were produced after the spring mating.

Peck & Whitcomb (1978) present pitfall catch data for *P. alarius* which also support the hypothesis of an annual cycle with spring mating. Their catch of males and females (immatures were not recorded) peaked in May instead of April, which may be consistent with the more northerly Arkansas study site resulting in a delayed "mating season." At the Arkansas site, males disappeared after May, whereas females were trapped through September. This pattern is similar to that shown at Horseshoe Bend, again corroborating my life history hypothesis.

A similar pattern in the hahniid *Neoantistea agilis* is also interpreted as an annual cycle with spring mating (Fig. 12). Males peaked in March and females were trapped from March to May. No immatures were trapped, suggesting that they spend their time within the leaf litter rather than walking on the ground surface. It would be interesting to know whether the few males that were trapped in August-November are old adults that survived to autumn or whether they are newly adult individuals that overwinter as adults. The absence of males in May, June, and July indicate that the latter hypothesis is more likely. *N. agilis* in Manitoba, Canada apparently displays a different life history, with male pitfall peaks in September (Aitchison 1984). Possibly the Manitoba populations are also annual, but a longer period is required for maturation in the cooler climate, so the mating is delayed until Autumn. Opell & Beatty (1976) suggest that the species is annual but has two periods of reproduction, in late March to late May and again in mid-August to mid-September. The species may facultatively reproduce during spring and/or autumn, with climate and other conditions determining the local life history pattern.

**Habitat selection.**—The four habitats sampled at Horseshoe Bend are all within 10 m of one another and adjacent to one another,

except that the grassy field border separates the agricultural from the forest habitats by a few meters. Since all habitats should be easily accessible to all spider species at the site, sampling within the small scale of this agroecosystem landscape enables a determination of the aggregate "habitat preferences" of the spider populations. This requires the assumption that numbers of individuals trapped broadly corresponds to the density of individuals in that habitat. Care must be taken since pitfall trapping data has often been shown to violate this assumption (Uetz & Unzicker 1976; Curtis 1980; Merrett & Snazell 1983; Topping 1993). Most potential sources of bias have been controlled for in this study. Temporal sources of bias were controlled by trapping simultaneously in all habitats for 24 hours at a time. Effects of weather on spider mobility were controlled for by simultaneous trapping at adjacent sites exposed to identical weather conditions. Interspecific variation in trap vulnerability is not relevant in this context because abundance comparisons are only made intraspecifically. I acknowledge that habitat architecture can influence the efficiency of the traps (Topping 1993), and that this factor was not controlled for in this study. Even if habitat architecture does affect pitfall catch, species habitat preference should still be identifiable unless architecture has an overwhelming effect on the trappability of species. Comparing catches of species with presumably similar locomotory abilities suggests that this is not the case. For example, *Grammonota inornata* was abundantly trapped in the no-tillage field and rarely trapped in the grass borders (84 and 6 adults, respectively) whereas another erigone linyphiid, *Idionella sclerata*, showed the opposite pattern (2 and 40 individuals, Table 4). Such examples of independent catches of apparently similar species in different habitats suggests that architecture is at least not the overriding factor determining pitfall catch, and that habitat preference of individual species can be examined despite this potentially confounding variable.

Some trends in habitat selection are suggested by examining the habitats in which the 46 clearly identifiable species in the February-August 1991 data set were trapped. Data for the 15 most abundant of these species are shown in Table 4. One immediately apparent feature is that few species were entirely re-

stricted to a single habitat. Although 37% of the species ( $n = 17$ ) were found in only one habitat, only one species, *Floricomus tallulae* (not in Table 4; forest,  $n = 8$ ) was represented by more than three individuals.

Another interesting feature of the habitat use list concerns those species which were trapped in all habitats except one. Of the 46 species, 24% ( $n = 11$ ) were present in three of the four habitats. Eight of these species avoided the forest: *Eridantes erigonoides*, *Erigone autumnalis*, *Florinda coccinea* (not in Table 4;  $n = 6$ ), *Walckenaeria spiralis* (not in Table 4;  $n = 7$ ), *Allocosa funerea*, *Pardosa atlantica*, *Pardosa milvina*, and *Glenognatha foxi*. The three remaining species all avoided the conventional tillage habitat: *Neoantistea agilis*, *Idionella sclerata*, and *Xysticus triguttatus* (not in Table 4;  $n = 6$ ). These results are consistent with my expectation that the only habitats that are "avoided" by species with otherwise general habitat requirements are the habitats at either end of a gradient from frequently and intensely disturbed and managed (conventional tillage field) to infrequently disturbed (forest). Species are less likely to avoid the intermediate no-tillage field and grassy field border habitats.

Six species (all linyphiids or lycosids) were trapped in all four habitats: *Ceraticelus emertoni*, *Eperigone fradeorum*, *Grammonota inornata*, *Tennesseelum formicum*, *Hogna timuqua*, and *Pirata iviei*. This represents 25% of the 24 species represented by at least four individuals in the data set (and thus theoretically capable of being found in all habitats given their level of activity density). Interestingly, four of the five most abundantly trapped species in Table 4 (*Erigone autumnalis*, *Pardosa atlantica*, *Glenognatha foxi*, and *Pardosa milvina*) did not occur in all four habitats. This is perhaps contrary to Abraham's (1983) assertion that dominant spider species in ecosystems tend to be habitat generalists. At Horseshoe Bend, some of the most abundant species are habitat specialists at least to the extent that they do not occur abundantly in the forest habitat.

Table 4 also presents results of statistical analyses of the habitat distribution of the 15 most abundantly trapped species ( $n > 19$ ). Two-way ANOVA's showed that all species except *Pirata iviei* displayed a significant habitat effect. *Pirata iviei* appears to range widely

in the floodplain habitats, but was not caught in numbers sufficient to show a significant habitat preference. About half of the remaining species showed a significant "month  $\times$  habitat" interaction, implying that the habitat "preference" of the species changed over time. In some cases, this may be a statistical artifact resulting from low capture rate during certain months.

One-way ANOVA's were performed on all data showing a habitat effect when blocked by month in the two-way ANOVA. Means separation by LSD indicated in which habitats the species were trapped significantly more or less often. Most of these abundant species were much more common in one or two habitats than in the remainder, in which they were rarely or never trapped. This pattern of habitat specialization was also observed in Maelfait & De Keer's (1990) study of spiders in pastures and their border zones.

*Forest species:* Only 2 of the 15 abundant species preferred the forest habitat, *Neoantistea agilis* and *Phrurotimpus alarius*. *N. agilis* was rarely trapped in either agricultural habitat and seems to avoid them. Its prevalence in the forest is consistent with previous collection data (Opell & Beatty 1976).

*Field border species:* The thin grassy field borders seem, at first glance, much less a distinct "habitat" than the fields and forest. However, grasslands in Georgia (mostly small strips and patches like the ones in this study) account for about 14% of the land in the state, and can serve as important reservoirs for both beneficial and destructive insects (Morrill 1978). Four species were characteristic of the grassy field borders: the lycosid *Allocosa funerea* and the linyphiids *Ceraticelus emertoni*, *Erigone autumnalis*, and *Idionella sclerata*. *Erigone autumnalis* definitely avoids the forest; none of the 212 individuals were trapped there. Another linyphiid, *Eperigone fradeorum*, was also trapped in considerable numbers in the grassy borders, though it showed a stronger affinity for the conventional-tillage agroecosystem. *Allocosa funerea* was also often trapped in the no-tillage agricultural field. This species has often been collected in grassy fields, meadows, and lawns, in addition to gardens and pine forests (Dondale & Redner 1983).

Duelli (1990) found few species which preferred the grassy margins between cultivated

fields and semi-natural (grassland/pasture) areas, and considered the grassy margins in his system to be ecotones, mainly important for harboring species more common elsewhere. However, I have documented several common spiders that were trapped predominantly in the meadow habitats at Horseshoe Bend, indicating that this is their primary habitat, and does not serve as ecotone for them. The grassy habitats at Horseshoe Bend undoubtedly also serve as secondary habitats for species which are more abundantly trapped in cultivated fields or forest. In particular, the grassy margins may provide a refuge for cultivated field populations during times when that habitat is disturbed by management practices.

*No-tillage field species:* *Hogna timuqua* was trapped in the no-tillage agricultural field significantly more often than in other habitats. Two other lycosids commonly trapped here were *Pardosa atlantica* and *Allocosa funerea*, though both had stronger affinities to other habitats. Two linyphiids, *Eridantes erigonides* and *Grammonota inornata*, showed strong preferences for the no-tillage habitat over the other three habitats. I hypothesize that these species must thrive in the thick herbaceous "straw-like" litter layer that is unique to this habitat. *Erigone autumnalis* was also trapped abundantly in this habitat and in the conventional-tillage field.

It seems at first surprising that species would "prefer" the no-tillage habitat to the extent of being much more rarely trapped in both the conventional tillage and the meadow habitats. However, Mangan & Byers (1989) showed that many old-field species remain during the establishment of no-tillage agroecosystems from old field habitats. Possibly the "no-tillage" species are adapted to life in early successional habitats. It seems that the no-tillage habitat may be to some extent ecologically similar to an old-field system for many of these species.

*Conventional-tillage field species:* The tetragnathid *Glenognatha foxi* was trapped abundantly in both agricultural habitats but rarely caught in the other two habitats. It is the only abundant species which showed no "preference" for either of the two agricultural habitats. The horizontal orb webs spun by this species were found from about 0.5–3.0 cm above the ground or litter surface of both habitats (Draney pers. obs.); presumably it is de-

pendent on habitat characteristics other than the ground surface architecture. The species has been found in a variety of mostly open, generally xeric situations (Levi 1980), including meadows, old field, saltmarsh, short grass, and cornfields, which are quite similar to sorghum fields. Their considerable ballooning ability (Crosby & Bishop 1936, as *Mimognatha foxi* McCook) makes them potentially beneficial colonizers of agricultural fields.

Besides *G. foxi* and *Erigone autumnalis*, four species were also characteristic of the conventional tillage agricultural field: *Pardosa atlantica*, *P. milvina*, and the linyphiids *Tennesseelum formicum* and *Eperigone fra-deorum*. *P. atlantica* was found in lower but considerable numbers in the no-tillage field and even in the grassy field border, whereas *P. milvina* was more restricted to the conventional tillage field.

**Maintenance of biodiversity in agroecosystems.**—Although more intensive sampling will undoubtedly yield additional species, it is clear that the four-habitat agroecosystem at Horseshoe Bend harbors a high diversity of species, similar in structure to that documented across an array of successional habitats elsewhere on the Piedmont Plateau (Berry 1966). Much higher species richness can be maintained in agroecosystems composed of a mosaic of habitats under different management regimes, as is the case at Horseshoe Bend, than in agroecosystems maintained as conventional monocultural landscapes. This is corroborated by the fact that Bailey & Chada (1968) trapped only 64 species from pitfalls in grain sorghum fields, compared with 112 species I trapped in the more complex sorghum/meadow/forest landscape at Horseshoe Bend. Habitat use patterns of individual spider species illustrate two mechanisms which may explain how landscape complexity results in higher spider diversity. First, many species seem to “specialize” in one or a few habitat types; populations may not be able to persist without these habitats. Thus, increasing the number of different habitat types will obviously increase the site-wide richness (gamma diversity) of the agroecosystem as a whole. Second, individuals are often found in habitats other than those in which the species is most abundant. Presumably these species often simply “spill over” to adjacent habitats during foraging and mate-searching behavior from

habitats where they are common. This results in higher species richness in each individual habitat (higher alpha diversity) via “mass effect” (Shmida & Wilson 1985). Diffusion of species into suboptimal habitats means these habitats may sometimes serve as refugia (*sensu* Duelli 1980), allowing species to persist in an ecosystem when their optimal habitat is disturbed by management practices. One practical effect of this is that species utilizing refugia may more rapidly recolonize their primary habitats after the disturbance (plowing, spraying, harvesting, etc.) subsides than would be the case if recolonization were solely by long-distance ballooning.

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