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ABUNDANCE AND ASSOCIATION OF CURSORIAL SPIDERS FROM CALCAREOUS FENS IN SOUTHERN MISSOURI

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ABSTRACT. I systematically sampled, by pitfall trap, spiders in three different but nearly contiguous fens (Seep, Prairie and Forested) as well as those in the surrounding habitat (Oak-hickory forest) in southern Missouri. Samples were taken biweekly from May through August. Fifty-five species of cursorial spiders were found, of these, 17 occurred only within one or more of the fens and not in the surrounding habitat. All habitats, and particularly fens, were dominated by wolf spiders. Jaccard's similarity coefficient showed spider faunas of the Seep and Prairie fens were more similar to one another than to that of the Forested fen. While both Seep and Forested fen habitats harbored spider species quite different from the surrounding Oak-hickory forest, many species from the Forested fen were also found in the Oak-hickory habitat (56.3%). Abundances of spiders were greatest in May and declined through summer in all habitats, except the Seep fen in which abundances remained fairly constant. Tests of interspecific association among species within Lycosidae, Clubionidae, and Gnaphosidae gave no evidence of negative associations of species, which could theoretically result from interspecific competition, among the three fen habitats. I conclude that the spider faunas associated with the fens are quite distinct from that of the surrounding habitat with each fen harboring a somewhat unique assemblage of spiders and that there is no evidence of competitive exclusion of species from the fen habitats.

The Ozark Mountains are a biologically rich area of the central United States with many endemic plant (Thom & Wilson 1980; Thom & Iffrig 1985) and animal species. Of the communities found there, fens are perhaps the most distinctive. Fens are boggy areas with saturated soils caused by seepage. Within the Ozark Mountains, fens are most common in the Salem Plateau region (Thom & Wilson 1980). Several unusual geological factors contribute to the abundance of fens in the Salem Plateau region. First, the region is characterized by Cambrio-Ordovician dolomite bedrock covered by a thick residuum formed from *in situ* weathering of the parent material. The residuum freely accepts and transmits water (Orzell 1983). Second, there are several regional springs that are recharged in the area. As water moves through the residuum from hillsides and uplands the soil becomes saturated. In lowland areas within the Salem Plateau region fens develop under the influence of a constant supply of cool water. The source of the water is thought to be springs recharged by storage groundwater (Aley 1978). Fed by cool-water springs, fens of Missouri support a flora more typical of latitudes much farther north.

Recent work shows that the flora of Missouri fens is markedly different from that of the surrounding vegetation (Orzell 1983). Yet, the arthropod fauna associated with fens is poorly known. Systematic sampling of fen spiders has not been done. The goal of my study was to describe the spiders associated with the various fen types in the Grasshopper Hollow Fen complex in southern Missouri. Additional objectives were to assess the seasonal abundance patterns of spiders, to assess if species exclude one another from some fens and to evaluate how unique fen spiders are, compared to those from the habitat surrounding the fens. A goal of my work is to provide knowledge about the biotic distinctness of the fens so that appropriate management practices of these protected and unique habitats can be initiated.

METHODS

The study was conducted in the largest (7 hectares) and most diverse fen complex in Missouri: Grasshopper Hollow Fen in Reynolds County. The complex is heterogeneous, being composed of several fens that differ somewhat vegetatively (Orzell 1983). One of the fens in the complex, the Seep fen, is heavily dominated by various species of sedges [*Carex interior* Bailey, *C. leptalea* Wahl. and *C. subserecta* (Olney) Britt.] and rush (*Juncus dudleyi* Wieg.). Another fen type, the Prairie fen, contains an interesting mix of fen (cord grass, *Spartina pectinata* Link.) and prairie plants (big bluestem, *Andropogon gerardii* Vitm.; Indian grass, *Sorghastrum nutans* (L.) Nash; prairie dock; *Silphium terebinthinaceum* Jacq.; and swamp orange coneflower, *Rudbeckia fulgida* Ait.). A third fen type, the Forested fen, contains the following calcifile tree species: *Quercus mulenbergii* Engelm., *Q. rubra* L., *Fraxinus americana* L., *Alnus serrulata* (Ait.) Willd., and *Carpinus caroliniana* Walt. The habitat surrounding the fen complex is mesic oak-hickory forest typical of southern Missouri (Nelson 1985).

I assessed vegetative structure at the study sites monthly. Foliage height diversity (FHD) was determined by the point-quadrat method using a calibrated (four 0.4 m intervals) pole that was diagonally placed at 1 m intervals along a randomly selected 8 m transect within each habitat. The number of stems contacting the pole at each height interval was recorded. Data generated from samples were input into the Shannon (1948) diversity index to give the foliage height diversity, as has been done by others (e. g., Willson 1974). The technique provides a measure of the structural diversity of the habitat, a feature than may strongly influence arthopods (Murdock et al. 1972).

Ten pitfall traps (13 cm diameter; 9 cm deep) were placed in 1989 within each fen and the surrounding habitat to sample cursorial spiders. Traps were placed at 5 m intervals along a randomly-placed 50 m transect, with the exception of the Forested fen which was less than 50 m in diameter. Here, traps were placed randomly within the habitat. Traps were placed in fens during the first and third week of each sampling month; sampling occurred on two weeks each month to reduce environmental pertebation to the protected study area. A mixture of ethylene glycol and water (1:1) was used as a preservative in traps. Spiders were sampled in May, June, July and August. Wooden covers raised above traps by legs allowed arthropod entry but discouraged mammals from entering and falling into traps. Pitfall traps do not give a true measure of density, rather they sample the number of cursorial spiders moving in an area for a given time or the "active density" (Uetz 1977). Yet, they are useful in that they allow continuous sampling in varied habitats and provide an adequate estimate of the number of species of cursorial spiders over a wide range of habitats (Uetz & Unziker 1976).

Several pitfall traps were disturbed during the study and could not be included in the analysis. Therefore, for some months, some habitats had fewer than 10 pitfall trap samples. Numbers of individuals from these pitfall traps were standardized to make them comparable to habitats that did not have disturbed traps. For example, two pitfall traps in May from the Prairie fen were disturbed. Numbers of spiders collected in the remaining eight traps were multiplied by 10/8. In June, all 10 traps in the Prairie fen were disturbed, apparently by a small vertebrate.

Fen and non-fen habitats were compared at the species level using Jaccard's (1908) coefficient,

$$S_j = a/a + b + c$$

where a is the number of species collected in both habitats A and B, b is the number of species collected in habitat B but not in habitat A, and C is the number of species collected in habitat A but not in habitat B.

Species identification was made by the author, except for several species of Lycosidae and Gnaphosidae, which were identified or their identity verified by systematists. Only adult specimens (with the exception of a few individuals whose color pattern and general morphology allowed unquestionable matching with mature individuals) are included in the data set since immatures could rarely be reliably identified to species.

I calculated the variance ratio (VR) to test simultaneously for significant associations among species present at the three fen habitats for members of the Lycosidae, Clubionidae, and Gnaphosidae. The variance ratio was calculated as

$$VR = S_t^2/\sigma_t^2$$

where S_t^2 is the variance in total species number and σ_t^2 is the total sample variance for occurrences of the S species in the samples from the three fens (see Schluter 1984). If VR > 1, then the species exhibit a positive association and if VR < 1, a negative association exists among the species at the fens. The statistic, W, was computed to test whether deviations of VR from 1.0 were significant. The statistic, W, equals N(VR), where N is the number of habitats; W has a 95% probability of falling between limits given by the chi-square distribution (see Schluter 1984)

$$\chi^2_{.025,N} < W < \chi^2_{.975,N}.$$

RESULTS AND DISCUSSION

A total of 55 species of cursorial spiders was collected from the fen and non-fen habitats (Table 1). These spiders represented eight families. Of these species, 17 were found only in one or more of the fens and not in the Oak-hickory forest. Only one species was restricted to just the Oak-hickory forest. Both Seep and Prairie fens contained fairly diverse wolf (8 and 11 species, respectively) and running (7 and 12 species, respectively) spider groups. Overall, the Prairie fen was the most speciose of the habitats sampled, while the Forested fen had the fewest number of species (Table 1).

Comparison of species similarity among the various habitats reveals several interesting features (Table 2). The coefficient of similarity between the spider faunas at the Seep and Prairie fens is quite high ($S_j = 0.4571$; Table 2), but both of these faunas are quite dissimilar to that found at the Forested fen. The Seep fen spider fauna is also not similar to that found in the Oak-hickory forest. The spider community associated with the surrounding habitat is truly much different than that found in the Seep fen. In contrast, the spider species associated with the Forested fen and the Oak-hickory forest are fairly similar ($S_j = 0.2727$; Table 2). Species associated with the Prairie fen show some similarities with those from the Oak-hickory forest ($S_j = 0.2500$; Table 2), but less so than species from the Forested fen. Overall, eight of the 55 species collected in the study were found only in pitfall traps placed in the Prairie fen. Moreover, since these data represent only three-trap months (due to disturbance in June), it is likely that one or more species endemic to the Prairie fen may have been missed. In sum, while the Prairie fen and particularly the Seep fen tend to harbor spider species unlike the surrounding non-fen habitat, the Forested fen contains species also found in the surrounding Oak-hickory forest.

Looking at individual spider species reveals similarities and differences among habitats at the species level (Table 1). *Pirata insularis* Emerton was found at all sites, but was particularly common in the three fen habitats. Seep and Prairie fens both shared a numerically abundant species, *Pardosa saxatilis* (Hentz) (Table 1). One species, *Pirata insularis*, a small wolf spider that is often found near water (Kaston 1981), comprised 64.4% of all individuals in the Seep fen.

The Forested fen and the Oak-hickory forest shared nine species in common. Particularly abundant species that they both contained were: *Schizocosa ocreata* (Hentz), *Drassylus novus* (Banks), *Gnaphosa sericata* (L. Koch) and *Xysticus fraternus* Banks. The overlap in species is not unexpected, given that both habitats are forests and therefore share many abiotic features. While the Forested fen was most similar to the Oak-hickory forest, it did share some species with the other fens. Most notable are *Pirata insularis*, a species common in all three fens, but rare in the non-fen habitat; *P. arenicola* Emerton, which was found only in the Forested and Prairie fens; and, *Drassylus creolus* Chamberlin & Gertsch, also a member of Prairie and Forested fens. Of interest is *Phrurotimpus borealis* (Emerton), a species common to Oak-hickory and Forested fens, but more common in the latter. The range of this species is reported to be east of the Mississippi River and north of Georgia (Kaston 1978). Its occurrence in southern Missouri is somewhat unexpected, since it is frequently found in more northern deciduous forests. Its presence in and near the Forested fen supports the hypothesis that the fens are refugia for species normally found at more northern latitudes.

In terms of community structure, the most distinctive spider assemblage occurred at the Seep fen. This community was characterized by a rather sparse spider fauna (20 species; Table 1) and an extreme numerical dominant in *Pirata insularis* (64.4% of all individuals). The structure of the spider community at the Seep fen parallels the relatively simple structural diversity (Fig. 1) of the fen's sedge-dominated vegetation.

At the family level, lycosids dominated all habitats, particularly fens (Fig. 2). Of all habitats, the Seep fen was most heavily dominated by lycosids, with 95.7% of all individuals belonging to the Lycosidae (Fig. 2). In contrast, the cursorial spider faunas associated with the Prairie fen, Forested fen and Oak-hickory forest were composed of 83.3%, 64.8%, and 58.4% lycosids, respectively (Fig. 2). A preponderance of wolf spiders in the samples probably reflects the pitfall trap sampling technique employed. As a measure of "active density", pitfall traps would be expected to differentially capture highly active spiders like lycosids. However, visual inspection and hand sifting through litter also revealed that lycosids were by far the most common spiders present in the fen study sites (pers. obs.). While

Table 1.—Species list and seasonal abundances for cursorial spiders from pitfall trap samples taken in 1989. Abundances corrected for missing pitfall traps (see text).

	Habitat			
Family	Seep	Prairie	Forested	Oak-hickory
Agelenidae				
Agelenopsis pennsylvanica (C. L. Koch)	0	2	3	0
Cicurina robusta Simon	2	0	0	0
Hahniidae				
Neoantistea magna (Keyserling)	1	9	0	2
Lycosidae				
Allocosa funerea (Hentz)	3	1	0	1
Arctosa virgo (Chamberlin)	0	0	0	29
Lycosa helluo Walckenaer	21	3	0	0
Lycosa rabida Walckenaer	8	24	0	0
Lycosa sp. A	0	0	8	17
Pardosa saxatilis (Hentz)	135	193	0	0
Pardosa moesta Banks	0	1	0	0
Pirata alachuus Gertsch & Wallace	18	5	14	15
Pirata insularis Emerton	391	28	87	2
Pirata arenicola Emerton	0	2	17	0
Schizocosa bilineata (Emerton)	2	29	0	1
Schizocosa crassipes (Walckenaer)	0	0	0	98
Schizocosa ocreata (Hentz)	3	11	77	51
Schizocosa saltatrix (Hentz)	0	8	0	2
Trabea aurantiaca (Emerton)	0	0	1	0
Gnaphosidae				
Callilepis imbecilla (Keyserling)	0	4	0	1
Drassylus aprilinus (Banks)	0	1	0	0
Drassylus covensis (Banks)	0	0	0	1
Drassylus creolus Chamberlin & Gertsch	1	5	3	0
Drassylus dixinus Chamberlin	2	1	0	0
Drassylus eremitus Chamberlin	2	1	0	1
Drassylus niger (Banks)	0	5	0	0
Drassylus novus (Banks)	0	0	18	17
Gnaphosa fontinalis Keyserling	0	0	0	4
Gnaphosa sericata (L. Koch)	0	0	29	41
Haplodrassus bicornis (Emerton)	0	0	0	3
Haplodrassus signifer (C. L. Koch)	0	4	0	0
Herpyllus vasifer (Walckenaer)	0	0	0	1
Rachodrassus exlineae Pl. & Sh.	0	0	0	2
Zelotes duplex Chamberlin	0	1	0	3
Z. hentzi Barrows	0	0	0	1
Clubionidae				
Castianeira descripta (Hentz)	1	1	0	0
Castianeira longipalpis (Hentz)	0	9	0	22
Castianeira variata Gertsch	6	0	0	0
Castianeira sp. A	4	0	0	0
Clubionoides excepta (C. L. Koch)	2	4	2	0
Micaria elizabethae Gertsch	0	2	0	0
Phrurotimpus alarius (Hentz)	0	0	19	7
Phrurotimpus borealis (Emerton)	0	0	11	4

Table 1.—Continued.

Family	Habitat: Seep	Prairie	Forested	Oak-hickory
Thomisidae				
Misumenops sp. A	2	3	0	0
Oxyptila sp. A	0	1	0	0
Philodromus sp. A	0	1	0	0
Tmarus sp. A	0	1	0	0
Xyticus emertoni Keyserling	0	0	0	12
Xyticus ferox (Hentz)	0	0	0	1
Xyticus fraternus Banks	0	0	19	27
Xyticus funestus Keyserling	0	2	0	1
Salticidae				
Onondaga lineata (C. L. Koch)	1	0	0	0
Paraphidippus sp. A	0	0	0	3
Sitticus sp. A	2	4	0	0
Salticid sp. A	0	0	4	0
Dictynidae				
Dictyna sp. A.	0	0	3	0
Total number of individuals	606	366	370	315

the Seep fen was heavily dominated by members of the Lycosidae, the Prairie and Forested fens contained significant numbers of non-lycosid spiders. Members of the Gnaphosidae and Clubionidae comprised substantial proportions of the total number of individuals at both the Prairie (6.0% and 4.4%, respectively) and the Forested fens (10.2% and 6.0%, respectively; Fig. 2). The Oak-hickory forest differed from the fens, particularly Seep and Prairie, in having large proportions of Gnaphosidae (20.3%) and Thomisidae (11.1%). In sum, family level comparisions somewhat mirror those at the species level; both the Seep and Prairie fen spider faunas were more similar to one another than they were to the Forested fen, while spiders from the latter was more similar to those from the Oak-hickory forest.

Abundances of cursorial spiders were greatest in May and declined through the summer in the Prairie and Forested fen and the surrounding Oak-hickory forest. In contrast, spiders from the Seep fen occurred in fairly constant numbers over the sampling season (Fig. 3). Differences among fens in seasonal trends in abundance are primarily due to the occurrence of *P. insularis*. Mature males and females were found in large numbers throughout the four month sampling period. In contrast, other species showed early summer peaks in abundance of mature individuals. Since few immatures were included in the analysis, species at the Prairie and Forested fens showed a decline in abundance over the summer. If immatures could have been included in the analysis, then spider abundances for these fens would probably not have declined in this way. Thus, differences in seasonal abundance patterns among fens (Fig. 3) reflect abundances of adults, not immatures and adults. Nonetheless, it is of interest that *P. insularis* exhibited a phenology fairly atypical of the species in this study; mature adults were abundant from May through August.

Table 2.—Jaccard's coefficient of similarity for comparisons of the presence/absence of species at the fen and non-fen habitats.

	Seep	Prairie	Forested	Oak-hickory
Seep	—	0.4571	0.1613	0.1667
Prairie		—	0.1892	0.2500
Forested			—	0.2727
Oak-hickory				—

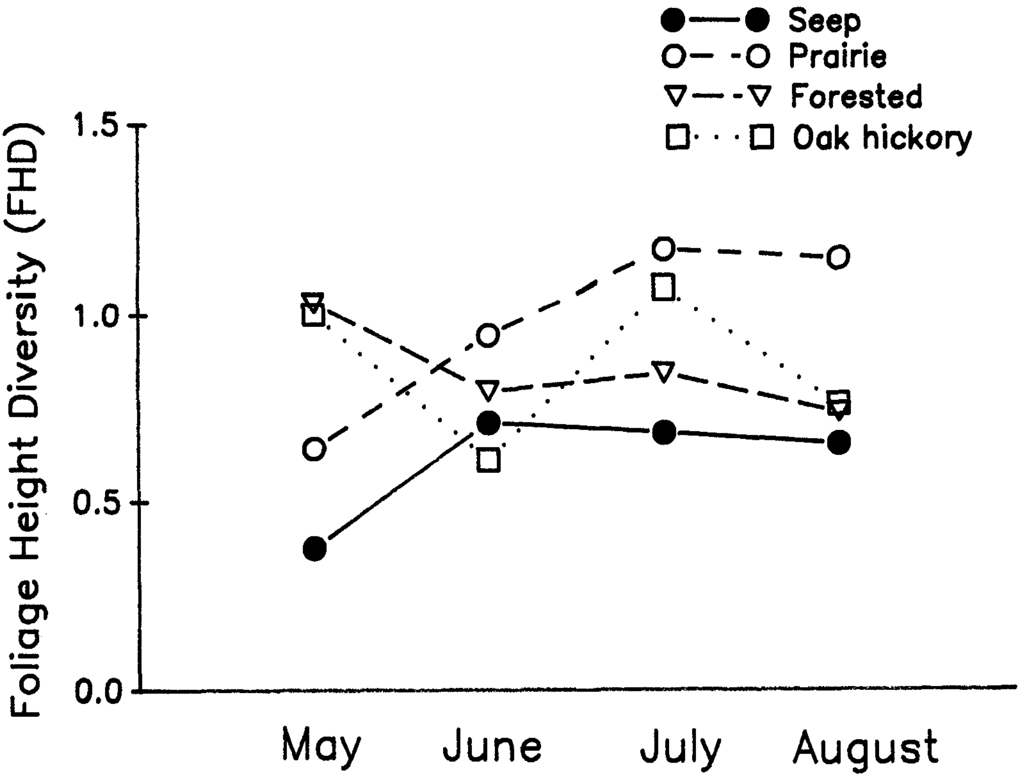

Figure 1.—Foliage height diversity (FHD) for fen and non-fen habitats during the four sample months.

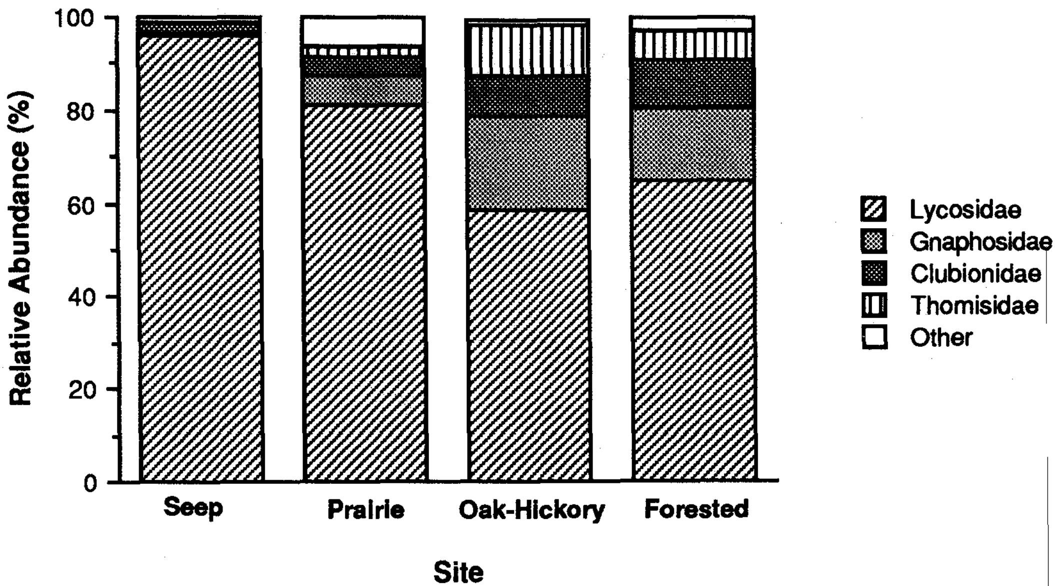

Figure 2.—Family composition of spiders sampled by pitfall trap at fens and surrounding non-fen habitat.

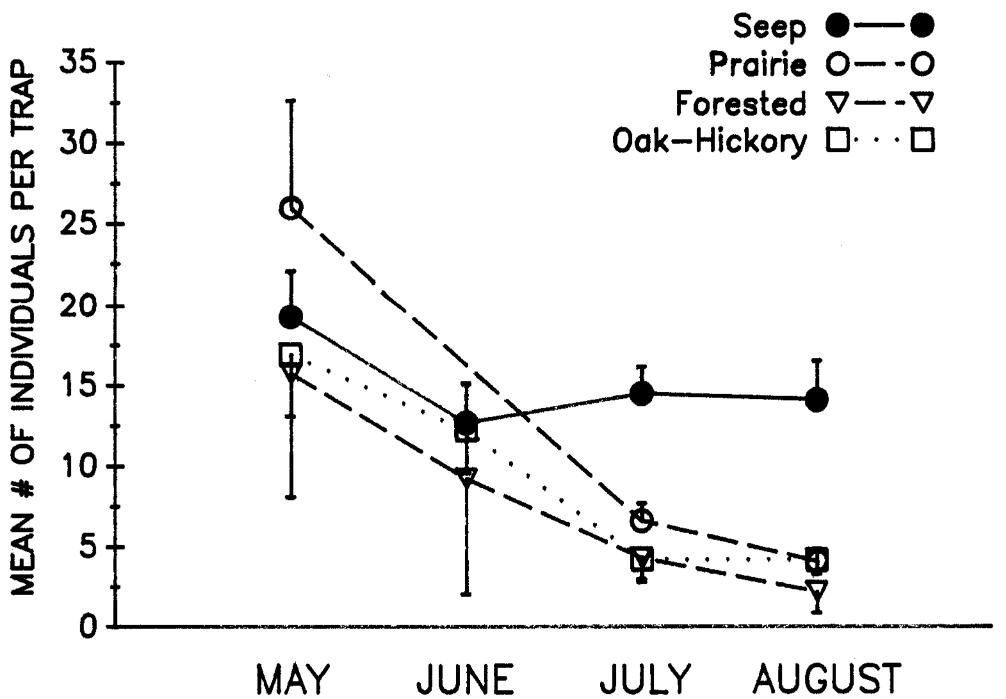

Figure 3.—Abundance of cursorial spiders sampled by pitfall trap at fens and surrounding non-fen habitat. Bars equal 1 SEM.

Females of *P. insularis* were collected with egg cases in June, July, and August. It is not clear if these represent multiple generations or one generation that breeds over a long period of time. That penultimate females were only found during the month of May argues in favor of the latter possibility.

Tests for interspecific association (Schluter 1984) within species of the Lycosidae, Clubionidae, and Gnaphosidae among the three fen habitats showed no negative associations between species (Table 3). These tests evaluate whether species of the relatively diverse wolf and running spider families show nonrandom patterns of presence/absence across the three fens. One might expect that members would preempt resource space within a fen and thereby prohibit the presence of another species of that family. That is, each fen might not have a full complement of species due to competitive exclusion from some fens by some species. The test for interspecific association however, gives no evidence for this conclusion. There is no interspecific competition acting to effect the observed pattern of presence/absence by wolf and running spiders in the fens.

CONCLUSIONS

My results show that spiders from the Prairie fen and particularly the Seep fen differ markedly from those from the surrounding Oak-hickory forest. In contrast, the spider fauna from the Forested fen is more similar to that at the Oak-hickory forest. Abundances of adult spiders declined over the summer in all habitats, except the Seep fen. Tests for interspecific association among wolf and running spider species at the fen habitats gave no evidence for competitive dis-

Table 3.—Results of Variance Ratio analysis as a test of interspecific species association among wolf and running spiders (Clubionidae and Gnaphosidae) among the three fen types. Schluter's (1984) Variance Ratio is VR. W is the test statistic associated with the variance ratio test. * = Number of spiders present. ** = Spider species show a significant positive association among the 3 fen habitats.

Guild	S*	VR	W	*P*
Wolf spiders	13	1.9	5.7	ns
Running spiders	20	1.4	4.2	<0.05**

placment. Furthermore, spiders collected from fens showed differences at the species and family levels among fen types. That cursorial spiders differ from fen to fen is noteworthy. Spiders, as generalist, mobile predators, might not be expected to respond to the somewhat subtle floristic differences between fen types. The fact that they do underscores the biotic differences between these habitats. Spiders, as common secondary consumers, are extremely important predators in natural ecosystems (Riechert 1974) and as such are excellent biological indicators of community- and ecosystem-level organization. Differences in spider faunas associated with habitats should indicate fundamental biological differences between those habitats. Implications of my findings are that management of the Grasshopper Hollow complex should incorporate the autonomy that exists between fen types. The fen complex should not be treated as a single unit with one management plan.

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