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Influence of Patch Size, Isolation, and Fire History on Hopper (Homoptera: Auchenorrhyncha) Communities of Eight Wisconsin Prairie Remnants

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Abstract

There is rising concern that the use of fire in managing small, isolated prairie remnants may be adversely affecting prairie-specialist insects. Concern that small remnants may be inadequate for conserving prairie insect diversity also exists. To address these issues, an analysis was made on a quantitative collection of hopper (Homoptera: Auchenorrhyncha) specimens collected in 1986-87. Hoppers were collected from eight dry prairie remnants in south central Wisconsin ranging in size from 0.1 to 17 ha. Collections yielded 21 new species records for the state. I analyzed the occurrence data for effects of remnant size, remnant isolation, average fire-return-interval (1 to 5 years), time-since-last-fire (0 to 4 years), and fire extent (all or part of a site burned) on hopper density, richness, and diversity. Analyses were done on all native species combined and on prairie-specialist species as a sub-group. I also analyzed the specialists individually. The data set revealed no striking, widespread effects of fire history, remnant size, or isolation on density, richness, or diversity. Remnants less than 1.5 ha in size, however, had markedly fewer specialists than those larger than 1.5 ha. Of the nine prairie-specialists, one (*Flexamia albida*) appeared sensitive to remnant size, and another (*Scaphytopius cinereus*) to time-since-last-fire. *F. albida* tended to be more prevalent on larger sites, and *S. cinereus* was more prevalent on areas that had gone the longest without fire. Average fire-return-interval seemed to have no effect on any specialist species. Sampling effort and year had far greater and more consistent influence than fire history, remnant size, or isolation.

Cover photo by Scott Sauer.

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Introduction

Invertebrates, especially insects, dominate the species diversity of terrestrial ecosystems (Wilson 1992), but only in recent years has much attention been given to them in the selection, design, and management of natural areas (Panzer 1988, Kremen et al. 1993, Hamilton 1995a, Panzer et al. 1995, Agosti et al. 2000, Metzler et al. 2005), and then only to a limited extent. This oversight is not due to lack of interest by conservation professionals, but rather to other factors. Foremost is the fact that vegetation defines terrestrial communities as a whole and provides the habitat upon which animals depend, therefore there is a practical need to first understand the vegetation of a natural area before examining other taxa. Unfortunately, resources are rarely adequate to progress much beyond the plant inventory stage. In addition, the taxonomy of many invertebrate groups is in such disarray that even the simplest of inventories often become hindered (New 1987). Even for well described taxa groups, there are often relatively few people skilled in collecting and identifying species. Lastly, for many invertebrates we know relatively little about their life histories and habitat requirements compared to plants and vertebrate animals. All these factors have combined to hamper our ability to intelligently incorporate invertebrates into natural area planning.

Progress, however, is being made. For tallgrass prairie systems, conservationists have begun to consider insects in preserve selection and management to a far greater degree than in the past. As a result, there has been rising interest and concern as to which insects are restricted to prairie remnants (Panzer 1988, Panzer et al. 1995, Metzler et al. 2005); how small and isolated a remnant can be and still have meaningful value to insect conservation (Panzer et al. 1995); and what effect prescribed fire has on prairie insects.

Concern about the possible negative effects of fire on prairie insects is nothing new (McCabe 1981, Opler 1981, Panzer 1988). But the concern has grown greatly in more recent years (Moffat and McPhillips 1993, Hamilton 1995a, Minno and Minno 1996, Reed 1997, Dietrich et al. 1998, Dietrich and Voegtlin 2001, Tooker and Hanks 2004). For a thorough discussion and literature review of this subject, see Panzer (2002).

Due to the highly fragmented nature of the prairie ecosystem today compared to the past, some entomologists are expressing deep concern that many prairie-restricted insects are being negatively affected, and possibly irreparably harmed, by the current use of fire in prairie management (Orwig 1992; Schlicht and Orwig

1992; Swengel 1996, 1998, 2001; Pyle 1997; Williams 1997, 1998; Orwig and Schlicht 1999; Dietrich and Voegtlin 2001; Swengel and Swengel 2007). There is evidence to support this concern (Swengel 1996, 1998, 2001; Panzer 1998, 2003; Harper et al. 2000). However, for the most part we do not yet fully understand which species are vulnerable to fire as it is typically used in prairie management, or how much recovery time each species requires before sites can be safely burned again. These are important questions, because fire is critical to the maintenance of prairie vegetation (Gleason 1913, Curtis 1959, Vogl 1974, Kucera 1981, Henderson 1982, Towne and Owensby 1984, Axelrod 1985, Knapp and Seastedt 1986, Pyne 1986, Gibson and Hulbert 1987, Hulbert 1988, Collins and Wallace 1990, Leach and Givnish 1996, Bowles et al. 2003), and is thus a necessary management tool that can not simply be abandoned as a precautionary measure. Instead, we need to learn more about fire effects on invertebrates in order to better safe guard the entire prairie ecosystem.

In 1989, graduate student Antje Lirken (University of Wisconsin-Madison Department of Zoology) gave me all the insect specimens collected during the course of her Master of Science project on spider community composition and structure in eight upland prairie remnants in south central Wisconsin. The specimens were collected in such a manor as to be useful in providing insights into the influence of fire history, remnant size, and remnant isolation on prairie insects. This paper covers the findings of the hoppers (Homoptera: Auchenorrhyncha), specifically leafhoppers (Cicadellidae), planthoppers (Fulgoroidea super family), and treehoppers (Membracidae). Leafhoppers dominated the collection, and no native spittlebugs or froghoppers (Cercopidae) were present.

I chose to analyze the hoppers, over other taxa groups in the collection, for three reasons. First, they have a high percentage of prairie-restricted or prairie-dependent species, especially among the leafhoppers (Whitcomb et al. 1986, Hamilton 1994, Whitcomb et al. 1994, Panzer et al. 1995). Second, they typically overwinter above ground in the litter and duff, and are thus considered by entomologists to be highly vulnerable to fire (Panzer 2002, Hamilton 1995a). Siemann et al. (1997) found Homoptera to be among the most sensitive to fire of the major taxonomic groups that they looked at. Lastly, their taxonomy is well understood, and leafhopper specialist Dr. K.G.A. Hamilton was graciously willing to identify the specimens.



RICH HENDERSON

Westport Drumlin State Natural Area, Dane County, contains dry to dry-mesic prairie, with a small bur oak savanna along its western edge. Dominant grasses include big and little blue-stem, Indian grass, side-oats grama, needle grass, and prairie drop-seed.



The University of Wisconsin Arboretum owns and manages one of the smaller sites studied, the Bolz Prairie, Dane County.



Oliver Prairie State Natural Area, Green County, includes an undisturbed, remnant dry prairie located on a west- and north-facing hillside.



The dry-mesic Black Earth Rettenmund Prairie, Dane County, occupies a low knob and ridge. The nonprofit Prairie Enthusiasts now own this predominantly forbs-rich state Natural Area, which previously was owned and managed by the Nature Conservancy.



The Muralt Bluff Prairie State Natural Area, Green County, occupies a ridge. Dominant prairie grasses in this dry prairie include little blue-stem, side-oats grama, Indian grass, and prairie drop-seed.



PHOTOS: RICH HENDERSON

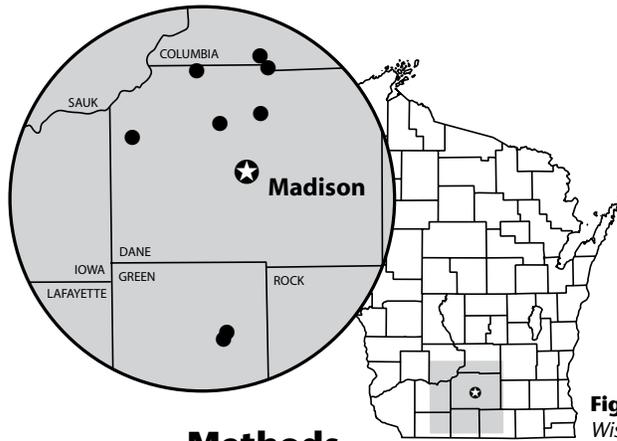


Figure 1. Location of Wisconsin study sites.

Study sites had a variety of burn histories. In some cases, entire sites were burned when fire was used. On others, only a portion of the site was burned. Years-since-last-fire was recorded for each of the prairies included in this study.



PHOTOS: KATHY HENDERSON

Methods

Study Sites

All eight prairie remnants are located in south central Wisconsin (Figure 1). They range in size from 0.1 ha to 17.0 ha (Table 1), and all support similar, relatively undisturbed, dry-upland prairie. The most prevalent grasses are side-oats grama grass (*Bouteloua curtipendula* [Michx.] Torr.), little blue-stem (*Schizachyrium scoparium* [Michx.] Nash.), panic grasses (*Panicum* [*Dichantheium* L.] species), and yellow Indian grass (*Sorghastrum nutans* [L.] Nash.). Also present in lesser amounts are prairie drop-seed (*Sporobolus heterolepis* A.Gray), needle grass (*Stipa spartea* Trin.), and some big blue-stem (*Andropogon gerardii* Vitman). Three of the sites are owned by the University of Wisconsin-Madison; two by private individuals; and one each by The Nature Conservancy, Green County, and Wisconsin Department of Natural Resources (Wisconsin DNR). Half of the sites are designated State Natural Areas within the Wisconsin DNR's Natural Areas Program.

Burn Histories

Burn histories for the sites were compiled from management records and are presented in Table 1. Three measures of fire history were considered for each site:

- 1) average fire-return-interval on the sampled area,
- 2) years-since-last-fire on the sampled area, and
- 3) fire-extent across the entire site.

"Average fire-return-interval" was calculated for the 12-year period prior to data collection (1974-1985). Prior to

Table 1. Study site characteristics. "Isolation Factor" is an index of the site's degree of isolation from other prairie remnants (see "Methods"). "Fire Return Interval" is the average fire return time (in years) to the sampled area within the site for the period 1974-1985. "Fire Extent" refers to the portion of the entire site burned when fires occurred.

Site	Size (Hectares)	Isolation Factor	Fire Return Interval	Fire Extent	Years since Fire	
					1986	1987
Muralt Bluff	17.0	0.51	2.75	Entire/Part	1	0
Hawkhill	16.2	1.02	5.0	Part	3	4
Black Earth	4.5	0.79	3.3	Part		1
Westport Drumlin	4.0	0.50	5.0	Entire/Part		0
Oliver	1.7	0.43	3.3	Entire	1	2
UW Farm	1.2	1.37	3.0	Entire		1
Bolz	1.0	0.58	2.5	Entire		0
Gravel Pit	0.1	1.77	1.0	Entire		0

1974, half of the sites (Hawkhill, Muralt Bluff, Westport Drumlin, and Bolz) had experienced no burning for many decades. The other half had been burned periodically for many years prior to 1974, but at approximately the same, to slightly longer, intervals than shown in Table 1. Total years under fire management prior to sampling were 18 years for Oliver, 23 years for Black Earth, 25 years for UW Farm, and at least 30 years for Gravel Pit (last 12 with annual fire). “Years-since-fire” is the number of years lapsed between specimen collection and the last time the sampled area had been burned. “Fire-extent” reflects how much of the site burned when fire occurred. I assigned sites to one of three categories:

- 1) sites always burned in their entirety,
- 2) sites that had no more than half of their area burned in any given year (in most cases it was no more than a third), and
- 3) sites where the burned portion varied from everything in some years to less than half in other years.

As a practical matter, it is likely that small spots escaped the fires even when the entire site was reportedly burned, but such areas would have been very small in comparison to the site as a whole.

Data Collection

The sampling history of the Lisken work is provided in Table 2. In 1986, three of the prairies (Oliver, Hawkhill, and Muralt Bluff) were sampled with sweep-net, D-vac, and pit-fall trap methods. Lisken found the sweep-net technique to be the most useful (i.e. easiest to use and reasonably effective) for spider sampling. Thus, it was the only technique she employed in 1987, when sampling was expanded from three to eight sites. The sweep-net technique proved the most useful of the three methods for sampling hoppers as well. A representative area of approximately 1.0 ha was sampled at each site (except for the small Gravel Pit Prairie, which was less than 1.0 ha in size). At sites sampled two years running, the same area was used both years.

Pit-fall traps consisted of plastic cups (8.5 cm in diameter and 9.5 cm in depth) set into the ground with the rim even with the soil surface. The cups were filled with ethylene glycol to about a third full. Approximately 60 cm above each trap a 20 cm x 20 cm piece of plywood mounted on nails served as a roof to prevent rain and debris from entering the traps. The pit-fall dates in Table 2 represent the end points of two-week periods during which the traps were left open. At Oliver, 16 traps were

Table 2. Sampling history of study sites (methods and dates). See “Methods” for explanation of sampling “effort”.

Site	Effort	1986			1987
		Sweep Net	D-Vac	Pit-fall	Sweep Net
Oliver	5	Aug. 12	Aug. 12	May 8, 21, June 11, Aug. 20, Sept. 17	July 9 Aug. 19
Hawkhill	5	Aug. 13	Aug. 13	May 13, 26, June 11, Aug. 21, Sept. 17	July 8, Aug. 3, 17
Muralt Bluff	4	Aug. 18	Aug. 18		July 9, Aug. 19
Westport Drumlin	3				July 8, Aug. 3, 20
Bolz	2				July 8, Aug. 20
Black Earth	2				July 8, Aug. 20
UW Farm	1				Aug. 20
Gravel Pit	1				Aug. 20

Table 3. Prairie-specialist hoppers found during the course of the Lisken study, along with the number of sites, number of specimens, known host plants, and generations per year.

Species	Sites	Specimens	Host(s) ^a	Voltinism ^b
<i>Laeicephalus unicoloratus</i> (Gillette & Baker)	8	255	blue-stems	>1
<i>Laeicephalus minimus</i> (Osborn & Ball)	7	260	side-oats grama	>1
<i>Flexamia pectinata</i> (Osborn & Ball)	7	105	side-oats grama	1
<i>Flexamia albida</i> (Osborn & Ball)	3	64	little blue-stem	1
<i>Scaphytopius cinereus</i> (Osborn & Ball)	4	51	forbs (<i>Amorpha</i>) ^b	>1
<i>Chlorotettix spatulatus</i> (Osborn & Ball)	4	46	little blue-stem	>1
<i>Bruchomorpha dorsata</i> Fitch	4	16	little blue-stem	1
<i>Bruchomorpha jocososa</i> Stal	4	12	little blue-stem	
<i>Polyamia herbida</i> DeLong	3	14	<i>Panicum</i> spp.	
<i>Extrusanus oryessus</i> Hamilton	2	5	sedges	1
<i>Memnonia flavida</i> (Signoret)	2	4	(native grasses)	1
<i>Mesamia ludoviciana</i> Ball	1	7	<i>Artemisia</i> / forbs	
<i>Memnonia panzeri</i> Hamilton	2	2	prairie drop-seed	1
<i>Polyamia apicata</i> (Osborn)	1	1	<i>Panicum</i> spp.	1
<i>Polyamia caperata</i> (Ball)	1	1	? <i>Panicum</i> ?	1
<i>Prairiana cinerea</i> (Uhler)	1	1	unknown	

^a Based on Whitcomb et. al. (1986) and Hamilton (1995a).

^b Panzer (1998).

used during each of the first three periods and 18 traps were used in the last two. At Hawkhill, 28 traps were used each period. D-vac suction sample points were 1 m² in size. Ten D-vac samples were taken at each site. Each sweep-net sample consisted of 20 sweeps. The sweep-net had a diameter of 38.1 cm and a handle length of 1 m. To avoid sweeping the same area twice, one sweep was made with each step forward and the arm extended. Ten sweep-net samples were taken from each site in August 1987. July 1987 sampling consisted of only five samples per site.

Each D-vac and sweep sample was emptied into a plastic bag and frozen for later sorting in the lab. The non-spider specimens were eventually placed in 70% ethyl alcohol, with one sample per vial, and given to the Wisconsin DNR's former Bureau of Research. In 1997, this material was sorted by order and identified to morpho-species. The number of individuals per morpho-species was tallied for each sample. At least two representative specimens of each morpho-species of hoppers were taken from each sample and sent to Dr. K.G.A. Hamilton of Agriculture Canada for identification. This was approximately 28% of the total material. Using the specimens identified by Dr. Hamilton as reference material, the remaining specimens were identified by Wisconsin DNR personnel.

Analysis

I analyzed the data using statistical software from SAS Institute Inc. (1990). Linear regressions were run comparing the effects of sampling effort, remnant size, remnant isolation, fire-return-interval, and years-since-last-fire on numbers of individuals (density), number of species (richness), Simpson index of diversity, and Shannon index of diversity. Analysis-of-variance (ANOVA) was used to test the effect of fire-extent. The analyses were run on three groupings of adult hoppers; all native species, non-wind-dispersed native species, and prairie-specialist species (see Panzer et al. 1997). Analyses were also run on the density of the eight most prevalent prairie-specialist species, and all leafhopper (Cicadellidae) nymphs. Most analyses were done on the more robust 1987 sweep-net data of late

Table 4. Homoptera collected during the course of the Lisken study and the number of species, adults, and immatures by family.

Family	Species	Adults	Nymphs
Cixiidae (planthoppers)	1	2	0
Delphacidae (planthoppers)	7	303	360
Issidae (planthoppers)	2	101	0
Flatidae (planthoppers)	1	1	0
Dityopharidae (planthoppers)	3	61	3
Caliscelidae (piglet bugs or planthoppers)	5	35	101
Cercopidae (spittle bugs or froghoppers)	1	1690	15
Cicadellidae (leafhoppers)	55	2182	2484
Membracidae (treehoppers)	3	102	15
Psyllidae (jumping plant lice)	?	8	--
Aphididae (aphids)	?	368	--

August (n=8 sites; 10 samples/site) (Table 2). The site characteristics (effect factors) were tested for independence from each other using paired linear regressions.

Analysis of sampling effort was accomplished by assigning an effort value to each study site based on the total sampling history at the site (Table 2). The more visits made to a site and the more methods used, the higher the sampling effort value. Values ranged from 1 (lowest) to 5 (highest). Comparisons were made between richness and sampling effort.

A measure of isolation was derived for each study site using the distances (km) from the study site to each of its three closest neighboring remnant prairies. The index value was calculated by averaging the distances, but with the shortest distance weighted by a factor of 4. The Index equaled $(4D_1 + D_2 + D_3) / 6$.

Prairie-specialist and wind-dispersed species were identified and assigned to their respective categories based on personal communications with Dr. K.G.A. Hamilton, Dr. Ron Panzer, and Dr. Robert Whitcomb, as well as Panzer et al. (1995) and Hamilton (1995a). Initially the specialists were divided into two sub-categories; highly restricted and moderately restricted. After, finding no differences between the two groups in response to the factors, they were merged into one category (Table 3).

Results

Lisken collected a total of 78 hopper species (Appendix 1). Table 4 shows the breakdown by family, along with numbers of individuals. Twenty-one species (27%) had not been recorded (published) from Wisconsin at the time of their identification in 1994 (Hamilton, personal communication). Sixteen (21%) are prairie specialists (Table 3). At the time of Dr. Hamilton's determinations, four of the taxa were undescribed species: *Extrusanus* sp., *Memnonia* nr. *grandis*, *Liburnia* sp., and *Oliarus* sp. Since then, the *Extrusanus* sp. has been named *E. oryssus* (Hamilton 1995b) and the *Memnonia* sp. has been named *M. panzeri* (Hamilton 2000).



Considered a fire-sensitive species, *Laevicephalus minimus* was the most frequently collected hopper.

SCOTT SAUER

Sampling Effort

As to be expected, there was a strong positive correlation between sampling effort and number of species found (Figure 2). This was the case for all native species combined ($R^2=0.76$, $P=0.005$) and prairie-specialists as a subset ($R^2=0.66$, $P=0.02$).

Remnant Size and Isolation

No significant correlations ($P<0.10$) were found between remnant size or isolation and native hoppers, both non-wind-dispersed species alone and all natives as a whole. This held true for all measures; density, richness, and the diversity indices. Prairie-specialists did exhibit a positive correlation ($R^2=0.52$, $P=0.04$) between remnant size and species richness (Figure 3), but not with the diversity indices or density. No correlation was found between prairie-specialists as a group and remnant isolation.

Densities of most prairie-specialist hoppers were not affected by remnant size, and none were affected by isolation. *Flexamia albida* (Osborn & Ball), however, showed a statistically significant positive correlation between remnant size and density ($R^2=0.80$, $P=0.003$) (Figure 4), and *Scaphytopius cinereus* (Osborn & Ball) showed a weak positive correlation ($R^2=0.48$, $P=0.06$). Cicadellidae nymph density correlated positively ($R^2=0.86$, $P=0.007$) with remnant size in the July data set ($n=6$ sites; 5 samples per site), but not in the larger August data set ($n=8$ sites; 10 samples per site). There was no correlation between Cicadellidae nymph density and isolation.



One hopper, *Flexamia albida*, appeared sensitive to remnant size, tending to be more prevalent on larger sites.

Fire History

For the variables of density, richness, and both diversity indices, no significant correlations were found between native hopper groups and any of the fire history factors (i.e. average return, years-since-last, and extent). Within the prairie-specialist group, no significant correlations were found between fire history factors and hopper density, or the two diversity indices. However, species richness seemed to be affected by fire-extent. ANOVA revealed statistically

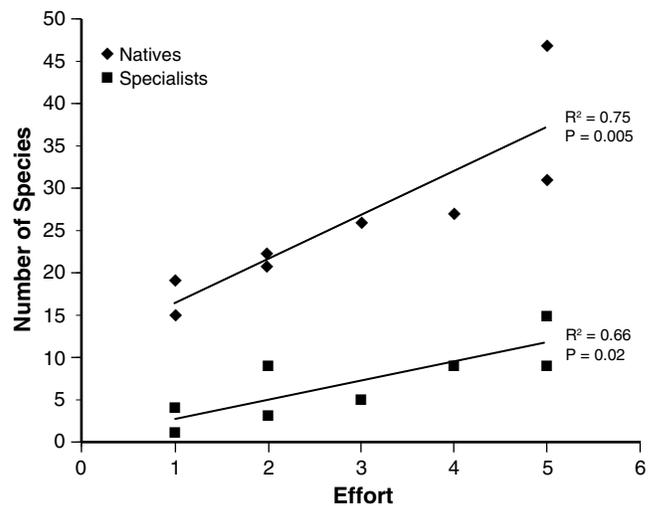


Figure 2. Pearson correlation regression between sampling effort (all sample methods and dates combined) and number of hopper species found (all native species combined and prairie specialists only). See methods for explanation of sampling effort.

significant differences among the three fire-extent categories ($F=5.22$; $df=2, 5$; $P=0.06$). Sites burned only in part had higher numbers of specialist species than those burned in their entirety (Figure 5). However, there was no significant correlation detected between specialist species richness and average fire-return-interval, or years-since-last fire.

Results of fire history influence on the eight individually tested prairie-specialist species are presented in Table 5. Presence and density of all specialists seemed to have been unaffected by the average-fire-return interval or fire-extent. As for years-since-last-fire, only *Scaphytopius cinereus* (Figure 6) showed any correlation. Density was highest with greatest time since last fire.

Interactions of Effect Factors

Paired regression analysis among the effect factors of remnant size, remnant isolation, fire-return-interval, and years-since-last-fire, yielded no statistically significant results. Only the factors of remnant size and fire-extent were not independent of each other. The four smallest sites were always burned in their entirety, and the four largest were mostly burned only in part.

Year Effect

There was a very consistent and strong year effect on density, richness, and the diversity indices for both all native hopper species combined and specialist hoppers as a subset. All measured response variables were higher in 1987 than in 1986 (Figures 7, 8, and 9). Cicadellidae nymph densities were also higher in 1987 than in 1986 (Figure 10). The 1986 to 1987 change-in-density of individual specialists also showed the same trend (Table 6).

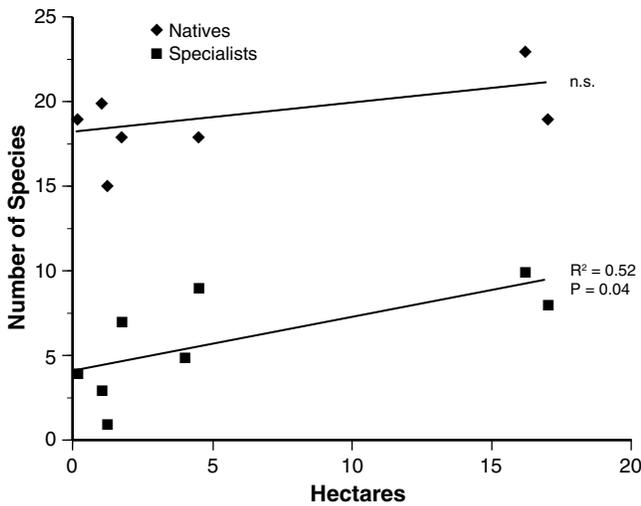


Figure 3. Pearson correlation regression between prairie remnant size and number of hopper species found (all native species combined and prairie specialists only) for sweep net data of August 1987. n.s.= not significant ($P>0.10$).

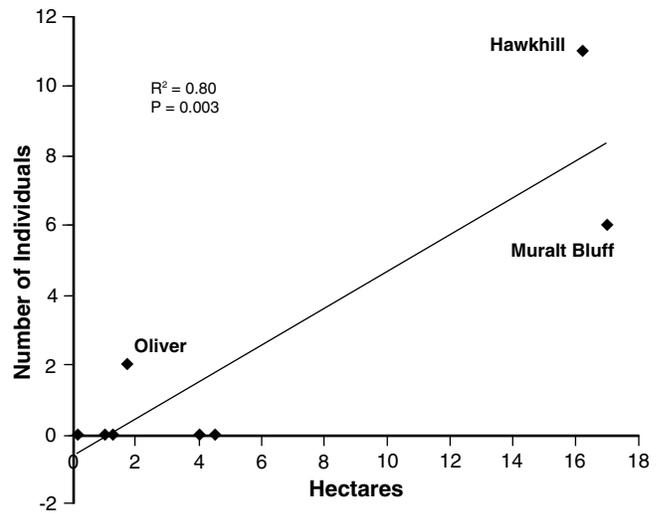


Figure 4. Pearson correlation regression between *Flexamia albida* density and prairie remnant size for sweep net data of August 1987.

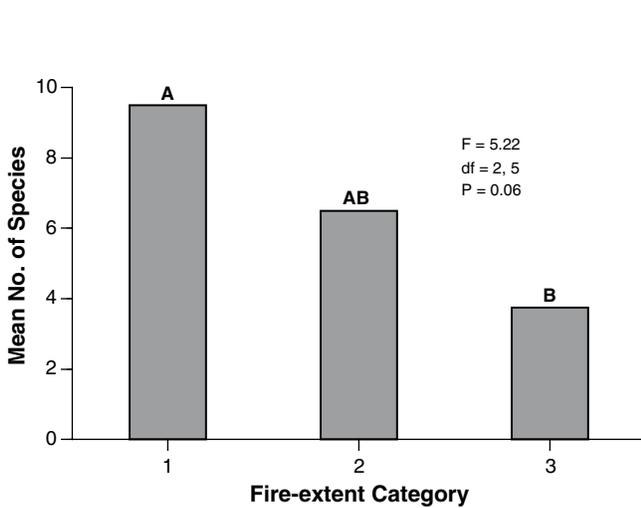


Figure 5. ANOVA of the mean number of prairie-specialist hopper species by fire-extent category for sweep net data of August 1987. Category 1=only part of the site burned each time, 2=in some years part of the site was burned and other years all of it was burned, 3=entire site burned each time.

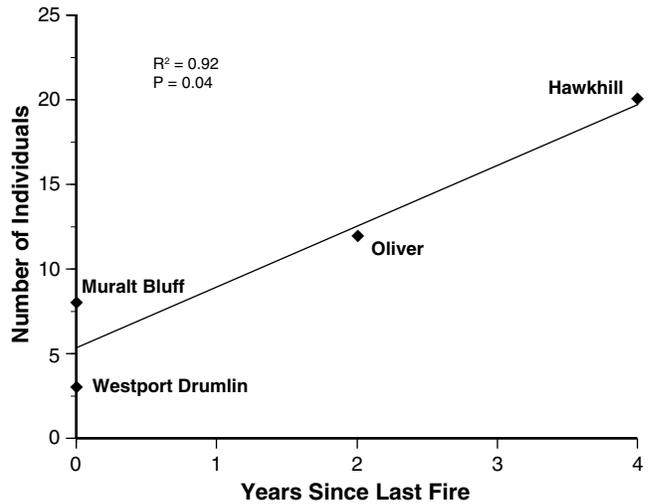


Figure 6. Pearson correlation regression between *Scaphytopius cinereus* density and years since last fire for sweep net data of August 1987.

Table 5. Effect of fire history on density of prairie-specialist hoppers using sweep net data from July (n=6 sites; 5 samples per site) and August (n=8 sites; 10 samples per site). “-”= not significant ($P>0.10$).

Species	Fire Return Interval		Fire Last		Fire Extent	
	July	Aug.	July	Aug.	July	Aug.
<i>L. unicoloratus</i> (G. & B.)	-	-	-	-	-	-
<i>L. minimus</i> (O. & B.)	-	-	0.88 (P=0.02)	-	-	-
<i>F. pectinata</i> (O. & B.)	0.91 (P=0.01)	-	-	-	-	-
<i>F. albida</i> (O. & B.)	-	-	-	-	-	-
<i>S. cinereus</i> (O. & B.)	-	-	-	0.96 (P=0.04)	-	-
<i>C. spatulatus</i> (O. & B.)	-	-	-	-	-	-
<i>B. dorsata</i> Fitch	-	-	-	-	-	-
<i>B. jocosus</i> Stal	-	-	-	-	-	-

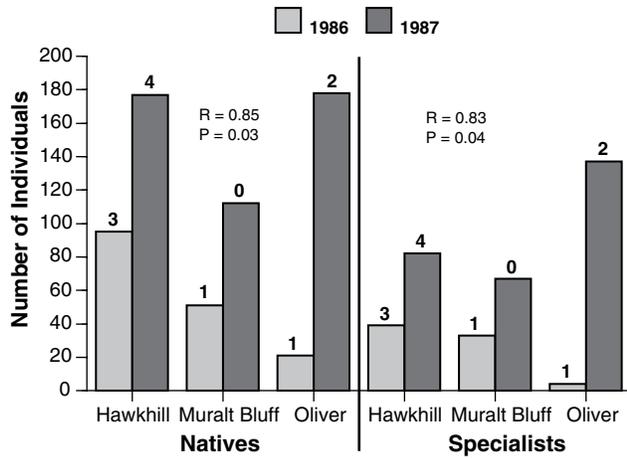


Figure 7. Effect of year (1986 vs. 1987) on hopper density for August sweep net data. The numbers above the columns are the years-since-last burned.

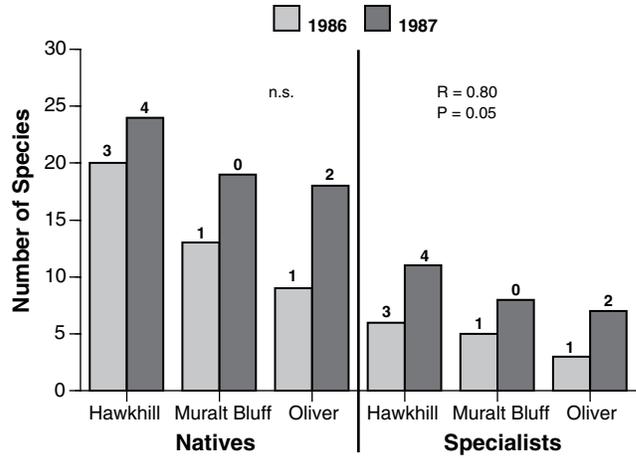


Figure 8. Effect of year (1986 vs. 1987) on hopper richness for August sweep net data. The numbers above the columns are the years-since-last burned. n.s.= not significant ($P>0.10$).

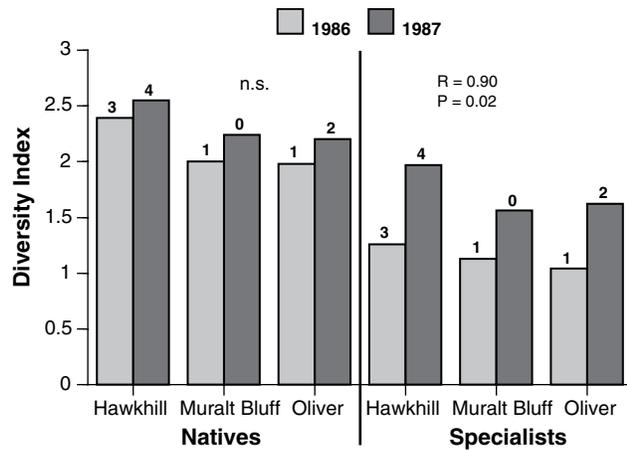


Figure 9. Effect of year (1986 vs. 1987) on diversity (Shannon Diversity Index) for August sweep net data. The numbers above the columns are the years-since-last burned. n.s.= not significant ($P>0.10$).

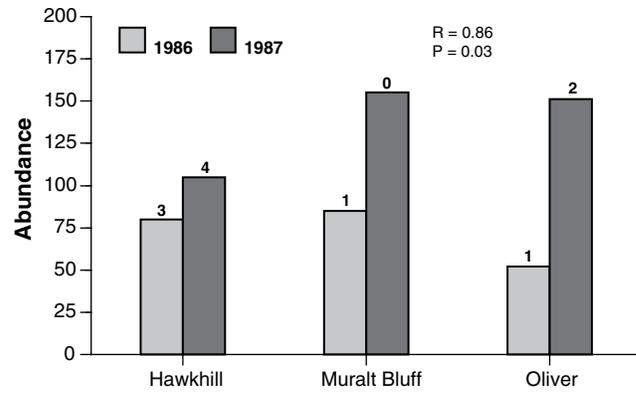


Figure 10. Effect of year (1986 vs. 1987) on Cicadellidae nymph density for August sweep net data. The numbers above the columns are the years-since-last burned.

Table 6. Change in density from 1986 to 1987 of prairie-specialist hoppers in August sweep net data. Values under the site names are the years since fire in 1986 and 1987, respectively. Percent change is in parentheses.

Species	Hawkhill (3 to 4)	Muralt Bluff (1 to 0)	Oliver (1 to 2)
<i>L. unicoloratus</i> (G. & B.)	0	+13 (62%)	+40 (>1000%)
<i>L. minimus</i> (O. & B.)	-3 (14%)	-4 (80%)	+40 (>1000%)
<i>F. pectinata</i> (O. & B.)	+1 (50%)	+2 (>1000%)	+24 (>1000%)
<i>F. albida</i> (O. & B.)	+10 (900%)	+4 (200%)	+2 (>1000%)
<i>S. cinereus</i> (O. & B.) ^a	+19 (>1000%)	+6 (300%)	+11 (>1000%)
<i>C. spatulatus</i> (O. & B.)	0	+4 (133%)	+14 (700%)

^a The increase from 1986 to 1987 (all sites combined) is significant ($P=0.03$, $r=0.86$).

Discussion

Study Limitations

The data from the Lisken collection is clearly not adequate for detecting weak or subtle effects or interactions among the site characteristics. To do so would likely require a pool of sites ten times larger than the eight used, and would have to include sites larger in size and burned less frequently than what were used. It is reasonable to assume, however, that the Lisken data set is adequate for detecting very strong widespread and consistent effects of remnant size, isolation, and fire history on native hoppers as a whole and prairie-specialist species as a subset. However, because long-unburned and very large remnants are not represented in the pool of study sites, it is possible that highly fire-sensitive and highly area-dependent species are missing from the analysis, thus biasing the results towards no detection of effects, even at the coarsest level.

In an attempt to address this concern, I compared the richness of prairie-specialist hoppers on the Lisken sites to the richness of specialists found on 100 remnants surveyed by Hamilton (1995a) in the northern part of the tallgrass prairie biome. I also compared the “commonness” of prairie-specialist species found on the Lisken study sites to the “commonness” of specialists found on 180 prairie remnants in Wisconsin surveyed for hoppers from 1994-2000 (Wisconsin DNR, unpublished data).

Hamilton assigned his 100 sites to one of six categories of hopper richness, along a continuum from depauperate to excellent. He did this by ranking the remnants based on the number of prairie-specialist he found at each, and then dividing the resulting list into six segments with approximately equal number of sites in each segment. Hamilton’s sites were a very diverse group including some of the largest and highest quality remnants known and many sites with minimum exposure to fire. A comparison of the Lisken to Hamilton sites (Table 7) indicates that the Lisken sites are not unduly depauperate in species. In fact, they appear to support above average richness of prairie-specialist hoppers.

Compared to the larger pool of 180 Wisconsin sites, however, it appears that specialist species very rarely encountered across the state may have been underrepresented on the Lisken study sites. Of 106 prairie-specialists

found across the state in the 1994-2000 survey, approximately 20% were found in each of following categories: 1) on one site only, 2) on two sites, 3) on 3-6 sites, 4) on 7-18 sites, and 5) on more than 19 sites. Thirty prairie-specialist hoppers were detected on the Lisken sites during 1986-87 or in subsequent surveys (Henderson, unpublished data). Their representation in the five “20%” categories were 0%, 7%, 23%, 27%, and 43%, respectively. Therefore, the Lisken sites as a group are weak in rarely encountered species, and thus of limited use in addressing the effects of site characteristics on those prairie hoppers. One cannot infer from this, however, that the lack of detection of very rarely found species on the Lisken sites is due to the sites’ fire history or size. Other factors would have to be ruled out, such as requirements for specialized (rarely encountered) habitat, edge of range considerations, and inadequacy of the survey collection methods to detect them, before such conclusions could be reached. Based on overall specialist richness and “commonness,” it seems that the Lisken sites are adequate for detecting, at minimum, strong effects of fire history and remnant size on prairie hopper communities.

Initial Response to Fire

In one of the first investigations into the effects of fire on prairie hoppers, Carpenter (1939) looked at a number of hopper species following a single spring burn, but found consistent responses from only six species. He found that one species declined, three remained unchanged, and two increased post-burn. Unfortunately, most studies since have stopped at the family level. Nagel (1973) and Van Amburg et al. (1981) found post-fire density declined for Cercopidae (spittlebugs or froghoppers), declined or remained unchanged for Membracidae (treehoppers), remained unchanged for Dictyopharidae and Fulgoroidea (planthoppers), and increased for Delphacidae (planthoppers).

The response of Cicadellidae (leafhoppers) has been more varied. Six studies have found an increase following fire, at least by mid- to late summer (Rice 1932, Cancelado and Yonke 1970, Hurst 1970, Nagel 1973, Dunwiddie 1991, Hartley et al. 2007). However, others have found significant initial declines, at least among some species, lasting through the first season post-fire (Bulan and

Table 7. Categorizing of the Lisken study sites based on number of prairie-specialist hoppers detected (after Hamilton 1995a).

Data Source	Depauperate (0-1)	Poor (2-3)	Fair (4-5)	Good (6-8)	Very Good (9-11)	Excellent (12-24)
Aug. 1987 Lisken sweep net	1	1	2	2	2	0
All Lisken data	1	1	2	0	3	1
All collecting on the sites ^a	0	0	2 ^b	1	1	4

^a Includes all Lisken data and results from surveys done after the Lisken study (Wisconsin DNR unpublished data). This data set likely comes closest of the three in matching Hamilton’s highly focused and skilled surveys that formed the basis of his rating system.

^b One of these sites was destroyed shortly after completion of the Lisken study, thus no additional collecting was done on it.

Barrett 1971, Mason 1973, Anderson et al. 1989, Siemann et al. 1997, Panzer 1998, Harper et al. 2000). From this evidence, it is safe to assume that initial response to fire among prairie hoppers is species specific, and therefore research must be pursued at the species level (Panzer 2002). Work done at the species level has been limited to this study, Mason (1973), Panzer (1998, 2002, & 2003), and to a very limited extent Harper et al. (2000).

For the most part, hoppers spend the winter as eggs in, or on, their host plants, or as nymphs (DeLong 1948). The over winter location for nymphs is presumably in the litter or at the base of the plants. Consequently, hoppers are generally considered especially vulnerable to fire (Hamilton 1995a, Siemann et al. 1997, Panzer 1998, 2002). There is strong evidence that single, dormant-season fires can cause significant, initial reductions in hopper abundance, but very rarely do they cause elimination of a species (Bulan and Barrett 1971, Mason 1973, Panzer 1998, 2002, 2003).

Panzer (1998), in a study of fire effects on prairie insects in the Chicago region, measured initial (early-season) post-fire abundance of 40 prairie-specialist hoppers (90% leafhoppers). The number of test trials per species ranged from 1 to 16, with a mean of 5.25. He found that fires significantly reduced initial abundance in 60% of the species, had no effect on 25% of the species, and stimulated an increase in 15% of the species. Most of the fire-neutral and fire-positive species were wet prairie specialists. Panzer presumed that fire consumed less of the litter, and thus caused less mortality, in wet sites than in upland, thus the lower rate of fire-sensitivity among wet prairie species. Of the upland species, 83% were fire-negative compared to only 17% of the wet prairie species.

A fire-effects study by Harper et al. (2000) on two prairie remnants in Illinois used enclosures to estimate in situ survival. They found *Deltocephaline* (Cicadellidae)

leafhoppers to have significantly lower numbers inside enclosures in burned areas than in unburned, but that *Typhlocybina* (Cicadellidae) leafhoppers responded just the opposite. The former group has a higher percentage of prairie-specialist species than the latter group. This agrees with Panzer's (2002) findings that remnant-dependent insect species are more likely to be fire-negative than remnant-independent species.

In contrast to the findings of Harper et al. (2000), Panzer (1998), and Mason (1973), analysis of the Lisken data did not detect negative effects of fire on hoppers. The data reveal no statistical differences in hopper density, for either natives in general or specialists as a subset, between areas burned that year (year-0) and areas that are 1, 2, or 4 years post-fire. This discrepancy is likely due to the time of year that the Lisken specimens were collected, mid-August. By then, the recovery or recolonization of many species may have already been well on its way, thus obscuring any initial declines. Panzer (1998) found 66% of the fire-sensitive species he tracked recovered within a year or less on larger tracts of prairie. Harper et al. (2000) found adults of *Laevicephalus minimus* (Osborn & Ball) starting to reappear in a burn treatment in central Illinois as early as mid-June. Wisconsin collection records for the 16 specialist hoppers found in the Lisken collection have dates of first adult activity to be May 26 and 31, June 3, 8, 20, and 24, and July 4 (Henderson, unpublished data). Thus, all these species had opportunity to rebuild (or recolonize) post-fire populations by mid-August. Mid- to late season sampling by Hurst (1970), Nagel (1973), and Van Amburg et al. (1981) may explain why they detected no negative effects from fire as well. For example, Dunwiddie (1991) found hopper (mostly leafhopper) abundance in July to be 33% to 50% lower following a spring burn than on the control, but by August populations recovered, and by September abundance was 100%



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higher on the burn than the control. Cancelado and Yonke (1970) found no statistical difference in hopper abundance in burned and unburned areas in April and May, but from June through September they found numbers to be statistically higher on the burned areas. This suggests an improvement in habitat may have resulted from the fire, such as more abundant or nutritious food.

The apparent recovery potential of hoppers post-fire suggests that when it comes to managing remnant prairie, knowing a hopper's initial response to fire may be of less relevance than knowing factors such as recovery time, primary method of recovery (i.e. in situ survival versus re-invasion), long-term survival under various fire-regimes, or population densities required for long-term survival. Answers to these questions are of more practical use to managers in planning burn regimes than knowing simply whether or not there is an initial decline.

Recovery Method

Knowing the primary means by which a fire-sensitive species recovers (i.e. in situ survival versus recolonizing) is of immense help in determining the need for, as well as size and location of, unburned refugia. Unfortunately, the Lisken data set lacks May/June data, and thus is of little help in addressing in situ survival.

The influence of refugia on recovery, however, is indirectly addressed by this study through the factors of fire-extent (presence of refugia) and isolation. Neither factor seemed to have any affect on overall native hopper density, richness, or diversity. Among the specialists, however, fire-extent did appear to have a significant effect on richness (Figure 5). There were no other effects of fire history on prairie-specialists as a group. This result would seem to support the idea that unburned refugia play an important role in post-fire rebuilding of populations of specialist hoppers and thus the retention of species over time. Unfortunately, in the limited dataset of this study, fire-extent was not independent of remnant size (Table 1). Both of these factors correlated with richness (Figures 3 and 5). Therefore, it is unclear in this study as to which was the driving force. It is also unclear why only richness and not diversity was significantly affected by these factors. The negative trend was there for the diversity indices, but the P values were >0.10 . Given that density of the specialists was not affected by fire extent and that remnant size was shown to affect species richness (see discussion below), it seems more likely that remnant size, rather than fire-extent, was the causative factor here.

Results from both Harper et al. (2000) and Panzer (1998) document relatively low in situ survival rates on average for many, if not a majority of, prairie-specialist hoppers. What seems to be lacking in the literature is documentation that recolonization is critical to the maintenance of specialist hopper richness (i.e. in situ survival is so low or non-existent in some cases that recovery will not occur without infusion of colonizers from elsewhere).

The use of enclosures in fire studies is an excellent way of confirming in situ survival and detecting initial reductions in abundance. But it is very difficult for enclosure studies to prove the absence of in situ survival. With organisms as small as hoppers, absence of proof is not proof of absence.

For example, the enclosure study by Harper et al. (2000), although focused at higher taxonomic levels, did happen to comment on one prairie-specialist leafhopper specifically, *L. minimus*, which was present on one of their two study sites. In the burn treatment, they found no specimens of this species within their 14 sample-points (7 enclosed and 7 open, each 0.8 m² in size) during their sampling period from late May to mid-June. *L. minimus* was detected, however, in both open and enclosed sample points in the nearby, unburned control, and thus demonstrated a very significant initial reduction of *L. minimus* due to fire. This was not proof of elimination from the site resulting from fire, however, for the surface area covered by the sample points was only approximately 1/10th of 1% of the burned prairie. The most that can be said from this example is that the density of *L. minimus* fell below a level that the survey method was capable of detecting, and that the species may or may not have been eliminated. By mid-June, the authors found adults of *L. minimus* in the open sample-points within the burned area. They speculated that this recovery was due primarily to recolonization from the nearby, unburned refugia. The contribution of in situ survival in their study is unclear, other than to say it was likely very small. Harper et al. (2000) also considered recolonization to play a major role in the recovery of Deltocephaline (Cicadellidae) leafhoppers, as a group.

Recovery due primarily to recolonization cannot be ruled out as a major factor in the Lisken study as well, but the case of the Gravel Pit Prairie gives support to in situ survival serving as a viable means of recovery for at least some fire-sensitive hoppers. Gravel Pit Prairie was the smallest, most isolated, and most frequently burned of the Lisken study sites (Table 1). After at least 10 years of annual burning of the entire site, it still retained four specialist hoppers: *Laevicephalus minimus*, *L. unicoloratus* (Gillette & Baker), *Flexamia pectinata* (Osborn & Ball), and *Bruchomorpha jocosus* Stal. The site was a minuscule island of prairie sod in a sea of corn and soybeans. The next closest patch of prairie sod was 1.1 km away, and was itself less than 0.1 ha in size. The next closest remnant after that was 1.9 km away and only 0.1 ha in size. At least three of the specialists found at the Gravel Pit Prairie are known to be very fire-sensitive (Harper et al. 2000, Panzer 1998). This example case suggests that recovery based on in situ survival alone, or at least recolonization from exceedingly small un-burned pockets, may routinely occur for some species.

In a study of leafhopper diversity in tallgrass prairie near Manhattan, Kansas, Mason (1973) found leafhoppers to be well represented in diversity and numbers in

an annually burned 65 ha plot. The area he sampled was several hundred meters from the nearest unburned prairie. Based on these site conditions, he assumed in situ survival was the primary means of leafhopper recovery following fire (Mason, personal communication).

Panzer (1998, 2003) considered both in situ survival and recolonization to be important means of population recovery. He specifically looked for in situ survival in three prairie-specialist leafhoppers (*Aflexia rubranura* [DeLong], *Memnonia panzeri*, and *Neohecalus lineatis* [Uhler]), and documented survival in 93% of the test trials. Survival occurred in 9 of 10, 8 of 9, and 4 of 4 trials, respectively. The host plant patches he looked at were completely burned, disjunct, and exceedingly small. They ranged in size from 4 m² to 32 m². Panzer also compared post-fire recovery rates between vagile and non-vagile species and found no statistical difference.

The evidence from Mason (1973), Panzer (1998, 2003), and this study suggests that, on average, in situ survival may play a significant role in hopper population recovery. It does not, however, diminish the possibility that some specialist hoppers may rely primarily (Harper et al. 2000, Panzer 1998, 2003), or even solely, on recolonization from nearby unburned refugia. At this time, sound documentation is simply lacking as to what degree hoppers are dependent, if at all, on recolonization for post-fire recovery. This places site managers in the position of leaving portions of sites unburned out of wise prudence, rather than firm knowledge of its necessity for the maintenance of specialist hoppers. Future work may yet rectify this situation. In the interim, Panzer's (2002, 2003) findings that recolonization accelerates recovery lends support to the practice of leaving un-burned refugia, if for no other reason than to allow for shorter average fire-return intervals, without loss of fire-sensitive leafhopper species, than would be possible if the entire site were burned at once.

Recovery Time

Determining when a population is recovered from fire is not necessarily a straightforward task. For sake of convenience, the following discussion of recovery time assumes recovery has occurred when population levels statistically meet or exceed those of a comparable unburned control. There is no assumption made here that this is the population level necessary for long-term persistence of a species, as discussed in the next section.

It appears that hoppers in general recover quickly from fire (i.e. within a year). The Lisen data show no effects of years-since-last-fire or average-fire-return-interval on native hopper density, richness, or diversity. Of the 12 specialist species in the August 1987 data, 10 were detected on sites burned that year (year-0). Of the two that were not, one (*Mesamia ludoviciana* Ball) was likely limited by absence of host plants, not recent fire, and the other (*Prairiana cinerea* [Uhler]) is simply rare. It is known from only six

sites in the state, but four of the six have histories of regular burning. Therefore, its absence is likely one of chance rather than recent fire. Dunwiddie (1991) observed that hopper numbers (mostly leafhoppers) started out in mid-July 33% to 50% lower on a burned treatment than on an unburned control, but by early August there was no difference, and by early September hopper numbers were 100% greater on the burned area than the unburned. Anderson et al. (1989) also reported reduced hopper numbers in July post-fire. Four other studies have also reported near 100% increases, by mid- to late summer, in overall abundance of hoppers (over 90% leafhoppers) on burned sites compared to unburned controls (Cancelado and Yonke 1970, Hurst 1970, Nagel 1973, Moya-Raygoza 1995). They generally attribute the increases to a greater quantity or quality of food in the post-fire environment. The findings of Siemann et al. (1997) and Harper et al. (2000) are more ambiguous. Siemann et al. found recovery lacking by end of year-0 in one year of their two-year study, but found no difference in numbers in the other. Harper et al. found recovery by late July post-fire at one of their two study sites, but not the other.

How quickly individual species, and especially prairie-specialists, recover from fire appears to be highly variable. Panzer (1998) looked at the mean recovery rates among 10 suites of prairie insects. Leafhoppers were the largest group. He detected no differences in recovery rates between specialists (remnant-dependent) and non-specialists (remnant-independent), wetland and upland species, vagile and non-vagile species, and contiguous and disjunct populations. The only factor that seemed to affect recovery rates was number of generations per year. Univoltine species tended to have longer recovery periods on average than multivoltine species ($P=0.068$).

The results from the Lisen data seem to indicate that prairie-specialist hoppers, as a group, as well as native hoppers as a whole, also recover quickly from fire (i.e. within a year). The data showed no effects from years-since-last-fire or average-fire-return-interval on density,



One hopper, *Scaphytopius cinereus*, appeared to be sensitive to time-since-last-fire, tending to be more prevalent on areas that had gone the longest without fire.

richness, or diversity on specialists. This is with most of the specialists in the study being univoltine (Table 3). When specialist species were looked at individually, however, the responses were mixed. For example, *Scaphytopius cinereus*, although present on year-0 sites, seemed to have progressively higher densities on sites with additional years since fire (Figure 6), suggesting that full recovery for this species may require multiple years. But this finding is at odds with Mason's (1973) and Panzer's (1998) work on this species, and may be the consequence of the Lisken data's small sample size. Mason and Panzer both found *S. cinereus*, which is a multivoltine species, to be either unaffected by fire or fully recovered by the end of year-0 post-fire. The Lisken data also hint at the possibility of *Laevicephalus* spp. populations not fully recovering by end of year-0. Instead, they seemed to reach their highest densities at year-1 post-fire, and then decline thereafter in absence of fire (Figure 11); the end result being no difference in abundance between sites at year-0 (late in the season) and sites at year-4 post-fire. Harper et al. (2000) and Panzer (1998) also did not find full recovery for *Laevicephalus* spp. by the end of year-0, even though they are multivoltine species. The other six specialists analyzed from the Lisken data were either unaffected by the burns or appeared fully recovered by August of year-0 (Table 5). In contrast, both the Mason (1973) and Panzer (1998) studies did not show full recovery by end of year-0 for four of them: *F. albida* (univoltine), *F. pectinata* (univoltine), *Bruchomorpha dorsata* Fitch (univoltine), or *Chlorotettix spatulatus* (Osborn & Ball) (multivoltine).

Other studies of prairie-specialist hoppers have found recovery of prairie-specialist leafhoppers to be generally fast (i.e. within a year), but not uniformly so. Fifty-seven percent of the specialist leafhoppers in Mason's (1973) study had frequencies of occurrence in the burn treatment equal to, or exceeding, those in the unburned control by the end of year-0 post-fire. In the Panzer (1998) study, hopper recovery tended to be slow among upland species, but fast among lowland species. Only 20% of the



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Fire frequency may not be a major concern for the fire-sensitive *Laevicephalus unicoloratus*, which remained present on one site after at least 10 years of annual burning of the entire site.

upland prairie leafhoppers he investigated recovered by end of year-0. Most of the rest recovered by the end of year-1, and a few took until the end of year-2 post-fire. Conversely, 83% of the wet prairie species were unaffected or recovered by end of year-0. Harper et al. (2000) found the density of Deltocephaline leafhoppers, as a group (which includes many prairie specialists), recovered by the end of year-0 at one of their two study sites, but only 35% recovered at the other. They thought this difference might be due to differing burn histories of the sites prior to the study.

Long-term Persistence on Fire Managed Sites

An obvious and conservative approach to deciding when to re-burn a given area, from the perspective of insect conservation, is to wait for populations levels to reach or exceed those found in long unburned conditions or in nearby unburned controls. Although logical, this approach may not necessarily be a valid way of assessing what burn frequency is safe for the long-term survival of a species, especially for species with high reproductive rates, such as hoppers. It is conceivable that the population levels reached in unburned conditions may be substantially higher than what is actually necessary for long-term viability. Conversely, in any given year, the population level on an unburned control might, by chance, fall below what is safe for the long-term viability, and thus be a poor goal at that point in time. An alternative approach may be to rely on estimates of total numbers within burned areas, rather than on relative comparisons to the unburned state. Of course, obtaining such estimates can be very time consuming, and even with good data in hand, land managers are still left with having to decide subjectively what population levels are adequate.

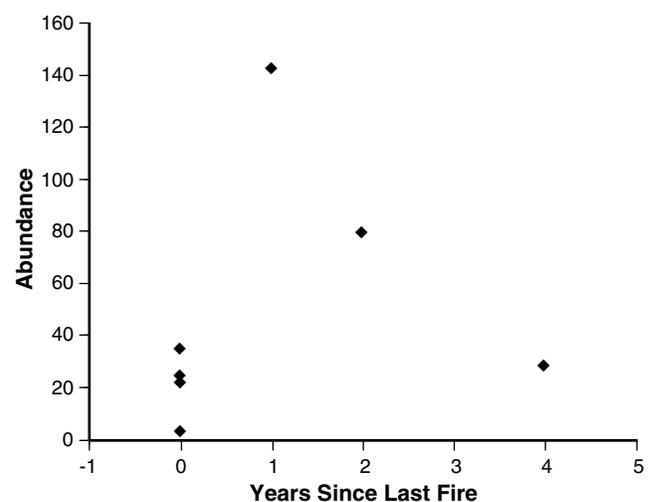


Figure 11. *Laevicephalus unicoloratus* (Gillette & Baker) and *L. minimus* (Osborn & Ball) density in August 1987 sweep net samples compared to years-since-last fire.

A more practical, and possibly superior, approach may be to collect empirical data from a number of sites of known burn histories and then look for trends in population densities and species presence/absence, as was done in this study and Panzer and Schwartz (2000). This approach, when covering long enough periods of time, has the best chance of accounting for stochastic events, such as extreme climatic variations, that may compound or mask the effects of fire. Of course, investigations of long-term, side-by-side plot comparison, such as Siemann et al. (1997), can also overcome the influence of stochastic events, but because the number of sites that can be studied in this way is limited, they lack applicability to a wider range of sites and conditions.

A number of entomologists (Pyle 1997, Williams 1997, Swengel 1998, Orwig and Schlicht 1999) have speculated that the burn regimes typically used in managing tallgrass prairie today (i.e. mean fire return intervals of 2 to 5 years on a given burn unit) may be causing the gradual loss of prairie specialist insects over time; a fire attrition hypothesis as described by Panzer and Schwartz (2000). The Lisken data, along with the work of Mason (1973), Siemann et al. (1997), and Panzer and Schwartz (2000) do not support this hypothesis for leafhoppers and related families. In the Lisken data, differences in fire frequencies that had been in place for 12 to 25 years appear to have had no significant effect on hopper density, richness, or diversity.

On a sand savanna complex in Minnesota, Siemann et al. (1997) looked at burn frequencies ranging from zero to nearly annual (9 out of 10 years) applied over a 30-year period. They found that the frequency of past burning was not reflected in significant differences in overall arthropod density, richness, or diversity despite observing decreased density and richness on year-0, post-fire sites during one of their two sample years. The proportion of Homoptera relative to other taxonomic groups, however, did decline with increasing burn frequency. Homoptera richness also declined significantly with increasing burn frequency in one sample year, but not the other. Homoptera density and diversity were not affected in either sample year.

Panzer and Schwartz (2000), in a study of Chicago region prairie remnants, compared a pool of “fire-managed” sites (n=26; mean fires per year=0.55) to a pool of “fire-excluded” sites (n=18; mean fires per year=0.03). They found a rich array of prairie-specialist leafhoppers (67 species) across all sites combined, but no loss of species richness or lowered mean population densities on fire-managed sites compared to fire-excluded sites. In fact, when fire-sensitive species (i.e. species that exhibit a decline in the year of a fire) were looked at as a separate group, fire-managed sites supported a greater number of species than fire-excluded sites, not less. Also, more species were restricted to fire-managed sites than to fire-excluded sites than might be expected by chance alone.

Useful insight on how often an area may be safely burned also can come from investigations of extreme cases, such as the case of Gravel Pit Prairie in the Lisken data and the work by Mason (1973). At least four prairie-specialist hoppers (*Bruchomorpha jocosus*, *Flexamia pectinata*, *Laevicephalus unicoloratus*, and *L. minimus*) were still present on Gravel Pit Prairie after a minimum of 10 years of annual burning of the whole site. The latter three have been documented as fire-sensitive (Panzer 1998, Harper et al. 2000). This extreme case suggests that post-fire recovery of some fire-sensitive specialist hopper species may be fast enough, or the decline inconsequential enough, that fire frequency may not be a major concern for them. Of course, 10 years may not be sufficient time to reveal accumulating impacts or to encounter stochastic environmental events that might lead to extirpation when combined with annual fire. Longer term case studies would be more enlightening.

Mason (1973) made a paired comparison between burned and unburned prairie in eastern Kansas. The treatment area, 65 ha in size, had been burned annually in spring for 23 years, while the control had remained unburned during that time. The sampled area within the burn was several hundred meters from the nearest unburned prairie (Mason, personal communication). Prairie-specialists comprised 33% (25) of the 75 leafhopper



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species present. Total numbers (measured by frequencies of occurrence) were lower in the burned area, but not species richness. The summed frequencies of occurrences within sample points were approximately 35% lower in the burn treatment than in the unburned control for all species combined and for specialists as a group. Of the specialist species, 43% had lower frequencies in the burn than the unburned control by 60% to 100% (mean of 80%). Fifty-seven percent were unchanged or slightly greater in the burned area. But, despite this evidence of detectable reductions in frequency and a moderately long distance to the nearest unburned refugia, there was no difference in species richness between treatment and control after 23 years of annual burning. Equal numbers of specialist species (23) and total species (60) were found in both burned and unburned treatments. Twenty-one of the 25 specialists had frequencies high enough to allow for species-specific comparisons. Only one of these, *Flexamia picta* Osborn, was not detected in the burn treatment. It had a mean frequency of 3.7 % in the control, and 0% in the burned area, an outcome that could just as easily be due to chance as due to fire.

Remnant Size and Isolation

Panzer et al. (1995) reported prairie-dependent butterflies of the Chicago region to be area sensitive and often absent from small sites. He has also found a strong linear log/normal relationship ($r^2=0.84$) between remnant size (1 to 600 ha) and richness of prairie-dependent leafhoppers (Panzer, personal communication). The Liskén data revealed a moderate effect of remnant size on hopper richness (Figure 3), but only if remnant size, rather than fire extent, was indeed the primary factor in reducing richness of prairie-specialist species in this study (see above discussion under "Recovery Method"). The Liskén data showed less area sensitivity of hoppers than what Panzer et al. (1995) found. The size of the Liskén remnants had to be below 1.5 ha before the number of specialist species per unit area markedly declined (Figure 3). To be fair, Panzer's work was based on species per site, not species per unit area. But even comparing the Liskén sites on a species per site basis, 1.5 ha still seems to be the cut off.

To obtain species per site information, Liskén data from 1986-87 were combined with hopper data collected from the same sites during 1995-2000 (Henderson, unpublished data). The five largest Liskén sites (1.7 to 17 ha) averaged 16 species each, while the three sites less than 1.7 ha in size averaged only six species each (Figure 12). This difference, however, may not be due entirely to remnant size. Sampling effort also may have played a role. The larger sites received approximately three times the sampling effort as the small sites. The mean index of sampling effort on the large versus small sites was 3.6 and 1.2, respectively (index categories ranged from 1 to 5).

Data from the Liskén sites do not support the idea that large sites inherently contribute more to prairie hopper

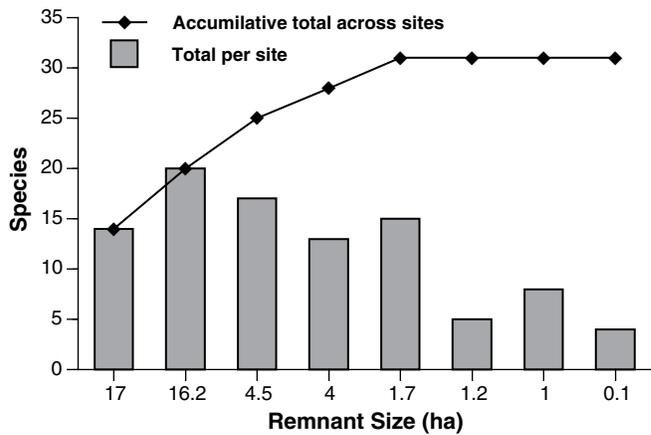


Figure 12. Accumulative species curve of prairie-specialist hoppers detected at the eight Liskén study sites during 1986-87 and in subsequent years. Number of species per site and accumulative number of species across sites are plotted against sites ordered by remnant size.

conservation than do small sites. The study's two largest sites combined held only 65% of the total specialist hopper richness among all the sites, and a site as small as 1.7 ha had three species not present on the four largest sites combined (Figure 12). This result is not likely attributable to differences in habitat among the sites, for they were chosen for similarity. These findings suggest that preservation focused only on the largest of sites may not be a wholly adequate approach for hopper conservation.

The data also do not support the idea that specialist hopper species will generally do better (occur at higher densities) with increasing remnant size. The one possible exception, *F. albida*, showed increasing numbers on the larger sites (Figure 4), but this result may be spurious. The 1995-2000 survey of prairie insects in Wisconsin found *F. albida* to be one of the more common prairie leafhoppers in the state (63 known locations), and to be very prevalent on even the smallest remnants. The 1995-2000 study also found *F. albida* to be on six of the eight Liskén study sites, and not limited to the three detected by the 1986-87 sampling. This suggests that the sampling timing or method used by Liskén may not have been best for detecting this species.

A difference in survey methods used to gather data between the Panzer and Liskén work may explain their differing results in regard to area sensitivity. Panzer et al. (1995) employed more highly trained and more intense survey methods than Liskén (Panzer, personal communication). It may be that the differences in the size of remnants looked at, 0.1 – 17 ha for Liskén versus 1 – 600 ha for Panzer, is a factor as well. Panzer's finding of increasing richness with increasing size could also simply be a result of an increase in habitat diversity that generally occurs with increasing remnant size, and not necessarily an inherent increase in richness per unit area with increasing remnant size. In other words, a small site of great habitat diversity

might harbor as many or possibly more species of prairie-specialist hoppers than a large site of uniform habitat. It may be that hoppers are more similar to plants in their area requirements than they are to larger insects, such as butterflies. Prairie plants seem to be far less area-sensitive than specialist butterflies. Plants seem to suffer very little species loss per unit area on small sites (Glass 1981, Simberloff and Gotelli 1982).

Year Effect and Sampling Effort

The Liskan data exhibited a consistent and strong year-effect (Figures 8-10 and Table 6), as well as a clear sensitivity to sampling effort (Figure 2). So strong was the influence of these factors that had they not been controlled for, they would have completely obscured the few effects of remnant size, remnant isolation, and fire history that were observed.

Of course the importance of controlling for sampling effort is a well known concept. These results simply underscore that fact as it applies to insects such as hoppers. Because standardizing quantification of insect numbers is not an easy task, and obtaining any information on less common specialist species is such a rare event, we tend to latch on to whatever information we can get. The results presented here remind us that we have to be careful how we use and interpret such data.

As for annual variation, Siemann et al. (1997) also detected its influence on hopper responses to fire frequency and time-since-last fire. The responses of density and species richness were more often than not different between the two years of their study. The findings from Siemann et al. and the Liskan data underscore the importance of controlling for annual variation in insect studies. They also suggest that fire effects on many prairie hoppers may be minor compared to year-to-year (annual) variations in population levels.

Conclusions

Because of the study's limitations (i.e. relatively small sample size and absence of both large and long-unburned sites in the sample), firm conclusions about the effects of remnant size, remnant isolation, or fire history on prairie hopper communities can not be drawn from this study, at least not in regard to subtle effects. The study sites, however, did support enough prairie-specialist species and had enough variation in size, isolation, and fire history, to be adequate at detecting dramatic and widespread effects of these factors.

No dramatic effects were found among native hoppers or, for the most part, among prairie-specialists, either individually or as a group. Density and diversity of specialists appeared to be unaffected, but specialist richness was sensitive to remnant size and fire extent. These factors, however, were not independent (i.e. the bigger the site, the less likely it was burned in its entirety), leaving open the

possibility that only one was causative. Evidence from individual species points more towards remnant size, rather than fire extent, as the causative factor. There were no individual species sensitive to fire extent, while one (*Flexamia albida*), possibly two (*Scaphytopius cinereus*), were sensitive to remnant size. Remnant size of approximately 1.5 ha was the cutoff below which specialist richness declined. As for the effects of years-since-last fire, only one out of nine prairie-specialists appeared sensitive (*S. cinereus*), but this result was contrary to both Mason's (1973) and Panzer's (1998) findings for *S. cinereus*. They found it to be unresponsive to fire.

In this study, sampling effort and year effect played far greater roles in predicting outcomes of hopper density, richness, and diversity than did remnant size, remnant isolation, or fire history. Not only does this reaffirm the need to control for these factors when researching the effects of fire on prairie insects, it also accentuates the study's finding of no dramatic, widespread, or long-term effects of fire on the prairie hoppers found at these sites.

From the results of this study and the other works referenced here in, it appears that effects of fire on prairie hoppers may be, for the most part, of short duration, subtle in nature, or non-existent. Research to date, however, has not ruled out the possibility that some rarely observed prairie-specialist species may be highly sensitive to fire and entirely dependent upon recolonization from unburned areas for post-fire recovery. Nor has it ruled out the possibility that at least a few prairie-specialists may routinely require nearby unburned refugia to rebuild reduced populations, or may need refugia in unforeseen, atypical years when in situ survival alone proves inadequate for post-fire recovery, in fact, the work of Panzer (1998) and Harper et al. (2000) hints that this might be the case for a few species. Therefore, from the perspective of prairie hopper conservation, it seems prudent to leave part of a given isolated prairie remnant unburned at any one time, until more conclusive evidence becomes available to support or reject such cautious action. Of course to be effective, the unburned portion must contain good representation of all host plant species present on site. Lastly, there are many prairie-specialists insect species, other than hoppers, to consider as well in the management of prairie remnants.



Appendix 1. Homoptera Species Found during the Study

“Category” is the group to which the species was assigned for analysis purposes (1=prairie specialist of highest order, 2=prairie specialist of moderate order, 3=native non-wind-dispersed, 4=native wind-dispersed, N=non-native).

“Numbers” reflects the total number of adults collected.

Family	Species	Category	Numbers	Family	Species	Category	Numbers
Aphididae	Aphididae spp.	-	368	Cicadellidae (<i>continued</i>)	<i>Macrosteles fascifrons</i> (Stal)	3	2
Caliscelidae	<i>Bruchomorpha dorsata</i> Fitch	2	15	<i>Macrosteles quadrilineatus</i> (Forbes)	4	28	
	1** <i>Bruchomorpha jocosus</i> Stal	2	12	<i>Memnonia flavida</i> (Signoret)	1	6	
	<i>Bruchomorpha oculata</i> Newman	3	1	1** <i>Memnonia panzeri</i> Hamilton	1	2	
	<i>Bruchomorpha tristis</i> Stal	3	2	* <i>Mesamia ludoviciana</i> Ball	1	7	
	<i>Peltonotellus histrionicus</i> Stal	3	1	* <i>Paramesus</i> sp.	N	1	
Cercopidae	<i>Philaneus spumarius</i> (L.)	N	1690	<i>Paraphlepsius irroratus</i> (Say)	4	18	
Cicadellidae	<i>Aceratagallia humilis</i> Oman	3	19	* <i>Pendarus stipatus</i> (Walker)	3	1	
	1** <i>Aceratagallia sanguinolenta</i> (Prov.)	4	21	<i>Polyamia apicata</i> (Osborn)	1	1	
	* <i>Alconeura rotundata</i> B.&D.	4	1	* <i>Polyamia brevipennis</i> (D.&D.)	3	1	
	<i>Amplicephalus inimicus</i> (Say)	4	581	1** <i>Polyamia caperata</i> (Ball)	1	1	
	<i>Anoscopus</i> spp.	N	3	** <i>Polyamia herbida</i> DeLong	1	14	
	<i>Aphrodes bicinctus</i> (Schk.)	N	18	1** <i>Prairiana cinerea</i> (Uhler)	1	1	
	<i>Athysanus argentarius</i> Metcalf	N	5	<i>Psammotettix lividellus</i> (Zetter.)	3	22	
	<i>Balclutha neglecta</i> (D.&D.)	4	10	<i>Scaphytopius acutus</i> (Say)	4	8	
	<i>Ballana</i> sp.?	-	4	<i>Scaphytopius cinereus</i> (O.&B.)	1	51	
	<i>Chlorotettix spatulatus</i> (O.&B.)	2	46	<i>Scaphytopius frontalis</i> (Van DuZee)	3	29	
	<i>Chlorotettix unicolor</i> (Fitch)	3	10	<i>Scaphoideus titanus</i> Ball	3	1	
	** <i>Deltocephalus flavicostatus</i> Van D.	4	3	<i>Xestocephalus superbus</i> (Prov.)	4	11	
	<i>Dikraneura angustata</i> B.&D.	3	171	Cixiidae			
	<i>Dikraneura mali</i> (Prov.)	3	2	* <i>Oliarus</i> sp. - New Species	3	2	
	<i>Diplocolenus configuratus</i> (Uhler)	3	13	Delphacidae			
	<i>Doratura stylata</i> (Boheman)	N	7	* <i>Liburnia</i> sp. - New Species	3	20	
	1** <i>Dorycara platyrhyncha</i> Osborn	3	1	<i>Liburnia campestris</i> (Van DuZee)	3	58	
	<i>Draeculacephala antica</i> (Walker)	4	20	* <i>Liburnia rotundata</i> (Crawford)	3	151	
	<i>Draeculacephala constricta</i> (D.&D.)	4	14	<i>Liburniella ornata</i> (Stal)	3	16	
	<i>Draeculacephala zaeae</i> Hamilton	4	3	<i>Liburniella</i> sp.	3	11	
	<i>Empoasca fabae</i> (Harris)	4	218	<i>Megamelus</i> sp.?	3	1	
	<i>Erythroneura</i> spp.	4	1	<i>Stobaera tricarianta</i> (Say)	3	1	
	<i>Exitianus exitiosus</i> (Uhler)	4	49	Dictyopharidae			
	<i>Extrusanus extrusus</i> (Van Duzee)	3	1	<i>Scolops angustatus</i> Uhler	3	30	
	1** <i>Extrusanus oryssus</i> Hamilton	2	5	* <i>Scolops perdix?</i> Uhler	3	1	
	1** <i>Flexamia albida</i> (O.&B.)	1	64	<i>Scolops sulcipes</i> (Say)	3	30	
	1** <i>Flexamia pectinata</i> (O.&B.)	1	114	Flatidae			
	<i>Forcipata loca</i> (DeLong & Cadwell)	4	20	<i>Metcalf pruinosus</i> (Say)	3	1	
	<i>Graminella</i> sp.	3	1	Issidae			
	<i>Gyponana</i> spp.	3	1	<i>Acanalonia bivittata</i> (Say)	3	99	
	<i>Jikradia olitoria</i> (Say)	3	1	* <i>Acanalonia conica</i> (Say)	3	2	
	<i>Laeviccephalus minimus</i> (O.&B.)	1	261	Membracidae			
	<i>Laeviccephalus unicoloratus</i> (G.&B.)	1	257	<i>Campylenchia latipes</i> (Say)	3	8	
	<i>Latalus personatus</i> Beirne	3	5	<i>Ceresa alta</i> (Walker)	3	1	
	<i>Latalus sayii</i> (Fitch)	3	1	<i>Vanduzeeia triguttata</i> (Burmeister)	3	93	
	<i>Limotettix osborni</i> (Scler.) (Ball)	3	5	Psyllidae			
				<i>Psylla</i> spp.	-	8	

* New (unpublished) state record at time of determination in 1994 with no known earlier specimens collected.

** New (unpublished) state record at time of determination in 1994 with older collections in existence.

1 Wisconsin records published since determination in 1994.

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