Species Richness of Insects on Prairie Flowers in Southeastern Minnesota

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Abstract. I systematically collected 3784 flower-visiting insects representing 287 species from 59 forb species in 4 prairie remnants and 4 prairie reconstructions (farm fields replanted to prairie plants) during 3 summers. Flower visitors included nectar and pollen feeders, parasitoids, and predators. Size of the site, time since planting of reconstructions and total flower number did not appear to influence the species richness of flower visitors on the sites. The presence of flowers throughout the summer and the presence of forb species that supported specialist insects appeared to increase insect species richness of sites. Certain forb species supported more than their share of insect visitors. Insect species richness was highest on sites of intermediate forb species richness. The native remnants had slightly higher insect species richness than the reconstructions when collection effort was equalized, but the reconstructions also supported many flower visitors. Of the 287 insect species, 105 were found on only one site, implying that even small remnants and reconstructions can contribute to the conservation of prairie insect species.

Key words: prairie insects; prairie forbs; prairie restoration; flower visitors; bees; species richness; insect phenology

Introduction

Many factors may be expected to influence species richness, i.e., the number of insect species present on a site. Many flower visitors are highly mobile (Johnson 1969); thus a landscape-level pool of species is available to colonize new sites, and to recolonize old ones if the sites meet the insectsquirements.

Large sites are expected to support more species than smaller ones, based on the greater variety of microhabitats on larger sites (Usher 1987). The degree of isolation of a site from other sites with established insect populations may influence species richness, because other sites are needed as sources of colonists for reconstructions or replacements of populations that have become locally extinct on native sites (Samways 1994).

Even for highly mobile flower visitors, the colonization and establishment processes take time: so native prairie sites are expected to have more insect species than reconstructions, and older reconstructions are expected to have more insect species than those that were planted recently.

Flower visitors include nectar and pollen feeders and their predators and parasites, so flowers themselves are the basic resources for the group. Differences in the forb community are expected to have strong effects on the insect community. The site resource level (number of flowers present) is a rough measure of the energy which is available for use by the flower visitors and is expected to limit the number of individual insects that can survive on a site (Bowers 1985). As the species richness of the forb community as a whole increases, insect species richness potentially can increase, but when many habitats are compared, the relationship between forb and insect species richness has been inconsistent (Neff and Simpson 1993). To elucidate this relationship in any habitat, we must examine the ways in which forb species serve as resources for different types of flower visitors. Many insect species complete their active life during only a few weeks of the summer; one way in which increased forb species richness can increase insect species richness on sites is by increasing the number of flowers in bloom throughout the season (Rathcke 1988).

On single sites, the relationship between forb and insect species richness is based in the forb species that are actually present and their visitors. Certain forb species may be especially valuable contributors to the insect species richness of their sites because they support specialists, are especially attractive to certain insect groups, and/or support unique species not found on other forbs. If certain forbs do increase the insect species richness of their sites, it may be possible to increase the insect species richness of reconstructed prairies by planting these forbs.

A variety of methods has been developed for estimating insect species richness on sites (Coddington et al. 1991). A major issue is collection effort. Making identical numbers of collections on each site is rarely possible when several sites are sampled, so site species richness is compared using the rates at which new species are found on the various sites. On any site, the first few collections will yield many species not seen before; as collections continue, fewer new species will be found per collection, yet it is unlikely that all the species on the site will be found. This diminishing return per collection can be displayed in a species accumulation curve like Figure 1. The slope of the curve indicates the rate at which additional collections yield additional species, and the extent of flattening of the curve with increasing number of collections indicates the completeness of sampling (Connor and McCoy 1979). Estimates of site species richness can also be made using truncated species accumulation curves (Janzen 1971).

Methods

Study Sites

All the sites are located in eastern Minnesota, USA, and all are managed. The sites vary in prairie plant area and number of forb species present (Table 1). The majority of the forb species are prairie plants but alien weeds are also present (Table 1). Plant names follow Great Plains Flora Association (1986).

Prairie Reconstructions. These are former agricultural areas that have been replanted to prairie vegetation.

Afton State Park (ASP), Washington County, contains several reconstructions. I sampled a 4.8 hectare field located at the NE 1/4 of section 10, T27N R20W, containing prairie grasses and four forb species planted 9 years before the study and managed by controlled burning. The soil is Ripon silt loam. The prairie area is bounded by old fields, second-growth woodland, and overgrown oak savanna remnants. The most recent burn was in the spring of 1989.

Table 1. Area, forb species number, age, total flower number in 1992, number of collections, total insect species, insect species in 17 randomly selected collections (mean of 5 values), and number of unique insect species collected for each site.

Site	Area, hectares#	Plant Spp##	Age in years	Total flower number 1992	No. of coll.	Total insect species	Ins spp. in 17 coll.**	Unique insect species***
Reconstructions								
ASP	4.8/4.8	6	9	113,600	17	33	33	2
CARP	32.4/16.2	25	1-4	93,000	89	128	55	15
CHR	243/10.0	31	1-15	40,500	107	112	46	12
LLRP	2.8/2.8	29	4	35,000	76	100	41	15
Native Sites								
AREM	1.6/1.6	13		11,000	47	86	51	14
CC	60.7/8.0	15		9,500	62	118	55	23
CEM	0.4/0.4	15		22,800	50	88	52	8
LV	13.5/7.5	22		16,000	57	95	50	16

Area that supported prairie plants/Area from which collections were made
Includes only those species with at least 100 flowers or infloresences blooming on at least one sampling date
**Number of insect species in 17 randomly selected collections
*** Number of insect species found on this site only

Carpenter Nature Center (CARP) in Washington County contains a 32.4-hectare reconstructed prairie at the NE 1/4 of Section 8, T27N R20W. One-quarter of the area was planted in 1988, one-quarter in 1989, one-quarter in 1990, and the remaining area in 1991. The reconstructions are managed by mowing during the first 2 years, followed by regular burning. The soil is Ripon silt loam. The area is bounded by agricultural fields. The site was burned in the spring of 1991.

Crow Hassan Park Reserve (CHR) in northwestern Hennepin County includes 243 hectares of reconstructed prairie replanted into former agricultural fields over the last 15 years. Forbs have been planted densely in a 10-hectare portion of the prairie area, located in the NW 1/4 of section 19, T120N R23W; new forb species have been added frequently since reconstruction began. The area is managed by controlled burning of parts of the area in different years. The soil is Hubbard loamy sand. The prairie area is bounded by restored deciduous woodland. The site was burned in the spring of 1991.

Long Lake Regional Park (LLRP) in Ramsey County contains a 2.8-hectare prairie reconstruction planted in 1987, located at the SE 1/4 of section 17, T30N R23W, and bounded by wetlands, trails, and an overgrown oak savanna remnant. A railroad right-of-way 100 meters from the site supports some prairie plants. This area is managed by burning, most recently in early spring of 1992. The soil is Zimmerman fine sand. I collected at LLRP in 1992 only.

Native Prairies. These are relatively undisturbed remnants.

Afton Remnant (AREM) is a 1.6 hectare remnant located on a bluff top in Afton State Park, Washington County at the N 1/2 of section 35, T28N R20W. It was somewhat overgrown but has been managed by brush cutting and burning since 1987; the most recent burn was in the spring of 1989, and extensive brush cutting was done in 1991. The soil is Ripon silt loam. The remnant is bounded by the bluff above the St. Croix river and by second-growth decidous forest.

Cedar Creek Natural History area (CC), Anoka County, contains a 60.7 hectare oak savanna area with two open meadows (approximately 5 and 3 hectares in area) containing many prairie plants located at the S 1/2 of section 34, T34N R 23W. Portions are burned in different years; the collection area was burned in 1990. The soil is Zimmerman fine sand. The meadows are bounded by oak savanna, and the area includes some wetlands.

Point Douglas Cemetery (CEM) is a 0.4 hectare pioneer cemetery directly adjacent to the Carpenter Nature Center Reconstruction at the SE 1/4 of section 5, T27N R20W. It has never been plowed, and the entire site was burned in 1989. The soil is Ripon silt loam. The site is bounded by agricultural fields and the section of the Carpenter Nature Center reconstruction that was planted in 1991.

Lost Valley State Natural area (LV), in Washington County is a protected area of 40.5 hectares including bluff prairie, shrubs, old field vegetation, and a small area still cultivated; about 1/3 of the area, the rocky bluff tops, supports prairie plants, at the S 1/2 of section 21 and the N 1/2 of section 22, T27N R20W. I sampled about half of this area, in the southern part of the site. Management of the area began in 1991 with brush cutting and burning of part of the site; this was continued extensively in 1992. The prairie areas are located on the Doreton rock outcrop complex, with very shallow loamy soil. The site is surrounded by agricultural areas and suburban development.

Collections

I counted the flowers or inflorescences of each forb species blooming on each site on each sampling date, using quadrat and line transect methods, and summed these for the entire year as an index of total resource level. I collected insects from the flowers by hand netting between 9 am and 4 pm on sunny or partly cloudy days when the temperature was between 20 and 35o C. The first collections were made in late May, and the last collections in late September. I made one 15-minute collection from the flowers of each forb species with at least 100 flowers or inflorescences open, from all forb species in all sites during 1991 and 1992, and limited collections in 1990, for a total of 505 collections (Table 1). From 1 to 53 collections were made from each forb species, depending on the length of blooming period and the number of sites on which it was present. I attempted to minimize overlap in collecting to avoid depleting the insect populations on the sites. All specimens were labelled according to site, date, and forb species, and were identified or confirmed by specialists.

Insect species were classified as predators, parasitoids, pollen feeders, pollen collectors, or cleptoparasites, and as specialists or generalists on plant species, genera, or families using standard references: Borror et al. 1989, Krombein et al. 1979, Opler and Krizek 1984, Scott 1986, Stone et al. 1965 (Table 2). Flower visitors were also defined as specialists if at least eight individuals were collected from only one plant species.

Table 2. Forb species presence on the eight sites, season, total collections made from each forb, total insect species collected, insect species unique to each forb, and ratio of percent insect species collected from each forb to the percent of total collections which were made from this forb.

Plant Species				Site					Season	Total	Total	Unique	Pctspp/
	ASP	CARP	CHR	LLRP	AREM	OC	CEM	LV		Col	Spp	Spp	Pctcol
Apiaceae													
Zizia aurea		x		x				x	early	8	34	5	
Asteraceae													
Achillea millefolium*		x	x	x	x			x	early-mid	10	18	4	3.15
Aster ericoides		x	x	x			x	x	v. late	11	46	3	6.15
Aster ontarionis								x	v. late	3	13	1	
Aster oolentangiensis			x	x	x	x	x	x	v. late	20	57	3	4.98
Aster sericeus			x	x				x	late	4	17	0	
Aster simplex		x		x			x		v. late	5	25	1	
Chrysopsis villosa			x	x					mid	5	12	1	
Cirsium arvense*		x							mid	2	9	2	
Cirsium discolor		x			x			x	late	9	21	2	
Coreopsis palmata			x						mid	3	4	0	
Crepis tectorum				x					early	5	8	0	
Erigeron strigosus		x		x					early	3	5	1	
Grindelia squarrosa				x					mid	2	6	0	
Helianthus rigidus		x	x	x		x	x	x	mid-late	27	39	7	2.63
Helianthus tuberosus		x	x				x		late	7	13	2	
Heliopsis helianthoides		x	x	x			x		early-mid	15	18	0	2.10
Liatris aspera			x			x		x	late	10	27	0	4.70
Liatris punctata								x	late	1	3	1	
Liatris pycnostachya			x						late	1	1	0	
Ratibida pinnata	x	x	x				x	x	mid	30	38	1	2.24
Rudbeckia hirta	x	x	x	x	x	x			mid	30	40	4	2.36
Solidago canadensis		x	x	x	x	x	x	x	late	20	62	7	5.40
Solidago nemoralis				x	x	x			mid-late	10	40	3	6.95
Solidago rigida		x	x	x		x	x	x	mid-late	20	62	2	5.40
Solidago speciosa		x	x	x	x		x	x	late	11	30	3	4.77
Vernonia fasciculata								x	mid	1	8	0	
Boraginaceae													
Lithospermum canescens						x			early	2	3	0	

Table 2 cont.

Brassicaceae												
Berteroa incana*				x					early	3	13	2	
Campanulaceae												
Campanula rotundifolia								x	early	1	4	1	
Fabaceae												
Amorpha canescens			x	x	x	x		x	mid	10	41	7	7.15
Dalea purpurea	x	x	x	x		x			mid	19	53	6	3.55
Dalea villosa				x					mid	2	7	1	
Desmodium canadense				x			x		mid	4	8	0	
Lupinus perennis			x						early	2	7	0	
Melilotus alba*			x	x					mid	9	19	0	
Melilotus officinalis*		x	x	x					early	7	15	2	
Trifolium pratense*		x							mid	1	2	0	
Vicia americana							x		v. early	1	4	0	
Iridaceae													
Sisyrinchium campestre			x						v.early	1	5	0	
Lamiaceae													
Agastache foeniculum		x	x	x	x				mid	31	48	4	2.74
Monarda fistulosa	x	x	x	x	x	x	x	x	mid	57	60	13	1.76
Nepeta cataria*					x			x	mid	6	18	0	
Pycnanthemum virginianum				x	x	x		x	mid	26	87	17	5.94
Stachys palustris		x				x			mid	4	12	0	
Liliaceae													
Allium canadense		x	x	x					mid-late	4	13	3	
Nyctaginaceae													
Mirabilis nyctaginea			x						early	1	3	0	
Polemoniaceae													
Phlox pilosa			x			x			early-mid	4	6	1	
Ranunculaceae													
Anemone canadensis			x						early	1	1	0	
Aquilegia canadensis								x	early	1	2	0	
Rosaceae													
Potentilla arguta		x	x						mid	2	8	0	

Table 2 cont.

Potentilla recta*	x	x							early-mid	3	15	0	
Rosa blanda		x	x				x		early-mid	4	8	0	
Rubus occidentalis								x	v.early	1	4	0	
Rubiaceae													
Galium boreale							x		early	1	6	3	
Scrophulariaceae													
Penstemon grandiflorus			x	x		x			early	15	36	5	4.46
Verbenaceae													
Verbena hastata	x				x				mid	5	13	1	
Verbena stricta		x							early-mid	5	10	0	
Total Plant Species on Site	6	25	31	29	13	15	15	22					
	ASP	CARP	CHR	LLRP	AREM	CC	CEM	LV					

X = presence of at least 100 flowers on that site on at least one sampling day
* = alien plant species

Tests of Factors Related to Insect Species Richness

I performed three analyses to determine whether native sites had more flower-visiting insect species than reconstuctions. First, I looked at all the collections in all the sites. I constructed separate species accumulation curves for all native sites and all reconstructions combined by randomizing the collections and recording the cumulative number of species as each new collection was added (Figure 1). This method compares the rates at which additional collections added species to the total species lists for native sites and reconstructions (Coddington et al.1991). I compared the slopes of the curves by log-log transformation and regression (Connor and McCoy 1979); a higher slope indicates a more species-rich site (Figure 1).

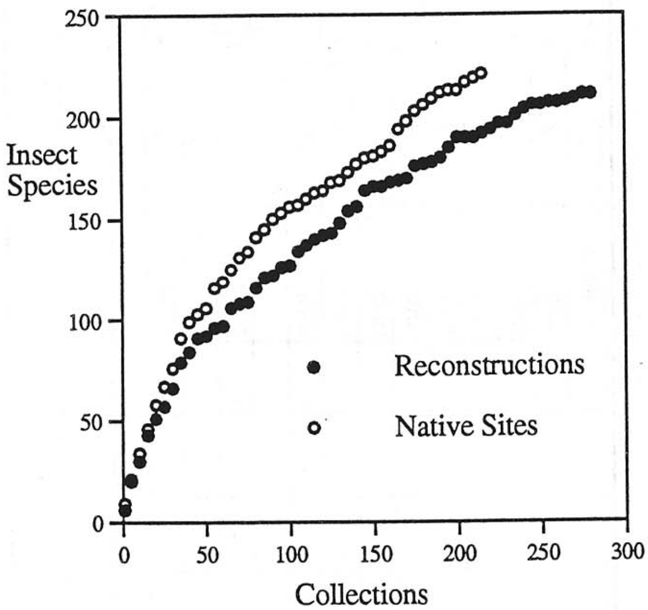

FIG. 1. Species accumulation curves for allnative sites combined and all reconstructions combined. Slopes of the log-log transformed curves are 0.599 for native sites, range 0.579-0.619; and 0.529, range 0.512-0.547 for the reconstructions.

Second, I treated the native sites and the reconstructions as replicates and compared mean species number per site using a 2-tailed t-test (unequal variances). To equalize collection effort among sites to the lowest collection effort (17 collections at ASP), I randomly selected 17 collections from each site (except ASP) and counted the species in this subsample. I repeated the randomization five times and used the mean species number as the site value for the t-test (values for 17 collections are shown in Table 1).

Third, I compared individual plant species that were found in both native and reconstructed sites. There were 28 species from which insect collections were made in both types of sites (Table 2). I equalized the collection number in native and reconstructed sites by using all collections from the type that had the lower number, and randomly selecting an equal number of collections from the type that had the higher number. This method made use of 282 of the 505 collections. I counted the insect species per plant species in the selected number of collections and compared the number in native and reconstructed sites using the Wilcoxon Signed-Rank test (Remington and Schork 1970).

Distance from Sources of Colonists

I identified possible sources of insect colonists using maps and by exploration near sites. At least 125 prairie and oak savanna remnants large enough to be mapped (about 8000 m2, or 90 X 90 meters appears to be the minimum size shown) exist in Washington County. (Source: Minnesota County Biological Survey Map Series no 1 (1990) Washington County). There are many more remnants too small to map, especially along the river bluffs and railroad tracks.

The rural/suburban Hennepin County site, CHR, is probably similar to the Washington County sites in having many remnants not too far away. This county has not yet been mapped by the Biological Survey. The LLRP site seems much more isolated by four-lane highways, heavy and light industry, trucking companies, and a few suburban developments, but it is separated by only a few hundred meters of woods from a remnant containing some prairie plants. A nearby railroad right-of-way contains some prairie plants. Only 21 mappable native vegetation remnants occur in Ramsey county, whereas Anoka County has at least 50 remnants, the largest one covering four sections (Minnesota County Biological Survey Map Series, Ramsey and Anoka Counties (1994)). The Cedar Creek site is the least isolated of the sites, because it is located in a less developed and less agricultural area than the others.

Phenology

I charted the phenology of all the insect species for which eight or more individuals were collected by listing the first and last dates of collection (Table 3). I noted the first and last date of collection from each forb species and recorded each as an early-, mid-, or late-season forb.

Insect and Forb Species Richness on Sites

I graphed insect species richness vs. forb species richness for each site, using both total insect species collected and insect species in 17 collections, fitted the curves, and calculated r2 for each (Figure 2).

Insect Species Richness Associated with Individual Forb Species

The number of unique insect species (insect species found on that forb only) are listed for all forbs in Table 2. As a measure of species richness, I calculated the percent of total insect species collected from the forb and divided this by the percent of all collections made from it. I limited this procedure to forb species with at least 10 collections, because the results become increasingly erratic with fewer collections ; this forced me to pool all the collections from each plant species, rather than examining all the plant species on a site-by-site basis. A high value indicates high insect species richness relative to other forbs from which insects were collected.

Table 3. Phenology of insects visiting prairie forbs.

Species	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25
1. *Bombus affinis*			X---	---	---	---	---	---X
2. *Bombus auricomus*			X---	---	---	---	---	---X
3. *Bombus bimaculatus*		X---	---	---	---	---	---X	
4. *Bombus fervidus*			X---	---	---	---	---	---X
5. *Bombus griseocollis*			X---	---	---	---	---X	
6. *Bombus impatiens*			X---	---	---	---	---	---X
7. *Bombus pennsylvanicus*					X---	---	---	---X
8. *Bombus ternarius*				X---	---	---	---X	
9. *Bombus vagans*			X---	---	---	---	---X	
10. *Andrena wilkella*	X							
11. *Andrena cressonii*	X							
12. *Andrena crataegi*	X							
13. *Andrena rudbeckiae*				X---	---X			
14. *Andrena placata*						X---	---	---X
15. *Andrena hirticincta*						X---	---X	
16. *Andrena helianthi*						X---	---X	
17. *Andrena simplex*						X---	---X	
18. *Andrena nubecula*						X---	---X	
19. *Andrena asteris*							X---	---X
20. *Anthophora furcata terminalis*		X---	---	---	---	---X		
21. *Ceratina calcarata* or *dupla*			X---	---	---	---	---	---X
22. *Tetralonia dubitata*	X							
23. *Melissodes subillata*			X---	---	---	---X		
24. *Svastra obliqua o.*				X---	---	---X		
25. *Melissodes trinodis*				X---	---	---	---X	
26. *Melissodes agilis*						X---X		
27. *Melissodes rustica*						X---	---X	
28. *Melissodes desponsa*						X---	---X	
29. *Melissodes dentiventris*							X---	---X
30. *Hylaeus mesillae m.*			X---	---	---	---	---	---X
31. *Hylaeus affinis*			X---	---	---	---	---	---X
32. *Colletes susannae*					X---X			
33. *Colletes simulans armatus*							X---	---X

June 1-15 June 16-30 July 1-15 July 16-31 Aug 1-15 Aug 16-31 Sept 1-15 Sept 16-25

Table 3 cont.

Species	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	
34. Lasioglossum paraforbesii	X	-	-	-	-	X			34.
35. Halictus ligatus			X	-	-	-	-	X	35.
36. Halictus confusus	X	-	-	-	-	-	-	X	36.
37. Evylaeus pectoralis	X	-	-	-	-	-	-	X	37.
38. Dialictus vierecki	X	-	-	-	-	-	-	X	38.
39. Dialictus rowheri	X	-	-	-	-	-	X		39.
40. Dialictus pruinosus	X	-	-	-	-	-	X		40.
41. Dialictus pilosus	X	-	-	-	-	-	-	X	41.
42. Dialictus pictus	X	-	-	X					42.
43. Dialictus lineatulus	X	-	-	-	-	-	-	X	43.
44. Agapostemon virescens	X	-	-	-	-	-	-	X	44.
45. Augochlorella striata	X	-	-	-	-	-	-	X	45.
46. Dialictus imitatus	X	-	-	-	X				46.
47. Dialictus albipennis	X	-	-	X					47.
48. Dufourea monardae				X	-	X			48.
49. Dialictus heterognathus				X	-	-	X		49.
50. Dialictus anomalus				X	-	-	X		50.
51. Agapostemon sericeus				X	-	-	-	X	51.
52. Agapostemon texanus	X	-	-	-	-	-	-	X	52.
53. Megachile relativa	X	-	-	-	-	-	-	X	53.
54. Megachile latimanus	X	-	-	-	-	-	-	X	54.
55. Hoplitis pilosifrons	X								55.
56. Heriades carinata				X	-	X			56.

June 1-15 June 16-30 July 1-15 July 16-31 Aug 1-15 Aug 16-31 Sept 1-15 Sept 16-25

Table 3 cont.

	Species	June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	
57.	Hylemya sp.	X	-	-	X					57.
58.	Systoechus sp.				X	X				58.
59.	Exoprosopa caliptera					X	-	X		59.
60.	Sphaerophoria sp.	X	-	-	-	-	-	-	X	60.
61.	Lejops stipatus	X	-	-	-	X				61.
62.	Allograpta obliqua			X	-	X				62.
63.	Eristalis transversus			X	-	-	-	X		63.
64.	Helophilus fasciatus			X	-	-	-	-	X	64.
65.	Toxomerus germinatus			X	-	-	X			65.
66.	Toxomerus marginatus			X	-	-	-	X		66.
67.	Syrphus sp.			X	-	-	-	-	X	67.
68.	Eristalis latifrons			X	-	-	-	-	X	68.
69.	Metasyrphus sp.				X	-	-	-	X	69.
70.	Sphaerophoria contigua					X	-	-	X	70.
71.	Helophilus latifrons					X	-	-	X	71.
72.	Eristalis tenax							X	X	72.
73.	Eristalis dimidiatus							X	X	73.
74.	Vanessa cardui	X	-	-	-	-	X			74.
75.	Atrytone delaware				X	X				75.
76.	Satyrium edwardsii				X	X				76.
77.	Cisseps fulvicollis				X	-	-	X		77.
78.	Colias sp.				X	-	-	-	X	78.
79.	Polistes fuscatus	X	-	-	-	-	-	-	X	79.
80.	Euodynerus foraminatus f.	X	-	-	-	-	-	X		80.
81.	Myzinum quinquecinctum				X	-	X			81.
82.	Philanthus ventilabris					X	X			82.
83.	Myzinum maculatum					X	-	X		83.
84.	Chauliognathus pennsylvanicus					X	-	-	X	84.
85.	Epicauta pennsylvanica					X	-	X		85.
86.	Luperaltica fuscula					X	-	-	X	86.
		June 1-15	June 16-30	July 1-15	July 16-31	Aug 1-15	Aug 16-31	Sept 1-15	Sept 16-25	

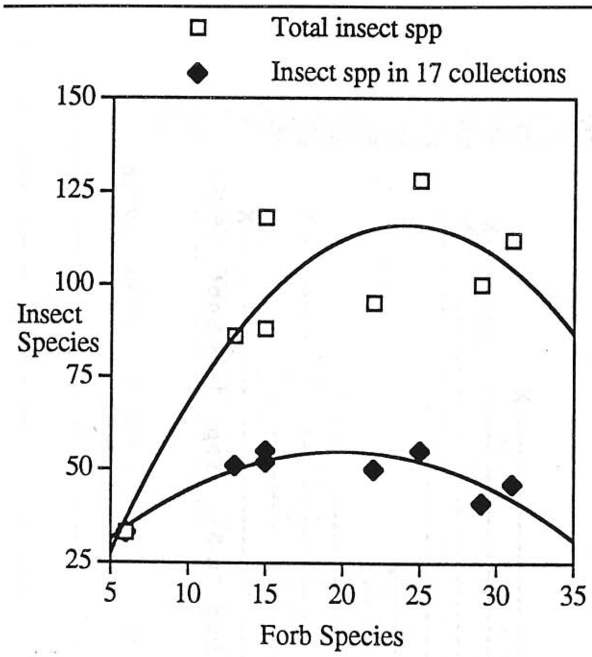

FIG. 2. Forb and insect species richness. Each symbol represents one site. For total insect species collected, $r^2 = 0.785$; for insect species richness based on 7 randomly selected collections (mead of 5 values), $r^2 = 0.789$.

Table 4. Ecological categories of flower visitors

Ecological category	Taxonomic group	Number of species
Nectar feeders	Lepidoptera	27
Pollen feeders	Syrphidae (Diptera)	28
	Coleoptera (Beetles)	3
Pollen collectors	Apoidea (Hymenoptera)	116
Cleptoparasites	Apoidea (Hymenoptera)	9
Parasitoids of flower visitors	Conopidae (Diptera)	6
	Chrysidoidea (Hymenoptera)	2
	Chalcidoidea (Hymenoptera)	1
Parasitoids of other insects	Bombyliidae (Diptera)	14
	Ichneumonoidea (Hymenoptera)	5
	Tiphioidea (Hymenoptera)	3
	Scolioidea (Hymenoptera)	3
	Calliphoridae (Diptera)	1
Predators	Sphecoidea (Hymenoptera)	40
	Vespoidea (Hymenoptera)	12
	Tachinidae (Diptera: larvae are predators)	8
	Pompiloidea (Hymenoptera)	4
	Hemiptera	2
	Matispidae	1

Results and Discussion

I collected 3784 insects representing at least 287 species, including predators, parasitoids, pollen feeders and collectors, and cleptoparasites. The pollen collectors included specialists and generalists (Table 4). Eighty-five insect species were found on native sites only, 67 species on reconstructions only, and 135 species on both native and reconstructed sites. One hundred and five insect species were found on one site only; 112 species were found on one plant only. Of the 287 species, 88 were represented by only one individual, 98 had from 2 to 5 individuals, 36 species had from 6-10 individuals, 22 had from 11 to 20 individuals, 26 species had from 21-50 individuals, and 17 species had more than 50 individuals.

Area of Sites

Little relationship existed between the area of a site and the number of insect species collected from it (Table 1). Many species were found on even the smallest sites. Area does not directly measure the amount of insect habitat, because resources (flowers and nesting sites) are distributed in an extremely patchy and variable manner within sites. The study sites were not isolated physically, and probably insects moved on and off of them.

Comparison of Species Richness of Native Sites and Reconstructions

Cumulative collections from all native sites combined yielded more species than cumulative collections on reconstructions; for example, 215 collections yielded 221 insect species in the native sites but only 192 insect species in the reconstructions (Figure 1).The slopes of the log-transformed species accumulation curves showed no overlap using an estimate of slope with 95% confidence intervals, indicating higher insect species richness in collections from the native sites overall, with statisical significance at the 0.05 level.

When the mean number of insect species per site for the four native sites and the four reconstructed sites (based on the means of five randomly selected groups of 17 collections) were compared using a 2-tailed t-test with unequal variances, the probability was 0.171. No significant difference occurred in insect species richness in native sites compared to reconstructions. The lack of statistical significance may be related to the much lower insect species richness at ASP compared to the other reconstructions, which caused a large variance in species richness values for the reconstructions.

Insect species richness of plant species growing in both native and reconstructed sites was compared. Of the 28 plant species with equivalent collection effort in native sites and reconstructions, 14 plants had more insect species in the native sites, 12 plants had more insect species in the reconstructions, and two had the same number of species in both. The difference was not significant based on the Wilcoxon Signed-Rank test.

Over all, more insect species were collected from all the native sites combined than from all the reconstructions combined, and fewer hours of collection were needed to find them (Figure 1). More insect species were found on native sites only than on reconstructions only. On the other hand, some of the reconstructions, especially CARP, had high insect species richness, even though more collections were required to find all these insects. Also, two of the three statistical approaches showed no statistically significant difference in insect species richness between the native and reconstructed sites. These results suggest that native sites had slightly higher insect species richness than reconstructions.

Distance from Possible Sources of Colonists

This variable was difficult to quantify. The CC site seemed to be the least isolated, and the LLRP site the most isolated from other prairie insect populations, but the other sites could not be compared on this basis.

Age of Reconstructions

No obvious relationship occurred between age of reconstruction and insect species richness (Table 1). Total Resource Level The reconstructions had more total flowers in 1992 than did the native sites (Table 1). No obvious relationship existed between total flowers and insect species richness. However, the measure of total resource level did not correspond with the ways flower visitors subdivided the resource, as discussed below.

Insect Phenology and Specialization

Phenology records were noted for the 86 species that had eight or more individuals: 20 species were collected during 1 month or less: six bee species, two flies, and two butterflies (Table 3). Thirty-two long-season species were present from June into September (24 bee species, six flies, and two wasps).

Fifty-seven bee species could be charted. The majority of the species fell into one of four groups:

1. Early-season bees. These were the first species seen, starting with the first collection date (May 29), and were not seen after mid-June. They were associated on my sites with certain early plant species, though they are recorded in the literature as visiting other plants. *Andrena wilkella*, *A. cressonii*, and *A. crataegi* were collected mainly from *Zizia aurea*, and *Tetralonia dubitata* and *Hoplitis pilosifrons* from *Penstemon grandiflorus*.
2. Mid-season bees were *Andrena rudbeckiae* on *Ratibida pinnata*, *Colletes susannae* on *Dalea purpurea*, *Dufourea monardae* on *Monarda fistulosa*, and *Heriades carinata* (generalist).
3. Late-season bees included *Andrena placata, A. helianthi, A. hirticincta, A. simplex, A. nubecula, A. asteris, Melissodes agilis, M. rustica, M. desponsa, M. dentiventris*, and *Colletes simulans armatus*. Most of these species are Asteraceae specialists.
4. Long-season bees were collected from June through August. All *Bombus* species were long-season bees, as were many halictids. All these species are generalists and shifted from plant to plant as the season progressed. Bumblebee numbers usually peaked on sites when the midseason flowers, especially *Monarda fistulosa*, bloomed, then dropped and increased again late in the season when the goldenrods and asters were in full bloom. Honeybees were generally rare on the prairie but visited the white and yellow sweetclovers early in the season, *Verbena stricta* and occasionally *M. fistulosa* in midseason, and the goldenrods and asters in the late summer.

Fly phenology: 17 species had eight or more individuals. The majority of the species were present for 8 weeks or more; no apparent patterns were related to subfamilies. In general, flies were more numerous late in the season. Syrphid flies, the most common flower visitors, were common from the end of June to the end of September.

Wasp phenology: only five species had eight or more individuals. Wasps were common in mid to late summer, except for *Polistes fuscatus* and *Euodynerus foraminatus*, which were present earlier.

Five Lepidoptera species had eight or more individuals. Only *Vanessa cardui* was seen early in the season; the remaining species were seen first in early to mid-July. *Cisseps fulvicollis* and *Colias spp.* persisted into mid-September, whereas *Satyrium edwardsii* and *Atrytone delaware* were not seen after early August. The sphinx moths, *Hemaris* spp., were seen mainly on *Monarda fistulosa.* during its blooming season, mid-July through August.

The beetles *Chauliognathus pennsylvanicus* and *Epicauta pennsylvanica* increased rapidly in early August to peak in late August and persisted into early September; they forage and mate in flowers of Asteraceae. The ambush bugs, *Phymata pennsylvanica*, also were seen in August.

Forb Species Richness

Insect species richness was highest at intermediate forb species richness on these sites (Figure 2). The relatively low insect species richness of the sites with the highest forb species richness is a bit surprising and may be related to unique site features.

Forb Phenology

There were 22 early species, (flowering during May and June), 24 mid-season species (July-mid August), and 13 late or very late species (mid August through September) (Table 3). The ASP site had only mid-season flowers, CARP and LLRP were especially rich in early flowers, and CEM and LV were especially rich in late flowers. The AREM site had few fall flowers.

Relationship of Forb Phenology and Insect Species Richness on Sites

Presence of flowers over a longer portion of the summer tended to increase the insect species richness of sites. Early generalist bees were found only on sites with early-season plants; for example, early andrenids such as Andrena commoda and A. crataegi, visited spring flowers at CARP, but were not found at CEM where early flowers were very limited. Most Asteraceae specialists were absent from AREM because of its lack of fall flowers, which are mainly Asteraceae; predators and parasites also tended to be found less frequently on sites with fewer fall flowers. ASP had only mid-season flowers and was very poor in insect species, lacking both specialists and many common generalists.

Insect Species Richness of Individual Forb Species

Insects that are specialists on my sites include *Osmia distincta, Tetralonia dubitata*, and *Hoplitis pilosifrons* on *Penstemon grandiflorus*; *Hoplitis cylindrica* on *Amorpha canescens*; *Colletes susannae* and *C. wilmattae* on *Dalea purpurea*; *Melissodes desponsa* on *Cirsium discolor*; *Andrena helianthi, Melissodes agilis*, and *Perdita albipennis* on *Helianthus* spp.; *Dufourea monardae* on *Monarda fistulosa*; *Andrena rudbeckiae* on *Ratibida pinnata*; *Andrena placata* on *Solidago* spp.; *Melissodes dentiventris* on *Aster* spp.and the *Hemaris* spp. on *Monarda fistulosa*. These insects are not found on sites without their plants.

Pycnanthemum virginianum and *Monarda fistulosa* supported the most unique insect species (those not found on any other forb); *Solidago canadensis, Amorpha canescens*, and *Helianthus rigidus* also supported many unique insects; unique insect species were collected from 33 of 59 plant species (Table 2).

Forbs that are especially species rich in visitors can be identified by a high ratio of percent of insect species collected to percent of total collections, if collection number is adequate for this test (Table 2). For example, *Amorpha canescens* had 2.0 % of the collections made, and 14.1 % of the total insect species, for a ratio of 7.1, whereas *Heliopsis helianthoides*, was poorer in insect visitors; it had 3.0 % of the collections and only 6.3 % of the insect species, giving a ratio of 2.1. *Amorpha canescens, Solidago nemoralis, Aster ericoides*, and *Pycnanthemum virginianum* had the highest ratios of visitors to collections, and *Rudbeckia hirta, Ratibida pinnata, Heliopsis helianthoides*, and *Monarda fistulosa* had the fewest insect visitors relative to the numbers of collections made. (The species to collection ratio may be a bit low for *M. fistulosa* because of the high number of collections thath were made from this plant).

Finally, some forb species are especially attractive to certain insect groups. For example, half the wasp species in the entire collection were found on *Pycnanthemum virginianum*; 37 bee species were collected from *Dalea purpurea*; *Liatris aspera* and *Monarda fistulosa* were the sources of the majority of bombyliids collected. Many syrphid flies were collected from *Heliopsis helianthoides*. *Lepidoptera* were found most commonly on *Monarda fistulosa, Liatris aspera*, and *Solidago speciosa*

Other forb species were visited rarely in these sites, especially *Phlox pilosa, Coreopsis palmata*, and *Desmodium canadense*.

Relationship of Forb Insect Species Richness to Site Insect Species Richness

Certain forb species listed above support specialist insects, others are attractive to generalists, some have strikingly rich insect visitor lists often including insects collected from no other plant, and other forbs are especially attractive to certain insect groups. Thus, forb species make unique contributions to the insect species richness of the areas in which they grow; experimental testing will be needed to determine the extent to which the presence of individual forb species affects insect species richness on a variety of prairie sites.

Conclusions

The species richness of the flower-visiting insect community on prairie sites was not related to the size and age of the site, number of individual flowers,or total forb species richness. Insect species richness of sites was increased by the presence of forb species that supported specialist insects and by the presence of flowers throughout the summer. Prairie forb species could be identified as resources for spring generalists, resources for fall generalists, and resources for specialists. Individual forb species supported unique portions of the flower visitor community on these sites. Over a variety of sites and with ample collections to sample visitor species richness, certain forb species are consistently more attractive to insects in general and to certain insect groups, than are other forbs. These results suggest that the insect species richness of reconstructions can be increased by the introduction of forb species that attract a wide variety of insect visitors.

Species tended to accumulate in older sites, as indicated by the slightly greater species richness in the native sites over all. The presence of many species on only one site indicates that even small prairie remnants should be preserved as insect conservation sites, and the presence of many unique insect species on reconstructions implies that reconstructed prairies also can be valuable sites for insect conservation.

Voucher Specimens and Species List

Voucher specimens are located in the authorollection and will be archived at the University of Minnesota Insect Museum and the University of Minnesota Herbarium. For a copy of the complete insect species list, write to the author.

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