FORAGING ECOLOGY OF SELECTED PRAIRIE WILDFLOWERS (*ECHINACEA, LIATRIS, MONARDA,* AND *VERONICASTRUM*) IN MISSOURI PRAIRIE REMNANTS AND RESTORATIONS

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Abstract: Pollinators of dominant prairie angiosperms were collected in the summers of 1998 through 2001 and examined for pollen loads. Data were collected on a restoration site, Litzsinger Road Ecology Center (St Louis County, Missouri), and a relict site, Paint Brush Prairie (Pettis County, Missouri). Statistical analysis of floral foraging preferences was performed, using the chi-square test for independence, and shows nonrandom floral visitation by the major species of prairie bumblebees (*Bombus,* Apidae) at plant species (or plant species groups). The small, short-tongued *Bombus impatiens* exhibits preference for Culver's root *(Veronicastrum virginicum),* while the large, long-tongued *Bombus nevadensis* primarily visits wild bergamot *(Monarda fistulosa).* The intermediate-sized prairie bumblebee, *Bombus griseocollis,* visits these plants but also composites in *Echinacea* and *Liatris,* thus displaying a generalist foraging strategy. The rare *Bombus fraternus* is strongly attracted to the flowers of milkweeds (*Asclepias* spp.). Bumblebees seldom visit rattlesnake master *(Eryngium yuccifolium),* which instead is strongly preferred by large and small species of sphecid wasps (tribes Bembicini and Philanthini, respectively). Many other smaller insects also visit these plants, and these smaller members of the above-described pollination guilds tend to be generalist foragers only on restorations. On remnants, however, some of the above-mentioned plants (as well as *Penstemon* spp.) are visited by oligolectic foragers that appear to be unable to move out of the remnants and colonize prairie restorations in the current landscape. The occurrence of large numbers of remnant-dependent prairie insects and the fact that prairie insect entomofaunas are poorly known are 2 strong arguments for the very great need for detailed, long-term studies of prairie insect biodiversity as well as concern for insects in restoration strategies. These pollinating insect populations do not use prairie grasses very much and are dependent on dicots. Thus insects and animals at higher trophic levels, such as prairie birds that feed their young on insects, are expected to be poorly represented in monocultures of prairie grasses. Such plantings might be called "prairie deserts," except that true deserts are remarkably rich in dicots, insects, and birds.

Key words: List?

The community ecology of pollinating insects of Missouri's prairie relicts and restorations is a fascinating area of research for many reasons, including the following:

- Missouri contains many fine conserved examples of prairie communities, more so than other states in the tallgrass prairie region (such as Illinois or Iowa). Hence these areas can be expected to support more intact communities than, say, the smaller and less numerous surviving prairie areas in these surrounding states.
- The entomofaunas of these prairie areas are poorly known, largely because the task of identifying collections of insects is daunting. Yet the opportunity exists to discover new species of Missouri prairie insects heretofore unknown in the state, as in the 3 new state records (for a bumblebee, a beefly, and a pseudomasarid wasp) reported here.
- Theoretically, the quantification of pollination niches sheds light on recent controversies in pollination biology, such as the debate over the relative importance of generalist *vs* specialist foraging strategies (see, for example, Waser, and others[1]).
- Since a significant portion of the prairie insects (as high as 25% for some groups, according to Panzer and others[2]) are remnant-dependent, comparisons of remnants and restorations identify those species that are present as floral visitors to a given plant in remnants but have been unable to disperse through the anthropocentrically-altered landscape to colonize restorations. This knowledge will be useful to restoration managers in future attempts to reintroduce these missing species onto suitable restoration sites.

In summary, this work is of great interest in both theoretical and applied spheres and provides a quantification of a qualitative approach to pollinator surveys of prairie plants in Macoupin County, Illinois, published by Charles Robertson in his classic *Flowers and Insects*[3]. In this paper, we consider plant–insect interactions in the month of July only [AU: other months are also reported]. Other seasons will be considered in followup papers; May–June visitations to *Penstemon* spp. were considered in Clinebell and Bernhardt[4].

While Robertson's[3] ambitious objective of documenting all floral visitors of all angiosperms in Macoupin County is

admirable, our objectives are more modest. We chose species that are abundant at Litzsinger Road Ecology Center (St Louis County, Missouri), that reflect a diversity of floral structure and corolla tube lengths (namely, from shortest to longest, *Echinacea, Liatris, Pycnanthemum, Veronicastrum,* and *Monarda*), and that might correlate with the varying tongue lengths of the several species of *Bombus* (bumblebees) known to occur on the site, as well as in other prairie remnants and restorations throughout the tallgrass prairie region.

METHODS AND MATERIALS

Methods employed here follow Clinebell and Bernhardt[4]. Common July-blooming plant species were chosen to represent a diversity of floral tube lengths in the hope that niche partitioning among workers of species of bumblebees (*Bombus* spp.) possessing varying tongue lengths could be detected, as suggested by similar partitioning reported by Clinebell[5] for bumblebee queens visiting flowers of other prairie plants in May and June at Konza Prairie Research Natural Area, Riley County, Kansas. Insects were collected randomly from the plant species compared, with some undercollection of the exotic honeybee *(Apis mellifera)* and large, conspicuous Lepidoptera (which are poor pollen transporters of the plants studied here, or rare and endangered, as the regal fritillary *[Speyeria idalia]*). Insects were killed in separate jars for each plant species and were pinned soon after collection to preserve the integrity of the pollen loads as much as possible. The number of pollen grains each insect carried was estimated by examining each specimen under the binocular microscope. Identification of pollens was made by staining pollen samples on a microscope slide with Calberla's solution and comparing the pollen grains to a reference collection of pollen slides at higher magnification.

While original contracts with the supporting agencies (Missouri Department of Conservation and Litzsinger Foundation) did not include pollen load analysis, this work has been carried forward. Without detailed pollen load analysis, collections of insects on flowers are not nearly as illuminating as the tables presented here, which not only identify true pollinators (as opposed to casual floral visitors) but also identify which species of insects are transporting major pollen loads.

The number of insects collected and analyzed for pollen loads here (approximately 700) exceeds the sample size from my dissertation[5] on the pollination biology of prairie penstemons (587). Aside from small sets of specimens donated to specialists in insect taxonomy, the entire collection is currently maintained at the Missouri Botanical Garden. A representative set of all pollinating species will be deposited at Enns Entomological Museum, University of Missouri, and subsets at the Field Museum and the Smithsonian Institution. A full collection of the pollen slides, as well as vouchers of plants studied, is also maintained at the Missouri Botanical Garden.

Statistical analysis of the data were made, and computation of Shannon–Wiener diversity indices for some of the collections were calculated.

RESULTS

Table 1 gives summary data for the late June–late July foraging behavior of the 3 most common species of *Bombus* on 5 of the most abundant summer-blooming prairie wildflowers at Litzsinger Road Ecology Center from 1998 to 2001. Table 1 is the organizing paradigm for this report. A cursory examination of the table shows that 2 species are extreme foraging specialists: the long-tongued *Bombus nevadensis* on the long corolla tubes of *Monarda fistulosa,* and the short-tongued *B. impatiens* on the short corolla tubes of *Veronicastrum virginicum* and *Pycnanthemum pilosum.* The 3rd species of bumblebee, *B. griseocollis,* with an intermediate tongue length, is seen to be a generalist, visiting all the wildflower species in the sample but most abundant on the composites.

Table 1 Foraging preferences of bumblebees at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2001

	***BOMBUS NEVADENSIS* (M/F)**	***BOMBUS IMPATIENS* (M/F)**	***BOMBUS GRISEOCOLLIS* (M/F)**
Veronicastrum virginicum[a]	0/0	21/34	27/4
Monarda fistulosa	0/59	0/3	9/8
Echinacea purpurea + *Liatris pycnostachya*	2/5	4/4	62/17
Total	2/64 (66)	25/41 (66)	98/29 (127)

[a]+*Pycnanthemum pilosum* [AU: how are this footnote and third row label "*Echinacea purpurea* + *Liatris pycnostachya*" different?]

Table 1 indicates numbers of male and female visitors. Looking only at the females (in July, mostly workers plus a few queens) is instructive. Male bumblebees do not contribute to the care of their offspring, they merely forage through the prairie looking for gynes (uninseminated queens), which appear from midsummer onward, depending on the species. The males mate with the gynes (the only individuals in the populations to survive winter), which then found new nests the following spring. The females of Table 1 are seen to provision the young of their species with pollen from different species of prairie wildflowers.

In other words, young of *Bombus impatiens* are largely made from the pollen (and nectar, the pollen pudding on which the young are nourished) of *Veronicastrum* and *Pycnanthemum;* young of *B. nevadensis* are made from *Monarda fistulosa,;* and even the more generalist *B. griseocollis* creates its offspring from prairie composites, in an excess of 50%, compared to an excess of 85% of young produced from the favored, non-overlapping food plant species in the 2 specialist species. Even though the 3 *Bombus* species are living in the same community, it is as if each is making its living in largely nonoverlapping universes.

The major goal of my work in Missouri Department of Conservation (MDC) remnant prairies was to see if similar patterns obtain. Vicissitudes of funding variation have resulted

in a smaller set of data for remnants (2000) than for restorations (1998 through 2001), and thus the results are somewhat equivocal, both because of sampling inequalities and because my work in the remnants diverged onto different prairie types than the more mesic Litzsinger site, but with some model validation. While we have 4 y of data from the restoration, and only 1 y of data from the remnants, work on the remnants will resume again in 2003. A 5th year of data from the restored prairie at Shaw Nature Reserve, Franklin County, Missouri (2002), validates the niche partitioning reported here, but is not included in this paper. We break down the discussion which follows by plant genus.

Monarda fistulosa

Table 2 shows the floral foragers (and their pollen loads) of this species for Litzsinger Road Ecology Center (LREC), while Tables 3 and 4 give the same information for Paint Brush Prairie (Pettis County, Missouri) and the forest light gap colony at Preston Flats East Vista in Caney Mountain Conservation Area (Ozark County, Missouri). (Tables 2–11 appear at the end of this paper.) At LREC the major floral visitor and pollen carrier is the worker caste of *Bombus nevadensis,* accounting for 42 of 94 insects collected or observed during latest [AU: what?] June–July of 1998 through 2000. Mean tongue (glossum+prementum) length for this species and caste is 8.2 mm (n=10), while the mean corolla tube length of the plant is 8.3 mm (n=10). Deposition of pollen is on the dorsal surface of the insect (nototribic) and is especially abundant on the dorsal thorax and basal portion of the wings.

Among the bumblebees, *Bombus nevadensis* workers are also the major floral visitor and pollen transporter for this *Monarda* at Paint Brush Prairie. In the forest light gap at Caney Mountain, *B. nevadensis,* a grassland species, is not present, and most of the pollen transport here is accomplished by workers of *B. bimaculatus,* a woodland species that also occurs in prairies. *B. bimaculatus* individuals have shorter tongue lengths than *B. nevadensis* and may not be as successful in procuring *Monarda* nectar, but nevertheless collect large amounts of pollen.

Bombus griseocollis

Bombus griseocollis (pooled data for all castes) was the 2nd most important transporter of pollen at both LREC and Paint Brush. This generalist forager possesses an intermediate tongue length (mean=6.2 mm, n=10) between the longer-tongued *B. nevadensis* and the even shorter-tongued *B. impatiens* (mean=4.5 mm, n=10).

At all 3 sites a variety of Lepidoptera, both large and small, visit the flowers but do not carry appreciable amounts of pollen, which was observed sparingly on 3 groups: clearwing moths (*Hemaris* spp., Sphingidae), silver spotted skippers (*Epargyreus c. clarus,* Hesperiidae), and great spangled fritillaries (*Speyeria cybele,* Nymphalidae). Because large butterflies seldom carry large pollen loads in these Missouri prairie plant species (data tables, this paper); because they are often not overly abundant; and because the opportunity to observe large, colorful butterflies is a great draw for the public to Missouri's public prairies, data on Lepidoptera are frequently a combination of captures and sight observations. When sight observations are included in the tables, they are assigned the "zero pollen load" category, which results in a slight underevaluation of their role in pollen transport.

Several interesting groups of insects collected on the remnants were not present in the restoration, including lepturine cerambycid beetles (flower longhorns, Caney Mountain), female bees in the genus *Anthophora* (Caney Mountain), and a white-pubescent beefly (family Bombyliidae, Paint Brush Prairie) with bright green eyes in life. All transported small amounts of *Monarda* pollen. Females of the megachilid bee *Megachile mendica* were also collected at Paint Brush, but these carried no pollen.

Overall, 15 species of insects were collected on *Monarda* flowers over 3 seasons at LREC (1998 through 2000, n=88 individual insects), while 29 species were collected at Paint Brush in 2000 (n=108 individual insects). The Shannon–Wiener diversity index[6] was greater at Paint Brush (H`=2.918) than at LREC ($H$`=1.900).

Monarda bradburiana

A small set (n=11) of pollinators of this species were collected at Valley View Glades on 11 May 2000. This set included 2 males of the dusted skipper *(Atrytonopsis h. hianna).* This taxon flies for only a few weeks in late April and early May, and "the larvae aestivate during the hot summer months and hibernate over winter, spending about ten months in the larval stage"[7]. It is thus important to document here the current occurrence of this species (limited in Missouri to Ozark glades) at Valley View Glades, since there is a very narrow window of opportunity to collect the adults. While these skippers carried no pollen, major pollen transporters include queens of *Bombus bimaculatus* and *B. griseocollis* and females of the xylocopid bee, *Hoplitis pilosifrons.* In June 2002 at Crescent Glade (Shaw Nature Reserve, Franklin County, Missouri), 8 of 15 queen bumblebees were *B. nevadensis,* the same species whose workers later harvest the majority of *M. fistulosa* pollen on prairies. This data set is not tabulated here.

Echinacea purpurea

This species (commonly called purple coneflower) is frequently used in prairie restorations, as at LREC and Shaw Nature Reserve, but in natural areas is limited to savannas, forest edges, and forest light gaps. The floral foragers of this species are shown in Table 5 at the end of this paper. At LREC the major transporters of pollen are males and workers of *Bombus griseocollis,* the bumblebee with intermediate size and tongue length. This bumblebee is a generalist forager, also visiting plants almost exclusively favored by longer-tongued bumblebees *(B. nevadensis)* and smaller, shorter-tongued bumblebees *(B. impatiens).* However, its modal food plants at LREC are composites in *Echinacea* and *Liatris,* as well as *Ratibida pinnata* (yellow coneflower), although the latter data are not tabulated here. These plants seldom are visited by the 2 specialist bumblebee species. It is noteworthy that the 3 specimens of the new Missouri record, *B. affinis,* were also collected on these

composites in the summer of 1998, one on *E. purpurea* and 2 on *Liatris pycnostachya.*

Table 5 shows that while *Bombus griseocollis* accounts for only about 50% of total floral visitors to purple coneflower, it accounts for about 90% of the major pollen carriers (defined as an insect carrying >50 pollen grains). The same preferences of *B. griseocollis* for *Echinacea purpurea* and of *B. nevadensis* for *Monarda fistulosa* can be readily seen in the prairie plantings around MDC's Powder Valley Nature Center (Clinebell, personnal observation). This is an example of niche partitioning that can be shown to school groups, as the 2 bumblebees are easy to tell apart in the field—the dorsal thorax of *B. nevadensis* has 3 stripes (yellow, black, yellow), while the dorsal thorax of *B. griseocollis* is solid yellow.

In the Caney Mountain colony of *E. purpurea* along the gravel road near Onyx Cave (light gap in forest), the major floral visitors are both males and females of the golden byssus skipper *(Problema byssus kumskaka).* A single *Bombus griseocollis* (and one *B. bimaculatus*) worker also carried pollen, as did a diversity of other Lepidoptera including pipevine swallowtail *(Battus p. philenor),* great spangled fritillary *(Speyeria cybele),* and 2 other skippers, the silver spotted *(Epargyreus c. clarus)* and Horace's dusky wing *(Erynnis horatius).* The same flower longhorn beetle as collected on *Monarda fistulosa* at Caney Mountain was also collected on purple coneflower. All of the above carried some pollen, with Lepidoptera pollen largely limited to the proboscis. The sample size here is small (n=25), with 10 of these being the golden byssus skipper. Because of the small sample size, I have not drawn up a table for this collection.

Echinacea pallida

Table 6 at the end of this paper shows the floral visitors at this species at Paint Brush Prairie (Pettis County, Missouri) in June 2000. The major pollinators of this species resemble those of *E. purpurea* at LREC in that bees are a major component; however, here the prevalent role of bumblebees is supplanted by a composite specialist in the Andrenidae, *Andrena helianthiformis,* which accounts for 22 of the major pollen carriers. By contrast, bumblebees account for only 7 of the major pollen carriers.

This population also resembles the *E. purpurea* colony near Onyx Cave in Caney Mountain Conservation Area in that Lepidoptera are a major component among the major pollen carriers. This is principally because of the great role played by the state-listed regal fritillary *(Speyeria idalia),* both sexes. Nine individuals were collected (2 females and 7 males) after several phone calls to MDC personnel from the field [AU: meaning?]. Relative visitations by sex and total numbers of individuals visiting flowers during the sampling periods were estimated and included in the table as 25 females and 50 males. Additional pollination carriers in Lepidoptera include several skippers (especially *Polites o. origenes*) and the swallowtail *Papilio polyxenes asterius.*

An additional population of *E. pallida* was studied May 15–16 in Ozark County at a roadside glade 3.0 mi (4.8 km) west of Missouri Highway 5 on Route W. Here floral visitors and pollen carriers were primarily medium-sized Lepidoptera, especially the variegated fritillary *(Euptoieta claudia),* American painted lady *(Vanessa virginiensis),* and the alfalfa butterfly *(Colias eurytheme).* Most of about 45 individuals carried small numbers (10 to 50) of pollen grains, usually on the proboscis and face but sometimes also on the legs. A few carried no pollen, and one variegated fritillary carried over 200 grains on the leg tips. These data are not tabulated here.

Echinacea simulata

This species was studied at Valley View Glades in Jefferson County, Missouri, on 6 June 2000. (The pollen of *E. simulata* is bright orange, while the pollen of *E. pallida* is pale yellow. Otherwise, these 2 species are nearly identical.) This data set resembles that for *E. pallida* at Paint Brush Prairie in that females of *Andrena helianthiformis* were important pollinators (n=7), while queens of *Bombus pennsylvanicus* were also important (n=4). Lepidopteran visitors included great spangled fritillaries and several skippers. One female great spangled fritillary was collected; it carried over 100 pollen grains on all body surfaces, while 4 others were observed visiting flowers. One skipper not collected elsewhere in this study was a female little glassy wing *(Pompeius verna).* These data are not tabulated here.

Liatris pycnostachya

Table 7 depicts pollinators of this species collected at LREC during July 1998, July 1999, and July 2001, while Table 8 gives comparable data for Paint Brush Prairie in July 2000. (Tables 7 and 8 appear at the end of this paper.) Both samples are small, due to the small population size at LREC and for unknown reasons at Paint Brush, where pollinator visitation rates were low in a large colony of prairie blazing star *(L. pycnostachya).* The major pollen carriers at LREC were males of *Bombus griseocollis,* as was the case with LREC *Echinacea purpurea* (hence the pooling of these 2 plant species in Table 1). The *Liatris* also attracted 2 workers of *B. affinis* (new Missouri state record), and a worker of the low-density conservative bumblebee species, *B. fraternus.* Lepidoptera accounted for about 20% of floral visits at LREC and about 5% at Paint Brush Prairie. Flower longhorn beetles (Cerambycidae: Lepturinae) also carried large pollen loads at Paint Brush Prairie, as did the grayling butterfly *(Cercyonis pegala).* These beetles and butterflies have not yet been collected at LREC.

Liatris aspera

A very interesting data set for this species (common name rough blazing star) was collected at Paint Brush Prairie in September 2000 (Table 9 at the end of this paper). Here males of *Bombus pennsylvanicus* are the major pollen carriers, as well as a single male of the conservative *B. fraternus.* These are the only occurrences of the males of these 2 bumblebees in this data set. A diversity of skippers was also collected here, but only the large silver-spotted *(Epargyreus c. clarus)* carried appreciable amounts of pollen. Large butterflies bearing heavy pollen loads included a female regal fritillary *(Speyeria idalia)* and a parsnip swallowtail *(Papilio polyxenes asterius).* The

genus *Liatris* is thus of great importance in prairie ecosystems in its support of 4 uncommon and conspicuous elements of the entomofauna: the regal fritillary, 2 rare bumblebees, and a flower longhorn beetle.

Liatris cylindracea

This species was studied at Valley View Glades in late August through early September, 2000. Here, 40 floral visitors were collected—39 consisting of a diverse set of Lepidoptera, and a single worker of *Bombus pennsylvanicus.* This species differs from the other species of *Liatris* in the greater role played by skippers and butterflies, most of which carried small pollen loads on the proboscis. The largest pollen loads were carried by 2 female pipevine swallowtails *(Battus p. philenor)*—130 and 310 pollen grains carried—and the bumblebee. The great diversity of skippers collected on this species include the silver-spotted *(Epargyreus c. clarus),* the Leonardus *(Hesperia leonardus),* the sachem (*Atalopedes campestris huron,* which accounted for 29 of the 40 individuals in the sample, about equally divided between males and females), the fiery *(Hylephila phyleus),* the clouded *(Euphyes vestris metacomet),* and the northern broken dash *(Wallengrenia egeremet)*. These data are not tabulated here.

Veronicastrum virginicum

This species was studied at LREC in late June through late July from 1998 to 2000. Major pollen carriers include males of *Bombus griseocollis,* which also visited heavily flowers of *Echinacea purpurea* and *Liatris pycnostachya;* and males and workers of *Bombus impatiens,* which did not visit other flowers in the data set with the exception of *Pycnanthemum pilosum.* Because *Veronicastrum* and *Pycnanthemum* shared this preponderance of *B. impatiens* visitation, these 2 plants are pooled in Table 1. The other unique feature of *Veronicastrum* in this data set is the large number of small halictid bees that visited these flowers but not the other plants in this survey. Of particular interest is the tiny halictid, *Dialictus imitatus.* Females of this species were major pollen carriers and transported loads of *Veronicastrum* pollen large enough to strain belief. *Veronicastrum* is also unique in the absence of visits from *Lepidoptera.* [AU: what about *Epargyreus*?] These data are depicted in Table 10.

Other Species Studied

Because focal genera were not always available for study, pollinators of additional co-blooming plants were also collected. These include *Asclepias viridis* (spider milkweed), *Grindelia* sp., *Houstonia* sp., *Oenothera macrocarpa,* and *Penstemon cobaea* in Ozark County, and fall composites in Pettis County. These data are not presented here due to space and time limitations. However, these additional collections provided some of the most exciting discoveries of the project. For the milkweed and penstemon, we found a promising indication of sexual dimorphism in the foraging behavior of the bee *Anthophora abrupta.* Here the females worked the penstemon (which provides both pollen for brood and nectar for the foraging female) while the males were encountered exclusively on the milkweed, which provides only nectar. The *Grindelia* at Long Bald was beetle-pollinated, almost exclusively by the scarab flower beetle (*Euphoria sepulchralis* Casey). The penstemons yielded a 3rd Missouri site along Missouri Route W in Ozark County for the Missouri-endangered masarid wasp *Pseudomasaris occidentalis,* and the *Oenothera macrocarpa* yielded females of the onagrad specialist bee *Sphecodogastra oenotherae* at Long Bald. Visiting the *Houstonia* was a new beefly for Missouri, *Poicilanthrax lucifer* (Fabricius). This is a medium-sized species with black and orange tinges on the wings.

Eryngium yuccifolium, co-blooming in July with the focal species at Litzsinger, is remarkable in that it does not attract bumblebees at all. Rather, its largest consistent pollinators are large (14 to 18 mm) sand wasps in the genus *Bicyrtes* (Sphecidae) and smaller (8 to 10 mm) sphecid wasps in the genus *Philanthus.* Curiously *Eryngium* also attracts a species flock (at least 6 species, both males and females, in several subgenera) of the very small (4 to 7 mm) colletid bee genus *Hylaeus.* These 3 groups are seldom encountered on other plant species in July at Litzsinger.

Comparison with Other Studies

Panzer and others[2] report a high level of remnant dependence in their studies of insect biodiversity in remnants and restorations in the Chicago area. Here they studied a few of the groups of flower-visiting insects, as well as a variety of herbivores, including grasshoppers and stinkbugs.

Reed[8] collected all flower visitors (for all flowering plant species producing at least 100 blossoms) from late May to late September on 4 remnants and 4 restorations in southeast Minnesota. Her data provide an interesting contrast to the set of floral visitors for a few plants species blooming mostly in July that are presented here. She reports the following distribution of floral visitors: 83 species encountered only on remnants, 73 from restorations only, and 129 from both types of grassland. Among her remnant-dependent species is the leaf-cutting bee (*Osmia distincta;* Megachilidae). This bee is also remnant dependent in a set of sites in Kansas, Missouri, and Illinois, where it is an oligolege of *Penstemon* spp.[5]. By contrast, a bee species Reed encountered only on 1 of her restorations, *Synhalonia hamata,* was encountered by Clinebell on *Penstemon digitalis* in both remnant and restoration sites. (The reason for citing Clinebell's dissertation rather than Clinebell and Bernhardt[4] here is that the reviewers collapsed the remnant *vs* restoration tables into a single listing of floral visitors for each *Penstemon* species, while the dissertation preserves separate restoration and remnant tables, as in this paper and in Reed[8].) Also by contrast, the andrenid bee *Andrena ziziae* Robertson (Andrenidae), which she collected only on a single restoration in her data set, has been encountered in the St Louis area on both remnants and restorations, where it is an oligolege of *Zizia aurea* (Apiaceae) (Clinebell, unpublished data). We are therefore far from being in a position to make definitive statements about the true prevalence of remnant-dependency. According to Williams[9] in a letter to the editor of the *Natural*

Areas Journal regarding Panzer and others[2], "Most insects you see on a prairie can be accurately identified by very few experts, each specializing in one or a few families. These experts are themselves endangered." It is thus critical to the future of science that biodiversity studies of prairie insects be pursued by as many students as possible. Otherwise, according to Williams, "the progress made by taxonomists early in this century will be relegated to old libraries and there will be no one capable of telling us the names of the organisms we see; and without names we can learn nothing about any one of them from research done in the past." Thus, the publication of data sets, such as provided by the above-cited authors and here are an important beginning that ultimately will yield the true level of remnant dependence in prairie insects. This is crucial information for the evaluation of restoration success and the establishment of restoration priorities, such as the need for insect species transplantation from remnants to restorations that provide appropriate habitat for a given rare insect species but lack that insect species.

I estimate it takes about 15 h (per hour of intense field collecting) to pin, spread, label, identify, and count pollen loads for the insect catch of a pollination study done in the manner I have described here. It is important to emphasize that most insects are pinned fresh (within 1 or 2 d of collection) in order to preserve the integrity of the pollen loads.

Variations in mean number of insects collected per hour (Table 11) require some explanation. In the case of *Monarda* at Paint Brush, there is some inflation due to the inclusion of insects observed but not collected (butterflies and *Xylocopa* bees). The higher visitation rate at Caney Mountain is an artifact of sampling methodology. Here insects were collected only from *Monarda,* while at LREC, 3 species were typically collected in a sampling bout simultaneously. Therefore tripling the LREC means would yield a comparable measure to the MDC sites, where only a single species was collected in 1 sampling bout. In other words, for example, tripling the LREC *Monarda* mean would yield a catch of about 24 insects per hour, which compares favorably to the mean of 19 for Caney Mountain.

The low mean number of pollinators collected per hour on *L. pycnostachya* at Paint Brush is puzzling. In spite of the fact that the population was large, insect activity was low on these flowers throughout the day. The high mean number of pollinators collected per hour on *L. aspera* is real and probably reflects the extreme scarcity of other blooming plants in the vicinity of this population of rough blazing star.

Little variation in pollinator activity was observed throughout the day, except that pollinator activity was sometimes low in the early morning when the plants were laden with dew. The one seasonal change observed was the collection of a few *Bombus impatiens* on *Monarda* and Asteraceae in late July, after their preferred food plant, *Veronicastrum virginicum*, was past bloom.

STATISTICAL ANALYSIS

LREC bumblebee data were analyzed for foraging preferences of the most abundant bumblebee species for pooled sexes, males alone, and females alone (1998–2000 data only). The test used is the chi-square test for independence. These results showed extremely significant foraging preferences for the females and very significant foraging preferences for the males. The data used in these calculations are similar to Table 1.

The pooled sex data, with the 2 *Bombus impatiens* flowers (*Veronicastrum virginicum* and *Pycnanthemum pilosum*) also pooled, yielded a data array with no expected values less than 5. Here the chi-square test statistic was 163.4, yielding an alpha much, much less than 0.005, and a strong rejection of the null hypothesis that the major bumblebee species are foraging randomly.

For the female-only (mostly workers, but including a few queens) data, the chi-square test statistic was 110.0, also yielding an alpha much, much less than 0.005, and also resulting in an extreme rejection of the null hypothesis that the females of the major bumblebee species are foraging randomly.

For the males, the *Monarda* data row was discarded, as only 7 males (of *Bombus griseocollis*) were encountered on this plant, resulting in too many expected values less than 5 to motivate legitimate use of the chi-square test. The *Bombus nevadensis* column was also discarded because only 2 males of this species were encountered, also resulting in low expected values. This left a 2×2 contingency table, which tests the preferences of males of *Bombus griseocollis* and *B. impatiens* for the composites versus *Pycnanthemum*+*Veronicastrum*. Here the chi-square statistic was 9.1, yielding an alpha less than 0.005 and again rejecting the null hypothesis of random foraging.

Additional data from the MDC sites would be required to perform comparable statistical analysis of the data sets of these sites.

CONCLUSIONS

For remnant prairies, we validate the strong preference of workers of *Bombus nevadensis* for *Monarda fistulosa* at the prairie restoration at LREC. The occurrence of *Echinacea purpurea* in Missouri grassland communities is an artifact of restoration practices, as this species does not occur in the natural grasslands of Missouri. Where *E. purpurea* does occur naturally (savannas and forest light gaps), our limited data suggest that skippers rather than bumblebees are the primary pollen carriers. By contrast, prairie and glade species of *Echinacea* frequently enjoy the pollination services of a composite specialist bee, *Andrena helianthiformis,* and to a lesser extent, females of *Bombus pennsylvanicus.* This suggests that a sizable population of *E. pallida* was established at LREC. [AU: verify; original unclear] Table 1 might well be expanded to include a new row for this coneflower and a new column for *B. pennsylvanicus.* In September and October at Litzsinger, males of *Bombus pennsylvanicus* are abundant on various fall composites (Clinebell, unpublished), and yet no females were collected in July. We do not yet know what the July-flying female *B. pennsylvanicus* are doing at Litzsinger, other than they are not visiting the focal plant species discussed in this paper. For completeness, we report that the male *B. nevadensis*—which are absent from our Table 1—emerge in August at Litzsinger

and forage on late summer composites (Clinebell, unpublished; M Arduser, MDC, personal communication, date?).

The sample size for *Liatris pycnostachya* at Paint Brush Prairie is insufficient to validate the preference of *B. griseocollis* for this species (although 2 individuals were collected carrying pollen), and we were unable to find sizable populations of plants of *Veronicastrum* in remnants of the Ozarks or the Osage Plains. We suspect that the restoration paradigm of little bumblebees *(B. impatiens)* and little halictids as the modal pollen carriers of this species would be validated if a natural population of Culver's root *(V. virginicum)* could be studied in the tallgrass prairie part of Missouri.

It is impressive that, when one considers the dominant modal co-blooming species of prairie plants at a given site and time, how little overlap there really is, as demonstrated in this paper. When plant species diversity is rich, pollinating insects in the tallgrass prairie partition the floral resources.

Studies similar to this one in other floristically rich prairies, and on these sites for other angiosperm species and at other times of the year, are greatly needed. While the task of counting pollen on each floral visitor is tedious, the technique is powerful in that the true major pollinators of a given species of prairie plant (as opposed to floral visitors which either transport little pollen or are rare visitors to a given kind of flower) are immediately discernible. Perhaps the most important aspect of this kind of study is the importance of avoiding Williams'[9] doomsday scenario, wherein we are truly in danger of losing the entomological taxonomic scholarship of the past. (The burning of the great classical library at Alexandria comes to mind.) Thus one should not be ashamed of making the attempt to identify prairie insects to species, no matter what the opinions of those who are unable to do so (and no matter how much time it takes), and especially those opinions regarding whether or not the ability to identify prairie insects is "real science." As I said in my presentation to the 18th North American Prairie Conference, there is so little known about prairie insects that field research on same is truly a fertile field for young workers to embrace. Perhaps the time is ripe for the aggressive promulgation of these much-needed and infinitely fascinating enterprises (as eloquently pleaded by Williams[9]), both in terms of deserved professional respect and the adequate funding that is needed but has been heretofore difficult to obtain. It is this author's experience that, though difficult, it is possible to obtain funding and heuristic support for the kinds of enterprises described herein.

SIGNIFICANCE OF THE RESEARCH

Pollen load analysis shows that despite visitation of all of the prairie plants studied here by a diversity of insect species, the pollination of each plant species at each site examined is accomplished by only a few major pollen transporters, and frequently by a single overridingly important pollen transporter. This can be seen by examining Tables 2 through 10.

Pollen load analysis also shows that there is an infrequency of mixed pollen loads, whereby the pollens of 2 or more species of plants account for a significant portion of the pollen load (defined here as greater than 10% of the total pollen grains on a stained pollen slide coming from a 2nd species of plant).

Pollen load analysis also shows that despite various Lepidoptera species' frequent floral visitations in summer prairie and glade floras, they seldom transport much pollen in comparison with bees, or even certain flower-visiting beetles. Clearly the tedious and time-consuming process of making pollen slides and identifying the pollens actually carried by insect floral visitors is a necessary component to the evaluation of the roles played by the various insect species in actually effecting pollination in self-incompatible prairie plants.

The most reassuring part of this research is that the patterns of floral choice reported here are preserved from year to year. Finally it is important to stress that the development of a fair degree of competence is necessary to carry out this kind of research. It is troubling to this author that the set of highly skilled workers who can identify insects is a dwindling and aging population. Yet, in the words of the late Al Gentry (affiliation?, personal communication, date?), one can answer so many interesting questions about how communities are organized if one carries out studies of community ecology at the species level, regardless of how unfashionable this work might be in the mainstream.

I have addressed 2 major dividends that accrue to this flavor of research: *(a)* the controversy over the relative importance of generalist and specialist foraging strategies in pollination biology, and *(b)* the need for information on remnant dependence. But there is yet a third, and this is the equilibrium theory of island biogeography[10]. Clearly, surveys conducted and published now on the array of insect visitors to a given species of prairie flowers on a given protected site will be valuable, decades from now, when future generations of workers seek to learn how well pollination guilds have been preserved on islands of prairie biota, whether they be remnants or restorations.

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Table 2 Floral foragers of *Monarda fistulosa* (Lamiaceae) *[MF]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2001†

	0 *MF* GRAINS	1–10 *MF* GRAINS	11–50 *MF* GRAINS	51–100 *MF* GRAINS	101–500 *MF* GRAINS	>500 *MF* GRAINS	OTHER POLLEN CARRIED	TOTAL
HYMENOPTERA								
Apidae: Apinae								
Bombus bimaculatus Cresson W			1		1			2
B. bimaculatus Cresson M			2	1				3
B. griseocollis DeGeer Q	2		1		1	1	c(2), d	5
B. griseocollis DeGeer W	1							1
B. griseocollis DeGeer M	2		3	1	4		a(2), d	10
B. impatiens Cresson W	2	1	2				a, e	5
B. nevadensis Cresson W+Q (1)	5		5	5	21	24	a(2), a+b, c(3), d, f+g	60
Apidae: Xylocopinae								
Xylocopa virginica L. F	1	2		3	1	1	c	8
Halictidae								
Agapostemon virescens (Fab.) M			1					1
Dialictus imitatus (Smith) F					3	1		4
Halictus rubicundus Christ M			1					1
Sphecidae								
Ectemnius ruficornis (Zetterstedt) F			1					1

Table 2 Floral foragers of *Monarda fistulosa* (Lamiaceae) *[MF]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2001† (Continued)

	0 *MF* GRAINS	1–10 *MF* GRAINS	11–50 *MF* GRAINS	51–100 *MF* GRAINS	101–500 *MF* GRAINS	>500 *MF* GRAINS	OTHER POLLEN CARRIED	TOTAL
LEPIDOPTERA								
Sphingidae								
Hemaris diffinis (Bdv.)			1					1
H. thysbe (Fab.)			2		1			3
Hesperiidae								
Epargyreus c. clarus (Cramer)	3	1	2					6
Polites coras (Cramer)	1							1
Nymphalidae								
Speyeria cybele	2	1	1				b	4
Papilionidae								
Pterourus g. glaucus (L.) F (black form)	1							1
Total	20	5	23	10	32	27		Σ=117

†Collection dates: 1998 Jul 9, 11, 27; 1999 Jun 17, 28, Jul 10; 2000 Jun 29; 2001 Jul 11, 18; *n*=1000+ plants
F=female, M=male, Q=queen, W=worker
a=Onagraceae, b=*Asclepias*, c=indeterminate (small, round, indeterminate), d=Asteraceae, e=*Veronicastrum*, f=Rosaceae, g=polyads ("bucky-balls"), h=large, reticulate
[AU: please check use of parens ( ) on names through all tables, for example DeGeer *vs* (DeGeer) in tables 2 and 3; also check consistency/accuracy—for example, *Epargyreus c. clarus* and *Epargyreus clarus clarus*]

Table 3 Floral foragers of *Monarda fistulosa* (Lamiaceae) *[MF]* at Paint Brush Prairie, Pettis County, Missouri, 2000 Jul 11–13‡

	0 *MF* GRAINS	1–10 *MF* GRAINS	11–50 *MF* GRAINS	51–100 *MF* GRAINS	101–500 *MF* GRAINS	>500 *MF* GRAINS	OTHER POLLEN CARRIED	TOTAL
COLEOPTERA								
small, black	1							1
DIPTERA								
Bombyliidae	2	1	1				a(1)	4
Syrphidae (9 mm)	1							1
HYMENOPTERA								
Apidae: Apinae								
Apis mellifera L. W	1					1		2
Bombus griseocollis (DeGeer) W	1					3		4
B. griseocollis (DeGeer) M	1							1
B. impatiens Cresson M	1							1
B. nevadensis Cresson W	1					7		8
B. bimaculatus W	1							1
Melissodes sp. F	1			1		1		3

Table 3 Floral foragers of *Monarda fistulosa* (Lamiaceae) *[MF]* at Paint Brush Prairie, Pettis County, Missouri, 2000 Jul 11–13‡ (Continued)

	0 *MF* GRAINS	1–10 *MF* GRAINS	11–50 *MF* GRAINS	51–100 *MF* GRAINS	101–500 *MF* GRAINS	>500 *MF* GRAINS	OTHER POLLEN CARRIED	TOTAL
Apidae: Xylocopinae								
Ceratina sp. F					3	1		4
Xylocopa virginica L. F	25							25
X. virginica (L.) M	1							1
Wasps								
1 (black)	1							1
2 (18 mm, black and yellow)	1							1
3 (9 mm, black and yellow)	5							5
Halictidae								
Agapostemon virescens F	1							1
A. virescens M	1							1
Augochlorella striata (Prov.) F	4							4
small, black	3		1	2				6
Megachilidae								
Megachile mendica Cresson F	3							3
LEPIDOPTERA								
Sphingidae								
Hemaris diffinis (Boisduval)	1							1
H. thysbe (Fab.)	2							2
Hesperiidae								
Atalopedes campestris huron (WH Edwards) M	4							4
Epargyreus clarus clarus (Cramer)	11							11
Polites coras (Cramer) F	1							1
Nymphalidae								
Danaus plexippus (L.)	1							1
Speyeria cybele (Fab.) F	5							5
S. cybele (Fab.) M [AU: no data?]								
Vanessa atalanta rubria (Fruhstorfer)	2							2
V. cardui (L.)	1							1
Satyridae								
Cercyonis pegala (Fab.) F	2	1						3
C. pegala (Fab.) M	1							1
Total	87	2	2	3	3	13		Σ=110

‡*n*=500 plants, at parking area nearest Missouri Route 65

F=female, M=male, W=worker

a=Onagraceae, b=Asteraceae (70% of pollen load), c=giant geodesic pollen grains, reminiscent of molecular structure of buckminsterfullerene (30%)

Table 4 Floral foragers of *Monarda fistulosa* (Lamiaceae) *[MF]* at Preston Flats East Vista, Caney Mountain Conservation Area, Ozark County, Missouri, 2000 Jun 22†

	0 *MF* GRAINS	1–10 *MF* GRAINS	11–50 *MF* GRAINS	51–100 *MF* GRAINS	101–500 *MF* GRAINS	>500 *MF* GRAINS	OTHER POLLEN CARRIED	TOTAL
COLEOPTERA								
Cerambycidae: Lepturinae								
Sp. 1			2	1				3
Sp. 2					1			1
DIPTERA								
Bombyliidae								
Exoprosopa sp. 1	2							2
Syrphidae	1							1
HYMENOPTERA								
Apidae: Apinae								
Anthophora abrupta Say F	2					3		5
Bombus bimaculatus M	4							4
B. bimaculatus W	8		1			8		17
B. griseocollis (DeGeer) G	1							1
B. impatiens Cr. W						1		1
Apidae: Xylocopinae								
Xylocopa virginica L. M	1							1
X. virginica L. F	2							2
Halictidae								
Augochlorella striata Prov. M			1					1
Augochlorella sp. F	2				1	1	a(1), b(1)	4
Megachilidae								
Heriades carinata Cresson F	1							1
Vespidae								
Wasp 1	1							1
LEPIDOPTERA								
Hesperiidae								
Achalarus lyciades (Geyer)	3	2						5
Thorybes pylades (Scudder) F		1						1
Nymphalidae								
Speyeria cybele (Fab.) F+M	10		1					11
Phyciodes tharos tharos (Drury)	1							1
Papilionidae								
Pterourus t. troilus (L.) F	2							2

Table 4 Floral foragers of *Monarda fistulosa* (Lamiaceae) *[MF]* at Preston Flats East Vista, Caney Mountain Conservation Area, Ozark County, Missouri, 2000 Jun 22† (Continued)

	0 *MF* GRAINS	1–10 *MF* GRAINS	11–50 *MF* GRAINS	51–100 *MF* GRAINS	101–500 *MF* GRAINS	>500 *MF* GRAINS	OTHER POLLEN CARRIED	TOTAL
Pieridae								
Colias eurytheme Boisduval M	1							1
Total	42	3	5	1	2	13		Σ=66

†*n*=50 plants
F=female, G=gyne, M=male, W=worker
a=pure load of circular, 45μm dia, b=pure load of oval, 15 μm long, 30 μm wide, cf *Vicia*

Table 5 Floral foragers of *Echinacea purpurea* (Asteraceae) *[EPUR]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2001‡

	0 *EPUR* GRAINS	1–10 *EPUR* GRAINS	11–50 *EPUR* GRAINS	51–100 *EPUR* GRAINS	101–500 *EPUR* GRAINS	>500 *EPUR* GRAINS	OTHER POLLEN CARRIED	TOTAL
DIPTERA								
Bombyliidae								
Exoprosopa sp.			1					1
Indeterminate	1							1
HYMENOPTERA								
Apidae: Apinae								
Bombus affinis Cresson W*						1		1
B. griseocollis (DeGeer) W	6				3	5	a(5), b, c(2), d	14
B. griseocollis DeGeer M	3		4	2	14	5	a(2), b(3), c, d	28
B. impatiens Cresson W	1					1	a(1)	2
B. impatiens Cresson M	2						a(2)	2
B. nevadensis W	1					1	d	2
B. nevadensis M	1							1
Apidae: Xylocopinae								
Xylocopa virginica L. F	2						c, g	2
Ceratina sp. F			1		1			2
Halictidae								
Agapostemon virescens (Fab.) F						1		1
Augochlorella sp. F					1			1
Dialictus pruinoides Robertson F			1					1
Dialictus sp. F	1		1	1	1	3	e	7
Halictus ligatus Say F						1	f	1
Megachilidae								
Heriades sp. F						1		1

Table 5 Floral foragers of *Echinacea purpurea* (Asteraceae) *[EPUR]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2001‡ (Contin-

	0 *EPUR* GRAINS	1–10 *EPUR* GRAINS	11–50 *EPUR* GRAINS	51–100 *EPUR* GRAINS	101–500 *EPUR* GRAINS	>500 *EPUR* GRAINS	OTHER POLLEN CARRIED	TOTAL
LEPIDOPTERA								
Arctiidae								
Cisseps fulvicollis (Hubner)			1					1
Hesperiidae								
Epargyreus c. clarus (Cramer)	1							1
Hylephila phyleus (Drury)		1						1
Polites coras			1					1
Nymphalidae								
Speyeria cybele (Fab.)	1**			1				2
Papilionidae								
Pterourus g. glaucus L. F (black form)	1			1				2
Total	21	1	10	5	20	19		Σ=76

‡Collection dates: 1998 Jul 9, 11, 18, 27; 1999 Jun 25, Jul 10, 30; 2000 Jun 29; 2001 Jul 18, 26; *n*=200 plants
F=female, M=male, W=worker
a=*Veronicastrum*, b=*Asclepias* pollinia, c=*Pycnanthemum pilosum*, d=*Monarda fistulosa,* e=*Vicia,* f=*Erigeron*, g=*Verbena*
*=new state record, **=sight record [AU: which site?]

Table 6 Floral foragers of *Echinacea pallida* (Asteraceae) *[EPAL]* at Paint Brush and Friendly Prairies, Pettis County, Missouri, 2000 Jun 14–15†

	0 *EPAL* GRAINS	1–10 *EPAL* GRAINS	11–50 *EPAL* GRAINS	51–100 *EPAL* GRAINS	101–500 *EPAL* GRAINS	>500 *EPAL* GRAINS	OTHER POLLEN CARRIED	TOTAL
COLEOPTERA								
Cerambycidae: Lepturinae					1			1
Chrysomelidae	4	1	1					6
Elateridae								
cf *Limonius griseus* Beauvois	1		2					3
HYMENOPTERA								
Andrenidae								
Andrena cf *beameri*	1							1
A. helianthiformis F				1	2	18	c(2)	21
A. helianthiformis M					1			1
Apidae: Apinae								
Bombus bimaculatus Cresson M				3				3
B. griseocollis (DeGeer) W						1	a	1
B. pennsylvanicus (DeGeer) Q						1		1
B. pennsylvanicus (DeGeer) W					2			2

Table 6 Floral foragers of *Echinacea pallida* (Asteraceae) *[EPAL]* at Paint Brush and Friendly Prairies, Pettis County, Missouri, 2000 Jun 14–15† (Con-

	0 *EPAL* GRAINS	1–10 *EPAL* GRAINS	11–50 *EPAL* GRAINS	51–100 *EPAL* GRAINS	101–500 *EPAL* GRAINS	>500 *EPAL* GRAINS	OTHER POLLEN CARRIED	TOTAL
Halictidae								
Agapostemon virescens (Fab.) F	1				1	3		5
Dialictus sp.						2		2
Halictus rubicundus F	1		1		1	2	c(4)	5
Megachilidae								
Megachile brevis F	1							[AU: 1?]
LEPIDOPTERA								
Geometridae	3						b(1)	3
Hesperidae (+25)								(25)
Atrytone l. logan (W. H. Edw.) M	1	1						2
Euphyes ruricola metacomet (Harris) M	1							1
Epargyreus c. clarus (Cramer)			1					1
Polites o. origenes (Fab.) F	2		1					3
P. o. origenes (Fab.) M	3	4	2	1			b(1)	10
P. themistodes (Latreille) F			2					2
P. themistodes (Latreille) M	2		1	1				4
Problema byssus kumskaka (Scudder) M		1						1
Nymphalidae								
Speyeria cybele M			2	1				3
S. idalia (Drury) F	(25+)		2					2 (+25)
S. idalia (Drury) M	1+(50+)		3	2	1		b(1)	7 (+50)
Papilionidae								
Papilio polyxenes asterius Stoll M					1			1
Lycaenidae								
Strymon melinus Hubner		1	2					3
Total	18	8	20	9	10	27		Σ=95 [Σ=96?] (+75)

†*n*=1000+ plants
F=female, M=male, Q=queen, W=worker
a=*Asclepias* sp. pollinia (5 on rear legs), b=Onagraceae, c=Asteraceae (not *Echinacea*)

Table 7 Floral foragers of *Liatris pycnostachya* (Asteraceae) *[LP]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–1999 and 2001‡

	0 *LP* GRAINS	1–10 *LP* GRAINS	11–50 *LP* GRAINS	51–100 *LP* GRAINS	101–500 *LP* GRAINS	>500 *LP* GRAINS	OTHER POLLEN CARRIED	TOTAL
HYMENOPTERA								
Apidae: Apinae								
Bombus affinis Cresson W*					1		c	1
B. bimaculatus Cresson Q					1			1
B. fraternus (Smith) W						1		1
B. griseocollis DeGeer Q					1			1
B. griseocollis DeGeer W					1			1
B. griseocollis DeGeer M	2		2		2	12	c	18
B. impatiens Cresson M					1		d	1
B. nevadensis Cresson W						2	a	2
B. affinis Cresson W*						1	b	1
Apis mellifera L. W				1		1	a	2
Apidae: Xylocopinae								
Xylocopa virginica L. F	1		1				e(2)	2
Ceratina dupla or *calcarata* F		1	1	1	1	1		5
Halictidae								
Agapostemon virescens (Fab.) F			1	1		1		3
Dialictus sp. F					1			1
Halictus ligatus Say F			1			4		5
LEPIDOPTERA								
Hesperiidae								
Erynnis baptisiae (Forbes) F			1					1
Hylephila phyleus (Drury) M	1							1
Polites coras (Cramer)	1							1
Papilionidae								
Pterourus g. glaucus L.					1			1
Total	5	1	7	3	10	23		Σ=49

‡Collection dates: 1998 Jul 28; 1999 Jul 30; 2001 Jul 28; *n*=50 blooming stems
F=female, M=male, Q=queen, W=worker
a=*Monarda*, b=*Pycnanthemum*, c=*Asclepias* pollinia, d=Rosaceae (?, 35 μm×50 μm) [AU: why "?"], e=small, round (15 μm dia, probably *Verbena*)
*=new state record

Table 8 Floral foragers of *Liatris pycnostachya* (Asteraceae) *[LP]* at Paint Brush Prairie, Pettis County, Missouri, 2000 Jul 11–13[†]

	0 *LP* GRAINS	1–10 *LP* GRAINS	11–50 *LP* GRAINS	51–100 *LP* GRAINS	101–500 *LP* GRAINS	>500 *LP* GRAINS	OTHER POLLEN CARRIED	TOTAL
COLEOPTERA								
Cerambycidae: Lepturinae					2			2
HYMENOPTERA								
Apidae: Apinae								
Apis mellifera L. W	1							1
Bombus bimaculatus M					1			1
B. griseocollis (DeGeer) M					2			2
Apidae: Xylocopinae								
Xylocopa virginica L. F	4						a(1)	4
Megachilidae								
Megachile mendica Cresson F	1							1
Halictidae	1							1
LEPIDOPTERA								
Hesperiidae								
Atalopedes campestris huron (WH Edwards) M	1	1	2					4
Epargyreus clarus clarus (Cramer)	1	1						2
Nymphalidae								
Speyeria cybele (Fab.)	1*							1
Satyridae								
Cercyonis pegala (Fab.) M		2	1	1	1			5
Total	10	4	3	1	6			Σ=24

[†]*n*=200 plants, at main parking area
F=female, M=male, W=worker
a=tricolpate, 30 μm dia, irregular circle to diamond-shaped
*=sight record [AU: which site?]

Table 9 Floral foragers of *Liatris aspera* (Asteraceae) *[LA]* at Paint Brush Prairie, Pettis County, Missouri, 2000 Sept 5–7‡

	0 *LA* GRAINS	1–10 *LA* GRAINS	11–50 *LA* GRAINS	51–100 *LA* GRAINS	101–500 *LA* GRAINS	>500 *LA* GRAINS	OTHER POLLEN CARRIED	TOTAL
HYMENOPTERA								
Apidae: Apinae								
Bombus bimaculatus F						1		1
B. fraternus M						1		1
B. pennsylvanicus (DeGeer) M	5				2	17	a(1)	24
Lepidoptera								
Hesperiidae								
Atalopedes campestris huron (WH Edwards) F	11	5	3					19
A. campestris huron (WH Edwards) M	3	4	10					17
Euphyes ruricola metacomet (Harris) M		1						1
Epargyreus clarus clarus (Cramer)	1	1		2	2			6
Polites coras (Cramer) F	1	4						5
P. themistodes (Latreille) F			3					3
P. themistodes (Latreille) M		2						2
Nymphalidae								
Junonia coenia Hubner	1							1
Speyeria idalia (Drury) F						1		1
Papilionidae								
Papilio polyxenes asterius Stoll						1		1
Pieridae								
Phoebis sennae eubule (L.)	4	1						5
Total	26	18	16	2	4	21		Σ=87

‡*n*=50 plants, 1000 m east of main parking area
a=large (52.5 μm dia), spiny pollen

Table 10 Floral foragers of *Veronicastrum virginicum* (Scrophulariaceae) *[VV]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2000†

	0 *VV* GRAINS	1–10 *VV* GRAINS	11–50 *VV* GRAINS	51–100 *VV* GRAINS	101–500 *VV* GRAINS	>500 *VV* GRAINS	OTHER POLLEN CARRIED	TOTAL
DIPTERA								
Conopidae								
Physocephala sp. M	2		1					3
Syrphidae (4.5 mm)	1							1
Tachinidae (13 mm)			1					1

Table 10 Floral foragers of *Veronicastrum virginicum* (Scrophulariaceae) *[VV]* at Litzsinger Road Ecology Center, St Louis County, Missouri, 1998–2000† (Continued)

	0 *VV* GRAINS	1–10 *VV* GRAINS	11–50 *VV* GRAINS	51–100 *VV* GRAINS	101–500 *VV* GRAINS	>500 *VV* GRAINS	OTHER POLLEN CARRIED	TOTAL
HYMENOPTERA								
Apidae: Anthophorinae								
Anthophora furcata terminalis Cresson F						1	b	1
Apidae: Apinae								
Apis mellifera L. W					1			1
Bombus bimaculatus Cresson W						2		2
B. bimaculatus Cresson M			1	1				2
B. griseocollis DeGeer W	1				1	2	e, e+g	4
B. griseocollis DeGeer M			1	1	17	8	a, e(2)	27
B. impatiens Cresson W					3	10	a, a+b	13
B. impatiens Cresson M				1	10	3	c, f	14
Apidae: Xylocopinae								
Xylocopa virginica L. F					2			2
Ceratina dupla or *calcarata* F		1						1
Colletidae								
Hylaeus m. modestus Say	1							1
Halictidae								
Dialictus imitatus (Smith) F		1				7		8
D. nr. *cattellae* Ellis F						1		1
D. nr. *rohweri* Ellis M				1				1
D. nr. *rohweri* F (or *D. rohweri* Ellis F)			1			2		3
Dialictus sp. 1 F						1		1
Halictus rubicundus (Christ) M			6	4	1			11
H. rubicundus (Christ) F	1			1			b+d	2
Megachilidae								
Chelostiloides exilis F			1					1
LEPIDOPTERA								
Hesperiidae								
Epargyreus c. clarus (Cramer)	1							1
Total	7	2	12	9	35	37		Σ=102

†Collection dates: 1998 Jul 9, 11, 27; 1999 Jun 17, 28, Jul 10; 2000 Jun 29; *n*=50+ plants
F=female, M=male, W=worker
a=*Echinacea purpurea*, b=Rosaceae, c=*Oenothera biennis*, d=*Tradescantia*, e=*Monarda fistulosa*, f=*Asclepias tuberosa* pollinia, g=Asteraceae

Table 11 Sampling times and mean number of pollinators collected per hour for tabulated plant species by site (1998–2000) [AU: 2001? see Tables 2, 5, 7]

PLANT SPECIES	SITE	DATE INTERVALS	TIME INTERVALS	TOTAL TIME (HOURS)	INSECTS/ HOUR
Monarda fistulosa	LREC	Jun 17–Jul 27	11 AM–5 PM	11.5	8.17
	Paint Brush	Jul 11–13	9 AM–5 PM	3	36.67
	Caney Mountain	Jun 22	9 AM–3 PM	3	19.00
Echinacea purpurea	LREC	Jun 25–Jul 30	11 AM–5 PM	12.5	4.16
E. pallida	Paint Brush	Jun 14–15	8 AM–11 PM	7	13.57
Liatris pycnostachya	LREC	Jul 28–30	12 PM–3 PM	3.5	8.86
	Paint Brush	Jul 11–13	8 AM–4 PM	3.5	6.86
L. aspera	Paint Brush	Sep 6–7	8 AM–6 PM	3	29.00
Veronicastrum virginicum	LREC	Jun 17–Jul 27	11 AM–4 PM	11.5	8.26