BEE-FLOWER INTERACTIONS ON AN OLD FIELD IN SOUTHEASTERN MICHIGAN

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Abstract. The mid-successional community of a 7.7 ha abandoned field surrounded by oak-hickory woods contained 57 species of native and naturalized flowers that were visited by 134 species of bee (including the introduced honey bee) in the 1972 and 1973 seasons. Flowering lasted from late April-early May to October, for 160 days in 1972, 171 days in 1973.

Nineteen "principal resource" flower species were abundant and broadly polyphilic, being visited by 28-49 bee species each. A few common or conspicuous flowers (*Rumex acetosella, Euphorbia corollata, Lithospermum croceum*) attracted few bees but were visited frequently by other insects.

Eleven bee species visited 14-39 flower species each; most of the others were moderately polytropic, but a few restricted their visitation to closely related taxa, including 10 species limited to *Solidago* and 4 species to *Compositae-Cynareae*, and two bees were found only on a single flower species each (*Dufourea monardae* on *Monarda fistulosa* and *Andrena rudbeckiae* on *Rudbeckia hirta*). Honey bees visited many flower species but ignored the bloom of some common ones (*Potentilla inclinata, Chrysanthemum leucanthemum, Solidago juncea*).

Flowering periods ranged from 15 days or less (*Crataegus crus-galli*) to 50 days or more (*Potentilla inclinata, Hypericum perforatum, Chrysanthemum leucanthemum*). These periods overlapped extensively, and 15-28 principal resource species were in bloom each 15-day interval from May 20 to September 1. Flight periods of native bees ranged from 17 (*Andrena rudbeckiae*) to 154 (*Ceratina dupla*) days; they also overlapped, and 32-61 species of bee were in flight per 15-day interval from May 5 to September 1.

Although numbers of bee species visiting floral resources in the course of the season were not closely correlated with resource diversity, the number per flower species was greatest early and late in the season, when there were relatively few flowers in bloom. The percentage of available bee species that visited a given flower species was greater for principal resources than for less important ones. Most of the flowers appeared to be adapted for visitation by many different bee taxa.

The pollen loads of polytropic bees often contained pollen from 3-4 species other than the one at which the bee was collected and occasionally from plants that did not occur on the field. Mixed loads were rare in bees that restricted visitation to a few flower species.

Within the last decade the open area of the field has been reduced, populations of some of the principal resource flowers have declined, and some woody species with short flowering periods have appeared. Eventually the flora is likely to approach that of the adjacent woodland community which supports a number of spring-flowering herbs but provides little bloom later on in the season. A less diverse bee fauna seems likely to characterize the field in the future.

INTRODUCTION

The observations reported here were made in the course of a long-term (1949-84) study of successional changes in the flora and fauna of a 7.7 ha abandoned field at the Edwin S. George Reserve, Livingston County, Michigan. This field, an open tract surrounded by oak-hickory woods, was probably cleared before 1850, then cultivated until 1925-26, since when it has not been subject to fires, grazing (except by deer, *Odocoileus virginianus*), or man-made disturbance of soil or vegetation (Evans 1975). For most of the study period, it has supported a prairie-like grassland with many species of flowering plants providing resources of pollen and nectar for bees and other insects. A detailed account of the relations between the flora and its bee visitors is in preparation. This paper is a preliminary report, focussing on the flowering seasons of 1972-73, when the diversity and abundance of bloom appeared to be at particularly high levels (72 species of herbs and 4 species of shrubs were recorded in flower) and when a concentrated effort was made to observe bee-flower interactions throughout the entire flowering season. Some additional records made in more recent years have been included to provide a more complete picture.

METHODS

Flower species were identified in the field after voucher material had been determined at the University of Michigan Herbarium. The field's flora was periodically inventoried, and records of the dates and duration of flowering were made at frequent intervals (in 1972-73, on 2-3 days every week) throughout the flowering season. Flower abundance was not generally quantified but was assessed visually in terms of limited or widespread occurrence and of conspicuousness, especially at the time of peak bloom. Observation of visitation by bees was usually made between 9:00 a.m. and 4:00 p.m. and on any given day was limited to a maximum of 30-40 minutes per flower species. Because of the need to shift attention from one resource to another as these were encountered in the field, changing from day to day in the course of the season, no orderly system of monitoring was developed. More attention was given to abundant resources when they were being heavily visited than was paid to them near the beginning or end of their flowering periods or to less frequently encountered species. It has not been possible to express the data in such terms as the numbers of bee visits per unit sampling effort on each flower species, and therefore statistical treatment has not been attempted.

Study of the bee fauna began with a preliminary survey by U.N. Lanham in 1957-58; he collected 81 species. In 1972-73, 134 species were taken. By 1984, 172 species had been recorded, of which 157 have been reported at one or more of 64 species of flower. The rapid movement of most bees and the small size of many species necessitated their collection for identification, but as familiarity with the bee fauna increased some species could be recognized without capture; an effort was made to avoid excessive removal of *Bombus* spp. and of oligotropic species, e.g., *Andrena rudbeckiae* and *Dufourea monardae*. Voucher specimens were taken with a net, placed in separate collecting tubes for each floral resource, and tentatively identified in the laboratory from keys and descriptions given in Mitchell (1960, 1962); they were subsequently submitted to specialists for corrected determination. Records were kept of the date of capture, the species of flower visited, and, when possible, the bee's behavior in gathering pollen and/or probing for nectar. Samples from pollen loads of selected bee visitors were transferred to glass slides, placed in glycerine jelly stained with fast green, and examined microscopically under high power; 200-300 pollen grains were generally counted from each sample. The assembled bees are in the author's collection, which will be placed in the University of Michigan Museum of Zoology.

The nomenclature of the plants reported follows that of Voss (1972, 1985) as far as possible and that of Fernald (1950) for the remainder except for the use of *Hieracium piloselloides* (see Voss and Böhlke 1978). Bee nomenclature follows that of Krombein, Hurd, Smith and Burks (1979).

THE FLORAL RESOURCES OF 1972-73

Bee visitation has been recorded for 57 species of flower that were observed in bloom in the 1972 and 1973 seasons. These

were distributed among 16 families (Table 1), consisting principally of Compositae (25 spp.), Rosaceae (9 spp.), and Leguminosae (6 spp.). The majority were indigenous species, but 17 were naturalized from Europe, several of which were fairly recent arrivals on the field: *Hieracium piloselloides* in 1963, *Carduus nutans* in 1966-67, *Centaurea maculosa* in 1969, *Cirsium arvense* in 1973. All of the plants had small flowers (the maximum corolla spread was 20-30 mm, in *Fragaria* and *Rubus*), but these were generally displayed in units of larger size: heads (*Hieracium, Monarda, Carduus, Cirsium*), panicles (*Solidago*), cymes (*Potentilla, Hypericum*), or umbels (*Asclepias*). Several structural blossom-types (Faegri and van der Pijl 1979) were represented: the dish- or bowl-shaped (*Fragaria, Potentilla*), the brush-shaped (*Antennaria, Carduus*), the disk-shaped (*Chrysanthemum, Rudbeckia*), and the flag-shaped (*Lespedeza, Desmodium*) -forms that pose differing problems for securing pollen and nectar. The predominant flower colors were yellow (22 spp.), white (15 spp.) and purple-pink (14 spp.); orange (2 spp.), blue (1 sp.), and greenish (3 spp.) flowers were also present, but no red flowers (all bees are regarded as red-blind, Proctor and Yeo 1972) were encountered. Most of the flower species present provided both pollen and nectar for bee visitors. However, the field's populations of *Antennaria fallax* and *A. neglecta*, both of which are dioecious, consisted almost wholly of pistillate individuals, producing no pollen, so that these early-season flowers were resources for nectar only. Since bees are not able to collect and utilize the pollinia of *Asclepias* for provisions, both *A. tuberosa* and *A. syriaca* must also have been visited only for nectar. In contrast, *Hypericum perforatum* seemed to produce little if any nectar (this was originally noted by Müller 1883) and appeared to be visited chiefly if not entirely for pollen. (Few of the flowers were large enough to facilitate measurement of nectar content, and no assessment of nectar production or flow was made.)

Flower species were categorized as (1) ''principal resources'' if their bloom was widespread and abundant over the field, conspicuous (to the observer) at the time of peak flowering, and heavily visited by bees; (2) ''supplemental resources'' if their bloom was either less abundant and conspicuous or less heavily visited (not only in terms of numbers of bee species attracted but also with respect to the numbers of bee visits recorded); and (3) ''subsidiary resources'' if only a low level of visitation (not more than 7 spp. of bee visitors nor more than 25 bee-visits recorded) was indicated. As shown in Table 1, nineteen species qualified as principal resources, each being visited by at least 28 (maximum, 49) species of bees and providing records of at least 100 (maximum, 506) bee visits; each had at least 2 (maximum, 12) species regarded as ''frequent visitors'' (defined here by 10 or more records of visitation). Of the 157 species of bee that were recorded as flower vistors, 148 have been taken at one or more of the principal resources.

Twelve flower species, each visited by only 10-21 species of bees and yielding fewer than 72 bee visits, were considered supplemental resources. Several of these (*Lespedeza virginica, Erigeron strigosus, Achillea millefolium*) bloomed widely and abundantly on the field but, as indicated in Table 1, yielded considerably fewer bee visit records than did any of the principal resource species. The native composite *Liatris aspera*, with 19 spp. of bee visitors and 126 bee visits recorded, is conservatively placed as a supplemental resource; it was visited frequently, however, by *Bombus* spp. and by *Apis*, and was generally widespread and abundant in late summer when the number of principal resources was small. Eighty bee species were recorded at supplemental resources, including 7 uncommon species not taken at principal resources.

The remaining 25 species of flower that bloomed in the 1972-73 seasons have provided little evidence of significant utilization by bees. They included three species (*Rumex acetosella, Lespedeza capitata, Euphorbia corollata*) that were both widespread and abundant but that, despite extensive monitoring, failed to show much bee visitation. Several species in this subsidiary resource category (*Spiraea alba, Aster azureus, A. lateriflorus, Cirsium discolor*) which generally attract bees when abundant were represented on the field by very few individual plants and thus produced a very small amount of bloom. Several others (*Desmodium marilandicum, D. sessilifolium, Tragopogon pratensis, Lactuca canadensis, Hieracium longipilum*) were often grazed on by deer so heavily that their flowering was severely diminished. As a group, these subsidiary resources were visited by 51 species of bee; one such resource, *Physalis heterophylla*, provided the only record of *Colletes latitarsis* obtained on the field.

TABLE 1. The floral resources for bees on Evans Old Field, Livingston County, Michigan, in 1972-73. Numbers of bee species visiting, and numbers of bee visits recorded, are given in parentheses.

1. ''Principal resource'' species (abundant, conspicuous, heavily visited):

ROSACEAE — *Rubus flagellaris* (45-144), *Crataegus crus-galli* (31-133), *Fragaria virginiana* (49-506), *Potentilla inclinata* (40-310). GUTTIFERAE — *Hypericum perforatum* (35-199). ASCLEPIADACEAE —*Asclepias tuberosa* (32-142). LABIATAE —*Monarda fistulosa* (32-417). RUBIACEAE —*Houstonia longifolia* (34-232). COMPOSITAE — *Solidago juncea* (36-188), *S. nemoralis* (40-196), *S. rigida* (41-266), *Antennaria neglecta* (33-101), *A. fallax* (28-130), *Rudbeckia hirta* (33-165), *Chrysanthemum leucanthemum* (29-102), *Carduus nutans* (34-243), *Centaurea maculosa* (34-145), *Hieracium aurantiacum* (45-365), *H. piloselloides* (36-278).

2. ''Supplemental resource'' species (less abundant and/or less heavily visited):

LILIACEAE — *Asparagus officinalis* (10-58). ROSACEAE — *Potentilla arguta* (13-51), *P. simplex* (15-60), *P. recta* (15-60). LEGUMINOSAE — *Trifolium repens* (13-66), *Lespedeze virginica* (10-54). ASCLEPIADACEAE — *Asclepias syriaca* (19-60). COMPOSITAE — *Liatris aspera* (19-126), *Erigeron strigosus* (14-22), *Achillea millefolium* (21-57), *Cirsium vulgare* (20-61), *C. arvense (19-71), Taraxacum officinale* (15-41).

3. ''Subsidiary resource'' species (mostly rare or with little bloom, few visits recorded):

POLYGONACEAE - *Rumex acetosella* (5-25). ROSACEAE — *Spiraea alba* (4-6), *Potentilla argentea (4-6). LEGUMINOSAE — Desmodium marilandicum (2-2), D. sessilifolium* (3-5), *Lespedeza hirta* (7-24), *L. capitata* (5-10). OXALIDACEAE — *Oxalis stricta* (7-15). POLYGALACEAE — *Polygala polygama (4-4). EUPHORBIACEAE — Euphorbia corollata* (3-3). ONAGRACEAE — *Oenothera fruticosa* (6-12), *O. biennis* (1-2). ASCLEPIADACEAE — *Asclepias viridiflora (1-1). BORAGINACEAE — Lithospermum croceum* (2-2). LABIATAE — *Hedeoma hispida* (3-4). SOLANACEAE — *Physalis heterophylla* (2-3). SCROPHULARIACEAE — *Verbascum thapsus* (2-3). COMPOSITAE — *Aster azureus* (2-3), *A. lateriflorus* (1-1), *Gnaphalium obtusifolium* (2-2), *Cirsium discolor* (2-4), *Krigia virginica* (3-7), *Tragopogon pratensis* (3-16), *Lactuca canadensis* (1-1), *Hieracium longipilum* (1-1).

THE FLOWERING SEASON

In 1972 and 1973, the flowering season, as estimated from the appearance of the first open flowers in the spring (*Antennaria neglecta*) to the last flowers producing pollen and nectar in the fall (*Solidago nemoralis*), lasted for 160 days (May 4 - October 10) and 171 days (April 24 - October 12), respectively. Despite an unusually late killing frost on June 9, 1972, the two seasons were nearly identical in the sequence and duration of flowering of most of the resource species; these features for the 1973 season are shown in Fig. 1 for the principal resources. The length of the flowering period of individual species varied considerably: two species (*Crataegus, Rubus*), both shrubs, had short flowering periods of approximately 15 days each, six species (*Potentilla, Hypericum, Houstonia, Rudbeckia, Chrysanthemum, Carduus*) flowered for

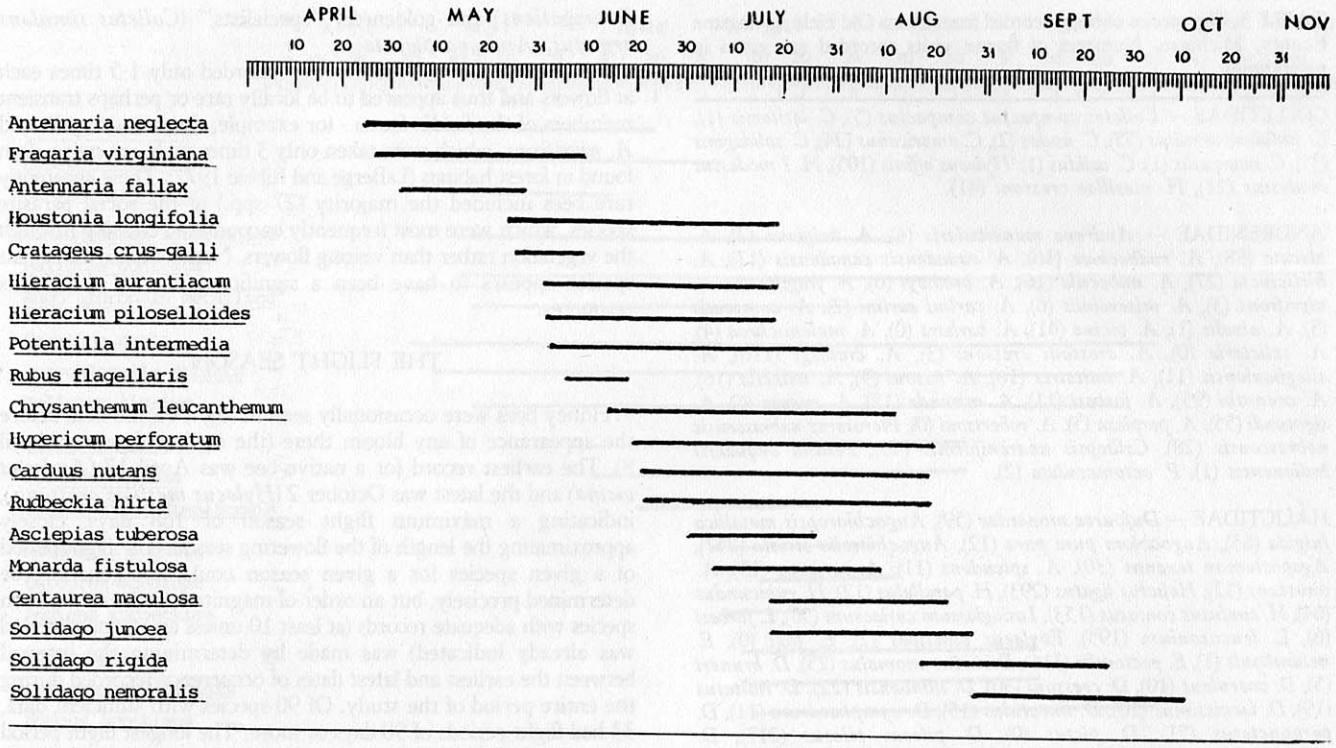

FIG. 1. Seasonal progression of flowering periods in 1973 for species serving as principal resources for bees on Evans Old Field, Livingston County, Michigan.

50 or more days each, and the remainder lasted from 3-6 weeks each. As in many other temperate-zone plant communities, seasonal patterns in flowering were evident: among the principal resources, several species (*Antennaria* 2 spp., *Fragaria*) limited their bloom to the spring, others (*Solidago* 2 spp.) to the late summer and early fall, and some (*Asclepias, Monarda*) to mid-summer. There was much overlap in flowering periods, however, and a commonly observed staggered sequence of bloom was evident, such that a number of resources were available to bees at any given time over a large part of the flowering season. Table 2 shows the numbers of principal resource and other bee-visited species that were in bloom in each of the successive 15-day intervals of the flowering seasons of 1972 and 1973. Although comparatively few species (9 or fewer) were available at the beginning and end of the season, from 15 to 28 were in bloom in each interval from May 20 to September 1; the greatest diversity occurred in July and early August. This continued high diversity does not of itself, however, guarantee an ongoing abundance of bloom. Indeed, the available records suggest that most of the principal resource species that began to flower early in the summer had either completed or passed the peak of their bloom by late July, whereas those which had their peak bloom at the end of the summer did not begin to flower until mid-August or later. The general impression was of a decreased abundance of bloom from the latter part of July to the middle of August. Ginsberg (1983) found evidence of a midsummer decline in flower abundance in an old-field community in central New York State.

TABLE 2. Numbers of species of bee-visited flowers blooming on Evans Old Field in successive 15-day periods of the season. (Based on data for 1972 and 1973).

	Number of flower species recorded in bloom		
Period	Principal resource species	Other species	Total species
1. May 5-19	4	3	7
2. May 20-June 3	8	7	15
3. June 4-18	8	13	21
4. June 19-July 3	9	14	23
5. July 4-18	12	14	26
6. July 19-August 2	11	16	27
7. August 3-17	9	19	28
8. August 18-Sept. 1	4	13	17
9. Sept. 2-16	2	7	9
10. Sept. 17-Oct. 1	2	4	6
For the entire season	19	38	57

THE BEE FAUNA

The bee species recorded from the field (Table 3) represent about 40 percent of the total number reported from the State of Michigan by Mitchell (1960, 1962) and are distributed by family as follows: Colletidae (11), Andrenidae (35), Halictidae (44), Megachilidae (30), Anthophoridae (37), and Apidae (15). The most prominent genera present were *Andrena* (31 spp.), *Dialictus* (15 spp.), *Nomada* (14 spp.), *Megachile* (11 spp.), *Bombus* (11 spp.), *Sphecodes* (10 spp.), *Colletes* (8 spp.), *Melissodes* (8 spp.) and *Osmia* (7 spp.). Except for the honey bee *Apis mellifera* and perhaps *Andrena wilkella* (see LaBerge 1964:306), all of the field's bees were native North American species. They ranged in size (body length) from 3.5-4 mm (*Hylaeus mesillae cressonii*) to 20-25 mm (queens of *Bombus nevadensis auricomus*); 37 species were less than 7 mm in length but the majority were of medium size (10-15 mm). They are divided almost equally between the so-called "long-tongued" and "short-tongued" bees. Forty-one species were social parasites that live in the nests of host bees and do not collect pollen to provision their young.

Twenty-seven species were observed at flowers 50 or more times each, accounting for 73.4 percent of the 5,422 flower visits that were recorded. With the exception of *Dufourea monardae*, to which special attention was paid because of its monotropic habits and its recent extension of range into Michigan (Bouseman 1976), all were regarded as major uses of the field's resources. The most abundant/active bee was clearly *Apis mellifera* (780 flower visits recorded), colonies of which were maintained on farms within 1-2 km of the field and which probably also nested as wild bees in

TABLE 3. The species of bees recorded from Evans Old Field, Livingston County, Michigan. Numbers of flower visits recorded are given in parentheses.

COLLETIDAE — *Colletes compactus compactus* (5), *C. latitarsis (1), C. simulans armatus* (55), *C. nudus* (2), *C. americanus* (24), *C. solidaginis* (35), *C. inaequalis* (1). *C. validus* (1). *Hylaeus affinis* (105), *H. ? modestus modestus* (21), *H. mesillae cressoni* (41).

ANDRENIDAE — *Andrena mandibularis* (4), *A. krigiana* (2), *A. placata* (88), *A. rudbeckiae* (16), *A. canadensis canadensis* (17), *A. hirticincta* (27), *A. nubecula* (16), *A. bradleyi* (0), *A. fragilis* (3), *A. nigrifrons* (3), *A. miserabilis* (6), *A. carlini carlini* (2), *A. commoda* (3), *A. nivalis* (1), *A. vicina* (41), *A. barbara* (0), *A. melanochroa* (4), *A. salictaria* (0), *A. cressoni cressoni* (3), *A. crataegi* (110), *A. alleghaniensis* (11), *A. imitatrix* (16), *A. nasoni* (9), *A. wilkella* (16), *A. ceanothi* (95), *A. forbesi* (11), *A. miranda* (12), *A. rugosa* (6), *A. sigmundi* (55), *A. perplexa* (5), *A. robertsoni* (0), *Pterosarus nebrascensis nebrascensis* (28), *Calliopsis andreniformis* (40), *Perdita bequaerti indianensis* (1), *P. octomaculata* (2).

HALICTIDAE — *Dufourea monardae* (59), *Augochloropsis metallica fulgida* (63), *Augochlora pura pura* (12), *Augochlorella striata* (257), *Agapostemon texanus (30), A. splendens* (11), *A. sericeus* (15), *A. virescens* (52), *Halictus ligatus* (293), *H. parallelus* (12), *H. rubicundus* (64), *H. confusus confusus (153), Lasioglossum coriaceum* (50), *L. forbesi* (6), *L. leucozonium* (195), *Evylaeus cinctipes* (2), *E. foxi* (0), *E. nelumbonis* (1), *E. pectoralis* (316), *Dialictus anomalus* (25), *D. bruneri* (5), *D. coeruleus* (10), *D. cressoni* (30), *D. illinoensis (22), D. imitatus* (19), *D. laevissimus* (10), *D. lineatulus* (15), *D. nymphaearum* (11), *D. perpunctatus* (51), *D. pictus* (0), *D. pilosus pilosus* (217), *D. supraclypeatus* (16), *D. tegularis* (14), *D. vierecki* (91), *Sphecodes confertus* (3), *S. cressoni* (4), *S. davisi* (0), *S. dichrous* (11), *S. heraclei* (2), *S. illinoensis* (0), *S. knetschi* (0), *S. persimilis* (0), *S. ranunculi* (2), *S. stygius* (14).

MEGACHILIDAE — *Stelis vernalis* (1), *Heriades leavitti* (23), *H. carinata* (66), *Hoplitis cylindrica* (3), *H. albifrons albifrons (1), H. pilosifrons* (71), *H. producta producta* (2), *Osmia lignaria lignaria* (3), *O. georgica* (4), *O. texana* (8), *O. distincta* (3), *O. pumila* (46), *O. atriventris* (16), *O. simillima* (3), *Megachile brevis brevis* (35), *M. mendica mendica* (50), *M. texana* (1), *M. inermis* (14), *M. montivaga* (13), *M. relativa* (16), *M. addenda* (4), *M. latimanus* (94), *M. albitarsis* (0), *M. frugalis frugalis* (1), *M. pugnata pugnata* (15), *Chalicodoma campanulae campanulae* (5), *Coelioxys octodentata* (9), *C. rufitarsis* (19), *C. alternata* (3), *C. modesta* (1).

ANTHOPHORIDAE — *Holcopasites calliopsidis calliopsidis* (7), *Epeolus bifasciatus bifasciatus* (1), *E. ? interruptus* (2), *E ? lanhami* (1), *E. pusillus* (11), *E. scutellaris* (18), *Triepeolus cirsianus* (2), *T. ? cressoni cressoni* (0), *T. simplex* (2), *Nomada ? armatella* (1), *N. cressoni cressoni* (40), *N. pygmaea* (24), *N ? sayi* (1), *N. vicina vicina* (4), *N. ? lepida* (0), *N. maculata* (13), *N. ? ovata* (1), *N ? perplexa* (2), *N. bishoppi* (0), *N. colorata* (1), *N. subrutila* (2), *N ? vincta vincta* (0), *N ? articulata* (3), *Melissodes communis communis* (13), *M. desponsa* (35), *M. dentiventris* (2), *M. nivea* (8), *M. rustica* (7), *M. subillata* (11), *M. tincta* (4), *M. wheeleri* (1), *Anthophora abrupta* (1), *A. walshi* (1), *A. furcata terminalis* (6), *Ceratina calcarata*, male (2), *C. dupla* (336), *Xylocopa virginica virginica* (2).

APIDAE — *Bombus affinis* (34), *B. terricola terricola* (6), *B. nevadensis auricomus* (33), *B. griseocollis* (38), *B. bimaculatus* (154), *B. impatiens* (60), *B. perplexus* (25), *B. vagans* (45), *B. borealis* (5), *B. fervidus fervidus* (22), *B. pennsylvanicus pennsylvanicus* (7), *Psithyrus ashtoni* (14), *P. citrinus* (5), *P. fernaldae* (3), *Apis mellifera (779).*

the adjacent woods; as its numbers built up through reproduction during the summer and as floral resources increased, *Apis* was on many days the predominant bee visitor on the field. Also abundant were several early season andrenids (*Andrena ceanothi, A. crataegi, A. sigmundi*); later on, a number of very small bees (*Hylaeus affinis, Evylaeus pectoralis, Dialictus pilosus, Augochlorella striata, Ceratina dupla*); and towards the end of the summer, several species of bumblebee (*Bombus bimaculatus, B. impatiens*) and goldenrod "specialists" (*Colletes simulans armatus, Andrena placata*).

In contrast, 62 bee species were recorded only 1-5 times each at flowers and thus appeared to be locally rare or perhaps transient members of the field's fauna - for example, *Andrena fragilis* and *A. nigrifrons*, which were taken only 3 times each, are more often found in forest habitats (LaBerge and Ribble 1972). These apparently rare bees included the majority (27 spp.) of the social parasite species, which were most frequently encountered cruising through the vegetation rather than visiting flowers. None of these infrequent species appears to have been a significant user of the field's resources.

THE FLIGHT SEASON

Honey bees were occasionally seen in flight on the field before the appearance of any bloom there (the earliest date was April 8). The earliest record for a native bee was April 17 (*Andrena vicina*) and the latest was October 2 (*Hylaeus mesillae cressonii*), indicating a maximum flight season of 168 days, closely approximating the length of the flowering season. The flight period of a given species for a given season could not generally be determined precisely, but an order-of-magnitude estimate for each species with adequate records (at least 10 unless an extended period was already indicated) was made by determining the interval between the earliest and latest dates of occurrence recorded during the entire period of the study. Of 90 species with sufficient data, 33 had flight periods of 90 days or more. The longest flight period was that of *Apis* (175 days), but 18 native species - all of them halictines except *Ceratina dupla* and including some of the smallest bees on the field (*Dialictus, Augochlorella, Evylaeus*) - had estimated flight periods of 120-154 days. In contrast, the flight period of 16 species was estimated at 30 days or less; all of the records of *Andrena rudbeckiae*, for example, were obtained within a span of 17 days. The only halictid in this category was *Dufourea monardae*, which was limited on the field to visiting a single resource (*Monarda fistulosa*); the other bees with short flight periods were for the most part either early season andrenids and colletids or late season specialists on goldenrods or other composites. An intermediate group of bees, including most of the species of *Bombus, Megachile*, and *Melissodes*, had estimated flight periods ranging from 35 to 88 days.

Fig. 2 provides examples of long, short and intermediate flight periods for selected species. It also illustrates the various seasonal patterns that were noted in the bees' foraging phenologies: (1) flight periods covering most of the flowering season (*Halictus ligatus, Augochlorella striata, Ceratina dupla*); (2) flight periods limited to spring and early summer, i.e., to May-June (*Andrena ceanothi, A. crataegi, A. sigmundi*); (3) flight periods limited to summer, i.e., to late June-early August (*Andrena rudbeckiae,*

TABLE 4. Number of species of bees visiting flowers on Evans Old Field in successive periods of the season. (Based on data for 1972 and 1973).

	Number of bee species			
Period	Taken 50 or more time each	Others	Total	No. spp. per fl.sp. in bloom
1. May 5-19	15	26	41	5.86
2. May 20-June 3	15	22	37	2.47
3. June 4-18	19	42	61	2.90
4. June 19-July 3	20	19	39	1.70
5. July 4-18	21	30	51	1.96
6. July 19-Aug. 2	18	25	43	1.59
7. Aug. 3-17	14	18	32	1.14
8. Aug. 18-Sept. 1	13	27	40	2.35
9. Sept. 2-16	6	23	29	3.22
10. Sept. 17-Oct. 1	5	14	19	3.17
For the entire season	27	107	134	2.35

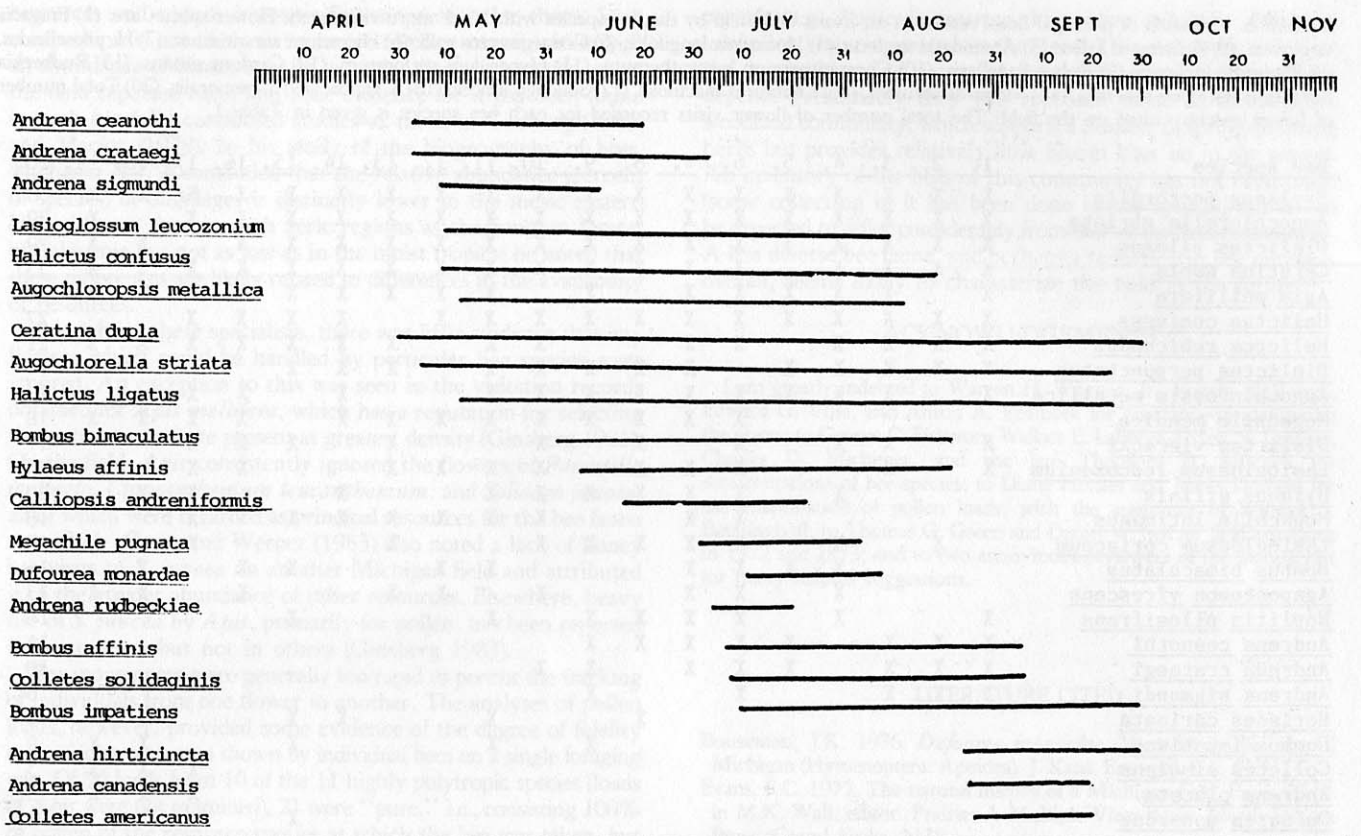

FIG. 2. Estimated maximum duration of flight periods of selected bee species on Evans Old Field, Livingston County, Michigan, based on earliest and latest dates of occurrence.

TABLE 5. Comparative success of floral resources in attracting bees on Evans Old Field, Livingston County, Michigan.

Floral resource	Flowering period (composite 1972–73	Number of bee species Visiting	Available	Percent visiting
PRINCIPAL				
Antennaria neglecta	April 24–May 24	33	66	50.0
Fragaria virginiana	April 25–June 11	49	75	65.3
Antennaria fallax	May 1–May 26	28	68	41.2
Houstonia longifolia	May 24–July 19	34	114	29.8
Crataegus crus-galli	May 25–June 7	31	66	47.0
Hieracium piloselloides	June 1–July 19	36	118	30.5
Hieracium aurantiacum	June 1–July 21	45	121	37.2
Potentilla inclinata	June 1–July 28	40	116	34.5
Rubus flagellaris	June 4–June 16	45	79	47.0
Chrysanthemum leucanthemum	June 12–August 9	30	97	30.9
Hypericum perforatum	June 19–August 16	35	92	38.0
Carduus nutans	June 20–August 17	34	92	37.0
Rudbeckia hirta	June 20–August 17	33	92	35.0
Asclepias tuberosa	June 29–July 26	32	79	40.5
Monarda fistulosa	July 6–August 10	32	82	39.0
Centaurea maculosa	July 17–August 23	34	54	63.0
Solidago juncea	July 18–August 29	36	81	44.4
Solidago rigida	August 18–September 20	41	73	56.2
Solidago nemoralis	August 29–October 10	40	58	69.0
OTHERS				
Erigeron strigosus	June 14–August 22	14	105	13.3
Euphorbia corollata	July 17–August 25	3	77	4.0
Lespedeza virginica	August 22–August 31	10	57	17.5

TABLE 6. Visitation of principal floral resources on Evans Old Field by the bee species with 50 or more visits each. Flower species are: (1) Fragaria virginiana, (2) Antennaria fallax, (3) Antennaria neglecta, (4) Houstonia longifolia, (5) Crataegus crus-galli, (6) Hieracium aurantiacum, (7) H. piloselloides, (8) Potentilla inclinata, (9) Rubus flagellaris, (10) Chrysanthemum leucanthemum, (11) Hypericum perforatum, (12) Carduus nutans, (13) Rudbeckia hirta, (14) Asclepias tuberosa, (15) Monarda fistulosa, (16) Centaurea maculosa, (17) Solidago juncea, (18) S. rigida, (19) S. nemoralis. (20) Total number of flower species visited on the field. The total number of flower visits recorded for each bee species is given in Table 1.

Bee species	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.	20.
Evylaeus pectoralis	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	30
Augochlorella striata	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	39
Dialictus pilosus	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	29
Ceratina dupla	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	33
Apis mellifera	X		X	X	X	X	X		X		X	X	X	X	X	X		X	X	28
Halictus confusus	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X			27
Halictus rubicundus	X	X	X	X		X	X			X	X		X	X	X	X	X	X	X	21
Dialictus perpunctatus	X	X	X	X	X		X	X	X	X	X		X	X	X					14
Augochloropsis metallica	X		X	X	X	X	X	X	X	X	X			X		X	X			17
Megachile mendica						X	X	X	X	X	X	X	X	X		X	X	X	X	18
Dialictus vierecki	X		X	X		X		X		X			X		X	X	X			17
Lasioglossum leucozonium	X		X			X	X	X		X	X	X	X			X	X			24
Hylaeus affinis				X		X	X	X	X	X	X			X			X	X		20
Megachile latimanus						X	X			X	X	X	X	X	X	X	X			18
Lasioglossum coriaceum		X		X		X	X	X	X	X			X				X			15
Bombus bimaculatus				X	X	X	X				X	X			X	X		X		16
Agapostemon virescens				X		X	X			X		X	X			X		X	X	13
Hoplitis pilosifrons	X			X		X	X	X	X		X				X					16
Andrena ceanothi	X	X	X		X	X	X	X	X											14
Andrena crataegi	X	X	X		X	X	X		X	X										10
Andrena sigmundi	X	X	X			X			X											6
Heriades carinata								X			X			X	X					7
Bombus impatiens									X		X				X			X	X	9
Colletes simulans																	X	X	X	3
Andrena placata																	X	X	X	3
Dufourea monardae															X					1

Dufourea monardae, Megachile pugnata); (4) flight periods limited to late summer and early fall, i.e., to late August-September (*Colletes americanus, Andrena candensis, A. hirticincta*).

As with the flowering periods of the plants, the flight periods of the bees can be arranged in a staggered sequence through the flight season, with much overlapping. Table 4 shows, however, that the species diversity of bee visitors in 1972-73 was maintained a fairly high level for most of the season, varying between 32 and 61 per 15-day interval from May 5 to September 1, with a peak in early summer and a low in the first half of August. Although numbers of bee species visiting floral resources in the course of the season were not closely correlated with resource diversity, the number of bee species per flower species was greatest early and late in the season, when there were relatively few flowers in bloom.

BEE - FLOWER INTERACTIONS

Table 5 compares the success of the 19 principal resource flowers in attracting visitors, in terms of the percent of bee species considered to be available (based on their estimated light periods) during a resource's flowering period that were actually recorded at that resource. These values ranged from 29.8% to 69.0% (considerably higher values than those obtained for most of the supplemental and subsidiary resources, e.g., *Lespedeza virginica*, 17.5%; *Erigeron strigosus*, 13.3%; *Euphorbia corollata*, 4.0%). Highest values were found for species blooming early in the season (*Fragaria, Antennaria*) or toward its close (*Solidago*), while relatively low values prevailed in mid-summer (*Chrysanthemum, Hypericum, Carduus*). Although some of the rare flowers, e.g., *Spiraea alba, Aster azureus, Cirsium discolor*, are known to be attractive to bees when their bloom is abundant, several common or conspicuous species (*Rumex acetosella, Euphorbia corollata, Lithospermum croceum*) also failed to yield many bee records (though they were visited frequently by other insects such as flies and butterflies). Small-flowered plants with low-growing and loosely arranged inflorescences (*Houstonia, Rumex*) were seldom visited by large bees, and the intricate flower structures (the flag-blossom type of Faegri and van der Pijl 1979) of *Lespedeza* and *Desmodium* seemed to discourage visitation by bees other than *Megachile, Bombus* and *Apis*.

Table 6 indicates the principal resources that were visited by the bee species for which 50 or more records are available. Eleven of these were broadly polytropic, visiting 13 or more of the principal resource species and 14-39 of all flower species at which bees were taken. Such a high degree of polytropy was made possible by the long flight periods of these bees. Michener (1979) has pointed out that male bees and females not collecting pollen are not usually very specific in their flower visiting habits. In the present study, field observation of pollen collecting and analyses of pollen loads (see below) indicated that these polytropic bees obtained pollen from most of the flower species which they visited.

In contrast, three of the bee species in Table 6 limited their visitation to very few resources: *Colletes simulans armatus* and *Andrena placata* to the three species of *Solidago* and, as noted above, *Dufourea monardae* to *Monarda fistulosa*. Other bees apparently restricting their visits on this field to a single flower species or to two or three closely related taxa included *Andrena rudbeckiae* on *Rudbeckia hirta*, a group limited to *Solidago* (*Colletes americanus, C. solidaginis, Andrena canadensis, A. hirticincta, A. nubecula, Pterosarus nebrascensis, Melissodes nivea, M. rustica, M. subillata, M. tincta*), and a group limited to *Compositae-Cynareae* (*Osmia texana, Megachile inermis, M. pugnata, Melissodes desponsa*). Most (but not all) of these bees are regarded as oligoleges throughout their geographic ranges, and most were found on the field in the latter part of the season (when the number of available flower species was small). As Michener (1954) has pointed out, oligolecty tends to divide available

resources and reduce interspecific competition for them. Such competition is not likely to be severe in plant communities with an abundance of bloom over an extended flowering season, as on the field reported here, and little evidence for it has been found in such carefully conducted studies as those of Ginsberg (1983) and Macior (1978). In his study of the biogeography of bees, Michener (1979) concluded that the relative abundance (percent of species) of oligoleges is distinctly lower in the mesic eastern United States than in such xeric regions as the Sonoran Desert of California but not as low as in the moist tropics; he noted that these differences are likely related to differences in the availability of resources.

Apart from these specialists, there was little evidence that any flowers which could be handled by particular bee species were ignored. An exception to this was seen in the visitation records obtained for *Apis mellifera*, which has a reputation for selecting the resources that are present at greatest density (Ginsberg 1981). On the field, *Apis* consistently ignored the flowers of *Potentilla inclinata, Chrysanthemum leucanthemum*, and *Solidago juncea*, all of which were regarded as principal resources for the bee fauna as a whole. Gross and Werner (1983) also noted a lack of honey bee visits to *S. juncea* on another Michigan field and attributed it to the greater abundance of other resources. Elsewhere, heavy use of *S. juncea* by *Apis*, primarily for pollen, has been reported in some years but not in others (Ginsberg 1983).

Bee movements were generally too rapid to permit the tracking of individuals from one flower to another. The analyses of pollen loads, however, provided some evidence of the degree of fidelity to particular resources shown by individual bees on a single foraging trip. Of 96 loads from 10 of the 11 highly polytropic species (loads of *Apis* were not examined), 21 were "pure," i.e., consisting 100% of pollen of the resource species at which the bee was taken, but the remaining 75 loads were "mixed" and contained pollen from 3-4 other species in addition to the one at which the bee was collected. The presence in some loads of pollen from plants not occurring on the field (tentatively identified as *Barbarea, Ilex, Cornus, Rhus*, and *Ericaceae*) indicated that some bees had previously visited other areas and habitats and were not restricted to the field's resources. In contrast to these polytropic bees, the individuals of species whose flower visitation on the field was limited to a few resources showed a much higher level of fidelity: of 74 loads examined from 11 species of specialist bees, 68 were "pure." Because fidelity restricts an individual to a particular kind of resource, that bee need not modify its behavior (on a given trip) to handle more than one blossom-type, and this may increase its efficiency as a forager.

CONCLUDING REMARKS

In the course of its historically short development, this small field community has acquired a large and diverse bee fauna. This has been made possible by the accumulation of a species-rich assemblage of herbaceous plants whose varied flowering phenologies have provided substantial supplies of pollen and nectar over an extended annual season. The coexistence of so many species of bees has been facilitated by differences in the timing and duration of their flight periods, by differences in the diversity and kinds of flowers they visited, and by differences in their life cycle characteristics (see Ginsberg 1983). Despite potential disturbance from a large population of honey bee visitors, there has been little evidence of interspecific competition among the native bees. However, the vegetation of the field is now shifting to a shrub stage, in which the total area of open field conditions preferred by many of the currently existing plant species is being steadily reduced; populations of some of the principal resource flowers have declined, and a number of woody species with short flowering periods (e.g., *Lonicera tatarica, Viburnum trilobum, Eleagnus umbellata*) have appeared in the flora. These changes will alter the composition and nature of the resources on which the bees depend. Presumably they will approach those of the adjacent woodland community, which supports a number of spring-flowering herbs but provides relatively little bloom later on in the season. An inventory of the bees of this community has not been made (some collecting in it has been done in the spring), but it can be expected to differ considerably from that of the field community. A less diverse bee fauna, and perhaps a reduction in bee numbers overall, seems likely to characterize the field in the future.

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