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The following is the established format for referencing this article:
Marlin, J. C. and W. E. LaBerge. 2001. The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. Conservation Ecology **5**(1): 9. [online] URL: http://www.consecol.org/vol5/iss1/art9/

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Report, part of Special Feature on Pollinator Decline

The Native Bee Fauna of Carlinville, Illinois, Revisited After 75 Years: a Case for Persistence

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ABSTRACT

As a follow-up to the observations of Charles Robertson from 1884 to 1916, we revisited the Carlinville, Illinois, area between 18 August 1970 and 13 September1972 to sample and identify bee species (Hymenoptera: Apoidea). We concentrated on collecting nonparasitic bees (and excluded *Apis* and *Bombus*) visiting 24 plant species that bloomed at various times of the year, and upon which Charles Robertson found many bee species. For example, we collected most intensively on spring-blooming *Claytonia virginica* and fall-blooming *Aster pilosus,* upon which Robertson reported 58 and 90 bee visitors, respectively. Bees were also collected on an opportunistic basis at some other plants. We updated the species names used by Robertson for revisions and synonymies. This paper summarizes a comparison of the two collections, made about 75 years apart at the same small geographic location.

The study considers 214 valid bee species that Robertson collected plus an additional 14 species found by us but not by Robertson. Of these 214, we collected 140 species. The absence of most of the remaining 74 species that we did not collect can be explained by examining their plant preferences. Robertson did not record 47 of these

74 species on the 24 plant species where we collected intensively, and he observed 19 more species on only one or two of the 24 plant species. Additionally, he observed 21 of them on only one of the 441 plants he studied. Of the bee species found by Robertson on the 24 plant species, we collected 82% on the same plant species.

The land uses and land cover on Macoupin County's 225,464 ha (558,080 acres), which bear directly on the type and availability of habitat for bees and their host plants, varied considerably over two centuries. For example, in the early 1800s, land cover was about 73% prairie and 27% forest. The estimated 59,792 ha (148,000 acres) of forested land in 1820 diminished to 24,644 ha (61,000 acres) by 1924. It then grew to 34,340 ha (85,000 acres) by 1962. Agriculture is the predominant land use; in 1967, 59% of the land was in harvested crops (primarily row crops) and 15% was in pasture. Despite habitat changes and the passage of 75 years, our 1970 and 1972 Carlinville collections show a high degree of similarity with those of Robertson, possibly because diverse habitats within the agricultural matrix contained the host plants and nesting sites required by the bees. We recommend that a third survey of this area be undertaken as part of a long-term study made possible by the meticulous 19th century records of Charles Robertson, which must be preserved.

KEY WORDS: Apoidea, Carlinville (Illinois), Hymenoptera, Robertson (Charles), agricultural habitats, bees, biodiversity, conservation, faunal survey, historical ecology, land use changes, pollinators.

Published: April 5, 2001

INTRODUCTION

The long-term impact of large-scale anthropogenic influences on the world's flora and fauna is the focus of considerable research and public interest. Substantial long-term data exist for many vertebrate species and floras in some parts of the world, but such information is rare for most invertebrates. Native pollinators can be key to maintaining biodiversity through their mutualistic relationship with many plant species. The economic and agricultural importance of bees (Hymenoptera: Apoidea) is illustrated by the recent impact of Old World honeybee mites in North America, which demonstrates the risks associated with over-reliance on a single species for pollination. A major impediment to documenting anthropogenic impacts is the lack of older, well-documented baseline collections of pollinators from specific localities to which subsequent resamples can be compared (Banaszak 1995*a,b,* Matheson et. al. 1996, Richards 1997).

Unlike social honeybees and bumble bees, most native bees are solitary. A lone female provisions brood cells and in each cell lays an egg that develops without further attention. Emergence of the young usually occurs in the following year. The emergence of many species coincides with the flowering of specific host plants. Thus, some bees are only active for a few weeks each year. Others are active for much of the growing season. Some bees exhibit varying degrees of cooperation with their sisters and mother. Bees have specific habitat requirements for nesting. Ground-nesting species dig burrows that contain one or more brood cells. Others nest in the pithy stems of plants like sumac (*Rhus* sp.). Still others nest in holes, dig chambers in wood, tunnel into embankments, or nest in crevices. An excellent introduction to the habitat requirements and foraging habits of bees is found in Stephen et al. (1969).

Robertson's work

The exhaustive, detailed collections of Charles Robertson provide a remarkable source of baseline data for long-term comparisons of many terrestrial plant and insect species from a specific locality. Between 1884 and 1916, Robertson observed and collected flower-visiting insects belonging to several orders. He collected in Macoupin County within a 10-mile (16-km) radius of Carlinville, Illinois, USA, about 50 miles (80 km) northeast of St. Louis, Missouri, USA. Robertson summarized his work in the book *Flowers and Insects* (Robertson 1929). Because of its private publication and limited distribution, this book is absent from most research libraries. Here, we provide an overview and summary of a forthcoming monograph discussing the re-collection of bees in the Carlinville area. A detailed version with species lists and commentary is planned for publication in the *Bulletin of the Illinois Natural History Survey.*

Robertson's book records over 15,000 insect visits to 441 flowering species. He lists 296 bee species. In addition to bees, he records visits by 367 other species of Hymenoptera, 446 Diptera, 99 Lepidoptera, 153 Coleoptera, 25 Hemiptera, and one Neuroptera species. Most of Robertson's plant and insect collection is at the Illinois Natural History Survey (INHS). Robertson's database is probably the oldest of its type for flower-visiting insects. Michener (2000) suggested that Carlinville must be one of the most carefully collected localities in the world.

Robertson (1858–1935) was the son of a pioneer doctor and druggist. The family's resources allowed Robertson the freedom to pursue his interests as a naturalist (Anonymous 1891:859). He did not earn advanced degrees, but took courses in zoology and botany at Harvard University and the University of Illinois. He was a professor of biology and Greek at Blackburn College in Carlinville for 18 years. Robertson's primary interest was the relationship between flowers and insects. Many of the insects that Robertson collected were not named at the time. He solved this problem by corresponding extensively with entomologists, sending them specimens for identification and describing well over 200 species and varieties himself. His renown among entomologists is evidenced by the fact that 20 species or subspecies bear the name *robertsonii.* Biographical information, insights on his collecting, and a five-page list of his publications are contained in Parks (1936).

Robertson left little first-hand information as to the intensity of effort that he devoted to collecting and observing, and only subjective insights into the relative abundance of species. Examination of his surviving records can help with reconstructing some of his methods and interpreting the value of the data for various purposes.

Flowers and Insects (1929) contains detailed information about visitors to flowers, including the species name and, in many instances, its sex. Abbreviations indicate activities such as feeding on pollen (f), sucking nectar and collecting pollen (sc), and exploratory visit (expl). The only stated indication of relative abundance is that some visitors to individual plants are described as frequent (fq) or abundant (ab). In a few instances, he listed separately the number of all visitors to a plant over a specified period, usually several days, without indicating hours of observation. Thus, a major limitation for using the data is the lack of specific numerical support for designating a bee as frequent or abundant on a given plant species. This is a common limitation with old data sets, which often are simply annotated species lists. Banaszak (1995*b:*18) mentioned similar subjective assessments of relative abundance in publications by Torka in 1919 and 1933, yet, he noted that species Torka described as "frequent" or "very frequent" are commonly found today. Krzysztofiak and Pawlikowski (1995:117) also commented on the difficulty of making quantitative comparisons with data collected prior to World War II.

Besides *Flowers and Insects,* the major documentation of Robertson's collecting effort is his insect voucher collection, with its four accession books containing over 25,000 handwritten entries for insects collected. These include the date, host plant, and sometimes other information. The numbers correspond to those on specimens in his insect collection. It is apparent that this was a reference collection not intended to contain all of the specimens that he observed or collected, or even to document visits to plant species. He probably kept more specimens of species when he was unsure of their taxonomic status. For example, *Bombus impatiens* is listed by Robertson as visiting many plants, but it is not represented in his collection at the INHS. *Melissodes bimaculata* was observed by Robertson on 67 plant species, but he kept specimens from only 17 plant species. He occasionally assigned a single number to a series of insect specimens of the same species collected on the same plant during a single day. The collection is reasonably consistent with Banaszak's (1995*b:*18) characterization of faunal studies at the turn of the century as, " ... collecting all encountered specimens of rare and less numerous species and some specimens of numerous or common species." Host plant information on other early bee collections was generally lacking (Mitchell 1960:7). Copies of two pages of Robertson's best preserved accession book are included here as Fig. 1 and Fig. 2. The early accession books are over 100 years old and are deteriorating, as are the labels on the collection, which contain only a number referring to the accession book entry. There is a need to computerize the data in the books and relabel the collection to prevent loss of this irreplaceable resource.

Fig. 1. A page of the Charles Robertson accession books for April 1892. Charles Robertson made corrections and updated names in the four books over several decades. Each entry includes the plant upon which the specimen was taken. *Click on the thumbnail image below to view the full-size image.*

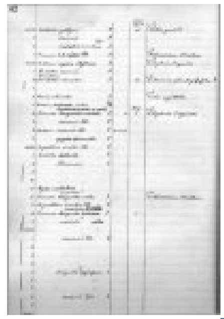
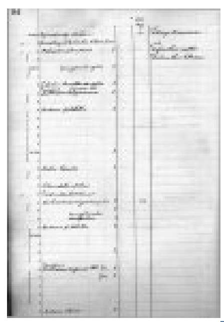


Fig. 2. An accession book page for August 1893, showing corrections and noting type specimens. The first of the four Charles Robertson accession volumes is deteriorating, and the others need preservation. *Click on the thumbnail image below to view the full-size image.*



The accession books are helpful in determining when Robertson gathered the bulk of his field data. Approximately 90% of his accession book entries are between 1884 and 1899. According to Parks (1936:85), " ... in 1880 he became a member of the faculty of Blackburn College, a position that he held for six years until he retired to give full attention to his studies on the ecological relationships existing between insects and plants within the Carlinville area." In 1898, he returned to teaching for 12 additional years. The accession entries are greatest during the years between his teaching appointments, when he presumably was free during the spring and fall collecting seasons.

Robertson traveled in a one-horse buggy over unimproved roads to conduct his fieldwork. This limitation made it difficult to monitor some plant species, especially those that bloomed only briefly. According to Parks (1936:87), he overcame some of the logistical difficulties by moving some plants into his own yard in the year before he intended to study them. Robertson's house stands today in the 300 block of Olive Street near Blackburn College. The surrounding neighborhoods still have considerable undeveloped space with varied terrain. This area is indicated as RN on the aerial photographs in Figs. 3, 4, and 5.

Fig. 3. Composite of four aerial photographs of the Carlinville, Illinois, area taken in October 1937 by the U.S. Department of Agriculture. The photos are filed in the University of Illinois Map Library as Macoupin County 1937 aerial photographs CK 4: 37, 39, 118, and 120. The individual letters on the photos are to help viewers quickly locate the same area. RN indicates the approximate location of Robertson′s neighborhood, a few blocks south of Blackburn College, where he taught. SR 4 and SR 108 are state highways. Locations A through E are common to all three photos, whereas F is common to 1937 and 1993, and G and H are common to 1968 and 1993. *Click on the image below to view a high-resolution copy of the composite.*

Fig. 4. Composite of six aerial photographs of the Carlinville, Illinois, area taken on 27 August and 21 September 1968 by the U.S. Department of Agriculture. The photos are filed in the University of Illinois Map Library as Macoupin County 1968 aerial photographs CK-1-JJ: 175, 177, and 178, as well as CK-3-JJ: 16, 17, and 20. The individual letters on the photos are to help viewers quickly locate the same area. RN indicates the approximate location of Robertson′s neighborhood, a few blocks south of Blackburn College, where he taught. SR 4 and SR 108 are state highways. Locations A through E are common to all three photos, whereas F is common to 1937 and 1993, and G and H are common to 1968 and 1993. *Click on the image below to view a high-resolution copy of the composite.*

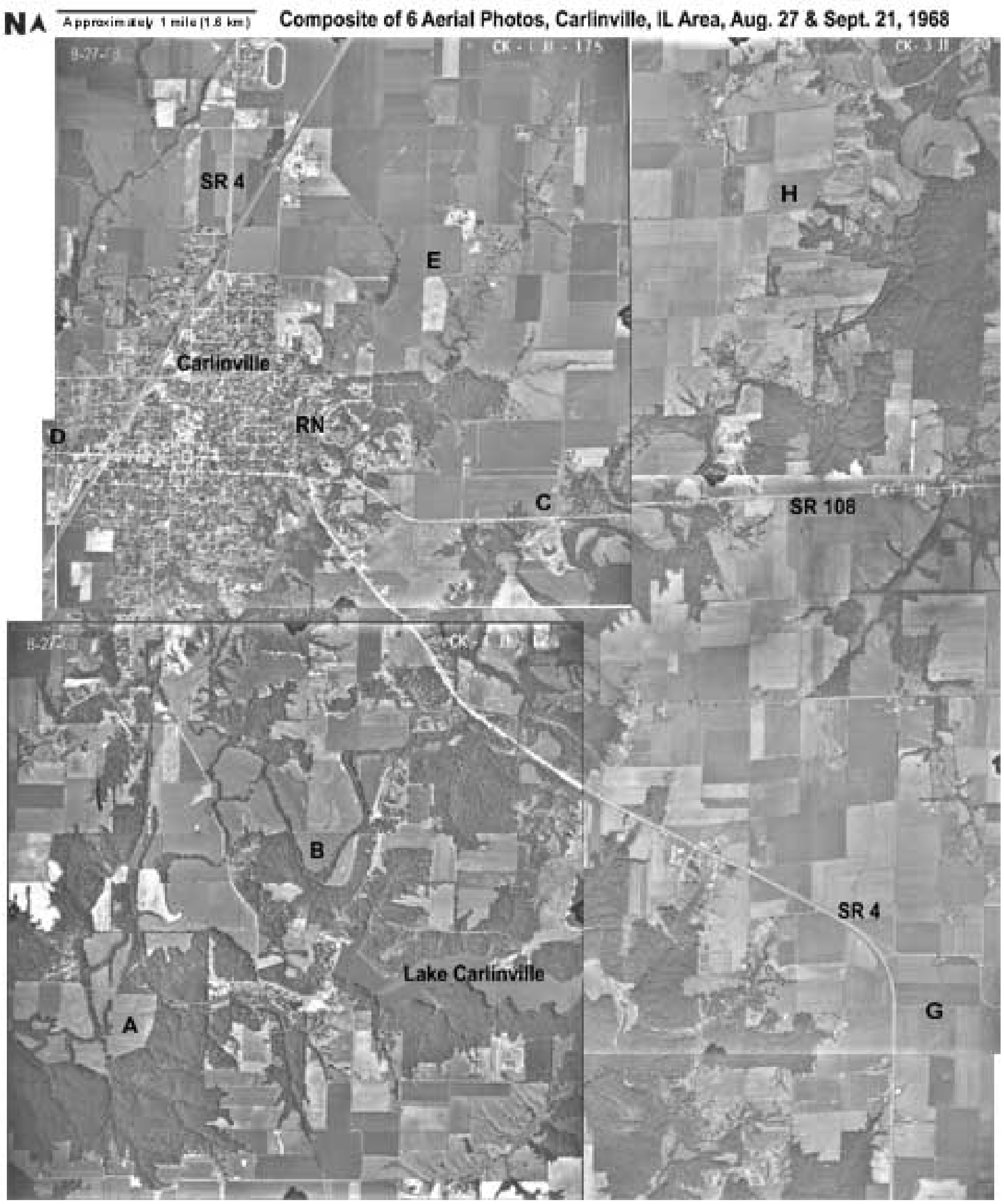


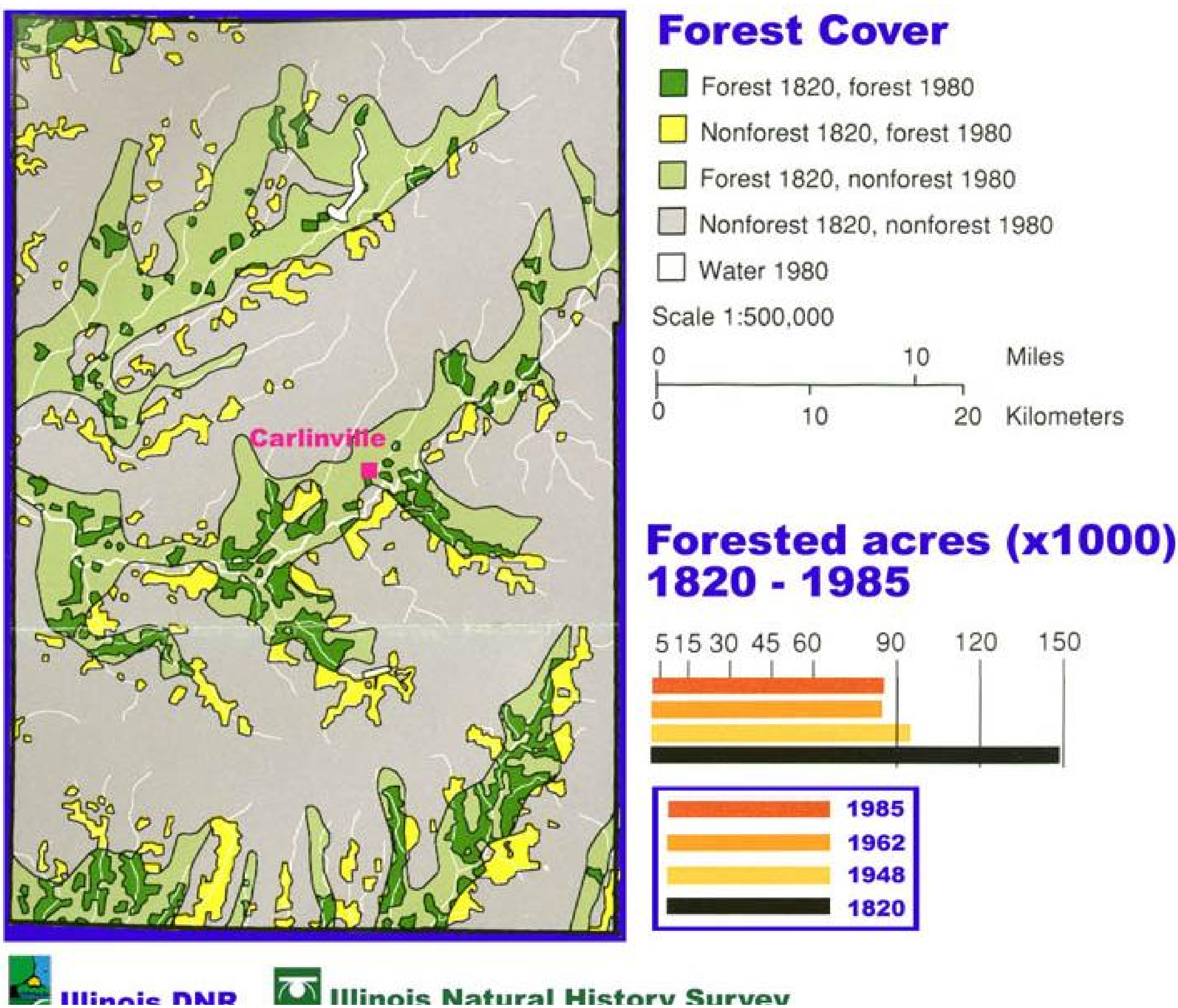
Fig. 5. Composite of four aerial photographs of the Carlinville, Illinois, area taken on 28 March 1993 by the Illinois Department of Transportation. The photos are filed in the University of Illinois Map Library as Macoupin County 1993 aerial photographs ST 41 498, ST 41 491, ST 40 489, and ST 40 491. The individual letters on the photos are to help viewers quickly locate the same area. RN indicates the approximate location of Robertson's neighborhood a few blocks south of Blackburn College, where he taught. SR 4 and SR 108 are state highways. Locations A through E are common to all three photos, whereas F is common to 1937 and 1993 and G and H are common to 1968 and 1993. *Click on the image below to view a high-resolution copy of the composite.*

The accession books provide insight into Robertson's methods. The entries indicate that he generally observed a few plants per day rather than trying to observe visitors to dozens of plant species each day. He was thus able to observe many species for significant periods of time over several years. For example, during October of 1886, he recorded visits exclusively to *Aster pilosus,* and presumably spent most, if not all, of his field time that month observing its visitors. Many plants show up for multiple years in the books, demonstrating that he did not rely on a single observation for his conclusions. He recorded visitors to *Aster pilosus* on 96 days during 16 years, *Aster novaeangliae* on eight days during three years, *Claytonia virginica* on 31 days during 10 years, and *Ipomoea pandurata* on 17 days during eight years.

Study setting

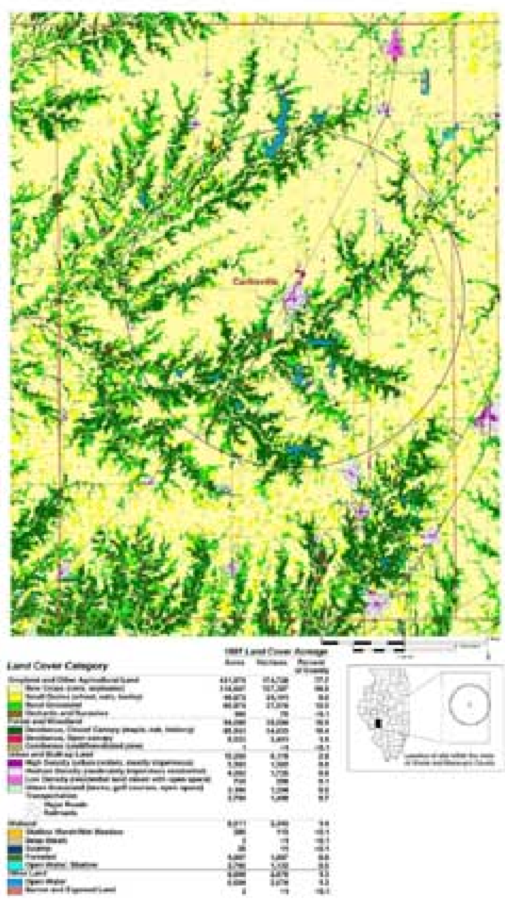
The land uses and cover on Macoupin County's 225,464 ha (558,080 acres), which bear directly on the type and availability of habitat for bees and their host plants, have varied considerably over the past two centuries. In the early 1800s, land cover was approximately 73% prairie and 27% forest. The estimated 59,792 ha (148,000 acres) of forested land in 1820 diminished to 24,644 ha (61,000 acres) by 1924, and then grew to 34,340 ha (85,000 acres) by 1962 (Iverson et al. 1989:17). Fig. 6 graphically illustrates the county's historic forest cover. Agricultural production has dominated much of the landscape, particularly the former prairie. In 1967, agriculture was the predominant land use, with 59% of the land in harvested crops (primarily corn and soybean row crops) and 15% in pasture. Estimates based on 1991 satellite images indicated that about 56.6% of the county was in row crops, 9% in small grains, 12% in rural grassland, and 16.9% (38,069 ha or 94,068 acres) in forest or open woods (Illinois Department of Natural Resources 1996:98). Fig. 7 displays the various amounts and types of land cover in the county based on Landsat data acquired primarily in 1991.

Fig. 6. Forest cover in Macoupin County, Illinois, in 1820 and 1980, with estimated coverage for some other years. It is likely that the dark green areas were forested over the entire period. The map and data are adapted from Iverson and Joselyn (1990).



Illinois DNR Illinois Natural History Survey

Fig. 7. Land cover of Macoupin County, Illinois, in the early 1990s. The area around Carlinville includes both heavily agricultural, flat prairie land and rough forested terrain along the major streams. The circle,11 miles (17.6 km) in radius, encompasses the study area. The map is based on Landsat Thematic Mapper (tm) satellinte imagery, 1991-1995, adapted from Luman et al. (1996) and the Illinois Department of Natural Resources (1996), reprinted with permission of the Illinois Department of Natural Resources, copyright 2000. *Click on the thumbnail image below to view the full-size image.*



Sizes and types of farms have changed over time, trending toward row crops and larger fields. The number of farms between 1890 and 1964 decreased by 40% while average farm size increased by 60%. The ascendancy of row crops led to decreases in the diversity of the agricultural economy and land cover. For example, the number of trees in apple orchards decreased from 122,500 in 1910 to 7,820 in 1964. Likewise, the number of milk cows decreased from 18,800 in 1945 to 3,900 in 1967 (Illinois Cooperative Crop Reporting Service 1969). By the 1960s, pesticide use on farmland was common. In southwestern Illinois in 1971, over 80% of the land in corn and soybeans was treated with herbicides. Over half of the corn in Illinois was treated with insecticide in 1971 (Illinois Crop Reporting Service 1972).

Robertson's study area included flat prairie areas primarily to the north and west of Carlinville, and the relatively rough, more forested land to the south and east carved by Macoupin Creek and its tributaries. The area thus provides habitat ranging from open prairie to hills with relatively dense tree cover. The creek and associated topographic relief provided many sites protected from intensive agricultural and residential development between the turn of the century and our survey in the early 1970s. Figs. 3 to 5 are composites of aerial photographs taken of the Carlinville area in 1937, 1968, and 1993, respectively. They illustrate the agricultural and wooded areas as well as the many fields bordered by trees. The photos were taken at different altitudes over the years, so the scale and resolution varies. It is possible to note changes that have occurred over the years, including the development of reservoirs and residential areas, and places where forest cover has increased or decreased. In some fields, the dotted patterns are orchards; in others they are harvested hay. Many features show up best when the electronic files are enlarged. The variety of terrain and collecting sites in the county is shown in Figs. 8, 9, 10, 11, and 12.

Fig. 8. The flat farmland immediately north of Carlinville provides little habitat diversity. The trees in the background in this 2000 photo are near a stream.

Fig. 9. Macoupin Creek floodplain southwest of Carlinville in 1971.

Fig. 10. Hillsides with open woods were fairly common around Carlinville, Illinois, in 1971. This hillside receives ample light and accumulates modest amounts of fallen leaves, providing good habitat for spring wildflowers such as *Claytonia virginica.*

Fig. 11. Flowering plants, including species of *Silphium, Echinacea,* and *Cirsium* along a Macoupin County, Illinois, farm access road in 1971. Patches of wildflowers were common along rural roads in the early 1970s, especially in hilly areas. In flat areas such as in Fig. 8, the space between the road and cultivated field was frequently narrow and likely to be mowed, making it difficult for flowering plants to mature.

Fig. 12. A field bordered by wooded hills south of Carlinville in 2000.

The increase in farm size and the maneuvering room required by large, modern farm machinery caused additional changes to the landscape. Early settlers planted hedges or erected fences between farms and fields. A traditional Illinois hedgerow is shown in Fig. 13. It consists of a narrow band of trees, grasses, and flowering plants. The hedgerows have provided habitat protected from plowing. Since 1950, thousands of kilometers of hedgerows have been removed as farm and field size have increased. Fence rows were also in decline during our survey. Fig. 14 shows a typical Illinois fence row. The small area on either side of the fence is protected from plowing. Hedge and fence rows presumably provide habitat for bees because they are unplowed, are not directly exposed to soil-incorporated corn insecticides, and harbor a number of plants that may provide a pollen source. They offer potential nesting sites for both ground- and stem-nesting bees. Additionally, these areas are often somewhat elevated because they trap water- and wind-driven soil particles, creating a low berm of earth. Fig. 15 pictures an overgrown fence row that extends from a road to a wooded area. Such features presumably provide protected corridors through which insects and other species can move about agricultural areas.

Fig. 13. Hedgerows of trees and shrubs were used to separate farms and fields, especially prior to the availability of wire fencing. Osage orange (*Maclura pomifera*(Raf.) Schneid.) was often planted in hedgerows. Hedgerows provide unplowed ground that has minimal exposure to incorporated corn insecticides, and hedgerows often provide nesting habitat and pollen sources for bees. The removal of hedgerows decreases habitat diversity.

Fig. 14. A typical fence row, which like hedgerows, provides some unplowed habitat in heavily agricultural areas.

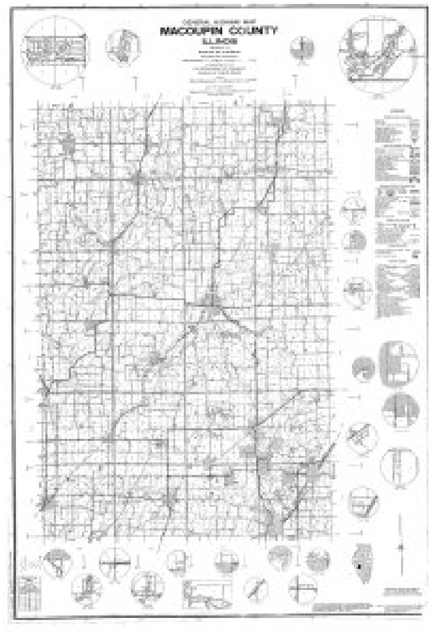
Fig. 15. A Macoupin County fence row overgrown with tallgrass, some trees, and other vegetation in the spring of 2000. The trees in the background stand at the edge of a ravine.

During our survey, several housing subdivisions were constructed in partially wooded areas around Carlinville. The construction process often included removing most of the vegetation from the sites, with the exception of a few large trees. Roadside spraying of herbicides for maintenance purposes occurred. The spray killed many trees and much of the vegetation along the roadside. This activity, which was also once prevalent along stream banks, could seriously reduce food resources for nearby bee populations. Fig. 16 shows a typical sprayed roadside.

Fig. 16. This 1971 photo shows plants killed along a roadside by herbicide used in maintenance programs. Herbicides were also used to control vegetation along streambanks. In areas where row crops dominate, such practices may severely limit the pollen available to bees.

The Carlinville area in 1970 provided a surprisingly wide range of habitats and land uses. Future researchers may refer to the accompanying aerial photographs to assess past conditions. A copy of the Macoupin County highway map used during the study is included as Fig. 17. It will be useful for locating sites, as several areas shown on that map have changed or have been developed. Of particular value may be railroad right-of-way corridors, many of which are being abandoned in Illinois. Such corridors currently harbor many native prairie plants.

Fig. 17. This electronic copy of the out-of-print 1965 edition of the Macoupin County Highway map was provided by the Illinois Department of Transportation (IDOT) and Illinois State Library. This edition was used by the authors while collecting the Carlinville area. It will prove useful during any future collecting effort, as it shows features that are not on current maps. It also provides a good representation of the density of the road net, rail rights-of-way, reservoirs, streams, and other features. IDOT publishes such maps for each county.



Click on thumbnail above for full-sized image (2,256 KB)

METHODS

The bees of the Carlinville area were re-collected beginning on 18 August 1970 and ending on 13 September 1972. W. E. LaBerge directed the project. Except for the first trip, J. C. Marlin made all of the field collections. Bees were collected within 16 km (10 miles) of Carlinville, the distance over which C. Robertson reported collecting. Future collectors may closely approximate this area by staying within 17.7 km (11 miles) of the Macoupin County courthouse. The amount of time spent collecting at various plants was recorded. An attempt was made to collect representatives of all bee species visiting the plants. Indiscriminate sweeping was employed most of the time, and special effort was made to individually collect any bees that were distinct or likely to be missed by general sweeping. It was usually necessary to stalk bees at plants such as *Ipomea pandurata* and *Vernonia missourica.* A long-handled net with three sections that bolt together was occasionally employed. This allowed the sweeping of *Salix, Prunus, Cercis,* and other short trees to a height of about 6 m.

Collecting focused on nonparasitic bees, based on the belief that their numbers would be more representative during the relatively short time available for fieldwork. Parasitic bees spend much of their time seeking host species nests instead of seeking pollen at flowers. Additionally, there were concerns about securing reliable species identification for some parasitic genera such as *Nomada.* Most bees collected were preserved. *Bombus* and *Apis* were not collected intensively as part of the study, although representative specimens of *Bombus* were collected and preserved. Parasitic bees were collected and preserved when present, but they are not considered in this paper. Most identifications were made by W. E. LaBerge, or by J. C. Marlin under the direction of LaBerge.

Because only two full years were available for collecting, the authors decided to focus their collecting on a manageable number of plants. Robertson's records were studied in an attempt to identify plants that were likely to collectively attract a large variety of bees. For example, spring-blooming *Claytonia virginica* and fall-blooming *Aster pilosus,* upon which Robertson reported 58 and 90 bee species, respectively, were singled out for special attention. Together, they were visited by about half of the bees that Robertson observed. *Prenanthes aspera* and *Lactuca canadensis* were not considered likely candidates, because Robertson observed only one common bee on each of them.

Sites for collecting were initially selected by looking for likely terrain or host plants. Frequently, suitable stands of flowers were found alongside the road or near it. Willows were often found along streambanks within 0.25

mile (0.4 km) of a bridge. Similarly, *Prunus* sp. and *Cercis canadensis* were often adjacent to roadsides. Open and partly wooded fields and hillsides occurred within easy walking distance of roads. Areas with railroads, abandoned roads, and winding streams provided habitat for numerous plants. Productive sites were revisited. When the weather was good, time spent driving across the study area was minimized in order to maximize collecting time.

We concentrated on 24 plant species that collectively bloomed during the entire growing season, were attractive to large numbers of species in a variety of genera, and were reasonably available for collecting. In total, 163 hours were spent collecting on the 24 plants, with a mean of 6.8 h/plant species and a range of 1.5-31 h/ plant species. For example, Marlin collected bees on these plant species at the following intensities: *Aster pilosus* for a total of 30 times over 13 d during two years; *Claytonia virginica*, 22 times on 10 d during two years; *Ipomoea pandurata*, 11 times on 8 d during two years; and *Aster novaeangliae* once for 2.5 h. Collections were made on an opportunistic basis at 43 other plants, seldom for more than a total of 30 min over the study period.

Robertson was meticulous in identifying and naming species, as well as in maintaining his collection. Most of the species names that he used are still valid or are readily updated. Many specimens from Robertson's collection were studied for generic revisions. The result is that the nomenclature of the collection is in reasonably good shape. In a few instances, there is some confusion between the species listed in his book and those in the collection, as with some species of *Hoplitis* and *Heriades.* There are also bees such as *Melissodes rustica* (Say), with which Robertson's *M. simillima* Rb. and *M. asteris* Rb. are synonymous. In other cases, such as *Andrena sayi* (Rb.), a modern revision found that the bees considered to be one species by Robertson actually belong to two species. *Dialictus admirandus* (Sandhouse) is unusual in that Robertson mixed it with at least four species. The fact that he kept only a reference collection makes it impossible to verify each entry to *Flowers and Insects,* yet the information for the vast majority of species appears to be reliable.

RESULTS

Allowing for taxonomic corrections and eliminating *Apis, Bombus,* and parasitic bees from consideration, this study considers 214 valid species collected by Robertson on all of the plants that he studied, and an additional 14 species found during the re-collection, making a total of 228 collected by either Marlin or Robertson. Marlin collected a total of 154 species. Of the 214 species collected by Robertson, 140 (65%), or all but 74, species were re-collected in the 1970s. Table 1 summarizes the results of the total collecting effort and the collections on the 24 intensively collected plant species.

Table 1. Number of bee species and collected at Carlinville, Illinois, USA, during 1884–1916 by C. Robertson, and during 1970–1972 by W. E. LaBerge and J. C. Marlin. This analysis excludes *Apis melifera, Bombus* spp., and parasitic bees.

	Total no. spp. in both studies	No. spp. 1884–1916	No. spp. 1970–1972	No. spp. unique to 1884–1916	No. spp. unique to 1970–1972	Robertson spp. re-collected (%)	Jaccard similarity index**	Sorensen similarity index**
Total no. bee spp. collected	228	214	154	74	14	65%	0.614	0.761
No. bee spp. on 24 selected plant species*	179	157	150	29	22	82%	0.715	0.883

* The present authors concentrated their collecting on 24 plant species on which Robertson found a relatively large number of species. Robertson collected on over 400 plant species.
**These indices are commonly used to measure the similarity of species in samples where the data include presence or absence. The indices equal one if similarity is complete, and zero if the sites or samples have

no species in common.

Most of the 74 species not re-collected were found by Robertson on relatively few of the 441 flowering plant species that he observed. For example, he found 21 of these bee species on only one of the 441 plant species, and seven other bee species were found on only two plant species. Robertson recorded 59 of the 74 species on fewer than 10 plant species, and 15 on between 10 and 22 plant species.

Robertson reported 157 species of bees on the 24 plant species upon which we subsequently concentrated. In total, 150 species were taken on these plants by Marlin, whose total included 128 species that were collected by Robertson. Thus, 82% of the species collected by Robertson on the 24 plants were re-collected on those plants about 75 years later.

The lack of quantitative data reported by Robertson limits our ability to make detailed statistical comparisons. A variety of similarity indices exist that measure the similarity of species in samples or at sites using only the presence or absence of the various species. The Jaccard index and Sorenson index are commonly used for this purpose. These indices equal one if similarity is complete, and zero if the sites or samples have no species in common. The Jaccard index is expressed as $C = j/(a + b - j)$, and the Sorenson index is $C = 2j/(a + b)$, where j is the number of species found common to both samples or sites, a is the number of species in sample A, and b is the number of species in sample B (Magurran 1988:95). For all bee species in the Carlinville resample, the Jaccard index value is 0.614 and the Sorenson index is 0.761. For bees on the 24 study plants, the Jaccard index value is 0.715 and the Sorenson is 0.883.

DISCUSSION

The Carlinville collections show a high degree of similarity, despite the passage of over 75 years. This is particularly true for the species collected on the 24 study plants. For comparative purposes, we calculated the similarity indices of live freshwater mussels collected at Henry, Illinois, in 1912 and 1966. The collections were made in the Illinois River, which had experienced a serious decline in water quality. The mussels, which have little ability to respond to changing water quality, declined from 24 to nine species during this time (Starrett 1971:386). The Jaccard index for these samples is 0.375 and the Sorenson index 0.545.

Much of the difference between the species collected by Robertson and those in our collection can be explained by host plant preferences. Some bees are generalists, obtaining pollen and nectar from a wide range of flowers. *Apis,* most *Ceratina,* and *Halictus* fall into this category, and are termed polylectic. Oligolectic bees forage for pollen on a limited number of related plants and may or may not show a similar preference for nectar sources. Monolectic bees generally exploit a single pollen source. Robertson provided a list of bees that he considered oligolectic (1926). Robertson (1925) and Stephen et al. (1969) discuss this topic. Bees are most likely to be found at their preferred pollen sources. This information, combined with Robertson′s designation of each bee′s relative abundance on host plants, provides a reasonable indicator of the likelihood of finding that species.

For example, Robertson found polylectic *Ceratina calcarata* Rb. on flowers of 47 plant species, including nine of the 24 plants resurveyed. It is reasonable to expect to re-collect such bees, barring a major change in that bee′s status. On the other hand, Robertson collected *Osmia albiventris* Cr. on only one plant species during his years of collecting, and it was not on one of the 24 plant species. Thus, it is no surprise that it was not recollected by us. *Cemolobus ipomoea* Rb. was found only on *Ipomoea pandurata* by Robertson, on which he listed it as abundant; he speculated that it was an oligolege. We collected this bee only on that plant. Today, this species is generally considered rare (Michener et al. 1994:156).

Fully 47 of the 74 bees species that we did not re-collect were found by Robertson on other than the 24 study plants. Thus, a majority of these bees did not show a preference for any of the plants on which our collecting was concentrated. An additional 11 bee species were previously observed by Robertson on only one of the 24 plants.

Information about a species′ relative abundance is also important when evaluating re-collection efforts. Cierzniak (1995:94) discussed the differences in bee fauna over a 10-year period in an agricultural area of western Poland. He pointed out that the differences in collected species in the samples often involved species that occurred infrequently in the area, and stated that confirming the occurrence often requires years of searching. Banaszak (1995*b:*18) also discussed the difficulty of finding rare species, especially those with insular sites where years of intensive search were needed to confirm their presence. Westrich (1996:7) pointed out that the European *Osmia dalmaica* has specialized habitat requirements and is known from only three Swiss cantons. No more than 6−10 females per year and site could be observed. In order to collect such a rare species, one must be in the right place at the right time.

Numerous factors influence whether or not a bee will be present at a specific plant when a collection is made. Among them are the presence of suitable nesting sites within flight range, the density of host plants, weather, and time of day. The emergence time of short-lived bee species is another critical factor. Thus, the mere presence of a host plant does not guarantee that all of its associated bees will be found.

Determining the relative abundance of a bee species, and especially whether it is truly rare, requires considerable study. For example, *Cemolobus ipomoea* was found by Robertson and Marlin only on *Ipomoea pandurata.* Any sampling effort ignoring this plant would most likely miss this bee. *Andrena alleghaniensis* is primarily an eastern bee. Robertson did not list it, but Marlin found a total of four specimens on three plants. Carlinville is at the edge of its range, which may expand or contract due to weather patterns, land management practices, and other considerations. It was probably absent or locally rare in the late 1800s. On the other hand, Robertson and Marlin each collected only one specimen of *Andrena lauracea* on *Sassafras variifolium* and *Prunus serotina,* respectively. Only two other specimens are known to science, both from Texas. It is reasonable to consider this species rare.

We did not collect 27 of the bee species found by Robertson on the 24 intensively surveyed plant species. Of these, Robertson observed 11 on only one of the plant species, with eight of those being recorded only as present. These bees could easily be present in the area, yet still be missed during the two years of re-collecting. The same is true for many of the species found on several of the 24 plants. At the other end of the spectrum, Robertson recorded *Melissodes nivea* on five of the 24 study plants, including *Aster pilosus,* where it was found frequently. We should have collected it if there was no change in its status. Another bee that we expected to collect is *Agapostemon splendens,* which Robertson found on four of the study plants. A specimen of this species collected at another site in central Illinois in 1965 is in the INHS collection. Thus, it was probably still in the area during our survey.

CONCLUSIONS

Although we expected changes in the composition and relative abundance of species comprising this diverse bee community, the Carlinville area bee fauna remained surprisingly intact between the late 1800s and 1972, when we resampled bees on 24 of the hundreds of plant species that Robertson originally surveyed. The faunal differences between Robertson's and our collections were largely restricted to rare bee species and to species usually found on other floral hosts upon which we did not collect. Thus, there was no evidence of a marked decline in the species composition of this rich bee community during the first seven decades of the past century, despite dramatic changes in land use and agricultural practices over much of the study area. It seems likely that the persistence of many species is directly related to the varied terrain near Carlinville. Although the relatively flat areas are intensively farmed and appear to provide little bee habitat, local landowners retained many other areas in woods, pasture, meadow, and other types of cover. As long as suitable amounts of host plants and such varied habitat remain, the associated bee species seem likely to persist.

Because of the work and meticulous records of Charles Robertson, the plants and flower-visiting insects of the Carlinville area in the late 1800s are well documented. The opportunity exists to undertake a new collecting and surveying effort involving local residents, botanists, and specialists on the other insects, including beetles, flies, butterflies, and wasps that Robertson observed. This third collecting effort could provide valuable insights for understanding resilience in guilds of pollinating insects and their floral hosts, as well as their response to rural anthropogenic changes over an unprecedented time period spanning more than a century.

RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article. To submit a comment, follow this link. To read comments already accepted, follow this link.

Acknowledgments:

The authors wish to acknowledge Vanessa Block, Jeffrey Brawn, James H. Cane, Michelle Garland, Chris Harris, George Krumins, Kenneth Robertson, Calvin and Cecelia Vonnahmen, Charles Warwick, Donald W. Webb, William Werner, Monte Wilcoxon, and Neal Williams for assistance and advice during the preparation of this manuscript.

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