Bees associated with Louisiana longleaf pine savannas

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BEES ASSOCIATED WITH LOUISIANA LONGLEAF PINE SAVANNAS

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Master of Science

in

The Department of Entomology

By
Chanda Sara Bartholomew
B.S., University of Kentucky, 2001
August 2004
I dedicate this thesis to my family, whose love, support, and encouragement has enabled me to get this far:

Frank & Gerrie Bartholomew  
  Julie Bartholomew  
  Orin Bartholomew  
  Ed Bartholomew  
  John & Doris Schneider

I would also like to dedicate this thesis to the memory of my grandparents and great-grandmother:

Frank & Charlotte Bartholomew  
  Billie E. Flynn

Finally, I would like to dedicate this thesis to the following individual, without his guidance as my undergraduate advisor, I would not have achieved my current success:

Dr. Kenneth V. Yeargan

“We are not free, separate, and independent entities, but like links in a chain, and we could not by any means be what we are without those who went before us and showed us the way.”

Thomas Mann

“Success is a science: If you have the conditions, you get the result”

Oscar Wilde (1854-1900)

ECOLOGY
The sun, the moon and the stars would have disappeared long ago, had they happened to be within the predatory reach of human hands.

Havelock Ellis  
(1859-1939)  
British Psychologist/Author
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ABSTRACT

Longleaf pine savannas are perhaps the most threatened ecosystems in North America. Despite a well documented and highly diverse flora, little has been published on insects in general and, in particular, on bees that provide the valuable service of plant pollination. Thus, the aims of this study were to: 1) survey bees found in two savanna types in southeastern Louisiana; and 2) contrast the diversity and species composition of these two savanna types. An ancillary goal was to contrast two collecting protocols for bees in the savanna habitat. Overall, a total of 3,407 bees were collected representing 125 species. Of these, there were two possible new species, 67 state records, and 23 range extensions. Upland savannas consistently showed higher richness and abundance than the wet savanna by about ten species and by many hundreds of individuals. Despite this, diversity statistics yielded no significant differences. Similarity indices between upland savanna sites were consistently more similar than to the wet savanna sites, suggesting greater compositional similarities within upland sites. Of the two collecting protocols compared, both were effective at collecting bees though pan traps showed a tendency to capture more species and individuals than malaise traps. There were several management implications of this research. First, a savanna in the early stages of restoration had a relatively high level of bee diversity suggesting pollinators are capable of rapid colonization or recovery in this ecosystem. Second, there was a trend toward increased bee abundance and richness after prescribed fires consistent with increased flowering after fires. Third, size of preserve appeared to have no effect on bee diversity. An important outcome of this study was creation of a checklist of bees with distributional and biological information for each species.
CHAPTER 1
INTRODUCTION
LONGLEAF PINE SAVANNAS

A savanna is a grassland ecosystem characterized by dominate warm season C_4 grasses and a discontinuous canopy (Frost et al. 1986; Platt 1999). In longleaf pine savannas, the overstory is mainly longleaf pine (*Pinus palustris* Mill.) and the understory contains a rich and diverse herbaceous and grassy layer (Walker & Peet 1983; Frost et al. 1986; Outcalt & Sheffield 1996). These savannas have high plant species diversity per unit area, and are among the most species-rich plant communities outside the tropics (Walker & Peet 1983; Walker 1993). Longleaf pine savannas vary from xeric sandhills to seasonally flooded flatwoods areas in peninsular Florida and along the southeastern Gulf Coastal Plain (Louisiana Natural Heritage Program 1987; Noss 1989).

Historically, savannas covered a significant portion of the southeastern United States. These communities originally ranged from southeastern Virginia south to central Florida and west into eastern Texas and may have covered as much as 60 million acres (Outcalt & Sheffield 1996). The extensive distribution of this unique ecosystem has been drastically reduced and is still declining (Outcalt & Sheffield 1996; Platt 1999). Estimates place the current distribution anywhere from 2% to 14% of its historical distribution (Hardin & White 1989; Noss 1989). Of the remaining longleaf pine ecosystems, most are second growth and heavily fragmented (Bridges 1989; Outcalt & Sheffield 1996).

Decline of longleaf pine savanna in the southeastern Gulf Coastal Plain has been mainly attributed to human interference. These savannas were used by early settlers for grazing livestock and were burned annually in late winter to increase abundance of new spring growth,
keep the range open, and suppress tick and chigger populations. Longleaf pine was used for timber and turpentine. Threats today include commercial and residential development, altered hydrology, fire suppression, and invasions by non-prairie species (Panzer 1988; Smith 1991).

Fires are required for longleaf pine savanna ecosystems to persist (Mutch 1970; Platt 1999). Studies of natural lightning cycles in the region have suggested that late spring and early summer fires were common before humans began their manipulation of the environment (Frost et al. 1986). These fires were quick and low to the ground, burning only the flammable litter that had accumulated since the last fire (Frost et al. 1986; Noss 1989). Fires ultimately kill all vegetation not fire resistant and stimulate growth and flowering of understory plants (Anderson et al. 1989; Howe 1994). Without fires, shrubs and non-fire resistant tree species increase and eventually displace most of the herbaceous plants (Louisiana Natural Heritage Program 1987; Outcalt & Sheffield 1996). Burning also increases species richness of herbs found in the understory (Folkerts et al. 1993). In addition, Whelan et al. (1980) found that the fauna tended to be more diverse and abundant in burned than in unburned areas.

**POLLINATION**

Of the estimated 250,000 species of modern angiosperms, over 90% are animal pollinated (Kearns et al. 1998). In longleaf pine savannas, roughly 70% of angiosperms are entomophilous or insect pollinated (Folkerts et al. 1993; Kearns & Inouye 1997). Pollinators visit these flowers in search of pollen and nectar. Insects collect pollen grains because they contain proteins, lipids, starches and sterols which are essential for development and survival (Wcislo & Cane 1996). Nectar is an energy-rich aqueous solution of sugars offered as a reward to pollinators (O’Toole & Raw 1991).
Mutualism between plants and pollinators is ancient, dating at least back to the Cretaceous period (Kearns & Inouye 1997). From the perspective of the plant, a successful pollinator is an animal that makes contact with the anthers and stigma, moves quickly between plants, and stays faithful to flowers of that species (Feinsinger 1983; Arroyo et al. 1985). Most plants have a wide range of pollinators, and most pollinators visit more than one plant species. However, not all of the pollinators that visit a plant are efficient pollinators (Bond 1994; Spira 2001). Over time, evolution has in some cases selected for traits that attract and maintain the most efficient pollinators, resulting in specialization to some degree (Feinsinger 1983; Bond 1994; Olsen 1997). This specialization can range from simple tubular corollas to bee-mimicking orchids.

A variety of threats interfere with mutualism of plants and their animal pollinators. These threats include habitat alteration, invasions of alien plants and animals, habitat fragmentation, and chemical poisoning by pesticides (Bond 1994; Spira 2001). Introductions of exotic pollinators also threaten native pollinator systems. Although important in agriculture, these introduced species (i.e. e. the European honeybee) potentially out-compete native pollinators (Kearns & Inouye 1997). Another potential threat is predation by the red imported fire ant (*Solenopsis invicta* Buren). This species attacks bee larvae and caterpillars (Spira 2001). Neff & Simpson (1997) reported that it was the only successful predator of adults of the bee *Andrena rudbeckiae* Robertson (Andrenidae).

A threat of major concern is habitat fragmentation. Increasing urbanization has reduced natural habitats to small patches, causing plant populations to become isolated in a sea of concrete and steel. Genetic diversity and fitness of these isolated plant populations may be reduced, rendering them vulnerable to local extinctions (Kearns & Inouye 1997; Schulke &
For pollinators, urban development and agriculture have significantly reduced the number of locations for nesting sites and wild patches of plants used for food and mating (Kearns & Inouye 1997). Fragmentation also reduces species richness and abundance of pollinator guilds. For some plant species, this means that the most effective pollinator may no longer exist in a particular fragment (Steffan-Dewenter & Tscharntke 1999). Despite potential harm that fragmentation can cause to pollinators and their host plants, preserving large tracts of land is difficult (Kearns & Inouye 1997).

Conversely, a recent study suggested that pollinators may not be as vulnerable to habitat fragmentation as previously thought (Donaldson et al. 2002). They found that pollinators were affected more by characteristics of habitat, such as types and numbers of plants present, rather than fragment size. The authors also found that species richness of bees, flies and butterflies were not affected by fragment size. However, abundance of certain species of bees and beetles were affected.

Effects these threats may have on plant-pollinator mutualisms are difficult to predict. Loss of a pollinator or two may have minimal effects if other pollinators fill the void (Spira 2001). On the other hand, loss of pollinators could be detrimental to plants that are self-incompatible, have a single pollinator, and/or propagate only by seeds (Kearns & Inouye 1997).

**BEES**

The largest and most important group of insect pollinators is bees (Hymenoptera: Apiformes). Bees can be generalists, specialists or cleptoparasites. Generalist bees are referred to as polylectic. Polyleptic species visit many plant species from different families to collect pollen for their larvae (Michener 1979; Wcislo & Cane 1996). Although polyleptic species visit many plant species, they tend to practice flower constancy. This occurs when a bee learns the
structure of a particular plant species and visits only that particular species while it is in bloom. Flower constancy is temporary (O’Toole & Raw 1991).

Specialists can be divided into two types: oligolectic or monolectic. Oligolectic species visit a few plant species within the same genus or within several related genera. Most oligolectic species tend to restrict their host plants to the same plant family. These bee species tend to have special modifications to aid in pollen collection and their life cycles tend to be univoltine and synchronized with that of their host plants (Michener 1979; O’Toole & Raw 1991; Wcislo & Cane 1996; Cane 2001). Monolectic species collect pollen from only one plant species (Michener 1979; Wcislo & Cane 1996). Most specialists tend to be oligolectic, and monolectic rarely occurs. Cleptoparasites are bees that invade nests of other bees and lay their eggs in the cells. Larvae develop on stored food of the host (Wcislo & Cane 1996).

Bees vary in their degree of socialization. They can be solitary, communal, quasisocial, semisocial, subsocial, primitively social, or eusocial (O’Toole & Raw 1991). Solitary bees are those in which the female builds a nest, and collects and stores food on her own (Wcilso & Cane 1996). A communal nest contains several females, but each female builds and provisions cells with no help from the other females. A quasisocial nest contains multiple mated females who help each other build and provision cells. This nest contains multiple cells in various stages of building and provisioning. A semisocial nest contains only a few mated females, has only a single cell being built and provisioned at a time, and the nest begins to show signs of labor division. A subsocial nest is one in which the female remains with her immature offspring, guarding and feeding them. She usually dies when her offspring reach maturity. A primitively eusocial bee nest contains an egg-laying queen and her worker offspring. The colony usually passes through solitary and subsocial stages first and is not usually perennial (O’Toole & Raw
1991). Eusocial colonies have one mated female, called a queen, whose sole purpose is to lay eggs. The offspring are unmated workers who feed and tend the larvae, forage, and protect the hive. These colonies are usually perennial. A well-known example of a eusocial bee is the honeybee (O’Toole & Raw 1991).

The oldest bees in the fossil record are from late Eocene Baltic amber (~56.5 million years ago). These bees are the more evolved long-tongued bees, suggesting that bees existed earlier than the late Eocene. The life cycle of bees is closely entwined with that of flowering plants, so bees probably arose at the same time or closely after angiosperms in the Upper Cretaceous (~145 million years ago) (Michener 1979).

Bees nearest relatives are sphecoid wasps. Bees differ from sphecids in that the larval diet shifted from insects to that of pollen (Michener 1979). Today, bees depend entirely on plants for their diet throughout their life cycles, and it is this trait that makes them effective pollinators (O’Toole & Raw 1991). Bees can be distinguished from their wasp ancestors by having branched hairs, which aids in pollen collection (O’Toole & Raw 1991; Wcislo & Cane 1996). In addition to pollen collection, some bees also forage for oils and nectar from plants (Wcislo & Cane 1996).

There are approximately described 20,000 species of bees, the vast majority of which are solitary, although some will nest in aggregations (O’Toole & Raw 1991; Wcislo & Cane 1996). Bees are often divided into two groups based on tongue morphology: long-tongued or short-tongued. These groupings are not necessarily monophyletic (Michener 2000). Long-tongued bees differ from short-tongued bees in that the two basal segments of the labial palpi are long and flattened, and the two apical segmented are shorter and cylindrical. In short-tongued bees the labial palpi have four cylindrical segments of equal length. Short-tongued bees tend to
forage on flowers with more open floral arrangements, like those found in the Asteraceae (Wcislo & Cane 1996). Short-tongued bees are in the families Stenotritidae, Colletidae, Halictidae, Oxaeidae, Andrenidae, Melittidae, and Ctenoplectridae. Long-tongued bees are larger, fly faster and have greater calorific needs. These bees tend to be more specialized on flowers with fused, tubular corollas, like those found in the Fabaceae (O’Toole & Raw 1991; Wcislo & Cane 1996). Long-tongued bees are in the families Fideliidae, Megachilidae, and Apidae.

Apiformes as a whole tend to be mostly diurnal, with daily activities greatly influenced by such factors as temperature, illumination thresholds, wind and precipitation (Michener 1979; Wcislo & Cane 1996). Most bees overwinter as post-defecated larvae. A few species can facultatively remain in diapause if conditions, such as drought, prevent their host plants from blooming (Wcislo & Cane 1996). Upon emergence, females mate, and for most species this will be the only mating. She carries enough sperm in her spermatheca to last all, or nearly all, of her reproductive life (Michener 1979). Females contain a mechanism whereby they control the sex ratio of their offspring. Bees, like most Hymenoptera, are haplo-diploid, which means that males arise from haploid or unfertilized eggs and females from diploid or fertilized eggs (Torre-Bueno 1989; O’Toole & Raw 1991).

Once she has mated, the female then proceeds to build her nest. Females of some solitary species nest in aggregations. These aggregations can be persistent or ephemeral and have some disadvantages, such as concentrating enemies in a local area (Wcislo & Cane 1996). Nest substrate preferences vary depending on the species. Substrate materials used by bees include soil, living or rotting wood, sandstone, plant or earthen materials, pre-existing cavities, snail shells, tunnels bored by other insects, tree cavities, pithy or hollow plant stems, and abandoned
rodent burrows. Once a nest site is chosen, some bees bring in other materials to refine their nests, such as mud, resins, pebbles, plant hairs, leaves and petals (Wcislo & Cane 1996; Cane 2001). A solitary bee nest consists of cells in which bees store a mixture of highly perishable pollen and nectar for the development of the larvae. To protect larvae and perishable food sources, females line cells with a waterproof secretion from their Dufour’s gland. The composition of the waterproof secretion varies depending on species (Michener 1979; Wcislo & Cane 1996).

Not all bees build nests. Cleptoparasitic bees invade nests of other bees and lay their eggs in completed or nearly complete cells. About 15% of genera or subgenera of bees contain at least one obligate parasite of other bees. These cleptoparasites will either aggressively enter the host nest or wait until the host has left before entering the nest. Once inside, the cleptoparasite will lay an egg in a concealed location within a cell. Once the egg has hatched, the cleptoparasitic larva kills the host larva and develops on the food stores of the host (Wcislo & Cane 1996).

Today, bees are most speciose in warm, xeric, temperate regions, such as deserts. Although containing a higher generic diversity, tropical regions have fewer overall species of bees than temperate regions (Michener 1979; Buchmann & Nabhan 1996; Wcislo & Cane 1996). For example, cleptoparasitic bees tend to be rarer in the tropics and more speciose in temperate regions (Wcislo & Cane 1996). In North America, regions with the richest bee faunas are the Sonoran and Chihuahuan deserts. Temperate grasslands tend to have richer bee faunas than tropical grasslands. However, bee faunas in northern grasslands are only moderate-sized (Michener 1979; Buchmann & Nabhan 1996).
Michener (1979) described a study done by Moldenke which examined bee faunas of the various bioregions of California. Moldenke found approximately 676 species in the southern chaparral areas, 668 species in the deserts (which includes the western part of the Sonoran), 589 species in the mountain forests, and 129 species on the coastal strip. Looking at faunal surveys in southeastern United States, Mitchell (1960, 1962) described 859 bee species for eastern United States. Michener (1947) listed 103 species for an upland savanna ecosystem near Hattiesburg, Mississippi.

Human activities affect bees, but we still are not completely sure how. Evidence of detrimental effects of fragmentation is widespread, but Cane (2001) stated that fragmentation may not affect bees. Instead, bees are more influenced by the characteristics of the fragment. If fragments contain suitable host plants and nesting substrates and materials, then bees may flourish in them. ‘Waste places’ such as hedgerows, field margins and embankments may be suitable bee habitats (Cane & Tepedino 2001). A more significant threat to bees may be introductions of non-native pollinators, specifically the European honeybee, *Apis mellifera* L. that can displace native pollinators through competition. Although good at pollinating some species of field crops, honeybees may not be as efficient as native pollinators (Kearns & Inouye 1997; Spira 2001). Effects of the above examples on bees are still not fully understood.

**JUSTIFICATION**

Longleaf pine savannas are one of the most threatened ecosystems in the United States, yet their entomological fauna is poorly known and understood. In Louisiana two longleaf pine savanna types can be found, upland savannas and wet flatwoods. Both of these savanna types are critical habitats for more state-rare species than any other ecosystem in the state, with many of these species being plants (Smith 1991). Frequent pollinators of these longleaf pine savanna
Although most pollinators in longleaf pine savannas are polylectic, there are a few oligolectic species (Folkerts et al. 1993). We know in deserts that greater than 60% of bee species are oligolectic, but we do not know anything about levels of specialization of bees in longleaf pine savannas.

The importance of bees to humans cannot be overstated. O’Toole & Raw (1991) state that 15% of our diet is derived from crops pollinated by bees, 15% of our diet is derived from meats and animal products fed by bee pollinated forage crops, and about a third of our diet is directly and indirectly dependent on bees. Regardless of their importance, estimates state that only approximately two-thirds of the world’s bee species have been named and described (Kearns & Inouye 1997). Nabhan (1996) observed that of the 16 federally protected plants in the southwestern United States, 14 of them still had unknown pollinators. How are we to devise a management strategy for such plants if their survival and pollination requirements are unknown? As a start, cataloging the pollinators of these plants is necessary to determine if pollinator deficiencies are factors contributing to their decline.

The global bee fauna is so poorly known that new species are still being described. This is the case for North America as well. Faunal surveys of bees will enhance knowledge of bee distributions and provide names and descriptions for unknown bees. Since we do not know the precise distributions of bees, knowing whether some are extinct, endangered or threatened is problematic.

**OBJECTIVES**

This project is part of ongoing research aimed at documenting insects inhabiting and dependent on longleaf pine savannas. The specific objectives of this study are:

1) to determine the optimal collecting method for bees in longleaf pine savannas;
2) to create a catalog of the bees found in wet pine flatwoods and upland longleaf pine savannas found in Louisiana; and

3) to compare and contrast the diversity of bees found in wet pine flatwoods with bees found in upland pine savannas.

Knowledge of bee composition in these ecosystems will give a broader picture of pollination processes. It will also provide baseline data that will be useful for future conservation and management strategies aimed at maintaining pollinator diversity and maximizing pollination rates.
CHAPTER 2
A COMPARISON OF COLLECTING METHODS FOR BEES IN LONGLEAF PINE SAVANNAS

Longleaf pine ecosystems are ecologically unique communities in the southeastern United States that are highly threatened. To preserve these communities, conservationists need to know what organisms are present and their biological attributes. Surveys represent a first step in this process. For some organisms this is easier than for others. Insects present challenges due to their diversity, mobility, and year to year fluctuations.

Because insects are so biologically diverse, one trapping method cannot be used for all of them. As a result, researchers test and modify collecting methods fairly frequently to determine which are best for the group of insects they want survey in a particular habitat. Various studies have been conducted looking at optimal collecting methods for certain groups (i.e. Liebherr & Mahar 1979, Carabidae in North America; Purcell & Elkington 1980, Cicadellidae in North America; Disney et al. 1982, Diptera in England). Juillet (1963) tested optimal collecting methods for flying insects in general, and determined that, of four methods used, each was good for only certain groups and each had its own advantages and disadvantages.

Malaise traps have traditionally been the method of choice for Hymenoptera (Matthew & Matthews 1971; Masner & Goulet 1981; Noyes 1989). Bee researchers have recognized that hand collecting provides better quality specimens and can generate host records and pollination data. This has become a preferred collection method for bees but it requires a considerable amount of effort relative to more passive collecting methods and can generate limited small samples. Furthermore, smaller bee species are often overlooked when hand collecting. A passive collecting method that works well for bees, especially oligolectic species, is pan traps (Leong & Thorp 1999).
With increasing interest in monitoring and surveying bees in conservation studies, determining an optimal collecting protocol is desirable. A group of bee researchers (Gretchen LeBuhn, Terry Griswold, Robert Minckley, Sam Droege, T’ai Roulston, James Cane, Frank Parker, Steve Buchmann, Vince Tepedino, Neal Williams, Claire Kremen and Olivia Messenger) developed a standardized collecting protocol to allow researchers to compare survey results. This protocol, the Bee Inventory (BI) Plot, is still in a preliminary stage. Researchers developing it have conducted various small experiments to devise the best method to collect the most bees with minimal time and energy. (For more information on this protocol and the research behind it refer to the following website: http://online.sfsu.edu/~beeplot.)

As a side project during the second year of my study, I compared the efficiency of two collecting protocols for bees in Louisiana longleaf pine savannas. One was the collecting protocol used throughout my study referred to as the malaise trap (MT) protocol. This protocol employed the use of a malaise trap, a flight intercept trap and hand collection. The second protocol was the BI Plot. This comparison was conducted at one upland longleaf pine savanna site (Sandy Hollow-South) over a four month period. A description of this site can be found in the Study Sites section of Chapter 3.

MATERIALS AND METHODS

Collection Methods

MT Protocol. Malaise traps are usually selected for their ability to collect many insects at one time with minimal effort. A Townes (1972)-style malaise trap can be fitted with pans below the median barrier, and used as a flight intercept trap as well. When an insect flying through the habitat hits the median barrier, it either flies up or drops down. If it flies up, it eventually finds its way into a cup (malaise trap). If it drops down, it falls into trays on the
ground (flight intercept trap). A combination malaise/flight intercept trap coupled with hand collection was considered an optimal protocol to collect bees in addition to other insect groups to be inventoried later by D. Prowell and C. Carlton (pers. comm.).

A Townes light-weight malaise trap (panel size: 178 cm long, 178 cm high in front and 110.5 cm high in back; John W. Hock Company, http://www.acceleration.net/jwhock) was placed in a one hectare plot at Sandy Hollow-South. Two rectangular plastic trays (81 cm x 17 cm x 10 cm) were placed below the median barrier for the flight intercept trap. An antifreeze solution was put in the trays and malaise trap cup to kill and preserve the insects caught. The solution consisted of a 1:2 mix of Prestone LowTox™ antifreeze and water with detergent added for a surfactant. Traps were run for one week periods, once every three weeks during 2003 on the following dates: 16 June, 10 July, 29 July, and 15 August.

Bees were hand collected by two individuals for 45 minutes on each trapping date. Bees were collected using a pocket net and killed in ethyl acetate killing jars. Plants that bees were collected on were recorded. Plants not easily identified to species in the field were collected for species-level determination. All plant species identified were verified by Diane Ferguson, curator of the Louisiana State University Herbarium. Plants have been deposited in the Louisiana State University Herbarium.

**BI Plot.** Within a one hectare plot, three 100-meter transects were marked. They were 25-meters from each other and/or the parallel edges of the plot. Along each transect, nine pans were placed at 10-meter intervals with 10 meters separating the end pans from the plot edge. Pans consisted of 27 white 6 oz. Solo™ brand bowls. Prior to placement into the plot, a third of these bowls were painted with Ace Hardware™ brand fluorescent yellow paint and a third with fluorescent blue paint. The remaining third were left white. In a small experiment done by Sam
Droege for the BI Plot, preliminary data showed that bowls painted with fluorescent paint (which reflects UV) caught significantly more bees than bowls without fluorescent paint ([http://online.sfsu.edu/~beeplot](http://online.sfsu.edu/~beeplot)). Pans contained a solution of one teaspoon of blue Dawn dish detergent used as a surfactant, diluted in a gallon of water. Pans were placed in the plot at approximately 9 am and removed in the afternoon at approximately 3 pm. In addition to pans, two individuals hand collected bees in the plot for 30 minutes in the morning after pan placement, and 30 minutes in the afternoon before pans removal. Hand collection time differed from the malaise trap protocol to fit that described by the BI Plot method. The MT protocol hand collection matched time periods at other research sites. Four samples were taken on the same dates as the MT protocol.

**Analysis**

An adjustment was required for the different durations bees were hand collected. Hand collection for the MT protocol totaled six hours and the BI Plot totaled seven hours (a hand collection sample was missed on the afternoon of 16 June). Hand collected bee totals for the MT protocol were multiplied by 1.17 to equate them to the BI Plot. Paired t-tests of means were calculated to determine if the two trapping protocols differed. Results were considered significant at the \( \alpha \leq 0.05 \) level of probability. Tukey-Kramer HSD was calculated to determine if there were differences among pan colors.

**Sorenson’s Index.** Sorenson’s Index was calculated between methods to obtain an estimate of similarity of species caught by each method. Sorenson’s Index is traditionally used to determine similarity between sites. It ranges from zero to one with sites of increasing similarity approaching one. It is calculated from the following formula:

\[
C_s = \frac{2j}{(a + b)},
\]
where \( j \) is the total number of species two sites have in common, \( a \) is the total number of species found in site a, and \( b \) is the total number of species found in site b (Magurran 1988). To make comparisons of the methods, each method was substituted for site in the formula.

**RESULTS AND DISCUSSION**

The MT protocol appeared to be inferior to the BI Plot at collecting bees (Table 2.1). The BI Plot produced nine additional species of bees and 1.5 times as many individuals compared to the MT protocol. The malaise trap captured 29 species and 137 individuals whereas the BI Plot captured 38 species and 184 individuals. Pooled totals for the two protocols, however, indicated differences were not significant for bee species captured (\( t = -1.82, df = 3, p = 0.16 \)) or for individuals captured (\( t = -1.23, df = 4, p = 0.28 \)).

<table>
<thead>
<tr>
<th>Table 2.1. Number of species and individuals collected by two bee collecting protocols.</th>
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<tr>
<td>Malaise Trap Protocol</td>
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<tr>
<td># of Species</td>
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<td>------------------------</td>
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<tr>
<td># of Species</td>
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<td># of Individuals</td>
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The MT protocol contained a component, the flight intercept trap, which was the least effective of all the methods tested at collecting bees (Table 2.1; Appendix A). This was expected because bees tend to fly up when they encounter an object. In a previous study comparing flight intercept traps with malaise traps, twice as many individual insects were collected in malaise traps, and flight intercept traps were found to be ineffective for collecting Hymenoptera (Noyes 1989).

To further compare trapping methods, I removed the flight intercept trap and hand collection data, and tested differences between the malaise trap and pans alone. Although pans alone did not catch significantly more species than the malaise trap (\( t = -1.216, df = 3, p = \))
pans collected a significantly higher number of individuals ($t = -4.009$, $df = 5$, $p = 0.0092$). This suggests that pans were more effective at attracting bees than the malaise trap.

Within the BI Plot, pan color was examined for differences in attractiveness to bees. White pans were found to catch significantly fewer species ($F = 15.39$, $df = 2, 9$, $p = 0.0012$) and individuals ($F = 10.51$, $df = 2, 9$, $p = 0.0044$) than either blue or yellow pans. White pans contained no fluorescent paint suggesting fluorescence is an attractant. These results agree with those found by Sam Droege in his study of bowl catches with and without fluorescent paint (http://online.sfsu.edu/~beeplot). All species captured in white pans were also captured in the blue and yellow pans. Elimination of white pans in favor of fluorescent colors would probably result in higher bee catches in Louisiana savannas. Despite this fact white pans will likely remain a part of the BI Plot because they have been found to attract oligolectic bee species in California (Leong & Thorp 1999).

Sorenson’s similarity index was calculated to determine if there was overlap among the species collected in each method. It was found that pans were least similar to hand collection. The malaise/flight intercept trap was also dissimilar to hand collection, although not as much. This indicates that a portion of the bees collected by each method probably represent different subsets of the overall bee fauna. Given this, pans or malaise traps should be used in combination with hand collection to obtain a more complete sample of the bee fauna in the habitat.

I became aware of the BI Plot mid-way through my study and results may have been compromised if I had chosen to switch from the MT protocol to the BI Plot. Thus, this small scale experiment was conducted to determine whether the use of the MT protocol compromised my results by missing a component of the bee fauna. Although pan trapping appeared to be slightly superior to malaise trapping, over time most bee species captured in the pan traps were
also collected in the malaise trap. I could not test whether pan traps ultimately capture all species found in the malaise trap because I did not extend the pan trap study over a long enough time period. Results of the comparison of protocols suggest the malaise trap provided a reliable indication of the bee fauna though the BI Plot might have produced larger numbers of individuals.

There are pros and cons of each protocol. The MT protocol requires considerably less effort than the BI Plot. Traps are easy to assemble, do not require designation of transects and plot measurements, and once in place, will last a full season. A negative aspect is that malaise traps are more expensive than pans (~$187 per trap from John W. Hock Company). Pans, however, have an advantage over malaise traps in terms of quality of specimens. The necessity of using a preservative (antifreeze) tends to produce greasy specimens that make distinguishing hair colors difficult. Conversely, pans alone tend to catch a biased subset of bees. In a study of creosote bush pollinators, pans were found to poorly represent the hand netted bee fauna (Cane et al. 2000). The following reasons for this disparity were suggested. First, bees forage in the horizontal stratum of their preferred host. If pans are not at the same height as preferred flowers, bees may not see the pans. Second, pans may simply be less attractive to bees than flowers (Cane et al. 2000).

In summary, it was found that the malaise trap protocol and the BI Plot are effective in capturing bees in Louisiana longleaf pine savannas. Because there is a need to standardize inventory methods for conservation, and bee experts have developed and agreed upon the BI Plot, that method should probably become the standard collecting method for bees. However, if research is focused on multiple groups of insects such as beetles, parasitic Hymenoptera, and
grasshoppers, the MT protocol would simultaneously satisfy requirements for collection of bees and other groups.
CHAPTER 3

BEES IN A WET PINE FLATWOODS AND THREE UPLAND LONGLEAF PINE SAVANNAS

Cataloging insects in particular habitats is not a new concept. Researchers have been surveying insects in North America for nearly a century (e.g. Leonard (1926), insects of New York; Graenicher (1930), bees of Miami, Florida). There is, however, renewed interest in surveying insects because of increased conservation awareness. Because bees are an important group of insects, many surveys of bees have been conducted in various habitats, but the vast majority of habitats have not been surveyed. The few surveys completed during the first half of the twentieth century could potentially compliment those completed recently. By repeating the initial survey years later, these checklists can be used to determine if anthropogenic effects have influenced the bee fauna in a particular habitat (Marlin & LaBerge 2001).

A famous survey of bees was undertaken by Charles Robertson at the beginning of the twentieth century in Carlinville, Illinois (Robertson 1929). In this survey, Robertson recorded observed visitors to flowers over a 33 year period. This survey provided the first extensive host association records for many bee species, and also provided descriptions of many new species of bees. Marlin & LaBerge (2001) repeated this survey at Carlinville, Illinois 75 years later, and compared it to Robertson’s original study. This second study was restricted to only 24 plant species. When completed they found that the bee fauna of the region had not changed significantly, despite changes in land use and agricultural practices.

Bee surveys undertaken in habitats similar to my study include the Minnesota prairies (Reed 1995), the Florida Everglades (Pascarella et al. 1999), the Chicago region (Pearson 1933), Mississippi savannas (Michener 1947; Forrest and Perry Counties) and Louisiana (Merritt 1978;
Calcasieu Parish). Michener (1947) conducted his survey in a savanna similar to Louisiana savannas, and, thus, it serves as a rough guide to the bee fauna a half century ago.

No comprehensive recent surveys of bees in longleaf pine savannas have been conducted and none have ever been done in Louisiana savannas. As a result, my research was undertaken to fill that gap. Specific goals were to determine the bee species that frequent savannas, and, thus, characterize the bee fauna, determine seasonality of bees, and document host plants used by bees. Through a literature search of bee distributions and biology, ancillary goals were to document regional affinities of the fauna, new state records, range extensions, and notable, rare and unusual species.

STUDY SITES

Abita Creek Preserve

Abita Creek Preserve (hereafter referred to as Abita Creek) is a wet pine flatwoods located in St. Tammany Parish in southeastern Louisiana. The preserve is owned by The Nature Conservancy and totals 338 hectares. It contains numerous plants considered rare, threatened or endangered by the Louisiana Natural History Program, such as the federally endangered Louisiana quilwort (Isoetes louisianensis Thieret). Abita Creek is managed through selective timber harvests and prescribed burns (The Nature Conservancy 2003). Soils of Abita Creek are mainly fine sandy loams of the Stough, Myatt and Prentiss series. The presence of hydric soils leads to flooding or water saturated soils for extended periods of time (Soil Conservation Service 1990a; Latimore Smith, pers. comm.).

Sandy Hollow Wildlife Management Area

Sandy Hollow Wildlife Management Area (hereafter referred to as Sandy Hollow) is an upland savanna located in Tangipahoa Parish in southeastern Louisiana. Sandy Hollow is
divided into two parts separated by a road (LA 10) and farmland (Fig. 3.1). The section located north of LA 10 is referred to as Sandy Hollow North (Sandy Hollow-N) and the section to the south of LA 10 is referred to as Sandy Hollow South (Sandy Hollow-S). These two sections were considered separate sites because of the distance and the inhospitable habitat separating them. Although little is known about bee foraging ranges, most solitary bees are thought to travel only a few hundred meters (Goulson 2003). A distance of 5.5 kilometers separating traps is sufficient to consider these two parts as separate sites.

Sandy Hollow is owned by the Louisiana Department of Wildlife and Fisheries, and is located about 10 miles northeast of Amite, Louisiana. In total it is 1496 hectares, with about 300 hectares in the southern tract. It is characterized by rolling hills, and soils that are of the Tangi-Ruston-Smithdale association. These soils are silt and fine sandy loams and are well-drained (Soil Conservation Service 1990b; Latimore Smith pers. comm.). Sandy Hollow is managed for upland game birds (i.e. quail and doves), thus, hunting is allowed (Louisiana Department of Wildlife and Fisheries 1993). It is managed with prescribed burns, and was burned annually in the winter up to a few of years ago. Currently, large sections are burned annually during the winter and biennially during the growing season (Jimmy Stafford pers. comm.).

**Camp Whispering Pines**

Camp Whispering Pines (hereafter referred to as Whispering Pines) is owned by the Southeast Girl Scout Council and has been managed as a long term site of longleaf pine restoration since the late 1960s (Noel 1996). This 200 hectare tract is undergoing restoration through the guidance of William Platt at Louisiana State University. Like Sandy Hollow, it has a rolling topography, as well as the well-drained Tangi-Ruston-Smithdale silt and fine sandy loam.
soils (Soil Conservation Service 1990b; Noel 1996). It is managed through biennial growing season burns conducted mainly during April and May.

Fig. 3.1. Map of Sandy Hollow Wildlife Management Area. Sandy Hollow-N is the larger, northern tract, and Sandy Hollow-S is the smaller tract to the south. Trap locations are marked with stars.
MATERIALS AND METHODS

Collection Methods

Malaise/Flight Intercept Traps. Four years of sampling were undertaken in four longleaf pine savanna sites, Abita Creek, Sandy Hollow-N, Sandy Hollow-S, and Whispering Pines. My study was conducted during 2002 and 2003. Two years prior to this, Prowell and Carlton sampled at Abita Creek, and these samples were processed and included in my study. Because of this extensive previous sampling at Abita Creek, more effort was placed on the upland savanna sites in my study.

1999-2001. Six Townes light-weight malaise/flight intercept traps (described in Chapter 2) were placed in two plant communities in Abita Creek (Fig 3.2). Three traps were placed in a thickly wooded community of slash pine and the other three traps were placed in an open grassy, forb community. Traps were run simultaneously for one week periods, once per month. During the first year (May 1999-April 2000) ten samples were taken on the following dates: 19 May, 16 June, 14 July, 11 August, 8 September, 6 October, 3 November, 16 December, 29 March and 18 April. During the second year (June 2000-May 2001) nine samples were taken: 6 June, 6 July, 1 August, 31 August, 29 September, 26 October, 1 December, 27 March and 1 May. All sites were burned on 2 May 2000 between the two years of sampling.

2002. During the third year, three malaise/flight intercept traps were placed at Abita Creek in open grassland sites. Three traps were also placed at Sandy Hollow-N. Traps were run for one week periods. At Abita Creek the following six samples were taken on the following dates: 17 May, 12 June, 10 July, 7 August, 6 September and 11 October. The following six samples were taken at Sandy Hollow-N: 10 May, 5 June, 3 July, 31 July, 30 August and 27 September. Tropical Storm Isidore came ashore in Louisiana on 24 September 2002 and
damaged one flight intercept trap at Sandy Hollow-N. As a result, only a malaise trap sample was collected from that site for that date. The following week (3 October 2002) hurricane Lili delayed running of the Abita Creek traps by one week. A prescribed fire at Abita Creek in the area of one trap took place 23 April 2002.

Fig. 3.2. Trapping sites (stars) at Abita Creek Preserve.

2003. During the fourth year two malaise/flight intercept traps each were run at Sandy Hollow-N, Sandy Hollow-S (Fig. 3.1), and Whispering Pines (Fig. 3.3). Traps were run simultaneously for one week periods. Eight samples each were taken from Sandy Hollow-N, Sandy Hollow-S, and Whispering Pines on the following dates: 5 May, 27 May, 16 June, 10 July, 29 July, 15 August, 12 September, and 1 October. Additional samples were taken on 17 April and 24 October at Sandy Hollow-N and Whispering Pines. An impending prescribed burn
Fig. 3.3. Trapping sites (stars) at Camp Whispering Pines. Arrow indicates movement of trap due to a fire after four collections.
postponed the placement of traps at Sandy Hollow-S and dog trials forced early removal after 1 October. A malaise trap sample was not taken at Whispering Pines for the 17 April sample date as well as at Sandy Hollow-S for the 12 September sample date. Sandy Hollow-N was burned just prior to trap placement on 17 April 2003. Sandy Hollow-S was burned sometime between 17 April and 5 May 2003, when the traps were placed at this site. Whispering Pines was burned 27 May 2003.

**Hand Collecting.** Hand collecting was added to the sampling methodology in the third year to obtain host plant records, collect species that possibly avoid traps, and obtain good quality specimens.

**2002.** Two individuals collected bees for 90 minutes at each savanna on each trap sample date for a total collection time of three hours (i.e. three hours at Sandy Hollow-N and three hours at Abita Creek). Bees were collected using a pocket net, killed in ethyl acetate killing jars, and placed in vials with host plant data recorded. Any plants not easily identified to species in the field were collected and pressed for species-level determinations.

**2003.** Hand collecting in the fourth year was done the same as for the previous year with the exception of the length of time spent collecting. Forty-five minutes were allocated to hand collecting in each savanna (Sandy Hollow-N, Sandy Hollow-S, and Whispering Pines) per sample date for a total time of 90 minutes each. Specimens of unknown plants were once again collected and processed for identification.

**BI Plot.** The BI Plot was conducted at Sandy Hollow-S, and these data are included here. Details of this method were given in the Materials and Methods section of Chapter 2.
Identifications

All bee identifications were made by the author and verified or corrected by Terry Griswold and Harold Ikerd of the USDA Bee Lab in Logan, Utah. Classifications follow that of Michener (2000). Voucher specimens have been deposited in the Louisiana State Arthropod Museum. All plant species identifications were verified by Diane Ferguson, curator of the Louisiana State University Herbarium. All plants have been deposited in the Louisiana State University Herbarium.

Data Analysis

Traps within sites were considered subsamples of sites to obtain a broader representation of each site. Thus, for all analyses, traps within sites were pooled.

Species Accumulation Curves. Species accumulation data and estimates were generated by the computer program, EstimateS (Colwell 2001). Species accumulation curves illustrate the accumulated total of species or individuals as a function of collection effort or accumulated individuals. Eventually the rate of addition of new species slows and the curve reaches an asymptote, suggesting the total number of species in a habitat has been approached. EstimateS was used to generate estimates of species diversity based on the number of species collected and their abundance. The estimate used was the abundance-based coverage estimate (ACE). ACE estimates species richness based on rare species with fewer than ten individuals (Colwell 2001).

Estimated Sampling Effort. Because multiple collecting methods were used, and durations of collecting (i.e. years) differed, an estimate of sampling effort was calculated. Using data from Chapter 2, where all three collecting methods were used simultaneously, the average number of species collected per MT/FIT trapping week was 7.25 species, per 1.5 hours of hand
collection was 7.25, and per 27 pans was 14.5. Using relative species catch, 1.5 hours of hand
collection was considered equivalent to one MT/FIT trapping week and one BI Plot sample (27
pans) was equivalent to two MT/FIT trapping weeks. This generated an estimate of overall
effort in trapping weeks.

Sorenson’s Index. The Materials and Methods section of Chapter 2 contains the formula
and calculation for this index.

RESULTS

Faunistic Data

Over the course of four years of collecting at four sites, 3,407 bees representing 125
species were collected (Table 3.1; see Appendix B for annotated checklist). Six families of bees
were represented: Colletidae (9), Andrenidae (12), Halictidae (34), Melittidae (1), Megachilidae
(29), and Apidae (40). Most of these families were represented at each site (see Appendix C for
list of the species collected by site). Of these species, 67 were new state records (Appendix D).
Two possible new species were collected from the genera *Hylaeus* (Colletidae) and *Coelioxys*
(Megachilidae). The most abundant and diverse genus was *Lasioglossum*. Twenty-three species
from 3 subgenera of this group of small halictids were collected. Thirteen species of
cleptoparasitic bees (parasites of other bees), representing eight genera were collected. Hosts of
six of these species were also collected. Eleven confirmed oligolectic species were collected
(18% of those with known biology). Most of these species were specialists on Asteraceae, but
specialists of *Callirhoe*, *Hibiscus*, and *Ipomoea* were also present (Appendix D). The majority
of host specific bees were restricted to or biased toward upland sites (nine of eleven species).
Many of these bees tended to be seasonally restricted to either spring (e.g. *Andrena rudbeckiae*
Robertson, *Diadasia afflicta* (Cresson), *Melitoma taurea* (Say), *Melissodes wheeleri* Cockerell)
or fall (e.g. *Colletes americanus* Cresson, *Andrena accepta* Viereck, *Melissodes boltoniae* Robertson, *M. dentiventris* Smith) to coincide with host flowering.

### Table 3.1. Summary of diversity of bees and sampling effort in four savanna sites. (ACP=Abita Creek, SHN=Sandy Hollow-N, SHS=Sandy Hollow-S, SH=Sandy Hollow, CWP=Whispering Pines, ACE=Abundance-based coverage estimate)

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<td><strong>Individuals</strong></td>
<td>230</td>
<td>415</td>
<td>317</td>
<td>962</td>
<td>889</td>
<td>540</td>
<td>1429</td>
<td>589</td>
<td>2018</td>
<td>427</td>
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<td>53</td>
<td>40</td>
<td>83</td>
<td>54</td>
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<td>79</td>
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<td><strong>MT/FIT</strong></td>
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<tr>
<td><strong>Trapping Weeks</strong></td>
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<td>54</td>
<td>18</td>
<td>132</td>
<td>18</td>
<td>20</td>
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<td>14</td>
<td>52</td>
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<td><strong>HC Hours</strong></td>
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<td>18</td>
<td>18</td>
<td>15</td>
<td>33</td>
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<td>108</td>
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<tr>
<td><strong>Estimate of Effort (Trapping Weeks)</strong></td>
<td>60</td>
<td>54</td>
<td>30</td>
<td>144</td>
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<td>31</td>
<td>91</td>
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<td>265</td>
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From a biogeographic perspective, the fauna is clearly eastern in its affinity (Appendix D). Forty-nine percent of the species with known distributions occur throughout eastern North America. A smaller proportion are restricted to the southeastern (19%), southern (5%), central (5%), northeastern (2%), and coastal (2%) United States. Several species are broadly distributed across North America (17%) and one, the honeybee, is exotic and globally distributed. Louisiana collections represent major range extensions for 10 species (Appendix D). Major range extension was applied here to species extending their ranges to Louisiana from the west or
Minor range extensions, small westward extensions of primarily eastern or southeastern species, were documented for 13 species.

With regard to rarity or densities of bees (Appendix D), the two types of savannas had similar percentages of rare, common, and very common species. Upland sites contained more abundant species (16%) compared to the wet site (4%). The wet site had more bees in the uncommon category (20%) than did upland sites (10%).

Habitat data are known for about one-third of the species (Appendix D). Sixteen species exhibit preferences for sandy soils. Of these, five species showed significant biases toward upland sites (four species were only found at upland sites) and none were biased toward the wet site (Appendix C).

**Overall Diversity**

Sampling effort was greatest at Abita Creek (144), followed by Sandy Hollow (91), and least at Whispering Pines (30) (Table 3.1). Even though Abita Creek had the most collecting effort, Sandy Hollow contained the most species. It was found that upland savannas in general had higher species richness and abundance than the wet savanna when effort was considered.

**Abita Creek.** After three years of collecting, a total of 962 bees representing 83 species were collected from Abita Creek (Table 3.1). The decreased catch during the third year is likely a consequence of reduced collecting effort. The species accumulation curve of the observed data levels off somewhat over the course of three years, but has not yet reached an asymptote (Fig. 3.4). The ACE estimate suggests this site has a total of about 110 bee species (Table 3.1). If accurate, there are approximately 30 more species frequenting Abita Creek.

Bee species at Abita Creek increased in number during the spring, generally peaked during June and July, and tapered off during the fall (Fig. 3.5a). The number of individuals
collected at this site showed a similar trend, with peak numbers during June and July (Fig. 3.5b). In both figures of seasonality, a noticeable peak occurred early during the season of the second year that was not present during the other two years of collection. One month prior to this June 2000 sample, all sites at Abita Creek were burned. This observed increase in bee species and individuals may be a consequence of increased foraging activity as a result of the fire. Even two months after the fire, the number of individual bees was nearly twice that of the samples collected during the previous year without a fire (Fig. 3.5b). Increased numbers of bee species were also observed during 2002, when compared to 1999. A portion of the sites were also burned just prior to my collecting season during 2002. This higher number of bees during 2001 and 2002 could reflect higher numbers of flowers due to the growing season fire (Platt et al. 1988). Bees may also be building up in numbers of individuals and species as the savanna advances in the restoration process.

Sandy Hollow. Two years of collecting at Sandy Hollow-N yielded 1,429 bees and a total of 80 species (Table 3.1). During one season of collecting, 589 individual bees representing 64 species were collected at Sandy Hollow-S (Table 3.1). When the two years of collections at Sandy Hollow-N are pooled with the single season of collection at Sandy Hollow-S, a total of 2,018 individuals of bees representing 94 species were collected (Table 3.1). The species accumulation curve for Sandy Hollow indicated that bee species were still accumulating (Fig. 3.4) and the ACE estimate placed total diversity at around 125 species (Table 3.1). Sandy Hollow-N and Sandy Hollow-S exhibited similar increasing curves. Both years of collecting showed the highest number of species occurred during the spring through July followed a decline during August. This was then followed by a slight rise during the fall in 2003 sites (Fig. 3.6a). The peak during July corresponds to an increase in the abundance of
*Lasioglossum (Dialictus)* spp. Abundance of individuals and species richness follow a similar pattern with higher overall numbers collected during 2002 (Fig. 3.6b). Once again, the peak during July corresponds to a large number of individuals of *Lasioglossum (Dialictus)* spp., particularly *L. (D.) coreopsis* (Robertson). Seasonality differed somewhat at Sandy Hollow-S in that there was a noticeable peak during spring, but a decline during June through July when Sandy Hollow-N and Abita Creek had relatively high numbers (Fig. 3.6). Sandy Hollow-S was extremely high in flowering plants, particularly *Rudbeckia hirta* L., during May, which may explain the high numbers of bees. As in other sites there was a slight increase during early fall except at Sandy Hollow-S.

![Species accumulation curves of Abita Creek (ACP), Sandy Hollow-N (SHN), Sandy Hollow-S (SHS), Sandy Hollow (SH), and Camp Whispering Pines (CWP).](image)

*Fig. 3.4.* Species accumulation curves of Abita Creek (ACP), Sandy Hollow-N (SHN), Sandy Hollow-S (SHS), Sandy Hollow (SH), and Camp Whispering Pines (CWP).
Whispering Pines. From a single season of collection, 427 individual bees representing 59 species were collected from Whispering Pines (Table 3.1). The species accumulation curves...
indicated that more bee species remain to be collected (Fig. 3.4). This would be expected for a single year of sampling. The ACE estimate peaks at around 80 species, suggesting 20 more species remain to be collected (Table 3.1). The seasonality graph indicates an undulating pattern of species richness throughout spring and fall (Fig. 3.7). Peak abundance of individuals occurs during late summer, in contrast to Sandy Hollow. This pattern may be indicative of management resulting in greater flowering during late summer.

**Species Composition Comparisons Between Sites**

The composition of bees collected at individual sites that were shared with all sites ranged from 40-55% (Appendix C). Species composition patterns are probably related to collecting effort. As effort increased from Whispering Pines to Abita Creek (Table 3.1), the number of species shared with other sites decreased and the number of unique species increased.

Sorenson’s similarity values show a tendency towards a higher similarity between upland sites than between upland and wet sites (Table 3.2). Averages of these values better illustrate this point (Table 3.3). In addition, there is year to year variation at Abita Creek, with the first year (1999-2000) being more distinct than subsequent years. A prescribed burn occurred between the first and second year, and this could have had a small homogenizing effect on the bee fauna.

**DISCUSSION**

In this study, 125 species of bees were collected from among four longleaf pine savanna sites in southeastern Louisiana. Based on a limited number of faunal surveys undertaken worldwide, Michener (1979) predicted that faunal lists obtained from local sites in the eastern United States would have no more than 300 species of bees. However, Michener conceded that exceptions of higher numbers of bee species may occur in more southerly locations, and in larger
survey areas. Given that my sites are not particularly large survey areas, my collection fits this prediction.

a)

![Graph showing seasonal phenology of Sandy Hollow bee richness](image)

b)

![Graph showing seasonal phenology of Sandy Hollow bee abundance](image)

Fig. 3.6. Seasonal phenology of Sandy Hollow bee richness (a) and abundance (b).
Fig. 3.7. Seasonal phenology of Whispering Pines bee richness and abundance.

Table 3.2. Sorenson’s similarity values between bee collecting sites. (ACP1=Abita Creek 1999-2000; ACP2=Abita Creek 2000-2001; ACP3=Abita Creek 2002; SHN1=Sandy Hollow-N 2002; SHN2=Sandy Hollow-N 2003; SHS=Sandy Hollow-S 2003; CWP=Whispering Pines 2003)

<table>
<thead>
<tr>
<th></th>
<th>ACP1</th>
<th>ACP2</th>
<th>ACP3</th>
<th>SHN1</th>
<th>SHN2</th>
<th>SHS</th>
<th>CWP</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACP1</td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>ACP2</td>
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<tr>
<td>ACP3</td>
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</tr>
<tr>
<td>SHN1</td>
<td>0.44</td>
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<td>0.53</td>
<td>1</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>SHN2</td>
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<td>0.48</td>
<td>0.69</td>
<td>1</td>
<td></td>
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<tr>
<td>SHS</td>
<td>0.47</td>
<td>0.67</td>
<td>0.56</td>
<td>0.66</td>
<td>0.68</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>CWP</td>
<td>0.51</td>
<td>0.63</td>
<td>0.57</td>
<td>0.66</td>
<td>0.68</td>
<td>0.62</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 3.3. Means (± SE) of Sorenson’s similarity values within and between the three savannas.

<table>
<thead>
<tr>
<th></th>
<th>Abita Creek</th>
<th>Sandy Hollow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abita Creek</td>
<td>0.57 ± 0.05</td>
<td></td>
</tr>
<tr>
<td>Sandy Hollow</td>
<td>0.53 ± 0.02</td>
<td>0.68 ± 0.01</td>
</tr>
<tr>
<td>Whispering Pines</td>
<td>0.57 ± 0.03</td>
<td>0.65 ± 0.02</td>
</tr>
</tbody>
</table>
Comparisons of my study with others from grassland sites in the eastern United States (i.e. Michener 1947; Reed 1995; R. Jean and P. Scott unpublished) provide insight into bee diversity of Louisiana longleaf pine savannas. Michener (1947) surveyed two savanna sites southeast of Hattiesburg, Mississippi. Sampling was conducted over an 18 month period, presumably by netting. Reed (1995) surveyed the insect fauna in restored and native prairies in Minnesota. This study was conducted over a three year period, from late May until Late September. R. Jean and P. Scott (unpublished) surveyed six sandy black oak savanna sites in northern Indiana and Illinois over several years.

Comparisons with these studies indicate that bee faunas in savannas are less similar with distance between sites and latitudinal differences. Michener (1947) was at the same latitude as Louisiana, only about 125 miles away, and was the most similar to my sites. He collected a total of 104 species. My study collected about 20 more species of bees than Michener (1947). However, because of different sampling methods and efforts, higher diversity in Louisiana cannot be assumed. Forty-five bee species were shared between the two surveys. Overall Reed (1995) collected 127 species of bees, which is similar to the number collected in my study. Between the two studies, however, only 28 species were shared. This comparison suggests a great deal of species turnover between what appear to be similar habitats from plant structural and diversity perspectives. R. Jean and P. Scott (unpublished) collected 224 species of bees, and 51 species were shared with Louisiana savannas. Both the Minnesota and Indiana/Illinois studies are many hundreds of miles away and at higher latitudes than the Mississippi study and the bee faunas are less similar to Louisiana. Also, one is a savanna and the other is a prairie, yet they are nearly equally dissimilar to Louisiana. Habitat category seems not to be as relevant as latitude and distance.
The importance of latitude and distance was also evident in a comparison with another survey of bees in Louisiana. Merritt (1978) sampled bees along roadsides throughout Calcasieu Parish in southwestern Louisiana on weekends over an 18 month period from April 1973 to September 1974. Bees were collected by hand net between 7 am and 2 pm. Calcasieu Parish soils are predominantly sand and marl, and are divided into two vegetation types: prairie and longleaf pine. Merritt recorded a total of 38 bee species. Of these, 27 were shared with those of the current study suggesting rather similar faunas in eastern and western Louisiana. The recovery of few bees by Merritt may have been due to the fact that only small patches of grasslands remained even 30 years ago, and the patches were too small to maintain significant bee numbers. Also, Merritt did not report any of the more difficult to identify species from genera such as *Lasioglossum*, which were found to contribute significantly to overall diversity in my study.

Bees are most diverse in the xeric regions of the world (Michener 1979). In the United States, these regions include deserts of the southwest and California. In fact, certain desert regions in the southwest contain over 600 bee species. Northern and more humid prairie regions only contain moderate-sized bee faunas. Tropical regions, although not well surveyed, appear to contain the poorest bee faunas. Longleaf pine savannas of the southeastern United States probably rank within the moderate-sized bee fauna group. Although a total of 125 bee species was collected from the four longleaf sites in Louisiana, the actual fauna is likely to be closer to 200 species, when considering the ACE estimates and limited overlap with Michener (1947). The missing species from Louisiana are most likely uncommon or rare species such as cleptoparasitic and oligolectic bees. For example, a literature search yielded several cleptoparasitic bees that were not collected in this study, but their hosts were. Cleptoparastites
are not as common as non-parasitic bee species and are, therefore, more difficult to collect. Of the 13 cleptoparasitic species collected in Louisiana, ten were rare (represented by only one or two specimens), two were uncommon (greater than two and less than five specimens), and only one was common.

Longleaf pine savannas have much lower levels of specialized bees than areas of high bee diversity such as deserts. Of the species with known biological information in my study, only 18% were oligolectic. On the other hand, deserts of North America contain greater than 60% oligolectic species. Unlike deserts, which have an ephemeral and somewhat unpredictable flowering schedule, longleaf pine savannas contain a continuum of flowers throughout the growing season. Polylectic may have arisen in bees of longleaf pine savannas as a consequence of a shifting but continuous resource. Greater polylectic was postulated to be the case for pollinators in general in longleaf pine savannas (Folkerts et al. 1993).

Finally, Michener (1947) stated that the bee fauna of the Gulf Coast states was poorly known. This is obvious with his collection of *Exomalopsis micheneri* Timberlake. The genus *Exomalopsis* had not been previously recorded further east than Texas. This parallels a bee collected in the current study, *Diadasia afflicta* (Cresson) (Appendix A). *Diadasia* has not been previously recorded further east than west Texas.

A preliminary examination of differences in bee diversity between the two savanna types studied in Louisiana showed a trend toward higher diversity in the upland savannas. This is consistent with previous comparisons of the moth fauna of upland and wet savannas in southeastern Louisiana, where higher moth diversity was found in an upland compared to a wet savanna (Landau & Prowell 1999). To make more accurate comparisons between savanna types, a standardized data set is required. This is the topic of Chapter 4.
Overall, this study resulted in a checklist of the bee species found in Louisiana longleaf pine savannas. This checklist will be a valuable resource for both researchers and conservation biologists. Updated distributional and biological information for each species in this checklist will aid conservationists by giving them a quick reference of biological attributes of species present.

Several management implications have arisen from this study as well. First, Abita Creek showed high diversity despite being in an early stage of restoration compared with upland sites that have been preserves for longer periods. This suggests that bees have the ability to either sustain themselves in poorly managed sites or to readily colonize from neighboring areas as sites are restored. This, in turn, suggests that bees are capable of rapid recovery in restored savannas. Second, a trend toward increased bee abundance and richness following prescribed fires at Abita Creek was observed. This suggests that management of savannas with fire enhances bee diversity.
Like most large ecosystems, longleaf pine ecosystem can be divided into smaller community types. In Louisiana, two longleaf pine savanna types are found, upland savannas and wet pine flatwoods. Upland savannas tend to have well drained soils and a rich and continuous layer of herbaceous plants. Wet pine flatwoods tend to have poorly drained soils and are considered floristically to be wetlands. The groundcover of wet pine flatwoods is dominated by sedges and grasses. However, both savanna types are notable because they contain more species of herbaceous plants than any other habitat in Louisiana (Smith 1991).

Because many savanna plants rely on bees for their reproduction and survival, anthropogenic effects on bees could potentially have detrimental repercussions to these ecosystems as a whole (Folkerts et al. 1993). Documenting bee diversity is a necessary first step in observing potential human induced changes over time. Because the savanna types found in Louisiana consist of different plant communities, the objective of this part of my study was to determine if and to what degree diversity and species composition of bees in the two savanna types were different.

Addressing this question required standardizing data obtained from each site in order to produce comparable data sets from the perspective of sampling effort, sampling technique, and sampling habitat. To accomplish this, data were subjectively removed from sites with the intent of producing data sets that had comparable sampling dates and effort. Two comparisons were made using different amounts of data. First, to contrast the wet with upland savannas, a large data set spanning multiple years was generated from Sandy Hollow and Abita Creek. A second
set of comparisons involving a much smaller data set for a single year was made among all four sites.

MATERIALS AND METHODS

Study Sites

For a description of the sites refer to Study Sites in Chapter 3.

Collection Methods

Collection methods are described in the Materials and Methods sections of Chapters 2 and 3.

Data Standardization

Standardization of the large data set for Sandy Hollow and Abita Creek involved several iterations of data removal. First, samples collected from the BI Plot at Sandy Hollow-S were removed because pans were only run at this one site. Next, hand collected samples from Sandy Hollow in 2003 were removed and only comparable samples from Sandy Hollow-N and Abita Creek for 2002 were included. Third, because half of the samples from Abita Creek were collected from wooded locations and this study was more concerned with open areas, samples collected from wooded areas at Abita Creek were removed. The months of March, November, and December were also removed from Abita Creek samples because those months were not sampled at the upland site. After these data extractions, there was still an excess of seven trap samples at Abita Creek in the first two years. The following seven trap samples were randomly selected and removed from the months of April, May, September and October because these months were near the beginning or end of the sampling season: 18 April 2000 (two traps), 1 May 2001 (three traps), 26 October 2000 (one trap), and 29 September 2000 (one trap). When
completed, the standardized data set contained a total of 53 trapping weeks and 18 hand collection hours for Abita Creek and Sandy Hollow.

For the second, smaller comparison of all sites, standardization was centered around one year of sampling because two of the sites (Sandy Hollow-S and Whispering Pines) were only sampled one year. Samples from the first two years of collection at Abita Creek were removed because they did not contain any hand collected samples and no upland sites were sampled then. All data collected from the BI Plot were removed because pan collecting was only done at Sandy Hollow-S. Next, all samples from Sandy Hollow-N for the first year of collection were removed to produce a single year that matched the other sites. To standardize the three upland sites the following sample dates not common to all sites were removed: 17 April, 1 October, and 24 October 2003 from Whispering Pines and Sandy Hollow-N. Finally, the following samples were randomly selected and removed from Abita Creek: 17 May (one-half of hand collection sample), 12 June (hand collection), 6 September (one trap), and 11 October 2002. When completed, the standardized data set contained a total of 14 trapping weeks and 10.5 hand collection hours per site.

**Diversity Comparisons**

**Shannon Diversity Index.** The Shannon diversity index is commonly used to compare habitats or samples (Magurran 1988). It assumes that all individuals were sampled randomly from a large population, and that all species are represented in the sample. The Shannon diversity index is calculated by the following equation:

$$H' = -\sum p_i \ln p_i,$$

(4.1)

where $p_i$ is the proportion of individuals of the ith species found in the habitat.
Magurran (1988) includes formulae to calculate variances, t-values, and degrees of freedom based on this diversity index. The formula for the variance is:

$$VarH' = \frac{\sum p_i (\ln p_i)^2 - (\sum p_i \ln p_i)^2}{N} + \frac{S - 1}{2N^2}$$  \hspace{1cm} (4.2)$$

In this equation, $p_i$ is taken from formula 4.1, $N$ is the total number of individuals collected from the habitat, and $S$ is the total number of species collected from the habitat.

The formula for calculating the t-value is:

$$t = \frac{H'_1 - H'_2}{\sqrt{\frac{VarH'_1 + VarH'_2}{2}}}$$  \hspace{1cm} (4.3)$$

In this formula $H'_1$ and $H'_2$ are the diversity index values for the two sites being compared, calculated from equation 4.1. Variances calculated from equation 4.2 for these same sites are also included.

The following equation is used to calculate the degrees of freedom:

$$df' = \frac{(VarH'_1 + VarH'_2)^2}{\left[(VarH'_1)^2/N_1 + (VarH'_2)^2/N_2\right]}$$  \hspace{1cm} (4.4)$$

The variables in this equation are the same as in the previous formulae (Magurran 1988).

Evenness is a measure of the relative abundance of each species in a habitat. If each species is equally abundant, evenness is one. To observe and contrast species biases, evenness was calculated using the following formula:

$$E = \frac{H'}{\ln S'},$$  \hspace{1cm} (4.5)$$

where $H'$ is the diversity index calculated from equation 4.1, and $S$ is the total number of species present in the habitat (Magurran 1988).
**Sorenson’s Index.** The Materials and Methods section of Chapter 2 contains the formula and calculation for this index.

**Rarefaction Curves.** Samples differ in numbers of species and individuals caught. To make comparisons of richness, one approach is to plot species accumulation as a function of number of individuals as opposed to sampling effort or date. This approach is called rarefaction because it standardizes samples to a common sample size (Gotelli & Colwell 2001). Rarefaction curves were generated using EstimateS (Colwell 2001).

**RESULTS**

**Sandy Hollow Compared to Abita Creek**

In this standardized comparison, Sandy Hollow contained ten more species and almost two and a half times as many individuals as Abita Creek (Table 4.1a). Sandy Hollow had a significantly lower Shannon diversity value than Abita Creek (p<0.05). Since there were more species and individuals at Sandy Hollow, this result was not expected. The lower evenness value at Sandy Hollow was suggestive of skewed samples. Inspection of the raw data revealed that a species at Sandy Hollow, *Lasioglossum (Dialictus) coreopsis* (Robertson) was particularly abundant. To determine the effect of this species on the summary statistics, diversity for both sites was recalculated, this time excluding *L. (D.) coreopsis* (Table 4.1b). Results indicated that evenness of the sites was similar and the Shannon diversity value at Sandy Hollow was higher, albeit not significantly.

A comparison of species composition of these sites showed that more bee species are shared than are unique to a particular site. Abita Creek shares 72% of its bee species with Sandy Hollow whereas Sandy Hollow shares only 64% of its bee species with Abita Creek. Sorenson’s similarity value indicates that these sites are 68% similar.
Rarefaction results mirrored results of the Shannon diversity index (Fig. 4.1). Sandy Hollow has a somewhat shallower curve than for Abita Creek when *L. (D.) coreopsis* is included (Fig. 4.1a). This indicates Sandy Hollow accumulates a lower number of species per individual than Abita Creek. *Lasioglossum (D.) coreopsis* is most likely having a “dilution” effect on the overall sample for Sandy Hollow. At the point where sample sizes are maximum and equal, 627 individuals, Abita Creek contains more species. When *L. (D.) coreopsis* is removed, diversity at both sites is more similar (Fig. 4.1b).

**Table 4.1.** Species richness, abundance, evenness, and diversity for Abita Creek and Sandy Hollow including (a) and excluding *Lasioglossum (Dialictus) coreopsis* (Robertson) (b). Means followed by the same letter are not significantly different at p<0.05.

<table>
<thead>
<tr>
<th></th>
<th>Abita Creek</th>
<th>Sandy Hollow</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td>66</td>
<td>76</td>
</tr>
<tr>
<td><strong>Individuals</strong></td>
<td>627</td>
<td>1553</td>
</tr>
<tr>
<td><strong>Evenness</strong></td>
<td>0.80</td>
<td>0.71</td>
</tr>
<tr>
<td><strong>Shannon Diversity Index (±SD)</strong></td>
<td>3.37 ± 0.04a</td>
<td>3.07 ± 0.04b</td>
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</tbody>
</table>

<table>
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<tr>
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<th>Abita Creek</th>
<th>Sandy Hollow</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
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<td>75</td>
</tr>
<tr>
<td><strong>Individuals</strong></td>
<td>598</td>
<td>1138</td>
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<tr>
<td><strong>Evenness</strong></td>
<td>0.80</td>
<td>0.79</td>
</tr>
<tr>
<td><strong>Shannon Diversity Index (±SD)</strong></td>
<td>3.34 ± 0.05a</td>
<td>3.40 ± 0.03a</td>
</tr>
</tbody>
</table>

**All Sites**

In a comparison of all sites, Sandy Hollow-S contained the greatest number of species followed by Sandy Hollow-N, Whispering Pines and last by Abita Creek (Table 4.2a). Evenness was roughly similar in all sites except for a lower value in Sandy Hollow-N. Shannon diversity indices of Sandy Hollow-S and Whispering Pines were significantly higher than Abita Creek and Sandy Hollow-N.
Fig. 4.1. Rarefactions curves for Abita Creek and Sandy Hollow including (a), and excluding *L. (D.) coreopsis* (b). (ACP=Abita Creek; SH=Sandy Hollow)
Table 4.2. Species richness, abundance, evenness, diversity, percent unique species for four sites including (a), and excluding *Lasiglossum (Dialictus) coreopsis* (Robertson) (b). Means followed by the same letter are not significantly different at p<0.05.

<table>
<thead>
<tr>
<th></th>
<th>Abita Creek</th>
<th>Sandy Hollow-N</th>
<th>Sandy Hollow-S</th>
<th>Whispering Pines</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td>37</td>
<td>48</td>
<td>54</td>
<td>45</td>
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<tr>
<td><strong>Individuals</strong></td>
<td>208</td>
<td>407</td>
<td>400</td>
<td>308</td>
</tr>
<tr>
<td><strong>Evenness</strong></td>
<td>0.87</td>
<td>0.76</td>
<td>0.85</td>
<td>0.88</td>
</tr>
<tr>
<td><strong>Shannon Diversity Index (± SD)</strong></td>
<td>3.13 ± 0.06a</td>
<td>2.94 ± 0.07a</td>
<td>3.39 ± 0.05b</td>
<td>3.36 ± 0.05b</td>
</tr>
<tr>
<td><strong>% Unique Species</strong></td>
<td>16</td>
<td>15</td>
<td>17</td>
<td>11</td>
</tr>
</tbody>
</table>

b)

<table>
<thead>
<tr>
<th></th>
<th>Abita Creek</th>
<th>Sandy Hollow-N</th>
<th>Sandy Hollow-S</th>
<th>Whispering Pines</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td>36</td>
<td>47</td>
<td>53</td>
<td>44</td>
</tr>
<tr>
<td><strong>Individuals</strong></td>
<td>189</td>
<td>295</td>
<td>353</td>
<td>303</td>
</tr>
<tr>
<td><strong>Evenness</strong></td>
<td>0.87</td>
<td>0.83</td>
<td>0.86</td>
<td>0.88</td>
</tr>
<tr>
<td><strong>Shannon Diversity Index (± SD)</strong></td>
<td>3.11 ± 0.07a</td>
<td>3.25 ± 0.06ab</td>
<td>3.43 ± 0.05b</td>
<td>3.33 ± 0.05b</td>
</tr>
</tbody>
</table>

The lower diversity and evenness in Sandy Hollow-N were suggestive of a species bias as seen in the previous comparison. To see if the same species, *L. (D.) coreopsis*, was skewing results for Sandy Hollow-N, diversity was recalculated for all sites with this species excluded (Table 4.2b). Evenness at Sandy Hollow-N approached that of the other three sites and the diversity value was midway between upland and Abita Creek sites.

Sorenson’s similarity values indicated greater similarity among upland sites than between upland and Abita Creek (Table 4.3). Clustering sites by similarity values placed upland sites together, with Sandy Hollow-S and Whispering Pines being the most similar (Fig. 4.2). Abita Creek, the single wet savanna site, was an outlier to upland sites.

Species composition of each site was contrasted by determining the percentage of unique and shared species (Table 4.2a). There were similar percentages of unique species at each site with the lowest number of unique species at Whispering Pines. When considering the upland
sites together, there were 45 unique species or 58%. However, the number of unique species in
the wet savanna might likewise increase if there had been replicated wet sites.

Table 4.3. Sorenson’s similarity index for pairwise comparisons between all four sites.

<table>
<thead>
<tr>
<th></th>
<th>Abita Creek</th>
<th>Sandy Hollow-N</th>
<th>Sandy Hollow-S</th>
<th>Whispering Pines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abita Creek</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandy Hollow-N</td>
<td>0.45</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sandy Hollow-S</td>
<td>0.53</td>
<td>0.71</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Whispering Pines</td>
<td>0.56</td>
<td>0.67</td>
<td>0.73</td>
<td>1</td>
</tr>
</tbody>
</table>

Fig. 4.2. Dendrogram of site similarity of species composition based on Sorenson’s similarity index (ACP=Abita Creek; SHN=Sandy Hollow-N; SHS=Sandy Hollow-S; CWP=Whispering Pines).

Once again, rarefaction results mirror the Shannon diversity values (Fig. 4.3). Sandy
Hollow-S and Whispering Pines showed consistent high species richness. Curves for Abita
Creek and Sandy Hollow-N are lower and very similar. Sandy Hollow-N shows the shallowest
slope than the other three sites, and this is most likely the result of the extremely abundant bee,
L. (D.) coreopsis (Fig. 4.3a). Sandy Hollow-N curve is more aligned with Whispering Pines when this species is removed (Fig. 4.3b)

Fig. 4.3. Rarefaction curves for all savanna sites including (a), and excluding L. (D.) coreopsis (b). (ACP=Abita Creek; SHN=Sandy Hollow-N; SHS=Sandy Hollow-S; CWP=Whispering Pines)
DISCUSSION

Results of this study indicate upland savanna sites contain a higher diversity of bees than the wet savanna site. Bee species richness and abundance was consistently higher in the upland savanna sites versus the wet savanna site, by about ten species and by many hundreds of individuals. Species composition of upland savanna sites was consistently more similar than to the wet savanna site. Differences among upland sites and the wet pine flatwood site could have many causes, rendering definitive resolution difficult. The most obvious causes, which I will discuss individually, include fire history and management, plant species composition, size and age of preserves, and soil type.

Fire management of the three preserves is similar in that they all employ growing season fires every other year (Table 4.4). However, Sandy Hollow differs from the others by a history of annual dormant season fires that are still employed over about half of the preserve. In Florida, fire season was found to have an effect on the timing of flowering of herbaceous plants in flatwood and xeric sandhill savannas (Platt et al. 1988). Fires during the growing season resulted in delayed, enhanced and more synchronous flowering within and among herbaceous plant species in both savanna types. Regardless of time of fire, peak flowering in both savanna types was in fall with more species flowering in flatwoods than sandhills.

Because fire season has an effect on the timing of flowering of herbaceous plants in savannas, it follows that fire season might also affect bee presence and abundance in savannas. Dormant season fires at Sandy Hollow do not appear to have a negative impact on the bee community because Sandy Hollow contained the highest richness and abundance of bees. Abita Creek bee diversity is high given the recent application of fires to that site. This suggests bees can recolonize sites fairly quickly in restoration of savannas, presumably from nearby sources.
Table 4.4. Fire management, age, size, and soil type in four study sites.

<table>
<thead>
<tr>
<th>Fire Management</th>
<th>Abita Creek</th>
<th>Sandy Hollow-N</th>
<th>Sandy Hollow-S</th>
<th>Whispering Pines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acquired</td>
<td>biennial</td>
<td>annual dormant; biennial growing</td>
<td>annual dormant; biennial dormant</td>
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<tr>
<td>Managed for</td>
<td>May 1996</td>
<td>mid-1980s</td>
<td>mid-1980s</td>
<td>late 1960s</td>
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<tr>
<td>Longleaf Pine</td>
<td>May 1996</td>
<td>mid-1980s</td>
<td>mid-1980s</td>
<td>early 1990s</td>
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<td>338</td>
<td>~1200</td>
<td>~300</td>
<td>200</td>
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<tr>
<td>Soil Type</td>
<td>poorly drained sandy loam</td>
<td>well drained silt-loam</td>
<td>well drained silt loam</td>
<td>well drained silt-loam</td>
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</tbody>
</table>

Plant species composition of the two savanna types differs and may affect bee species presence in these habitats. Latimore Smith (Louisiana Nature Conservancy) speculates that Sandy Hollow probably contains 100-200 more species of plants than Abita Creek (pers. comm.). He further suggested that a good quality upland longleaf pine site would have more plant species per area than a good quality wet pine flatwoods. If bee diversity is related to flowering plant diversity and upland sites in Louisiana have more flowering plant species per area, then upland sites should be able to support higher bee diversity. Results of my study are consistent with this suggestion.

Another striking difference among the four sites that might affect bees is their sizes and ages (Table 4.4). Sandy Hollow-N is by far the largest of the four sites. Larger areas are likely to produce higher numbers of bee species (Michener 1979). This fits to some extent as high richness and abundance was observed at Sandy Hollow-N. However, diversity is not directly related to size. Sandy Hollow-S is approximately a third the size of Sandy Hollow-N and yet its bee fauna was significantly more diverse. Whispering Pines is a smaller site than Abita Creek, yet it had significantly higher diversity.
In terms of management history, there is not a direct relationship with length of time a preserve has been managed as a longleaf pine savanna. Whispering Pines and Sandy Hollow-S have comparable diversity levels, yet Sandy Hollow-S has been managed for longleaf pine more than a decade longer. Abita Creek is the most recently restored site and it has a diversity approaching the older sites. This is a positive outcome for restoration of these particular community types.

Finally, differences in diversity could be attributed to nesting preferences of soil nesting bee species. Bee families Andrenidae, Melittidae, Oxaeidae, and Fideliidae are composed entirely of soil nesting species. In addition to these families, members of the families Colletidae and Apidae are also soil nesting (O’Toole & Raw 1991). Upland savannas tend to have sandier soils than wet pine flatwoods. This sandier soil is easier for bees to build nests. Also, upland savannas tend to be drier, and ground nests would be less likely to flood in uplands (Folkerts et al. 1993). Therefore, differences in the diversity of upland savanna sites compared to the wet savanna site may be related to soil drainage and type. There are more species of bees with preferences for sandy, well-drained soils than compact, hydric, clay soils (Appendix B). Thus, higher diversity at upland sites may be due, in part, to a higher number of sandy soil preferring bees such as *Svastra atripes atrimitra* (LaBerge) and *Andrena rudbeckiae* Robertson.
CHAPTER 5

SUMMARY

My study was a part of a larger study aimed at describing insects in longleaf pine savannas in Louisiana. The goal was to fill a gap in our knowledge of bees. Because these savannas are rich in herbaceous, flowering plants, many of which are rare or threatened, documenting their potential pollinators may help in their protection. Bees are probably the most important group of pollinators due to their entire reliance on flowers (O’Toole & Raw 1991; Michener 2000).

One important outcome of this study was a checklist of bee species in Louisiana longleaf pine savannas. This is the first list of bees in a pine flatwood and upland savanna in Louisiana as well as the first list of bees by habitat for Louisiana. This checklist will aid researchers and conservation biologists by providing a list of bee species frequenting and in some cases dependent upon the savanna ecosystem. Distributional and biological information provided with this list indicated 67 new state records, 23 range extensions, and two possible new species. The bee fauna was found to have strong affinities with that of the eastern United States.

Several species were found to prefer sandier soils and, of these, five were biased toward upland sites. These five species are: *Andrena rudbeckiae* Robertson, *Nomia nortoni nortoni* Cresson, *Lasioglossum (Dialictus) pilosus pilosus* (Smith), *Megachile exilis parexilis* (Mitchell), and *Svastra atripes atrimitra* LaBerge. Three species have been reported to be associated with prairies or grasslands and are likely candidates for savanna dependent species. Two of these species, *Colletes productus* Robertson and *Diadasia afflicta* (Cresson), were rare and only collected at the upland sites (Whispering Pines and Sandy Hollow-S, respectively). *Diadasia afflicta* was previously only recorded from the central states, so Louisiana represents a
significant eastward range extension. It is a specialist on the plant genus *Callirhoe*, which is associated with longleaf pine savannas in Louisiana. *Colletes americanus* Cresson, a specialist on Asteraceae and a fall flying species, has been reported from prairies in the eastern United States. It was more common at upland sites.

Eighteen percent or eleven species were specialists on primarily Asteraceae, but also on *Callirhoe, Hibiscus*, and *Ipomoea*. The majority of host specific bees were restricted to or biased toward upland sites (nine of eleven). Many of these species tended to be seasonally restricted to either spring or fall to coincide with host flowering.

A second objective of this study was a comparison of diversity levels for bees in two longleaf pine savanna type, upland and a wet pine flatwoods site. My study indicated higher richness and abundance of bees in upland versus the wet flatwood savanna. The upland sites consistently contained a higher number of species and individuals. Two upland sites had significantly higher diversity than the flatwood savanna. No definitive conclusions will be drawn about factors contributing to differences in diversity among sites. However, the size of the preserve appeared to be less important than floral diversity and soil type.

Lastly, the best collection method for bees in longleaf pine savannas was tested on a small scale to insure collection methods adequately sampled bees. At one site studied over a three month period, a pan trapping protocol (BI Plot) collected a higher number of species and individuals than a malaise trapping protocol though differences were not significant. Over the course of the study, all the malaise traps combined caught most of the species collected by the pans. Both trapping protocols tested were fairly effective in capturing bees suggesting researchers should pick whichever method better satisfies requirements of their research goals.
There are several management implications of this research. First, and perhaps most importantly, a newly acquired longleaf pine savanna in the early stages of restoration, Abita Creek, contained a high diversity of bees though somewhat less than the upland sites. In the first year of this study, only three years after the preserve was established, 51 species of bees were collected. By the third year of the study and two fires later, 83 species had been collected on the site. This is an encouraging result because it suggests that bees either eke out an existence in poorly managed sites or readily colonize sites from neighboring areas as sites are restored. This study was conceived because of a concern over whether prairie restoration in eastern Louisiana would succeed without attention to pollinators. Although not definitive, this study suggests that pollinators are capable of rapid buildup or recovery in newly restored savannas, an ecosystem similar in plant structure and diversity to prairies.

A trend toward increased bee abundance and richness was observed at Abita Creek after prescribed fires. Lower overall diversity was observed in the first year of my study, prior to a fire, compared to each of two years after fires were added to the management regime. If fires result in greater floral biomass as demonstrated by Platt et al. (1988), then higher bee diversity is expected with increased fires because flowers are likely to be a limiting resource for bees. This suggests that fire management should have a positive effect on bee diversity in general.

Comparisons of multiple sites in the upland savanna region allowed for some insight into the effects of preserve size on bee diversity. Two of the smaller sites, Sandy Hollow-S and Whispering Pines, had significantly greater diversity than the largest site, Sandy Hollow-N. This finding supports another study (Donaldson 2002) that indicated fragment size had little or no affect on the bee community and richness. Even small, privately owned preserves, like Whispering Pines, where habitat protection is only one of several missions, are capable of
serving as reservoirs for bees. These bees will be available for future colonization as other savanna sites are acquired and restored.
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oligolectic and nonoligolectic bees associated with a vernal pool plant. Ecological 
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Liebherr, J., and J. Mahar. 1979. The carabid fauna of the upland state oak forest in Michigan: 


Linsley, E. G. and J. W. MacSwain. 1957. The nesting habits, flower relationships, and parasites 
of some North American species of Diadasia (Hymenoptera: Anthophoridae). The 

Litte, M. 1977. Aspects of the social biology of the bee Halictus ligatus in New York state 


Louisiana Natural Heritage Program. 1987. The natural communities of coastal Louisiana, 
classification and description. Louisiana Department of Wildlife and Fisheries.100-103.

American bees of the families Apidae, Meliponidae, Bombidae, Euglossidae and 

Princeton, New Jersey.


APPENDIX A: BEE TRAPPING DATA FOR TWO COLLECTING PROTOCOLS

Table A.1. Numbers of individuals per species collected by the malaise trap protocol. Species are listed alphabetically.

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<th>Species</th>
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<td>7/29</td>
<td>8/15</td>
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72
Table A.1. Continued.

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Table A.2. Numbers of individuals per species collected by the BI Plot. Numbers below pans indicate dates where 1=16 June, 2=10 July, 3=29 July and 4=15 August.

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<td><strong>Total Individuals</strong></td>
<td>4 3 5 2</td>
<td>8 6 10 15</td>
<td>6 7 8 7</td>
<td>81</td>
<td>21 51 12 19 103</td>
<td></td>
</tr>
<tr>
<td><strong>Total Species</strong></td>
<td>3 2 3 2</td>
<td>6 4 7 9</td>
<td>5 5 5 7</td>
<td>23</td>
<td>11 15 9 8 23</td>
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APPENDIX B. ANNOTATED CHECKLIST OF BEE SPECIES COLLECTED IN EASTERN LOUISIANA LONGLEAF PINE SAVANNAS

This checklist contains all the species collected during this study with added biological and distributional data. If host or nesting preferences are not mentioned, they are not known. Information is from Mitchell (1960; 1962) and Krombein et al. (1979) unless otherwise stated. Species are listed phylogenetically.

Colletidae

Colletes americanus Cresson

Distribution: Que., Man., and eastern U. S.

LA Collection Records: Aster dumosus

Notes: solitary and soil-nesting; favors high prairies; oligolege of fall flowering Asteraceae; Epeolus pusillus Cresson may parasitize nests; flies from Aug to Nov (Pearson 1933)

Colletes banksi Swenk

Distribution: MI and NY, south to FL and LA

Notes: solitary and ground-nesting; flies from mid-Apr to mid-Jul; range extension and state record

Colletes distinctus Cresson

Distribution: NC south to FL and LA

LA Collection Records: Trachelospermum difforme

Notes: flies from Mar to Jun; range extension and state record

Colletes latitarsis Robertson

Distribution: FL to LA, north to NY, MI and WI
Notes: solitary and soil nesting; favors sand dune and upland associations; flies from Mar to Sep (Pearson 1933); state record

**Colletes nudus Robertson**

Distribution: FL to LA, north to WI, Ont. and MA

LA Collection Records: *Trachelospermum difforme*

Notes: solitary and soil nesting; flies from Jul to Aug; state record

**Colletes productus Robertson**

Distribution: MA, west to WI, south to GA and AL

Notes: favors high prairies; flies from Apr to Jul (Pearson 1933); range extension and state record

**Hylaeus ?n. sp.**

Distribution: unknown

**Hylaeus affinis (Smith):**

Distribution: Eastern U. S. from New England west to MN, south to LA and GA

Notes: flies from Apr to Oct; state record

**Hylaeus confluens (Smith)**

Distribution: NJ south to FL, west to LA

LA Collection Records: *Agalinis linifolia, A. tenuifolia, Cyrilla racemiflora, Eriocaulon decangulare, Eryngium yuccifolium, Hypericum cistifolium, Oxypolis filiformis*

Notes: flies from Mar to Oct

**Andrenidae**

**Andrena sp. 1**

Distribution: Unknown
Collected from: *Krigia caespitosa*

**Andrena sp. 2:**

Distribution: Unknown

**Andrena accepta Viereck:**

Distribution: Widespread throughout N. America

LA Collection Records: *Helianthus angustifolius, H. hirsutus*

Notes: nests in soil; nests found in desert scrub; oligolege of Asteraceae, especially *Helianthus*; flies from Aug to Sep (LaBerge 1967; Rozen 1973); state record

**Andrena rudbeckiae Robertson**

Distribution: MI, south to TX, and from CO east to NC

LA Collection Records: *Helenium flexuosum, Rudbeckia hirta*

Notes: oligolege of Asteraceae, especially *Ratibida*; nests in deep alluvial sand deposits; flies from Jun to Aug (LaBerge 1967)

**Andrena confederata Viereck**

Distribution: CT, south to northern FL, west to eastern TX, OK, and southern IL

Notes: polylectic; flies from Mar to May (Bouseman & LaBerge 1979); state record

**Andrena ilicis Mitchell**

Distribution: NY to northern FL, west to KS and TX

Notes: flies from Apr to May (LaBerge 1971); state record

**Andrena morrisonella Viereck**

Distribution: MN to the New England states, south to GA and LA

Notes: flies from May to early Jun (LaBerge 1971); range extension and state record
Andrena ?unicostata LaBerge:

Distribution: TX and OK and LA

Notes: visits Salix; biological data lacking (LaBerge 1971); range extension and state record

Protandrena compositarum (Robertson)

Distribution: MD to GA, west to IL and LA

LA Collection Records: Aster dumosus

Notes: collects from Asteraceae; flies from Sep to Oct; range extension and state record

Protandrena sp. 1

Distribution: unknown

LA Collection Records: Helianthus angustifolius

Panurginus polytrichus Cockerell

Distribution: TX to MS

LA Collection Records: Rubus argutus?

Notes: genus primarily western, only three species occur east of Mississippi River; polylectic; nests in sandy soils; solitary; nests gregariously; flies from Mar and Apr; probable nest parasite Holcopasites rozeni (Neff 2003)

Perdita boltoniae chrysopsina Timberlake

Distribution: NJ south to FL and LA

Notes: flies from Jul to Oct; range extension and state record

Halictidae

Nomia nortoni nortoni Cresson

Distribution: NC to FL, west to CO and Mex.
LA Collection Records: *Chamaecrista fasciculata*

Notes: prefers sandy loam soil; most abundant where soil is sandy; nests in ground in aggregations; flies from Jul to Nov (Cockerell 1934)

*Agapostemon splendens* (Lepeletier)

Distribution: Ont. and ME to Sask., south to FL, AL, MS, LA, TX, NM, AZ, and Mex.

LA Collection Records: *Chamaecrista fasciculata, Ludwigia alternifolia*

Notes: common to sandy regions of the Central and Eastern states; most common species of this genus in southeastern U. S.; nests almost exclusively in sandy soil, in aggregations or alone; polylectic; flies throughout season (Stevens 1921; Knerer & Atwood 1962; Roberts 1968; Roberts 1969; Roberts 1972; Eickwort 1981; Moure et al. 1987)

*Halictus ligatus* Say

Distribution: N. America south through C. America to northern S. America.

LA Collection Records: *Coreopsis tripteris, Eurybia hemisperica, Helenium flexuosum, Helianthus angustifolius, H. hirsutus, Hydrolea ovata, Rudbeckia hirta, Vernonia gigantea*

Notes: primitively eusocial; polylectic; preference for Asteraceae; nest in the ground, no preference to soil type; flies year-round (Knerer & Atwood 1962; Litte 1977; Michener & Bennett 1977; Ginsberg 1985; Moure et al. 1987; Packer & Knerer 1987)

*Halictus parallelus* Say

Distribution: Ont. and NJ to FL, west to MT, WY, CO, NM and TX

LA Collection Records: *Ceanothus americanus, Helenium flexuosum, Rubus argutus?, Rudbeckia hirta*
Notes: polylegic; flies from Mar to Nov (Moure et al. 1987); nest aggregation observed at Camp Whispering Pines; appeared to have some form of sociality; a single female observed guarding the nest entrance, while others flew in; state record

*Halictus rubicundus* (Christ)

Distribution: Holarctic

Notes: facultatively social; nests primarily in sandy-loam soil in dense aggregations; polyleptic; flies from Mar to Sep (Knerer & Atwood 1962; Moure et al. 1987; Potts & Willmer 1997; Soucy 2002); state record

*Lasioglossum (Dialictus) admirandus* (Sandhouse)

Distribution: MN to NS, south to LA and FL

LA Collection Records: *Boltonia diffusa, Ceanothus americanus, Chamaecrista fasciculata, Cirsium horridulum, Eryngium yuccifolium, Helenium flexuosum, Lespedeza bicolor, Rhus copallina, Rudbeckia hirta*

Notes: flies from Mar to Sep (Knerer & Atwood 1962); state record

*Lasioglossum (Dialictus) apopkensis* (Robertson)

Distribution: NC to FL, MS and LA

LA Collection Records: *Chamaecrista fasciculata, Eryngium yuccifolium*

Notes: flies from Feb to Oct; range extension and state record

*Lasioglossum (Dialictus) coeruleus* (Robertson)

Distribution: MN to MA, south to GA and LA

Notes: primitively social; nests in decaying logs; utilizes abandoned beetle burrows; flies from Apr to Oct (Knerer & Atwood 1962; Stockhammer 1967); state record
**Lasioglossum (Dialictus) coreopsis (Robertson)**

Distribution: IL and MI to MA, south to FL and LA


Notes: flies from Apr to Sep; range extension and state record

**Lasioglossum (Dialictus) creberrimus (Smith)**

Distribution: NC to FL and LA

LA Collection Records: Agalinis linifolia, A. tenuifolia, Eriocaulon decangulare, Helianthus angustifolius, Hypericum cistifolium, Rhexia lutea, Sabatia campanula

Notes: flies from Mar to Sep; state record

**Lasioglossum (Dialictus) illinoensis (Robertson)**

Distribution: MN to NS, south to AR, GA and LA

LA Collection Records: Chamaecrista fasciculata

Notes: flies from Mar to Oct; state record

**Lasioglossum (Dialictus) imitatus (Smith)**

Distribution: entire region east of the Mississippi River

LA Collection Records: Chamaecrista fasciculata, Eryngium yuccifolium, Eupatorium rotundifolium, Hydrolea ovata, Hypericum cistifolium, Rhexia alifanus, Rhus copallina,
Notes: recently reported as adventitive in California; observed nesting in clay, sand and rich loam of city flower boxes in Ontario; flies from Apr to Oct (Knerer & Atwood 1962; Ascher 2001); state record

*Lasioglossum (Dialictus) laevisimus* (Smith)

Distribution: MN to NS, south to LA and GA

Notes: primitively eusocial; prefers to nest in sandy soil; flies from Mar to Oct (Knerer & Atwood 1962; Batra 1987); state record

*Lasioglossum (Dialictus) pilosus pilosus* (Smith)

Distribution: CO and MN to NS, south to GA and LA

LA Collection Records: *Ceanothus americanus, Diodia teres*

Notes: nests gregariously in open sand dunes; parasitized by *Sphecodes atlantis* Mitchell; flies from Mar to Oct (Knerer & Atwood 1962); state record

*Lasioglossum (Dialictus) platyparius* (Robertson)

Distribution: MN, MI and MD, south to TN, GA and LA

Notes: cleptoparasitic on other sweat bees; flies from Apr to Sep; range extension and state record

*Lasioglossum (Dialictus) rahleighensis* (Crawford)

Distribution: NC to FL, west to LA

Notes: flies from May to Sep; range extension and state record

*Lasioglossum (Dialictus) reticulatus* (Robertson)

Distribution: IL and MI, south to FL and LA

Notes: flies from Mar to Sep; range extension and state record
**Lasioglossum (Dialictus) tegularis (Robertson)**

Distribution: MN to NH, south to TX, LA and FL

LA Collection Records: *Ceanothus americanus, Helenium flexuosum*

Notes: life history details unknown; flies from Mar to Oct (Knerer & Atwood 1962); state record

**Lasioglossum (Dialictus) versatus (Robertson)**

Distribution: MN to Ont., south to GA and LA

Notes: primitively social; nests in hard soil; parasitized by *Paralictus*; flies from Mar to Oct (Knerer & Atwood 1962; Michener 1966)

**Lasioglossum (Dialictus) sp. 1**

Distribution: unknown

LA Collection Records: *Ludwigia alternifolia, Rhus copallina*

**Lasioglossum (Dialictus) sp. 2:**

Distribution: unknown

LA Collection Records: *Chamaecrista fasciculata, Helenium flexuosum, Rhus copallina*

**Lasioglossum (Dialictus) sp. 3:**

Distribution: unknown

LA Collection Records: *Boltonia diffusa, Callicarpa Americana, Ceanothus americanus, Eryngium yuccifolium, Hydrolea ovata, Hypericum cistifolium, Ludwigia pilosa, Rhexia alifanus, Rhus copallina, Rudbeckia hirta*

**Lasioglossum (Dialictus) sp. 4:**

Distribution: unknown

LA Collection Records: *Hydrolea ovata, Pycnanthemum albescens, Rhexia alifanus,*
**Lasioglossum (Dialictus) spp.:**

Distribution: unknown

LA Collection Records: *Eryngium yuccifolium*

Notes: collective group of males; because this subgenus in desperate need of revision; many males not described and cannot be placed to species; some may be undescribed males of above species, but it is possible there is one or two new species represented in this group

**Lasioglossum (Evylaeus) arcuatus (Robertson)**

Distribution: NS to FL, west to CO and ND

Notes: life history details unknown; flies from Mar to Sep (Knerer & Atwood 1962); state record

**Lasioglossum (Evylaeus) nelumbonis (Robertson)**

Distribution: ME to MN, south to TX and FL

Notes: flies from May to Aug (Knerer & Atwood 1962)

**Lasioglossum (Evylaeus) pectoralis (Smith)**

Distribution: NS to FL, west to WI, NE and TX

LA Collection Records: *Rudbeckia hirta*

Notes: occurs in sandy areas of Canadian Shield; flies from Mar to Nov (Knerer & Atwood 1962); state record

**Lasioglossum (Evylaeus) sp.**

Distribution: unknown

**Lasioglossum (Hemihalictus) lustrans (Cockerell):**

Distribution: IN and MI to VA, south to TX and FL

LA Collection Records: *Pyrrhopappus carolinianus*
Notes: solitary; oligolectic on *Pyrrhopappus*; nests found in soil consisting of clay; nests in aggregations; males as oligolectic as females, highly unusual trait for bees; flies from Apr to Sep (Michener 1947; Daly 1961)

**Sphecodes atlantis** Mitchell

Distribution: MN and Ont. to New England states, south to TX and FL

Notes: cleptoparasitic on nests of *Lasioglossum (Dialictus) pilosus pilosus* (Smith); flies from May to Sep; state record

**Sphecodes dichrous** Smith

Distribution: MN to NS, south to LA and GA

Notes: cleptoparasite on nests of *Halictus rubicundus* (Christ); flies from Apr to Sep; range extension and state record

**Augochlora pura pura** (Say)

Distribution: Que. and ME to MN, south to TX and FL

LA Collection Records: *Chamaecrista fasciculate, Diodia teres, Hydrolea ovata*

Notes: nests in decaying wood; solitary; polylectic; flies throughout season (Sandhouse 1937; Knerer & Atwood 1962; Stockhammer 1966; May 1972; Brown & Ramberg 1985; Moure et al. 1987)

**Augochlorella striata** (Provancher)

Distribution: throughout eastern N. America

LA Collection Records: *Aster dumosus*

Notes: primitively social; polylectic; prefers to nest in well-drained locations in clay or clay loam soils, and in aggregations; flies from Apr to Oct (Sandhouse 1937; Knerer & Atwood
Augochloropsis metallica fulgida (Smith)

Distribution: MI to New England states, south to FL and LA

LA Collection Records: *Aster dumosus*, *Callicarpa americana*, *Chamaecrista fasciculata*, *Helenium flexuosum*, *Helianthus angustifolius*, *Hibiscus aculeatus*, *Pycnanthemum tenuifolium*, *Rubus argutus?*, *Solidago rugosa*,

Notes: polylectic; flies from May to Oct; state record

Melittidae

*Melitta americana* (Smith)

Distribution: ME to FL and LA

Notes: flies from Apr to Jul (Snelling & Stage 1995); range extension and state record

Megachilidae

*Heriades leavitti* Crawford

Distribution: IL to ME and NB, south to FL and LA

LA Collection Records: *Cirsium horridulum*

Notes: nests in borings below branches in sand-scrub areas; polylectic; flies from Mar to Oct (Krombein 1967); state record

*Hoplitis pilosifrons* (Cresson)

Distribution: Que. and MA to FL, west to Alta., CO and TX

LA Collection Records: *Rubus argutus?*

Notes: nests in pithy dead stems; flies from Apr to Aug; state record
**Hoplitis truncata (Cresson)**

Distribution: ND to Que. and ME, south to FL and LA

Notes: polylectic; flies from Mar to Jul; state record

**Osmia subfasciata subfasciata Cresson**

Distribution: NJ to FL, west to southern CA

Notes: polylectic; nests in cavities; univoltine in Texas; weakly protandrous; flies from Mar to Jun (Krombein 1967; Neff & Simpson 1992); state record

**Osmia georgica Cresson**

Distribution: MA to MI, south to FL and TX

Notes: nests in borings and uses leaf pulp for cell partitions; flies from Mar to Aug (Hartman 1944; Krombein 1967; Hawkins 1975); state record

**Osmia collinsiae Robertson**

Distribution: MN to ME, south to LA and NC

Notes: flies from Apr to Aug; range extension and state record

**Osmia sandhouseae Mitchell**

Distribution: New England states to FL, west to TX

Notes: flies from Feb to Jun; state record

**Anthidiellum notatum notatum (Latreille)**

Distribution: MA to IL, south to FL and LA

Notes: polylectic; flies from Apr to Sep (Turell 1976; Merritt 1978)

**Anthidiellum perplexum (Smith)**

Distribution: NC to FL and LA

LA Collection Records: *Galactia volubilis, Hypericum cistifolium*
Notes: polylectic; flies from Apr to Oct (Turell 1976); range extension and state record

**Stelis louisae Cockerell:**

Distribution: eastern N. America

LA Collection Records: *Eupatorium rotundifolium*

Notes: cleptoparasite of nests of *Chalicodoma angelarum* and *C. campanulae*; flies from Mar to Oct (Parker & Bohart 1979; Parker et al. 1987); state record

**Trachusa zebrata (Cresson)**

Distribution: MI, south to LA, west to SD, NE, CO and NM

Notes: flies from Aug to Oct; state record

**Coelioxys sayi Robertson**

Distribution: NY to FL, west to NE, CO and AZ

LA Collection Records: *Helianthus angustifolius, Lespedeza bicolor*

Notes: cleptoparasitic on nests of *Megachile brevis* Say and *M. mendica* Cresson; flies from Apr to Oct (Krombein 1967; Baker 1975)

**Coelioxys ?n. sp.**

Distribution: unknown

**Coelioxys mexicana Cresson**

Distribution: NC to FL, west to TX

LA Collection Records: *Liatris squarrosa*

Notes: cleptoparasitic; flies from Apr to Nov

**Megachile albitarsis Cresson**

Distribution: MI and IN to NC and FL, west through TX to AZ
LA Collection Records: *Boltonia asteroides, Croton capitatus, Diodia teres, Eriocaulon decangulare, Helianthem flexuosum, Helianthus angustifolius, H. hirsutus, Hypericum cistifolium, Hyptis alata, Lespedeza bicolor, Liatris squarrosa, Pycnanthemum tenuifolium, Rudbeckia hirta, Vernonia gigantea*

Notes: lines its nest cells with cut petals and/or leaves; polylectic; flies from May to Sep (Mitchell 1937)

*Megachile parallela* Smith


LA Collection Records: *Helianthus angustifolius*

Notes: nests in ground and uses cuttings from *Spiraea* and *Trifolium* for nests cells; flies from Jun to Sep (Mitchell 1937); state record

*Megachile campanulæ* (Robertson)

Distribution: New England states to GA, west to TX and NE

Notes: Nests found in side of a garage, open wooded areas, sand scrub areas, and vertical clay banks; flies from Jun to Sep (Mitchell 1937; Krombein 1967)

*Megachile exilis parexilis* (Mitchell)

Distribution: MD and IN to FL, west to AZ

LA Collection Records: *Lespedeza bicolor*

Notes: nests in borings; flies from Mar to Oct (Mitchell 1937; Krombein 1967); state record

*Megachile georgica* Cresson

Distribution: NJ to FL, west to AR and TX

LA Collection Records: *Helianthus hirsutus, Lespedeza bicolor, Lobelia floridana,*
Notes: nests in borings; flies from Apr to Sep (Mitchell 1937; Krombein 1967); state record

*Megachile rugifrons* (Smith)

Distribution: NE to MI and NC, south to TX and FL

LA Collection Records: *Hypericum cistifolium*

Notes: flies from Apr to Jul (Mitchell 1937); state record

*Megachile petulans* Cresson

Distribution: FL to NJ and PA, west to Dakotas, NE and AZ, south to LA

LA Collection Records: *Ceanothus americanus, Chamaecrista fasciculata, Diodia teres, Galactia volubilis, Helianthus flexuosum, Helianthus angustifolius, H. hirsutus, Ilex glabra, Lespedeza bicolor, Pityopsis graminifolia, Rhus copallina, Rudbeckia hirta*

Notes: polylectic; flies throughout season (Mitchell 1937)

*Megachile brevis brevis* Say

Distribution: throughout N. America

LA Collection Records: *Helianthus flexuosum, Helianthus angustifolius, Lespedeza bicolor, Rhexia alifanus, R. mariana*

Notes: solitary; nests in any pre-existing cavity, using pieces of leaves and petals to construct cells; highly mobile; polylectic; cleptoparasites include *Coelioxys octodentata, Coelioxys novomexicana, Coelioxys salinaria, Coelioxys sayi*; flies throughout season (Hicks 1926; Mitchell 1935; Michener 1953; Pengelly 1955; Packer 1987)

*Megachile brevis pseudobrevis* Mitchell

Distribution: NC to FL and LA
LA Collection Records: *Agalinis linifolia*, *Aster adnatus*, *Hypericum crux-andreae*, *Lespedeza bicolor*, *Rhus copallina*

Notes: polylectic; nests near center of tufts of grass; cells constructed of plant material; flies from Apr to Oct (Packer 1987)

*Megachile mendica* Cresson

Distribution: throughout U. S.


Notes: nests observed in sandy soil as well as rose canes; polylectic; flies throughout season (Mitchell 1935; Pengelly 1955; Krombein 1967; Williams et al. 1986; Neff & Simpson 1988)

*Megachile texana* Cresson

Distribution: throughout N. America

LA Collection Records: *Chamaecrista fasciculata*, *Diodia teres*, *Helianthus hirsutus*, *Lespedeza bicolor*, *Orbexilum pedunculatum*, *Rhus copallina*, *Rudbeckia hirta*, *Tephrosia virginiana*

Notes: nests in any pre-made hole in ground; flies throughout summer (Mitchell 1935; Pengelly 1955; Krombein 1970; Eickwort et al. 1981)

*Megachile oenotherae* (Mitchell)

Distribution: NJ to TX, OK and LA
Notes: nests found in abandoned *Andrena macra* Mitchell burrows in sandy loam soil; exclusively uses *Oenothera* petals and leaves for nest materials; flies in spring when *Oenothera* flowers (Sivik 1954); state record

*Megachile xylocopoides* Smith

Distribution: LA and FL, north to MD

LA Collection Records: *Helianthus heterophyllus, H. hirsutus, Rhus copallina*

Notes: polylectic; nests found in open wooded and sand scrub areas; flies from Mar to Sep (Mitchell 1937; Krombein 1967)

*Megachile frugalis frugalis* Cresson

Distribution: PA and NJ to FL, west to CA

LA Collection Records: *Helenium flexuosum, Trachelospermum difforme*

Notes: polylectic; flies from Apr to Jul; state record

*Megachile inimica sayi* Cresson

Distribution: PA to FL, west to CA

LA Collection Records: *Liatris squarrosa*

Notes: polylectic; flies from Jul to Sep (Krombein 1967); state record

**Apidae**

*Xylocopa micans* Lepeletier

Distribution: southeast VA to FL, west along Gulf Coast states to TX

LA Collection Records: *Eryngium yuccifolium, Lespedeza bicolor, Rhus copallina, Rudbeckia hirta,*

Notes: polylectic; nests in dead, sound privet; flies throughout season
**Xylocopa virginica virginica** (Linnaeus)

Distribution: New England, south to central FL, west to NE, KS, OK and eastern TX

LA Collection Records: *Agalinis tenuifolia, Bidens aristosa, Chamaecrista fasciculata, Clethra alnifolia, Croton capitatus, Cyrilla racemiflora, Eryngium yuccifolium, Euthamia leptocephala, Helianthus heterophyllus, H. hirsutus, Liatris squarrosa, Pycnanthemum albescens, Rudbeckia hirta, Trachelospermum diffurm*

Notes: polylectic; nests in dead, sound wood of many tree species, including structural timbers; this tendency makes it something of a pest; flies throughout season (Ashmead 1894; Hurd 1958; Krombein 1967; Grissell 1975; Gerling & Hermann 1978; Hurd 1978; Barrows 1983; Gerling et al. 1989)

**Ceratina cockerelli** H. S. Smith

Distribution: SC, GA and FL, west to TX

Notes: polylectic; nests in dead, cut stems of sea-oats; flies from Jan to Sep (Daly 1973)

**Ceratina calcarata** Robertson

Distribution: Que. to GA, west to Man., south to TX

Notes: polylectic; nests in borings in sumac pith; females similar to *C. dupla* and require males for positive identification; solitary; flies from Mar to Oct (Rau 1928; Daly 1973; Ginsberg 1985; Johnson 1988); state record

**Ceratina strenua** Smith

Distribution: NY to GA, west to WI, MO, KS, OK and TX

Notes: polylectic (Daly 1973); state record

**Nomada erigeronis** Robertson

Distribution: LA, KS and NE, northeast to MA
LA Collection Records: *Rudbeckia hirta*

Notes: cleptoparasitic; range extension and state record

*Nomada aff. lehighensis* Cockerell

Distribution: MI to NS, south to GA

Notes: cleptoparasitic; flies from Mar to Jul; range extension and state record

*Doeringiella donata* (Smith)

Distribution: WI to New England states, south to GA and LA

LA Collection Records: *Helianthus angustifolius*

Note: cleptoparasitic on nests of *Melitoma taurea* Say; flies from Jul to Oct (Robertson 1914); range extension and state record

*Doeringiella lunatus concolor* (Robertson)

Distribution: MN to PA, south to FL and TX

Notes: cleptoparasitic on nests of *Melissodes bimaculata bimaculata* (Lepeletier); flies from May to Sep

*Doeringiella sp. 1*

Distribution: unknown

LA Collection Records: *Rudbeckia hirta*

Notes: cleptoparasitic

*Epeolus lectoides* Robertson

Distribution: IL to New England states, south to GA and LA

LA Collection Records: *Rudbeckia hirta*

Notes: cleptoparasitic; flies from Jun to Sep; range extension and state record
**Epeolus scutellaris Say**

Distribution: MN to NS, south to TX and NC

LA Collection Records: *Helianthus angustifolius*

Notes: cleptoparasitic; flies from Jun until Sep; state record

**Holcopasites calliopsidis (Linsley)**

Distribution: MT to NY, south to TN, TX and AZ

Notes: cleptoparasite on nests of *Calliopsis andreniformis* Smith and *Pseudopanurgus* sp; flies from Jun to Aug (Hefetz et al. 1982); state record

**Diadasia afflicta (Cresson)**

Distribution: NM, TX and LA, north to NE

LA Collection Records: *Callirhoe papver*

Notes: genus occurs entirely in southwestern United States; oligolectic on *Callirhoe*; flies from Apr and May; occurs in grasslands and open woodlands; nests in areas of hard-packed, fine, sandy loam (Lutz & Cockerell 1920; Linsley & MacSwain 1957; Adlakha 1969; Snyder & Barrows 1976; Neff et al. 1982; Neff & Simpson 1992); range extension and state record

**Melitoma taurea (Say)**

Distribution: NJ to FL, west to IL, KS, MO and LA

Notes: oligolectic on *Ipomoea*; alights on water; nests in compact, clay soil; cleptoparasite is *Doeingiella donata* (Smith); flies from Jun to Sep (Ashmead 1894; Robertson 1914; Lutz & Cockerell 1920; Davis 1926; Linsley & MacSwain 1958; Michener 1975); range extension and state record

**Ptilothrix bombiformis (Cresson)**

Distribution: KS and IL to NJ, south to TX and FL
LA Collection Records: *Cyrilla racemiflora, Hibiscus aculeatus, Hypericum cistifolium*

Notes: oligolectic on *Hibiscus*; nests in hard, clay soils; alights on water; solitary, but nests in dense aggregations; flies from Jun to Aug (Grossbeck 1911; Knab 1911; Robertson 1914; Robertson 1918; Lutz & Cockerell 1920; Robertson 1925; Davis 1926; Rau 1930; Michener 1947; Rust 1980; Michener 2000)

*Eucera dubitata* (Cresson)

Distribution: MN to PA, south to SC and TX

LA Collection Records: *Rubus argutus?*

Notes: flies from Apr to Jun; state record

*Eucera fulvohirta* (Cresson)

Distribution: NC to GA and LA

Notes: flies from Apr to May (Lutz & Cockerell 1920); range extension and state record

*Melissodes boltoniae* Robertson

Distribution: PA to MN, south to FL and TX

LA Collection Records: *Aster dumosus*

Notes: oligolectic on Asteraceae; flies from Aug to Sep (Lutz & Cockerell 1920; LaBerge 1961)

*Melissodes dentiventris* Smith

Distribution: Southeastern Can., MA, west to KS, south to GA and TX

LA Collection Records: *Aster adnatus, A. dumosus, Helianthus hirsutus*

Notes: oligolectic on Asteraceae especially Astereae and Heliantheae; flies from Sep to Oct (Lutz & Cockerell 1920; LaBerge 1961); state record
Melissodes tincta LaBerge

Distribution: MN and MI, south to TX and FL

LA Collection Records: Helianthus angustifolius, H. heterophyllus, H. hirsutus,

Notes: oligolege of fall Asteraceae; flies from Aug to Dec (LaBerge 1961)

Melissodes wheeleri Cockerell

Distribution: AZ to LA and north to ND and MI

Notes: oligolectic on Asteraceae; flies from Apr to Oct (Lutz & Cockerell 1920; LaBerge 1961)

Melissodes (Eumelissodes) sp. 1

Distribution: unknown

Melissodes (Eumelissodes) sp. 2

Distribution: unknown

Melissodes bimaculata (Lepeletier)

Distribution: ND south to northeastern NM, east to ME in the north and to northern FL

LA Collection Records: Helianthus hirsutus, Lespedeza bicolor

Notes: polylectic; observed nesting in an open field under a flat stone; flies from May to Oct (Ashmead 1894; Lutz & Cockerell 1920; LaBerge 1956); special interest is collection of a specimen that keys to southern Florida endemic subspecies Melissodes bimaculata nulla; its presence in Louisiana should be investigated further

Melissodes communis communis Cresson

Distribution: southeastern AZ north to ND and east to Atlantic and Gulf Coast

LA Collection Records: Helianthus hirsutus

Notes: polylectic; flies from Jun to Aug (Lutz & Cockerell 1920; LaBerge 1956)
**Melissodes comptoides** Robertson

Distribution: NJ to FL, west to SD, CO and AZ

LA Collection Records: *Chamaecrista fasciculata*

Notes: polylectic; flies from Apr to Oct (Lutz & Cockerell 1920; LaBerge 1956)

**Melissodes tepaneca** Cresson:

Distribution: KS, IL and NC, south through TX and Mex. to Panama

Notes: polylectic; flies from late Mar to Nov (Lutz & Cockerell 1920; LaBerge 1956)

**Melissodes (Melissodes) sp.**

Distribution: unknown

**Svastra aegis** (LaBerge):

Distribution: TX to FL, north to NC

LA Collection Records: *Coreopsis tripteris, Helianthus simulans*

Notes: flies from Jul to Oct (LaBerge 1956)

**Svastra atripes atrimitra** LaBerge

Distribution: NJ south to FL, west to LA

LA Collection Records: *Chamaecrista fasciculata*

Notes: polylectic; does not appear to collect pollen from Asteraceae; restricted sandy soils; nests in aggregations; flies from Jul until Nov (LaBerge 1956; Cane 1995)

**Svastra atripes atripes** (Cresson)

Distribution: IL, MO and LA, west to NM and CO

Notes: may prefer sandier soils; flies from Mar to Oct (Lutz & Cockerell 1920; LaBerge 1956)
**Svastra petulca petulca** (Cresson)

Distribution: eastern TX north through KS to IL, east to FL, and north to NJ

LA Collection Records: *Coreopsis tripteris, Helium flexuosum, Helianthus hirsutus*

Notes: flies from Apr to Sep (Lutz & Cockerell 1920; LaBerge 1956)

**Anthophora abrupta** Say

Distribution: NY to FL, west to MI, south to LA and TX

LA Collection Records: *Ilex glabra*

Notes: nests in dense aggregations in clay embankments or adobe structures; flies from Mar to Sep (Lutz & Cockerell 1920; Norden & Scarbrough 1982; Schneider 1982; Brooks 1983; Norden 1984; Stone 1994; Batra & Norden 1996; Batra 1997)

**Bombus pennsylvanicus** (Degeer)

Distribution: Que. and Ont., south to FL, west to MN, SD, NE, CO and NM

LA Collection Records: *Chamaecrista fasciculata, Cirsium horridulum, Salvia azurea, Vernonia gigantea*

Notes: nests under a heavy mat of grass on or beneath the surface of the ground; recorded nesting in an abandoned squirrel habitation; social; polylectic; flies throughout season (Rau 1924; Milliron 1967; Williams 1994); state record

**Bombus fraternus** (Smith)

Distribution: NJ to FL, west to ND, SD, NE, CO and NM

Notes: flies from Mar to Nov (Lutz & Cockerell 1920; Williams 1994)

**Bombus bimaculatus** Cresson

Distribution: Ont. and ME, south to FL, west to IL, KS, OK and LA

LA Collection Records: *Pycnanthemum albensens, Trachelospermum difforme*
Notes: flies from Mar to Sep (Lutz & Cockerell 1920; Williams 1994)

**Bombus impatiens** Cresson

Distribution: Ont. and ME, south to FL, west to MI, IL, KS and LA

LA Collection Records: *Agalinis tenuifolia, Ceanothus americanus, Centrosema virginianum, Chamaecrista fasciculata, Cyrilla racemiflora, Eryngium yuccifolium, Eupatorium rotundifolium, Euthamia leptosephala, Helianthus heterophyllus, H. hirsutus, Hydrolea ovata, Hypericum cistifolium, Lespedeza bicolor, Liatris squarrulosa, Lobelia floridana, Pycnanthemum albens, Rhexia alifanus, Tephrosia spicata*

Notes: social; nests in sandy locations; flies from Mar to Nov (Lutz & Cockerell 1920; Plath 1927; Townsend 1951; Williams 1994)

**Bombus griseocollis** (Degeer)

Distribution: Que. south to FL, west to BC, WA, OR and northern CA

LA Collection Records: *Ceanothus americanus, Chamaecrista fasciculata, Cirsium horridulum, Cyrilla racemiflora, Eupatorium rotundifolium, Hibiscus aculeatus, Hypericum cistifolium, Lespedeza bicolor, Liatris pycnostachya, L. squarrosa, Pycnanthemum albens, Rhexia alifanus, R. lutea, Rudbeckia hirta*

Notes: social; polylectic; known to daub nest intruders with honey as a defense; flies from Feb to Aug (Fuller & Plowright 1986; Williams 1994); state record

**Apis mellifera** Linnaeus

Distribution: worldwide

LA Collection Records: *Ceanothus americanus, Chamaecrista fasciculata, Coreopsis linifolia, Cyrilla racemiflora, Diodia teres, grass, Helianthus angustifolius, H. heterophyllus, H. hirsutus, Hydrolea ovata, Liatris aspera, L. pycnostachya, Rhus copallina, Rubus argutus?
Notes: non-native; social with persistent colonies in cavities; polylectic; flies throughout season (Lutz & Cockerell 1920; McNally & Schneider 1996)
APPENDIX C: ABUNDANCE OF BEE SPECIES BY SITE AND YEAR IN EASTERN LOUISIANA LONGLEAF PINE SAVANNAS


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APPENDIX D: SUMMARY OF BEE BIOLOGY, DISTRIBUTION, AND RARITY FOR SPECIES COLLECTED IN EASTERN LOUISIANA LONGLEAF PINE SAVANNAS

Species are listed phylogenetically. (R=rare [1-2 individuals]; U=uncommon [3-5]; C=common [6-20]; VC=very common [21-50]; A=abundant [>50]; E=eastern; SE=southeastern; S=southern; Co=coastal (Atlantic); Ce=central; G=global; NA=North America; NE=northeastern; Cl=cleptoparasite; O=oligolege; P=polylege)

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<th>Species</th>
<th>Upland Rarity</th>
<th>Flatwoods Rarity</th>
<th>Range</th>
<th>Minor Range Extension</th>
<th>State Record</th>
<th>Major Range Extension</th>
<th>Host Use</th>
<th>Host &amp; Habitat Preferences</th>
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<th>Major Range Extension</th>
<th>State Record</th>
<th>Recorded Flight</th>
<th>Observed Flight in LA</th>
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<th>Host &amp; Habitat Preferences</th>
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VITA

Growing up in Seattle, Washington, Chanda Bartholomew was always interested in the outdoors, especially the insects. Upon graduation from Garrard County High School in Lancaster, Kentucky, she enrolled in the entomology program at the University of Kentucky, where she graduated in May of 2001. While at the University of Kentucky, she worked as an undergraduate in an entomology lab. Upon completion of her bachelor’s degree, she continued in entomology, pursuing a master’s degree at Louisiana State University. She plans to graduate August 2004.