The Ant (Hymenoptera: Formicidae) Fauna of Black Belt Prairie Remnants in Alabama and Mississippi

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Abstract - Extensive areas of prairie were once found in the southeastern United States; however, in the last 200 years much of this habitat type has been destroyed. The largest of these prairie regions, the Black Belt Prairie, extends through portions of Alabama, Mississippi, and Tennessee. The ant fauna of these endangered grasslands has not been well documented; therefore, a survey was initiated, with collections made at 23 Black Belt Prairie remnants in Alabama and Mississippi during a four-year period. A total of 53 ant species, in six subfamilies and 25 genera were collected. Six exotic species were collected, and 11 species were found to be restricted to trees within the prairie, resulting in 36 species that likely represent the true prairie fauna.

Introduction

> "In the fields the grass is short, no bush; the soil in places is a lead color, yellow underneath, within the abode of the ants, and very stiff."
>
> - Benjamin Hawkins (1938) on traveling through a Black Belt Prairie in Lowndes County, AL in 1798–99.

Prior to European settlement, the southeastern United States had several regions dominated by grasslands or prairie (DeSelm and Murdock 1993, Peacock and Schauwecker 2003). One such region, called the "Black Belt," extends in an arc from McNairy County, TN to Russell County, AL. Instead of being a continuous swath of open grassland, the historic landscape of the Black Belt was a heterogeneous landscape of prairies and several types of forest (see Barone 2005 for extensive references). Surveys conducted by the General Land Office in the 1830s suggest that prairies once covered at least 144,000 hectares of the Black Belt (Barone 2005). Since that time, more than 99% of these prairies have been lost to agriculture and urban development (Noss et al. 1995). Remaining remnants of prairie are threatened by further development, erosion, and the encroachment of *Juniperus virginiana* L. (Cupressaceae) (Eastern Red Cedar), the latter probably as a result of fire suppression. The Mississippi Natural Heritage Program gives Black Belt Prairie remnants a ranking of S1, meaning they are "critically imperiled" within the state due to extreme rarity or factors making their biota vulnerable to extirpation (Mississippi Museum of Natural Science 2005).

The presence of the prairies in the Black Belt is due, in part, to the region's distinctive soils that are derived from a Selma chalk bedrock

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that was formed from Cretaceous marine deposits laid down when the Mississippi embayment occupied the region (Lowe 1921). These calcareous loamy soils have a pH in the 7.5–8.5 range, and in some areas have a dark color, hence the name "Black Belt." However, much of the land with these rich, dark soils has been converted to agriculture, and remaining prairie remnants are often found on marginal light gray soils where the chalk is close to the surface.

Today, small remnants of these prairies may be found along roadsides, fencerows, gas, rail, and powerline right-of-ways, and on marginal lands not suitable for agriculture. These prairie remnants support a diverse and distinct flora and fauna, including species of plants and insects that otherwise are found primarily in the Great Plains as well as several endemic species of insects. These disjunct distributions, along with endemic species and fossil evidence, suggest that Black Belt prairies may have had a prehistoric link to the Great Plains and served as a refugium for the prairie biota during the last glacial period (Brown 2003).

Floristic surveys of Black Belt prairie remnants have revealed a distinct plant community similar to that of the Great Plains of central North America, with several rare or critically imperiled plants (Leidolf and McDaniel 1998, Schuster and McDaniel 1973). This community is dominated by grasses (Poaceae), with *Andropogon gerardii* Vitman (Big Bluestem)*, Bouteloua curtipendula* (Michx.), *Panicum virgatum* L. (Switch Grass), *Schizachyrium scoparium* (Michx.) (Little Bluestem), *Sorghastrum nutans* (L.) Nash (Indian Grass), and *Sporobolus vaginiflorus* (Torr. ex Gray) being the most common. The most prominent forbs include those in the Asclepidaceae (*Asclepias* spp. [milkweeds]), Asteraceae (*Chrysopsis camporum* (Green) [Golden Aster], *Ratibida pinnata* (Vent.) [Prairie Coneflower], *Liatris* spp. [blazing stars], *Silphium laciniatum* L. [Compass Plant], *S. terebinthinaceum* (Jacq.) [Prairie Rosinweed]), and Fabaceae (*Dalea candida* (Mich.) [White Prairie Clover] and *D. purpurea* Vent. [Purple Prairie Clover]). Barone and Hill (2007) provide a more complete floral description.

Previous faunal surveys of these prairies have been limited to a few taxa, but they have revealed an interesting fauna, including: 1160 species of moths, with 57 disjunct and one endemic species; 33 species of Acrididae (grasshopper), with one disjunct species; four disjunct species of Cerambycidae (long-horned beetle), two of which feed on *Asclepias* spp. (milkweed); an endemic Carabidae (flightless ground beetle); and a disjunct species of Apidae (bee) that forages only on Purple Prairie Clover (R.L. Brown, unpubl. Data; Brown 2003; Hill 2007; Landry and Brown 2005; MacGown and Schiefer 1992; Schiefer 1998).

Ants are typically the most dominant and influential force in terrestrial ecosystems, and as such, may be among the most promising groups of animals for inclusion in community-based studies due to their contributions to ecosystem function (Agosti et al. 2000, Hölldobler and Wilson 1990). They directly and indirectly affect faunal and floral groups by predation, scaveng-

ing, tending homopterans, protecting certain plants, dispersing seeds, and aiding in nutrient and soil turnover (Agosti et al. 2000, Gorb and Gorb 2003, Hölldobler and Wilson 1990, Shultz and McGlynn 2000, Wheeler 1910). Ants are also of interest because of the putative deleterious effects caused by non-native species, especially the imported fire ants (*Solenopsis invicta* Buren, *S. richteri* Forel, and their hybrid *S. invicta* x *richteri*), which negatively affect human endeavors and may reduce biodiversity in the communities they invade (Gotelli and Arnett 2000, Kaspari 2000, Morris and Steigman 1993, Porter and Savignano 1990, Vinson 1997). Given the ecological importance of ants, documenting the ant fauna of endangered ecosystems, such as the Black Belt Prairie, could provide useful information for guiding current management and future conservation/restoration projects in those systems.

Methods

Study sites throughout the Black Belt were sampled to ensure that a comprehensive picture of the fauna, including any latitudinal variations, was developed (Fig. 1). Sites were chosen based on their accessibility and relative floral intactness. The level of past disturbance did vary, but most of the sites experienced relatively little human disturbance during this study. Sites experiencing disturbance consisted of several roadside prairies being partially mowed, and the site in the Tombigbee National Forest was burned during the early spring of each sample year. Almost all of the sites are within or near

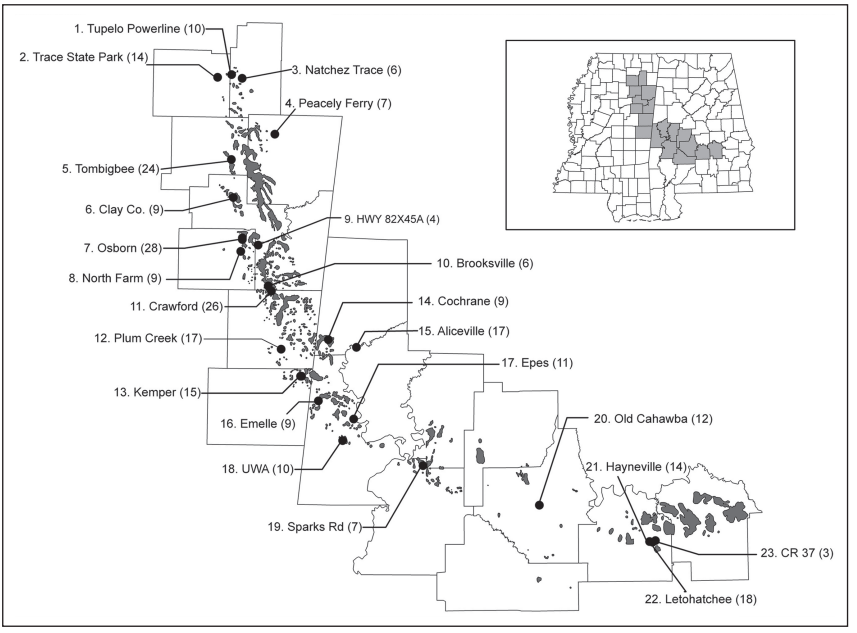

Figure 1. Map showing historical prairie remnants, based on General Land Office Surveys in the 1930s (from Barone 2005), location, site number, and number of ant species collected during this survey.

the boundaries of known historic prairies, as described by Barone (2005) based on General Land Office plat maps from the 1830s and 1840s (Fig. 1).

Twenty-three prairie remnants (Fig. 1, Table 1) were surveyed from June 2003 through July 2007. Three sites–Crawford, Osborn, and Tombigbee National Forest–were studied more intensively during the initial phase of the study. These sites were sampled twice a month from June to October in 2003 and from April to December in 2004, then revisited every three months throughout the study period. The remaining sites were sampled monthly from April to October for at least one year subsequent to their discovery. After the first sampling year of a site, it was re-visited several times across seasons and years to ensure that it had been sampled effectively.

From June to October, 2003 and from April to December, 2004, ants were collected at the Crawford, Osborn, and Tombigbee sites using a variety of collecting techniques including baiting, hand collecting, and pitfall traps. Hill et al. (2008) provide a more detailed explanation of the procedures used at these sites. On subsequent dates, these sites as well as the other 20 sites were sampled by baiting with cookies, (Keebler Sandies Pecan Shortbread®), by sifting through soil, grass duff, and cedar litter, and by active searching. Searching consisted of looking for nests and foragers on the open ground and on or inside stems and other plant parts. As Eastern Red Cedars are common components of unburned prairies, and often the main target of management activities, an effort was also made to collect ants that occurred on these trees

Table 1. List of study sites with their latitude and longitude.

Site	County	Latitude, longitude
Mississippi		
Tupelo Powerline	Lee	34°14'26"N, 88°48'39"W
Trace State Park	Pontotoc	34°15'24"N, 88°53'12"W
Natchez Trace National Park	Lee	34°15'24"N, 88°45'22"W
Peacely Ferry Road	Monroe	34°00'20"N, 88°34'23"W
Tombigbee National Forest	Chickasaw	33°55'39"N, 88°51'18"W
Clay County	Clay	33°43'52"N, 88°49'44"W
Osborn	Oktibbeha	33°30'41"N, 88°44'08"W
MSU North Farm	Oktibbeha	33°27'43"N, 88°45'31"W
HWY 82 X 45A	Lowndes	33°29'17"N, 88°39'38"W
Brooksville	Noxubee	33°15'52"N, 88°33'19"W
Crawford	Lowndes	33°18'01"N, 88°36'38"W
Plum Creek	Noxubee	33°06'01"N, 88°31'14"W
Kemper County	Kemper	32°52'24"N, 88°29'28"W
Alabama		
Cochrane Recreational Area	Greene	33°04'21”N, 88°15'52"W
Aliceville	Pickens	33°14'09”N, 88°24'15"W
Emelle	Sumter	32°46'38"N, 88°18'50"W
Epes	Sumter	32°41'49"N, 88°07'11"W
University of West Alabama	Sumter	32°36'17"N, 88°11'35"W
Sparks Road	Marengo	32°29'18"N, 87°44'44"W
Old Cahawba	Dallas	32°18'44"N, 87°07'33"W
Hayneville	Lowndes	32°08'51"N, 86°32'30"W
Letohatchee	Lowndes	32°08'29"N, 86°30'35"W
County Road 37	Lowndes	32°08'56"N, 86°29'44"W

and in their litter to investigate their effect on ant species composition in the prairie. Specimens were collected in 90% ethanol, then were pinned and labeled, and identified. Ants were also sorted from stored pitfall trap samples taken by the Mississippi Entomological Museum (MEM) at the Osborn and Crawford sites in the early 1990s. Voucher specimens have been deposited in the MEM.

Results

A total of 52 ant species including the hybrid fire ant *Solenopsis invicta* x *richteri,* representing 6 subfamilies and 25 genera, were collected (Appendix 1). The most diverse subfamilies included the Myrmicinae with 30 species and the Formicinae with 12 species. The most diverse genera were *Pyramica* with seven species and *Pheidole* with five species. Six exotic species were collected including the imported fire ants (*S. invicta* and *S. invicta* x *richteri*), *Brachymyrmex patagonicus* Mayr, *Cyphomyrmex rimosus, Pyramica margaritae*, and *P. membranifera*. Eleven native species were found to only be associated with cedar or other trees within the remnants. The remaining 35 native species likely represent the true prairie ant fauna. Imported fire ants were collected at all the sites, with the hybrid fire ant, *S. invicta* x *richteri,* collected at the sites from Plum Creek northward (16 sites), while the red imported fire ant *S. invicta*, was collected at the sites south of the Plum Creek site (7 sites). The native species collected at the most sites were *Monomorium minimum* (23 sites), followed by *Forelius mccooki* (17 sites), and *Pheidole tysoni* and *Solenopsis c.f. molesta* (16 sites both). Two species found in this survey, *Hyponera inexorata* and *Pheidole lamia*, represent new state records for Alabama.

The number of species at individual sites ranged from a low of three at the County Road 37 site, a small (0.011 ha) roadside remnant, to highs of 28, 26, and 24, represented by the Osborn, Crawford, and Tombigbee sites, respectively. All three of these latter remnants are found in Mississippi and are large (more than 6 ha.) and protected. The Letohatchee site, a roadside remnant (0.11 ha), was the most diverse site in Alabama with 18 species. The mean number of species per site was 12.35, and 10 of the sites contained at least this many species.

Discussion

The results of this survey indicate that Black Belt Prairie remnants support a relatively diverse ant fauna. Typically, the most abundant ant species within a remnant are *Forelius mccooki* (McCook) followed by several Myrmicines such as *Monomorium minimum* (Buckley), imported fire ants (*Solenopsis* spp.), *Solenopsis* c.f. *molesta* (Say), *Pheidole tysoni* Forel, and *Crematogaster lineolata* (Say); although species composition and abundance varies depending on the amount of disturbance (based on area, native/exotic plant ratio, etc.) at the site, with imported fire ants apparently being more dominant

on highly disturbed sites (J.G. Hill, pers. observ.). The ant fauna of Black Belt Prairies are similar to that of the southern portion of the tall grass prairie biome of Arkansas, Texas, and Oklahoma where the subfamily Myrmicinae and the genus *Forelius* also make up dominant components of the fauna (Trager 1998; M. Warriner and J.G. Hill, unpubl. data). However, Hill et al. (2008) indicated that the ant fauna of prairie remnants was significantly different and more diverse than pastures on similar soils in the Black Belt of Mississippi, and that prairie remnants supported a significantly different but less diverse ant fauna than the forests of the region. The ant fauna of Black Belt Prairies also differs from the fauna of other naturally occurring open habitats in the Southeastern United States, such as coastal dunes or sandhill/pine savannah habitats, based on faunal lists from these habitats compiled from MacGown and Hill (2007), Hill and MacGown (2008), and Graham et al. (2004). Notable ants that occur on Black Belt prairie remnants include *Dolichoderus pustulatus*, *Polyergus montivagus*, *Hypoponera inexorata*, *Pyramica bimarginata*, *Pheidole lamia*, and *Pheidole pilifera*. *Dolichoderus pustulatus* was found apparently nesting in a clump of Indian Grass at the Letohatchee site. Specimens of *D. pustulatus* in the MEM were collected from the Osborn and Crawford sites in pitfall traps run in the late 1990s, but no recent specimens were found at those sites despite extensive searches. *Polyergus montivagus* was collected in pitfall traps from the Tombigbee prairie site (Hill and Brown 2005). *Hypoponera inexorata* is a subterranean species that can be collected by sifting soil taken from the base of grass clumps or cedar trees. This species was not listed as occurring in Alabama in MacGown and Forester (2005), thus the collections made during this survey from the Aliceville, Sparks Road, and Old Cahawba sites represent new state records for Alabama. Smith (1927) lists *H. inexorata* from A and M College, MS (now Mississippi State University), the campus of which lies at the edge of the Black Belt and still contains prairie remnants. One colony of this species, containing several queens, was found underneath a hybrid fire ant colony. *Pyramica bimarginata* was found in pitfall samples taken in the early 1990s from the Osborn site, and despite extensive searches during this survey no additional specimens were discovered. Three specimens of *Pheidole lamia* were collected at the Aliceville site, a small (0.107 ha) roadside remnant. Specific microhabitat information for this collection could not be determined; however, this species has been found to inhabit the soil in large stands of Indian Grass and Big Bluestem in the similar Jackson Prairie further south in Mississippi. (J.G. Hill, pers. observ.). This species is a new state record for Alabama based on MacGown and Forester (2005). *Pheidole pilifera* was only found at the three largest and most floristically intact sites—Crawford, Osborn, and Tombigbee—indicating that this species may inhabit only the less disturbed remnants. Hill (2006) reported observations of this species feeding on seeds of Switch Grass during the fall of 2005; however, in the fall of 2006, *P. pilifera* was observed ignoring seeds of that species completely in favor of seeds of an undetermined grass a few weeks earlier than the 2005 observations.

Several ant species inhabit the soil and litter that accumulates around the bases of clump grasses such as Bib Bluestem, Switch Grass, Little Bluestem, and Indian Grass. These include *Brachymyrmex depilis*, *Myrmecina americana*, *Pyramica creightoni*, *P. dietrichi, P. margaritae*, *P. membranifera*, *P. talpa*, and *Pheidole lamia*. Most of these species are typically found in forest leaf litter; however, they also seem to be adapted to this microhabitat of open prairies. All of the above mentioned litter-dwelling species were absent from the Tombigbee prairie, which is burned in entirety annually resulting in the loss of the microhabitat that these species require. Most of these species may also be found in the litter under Eastern Red Cedar trees, but are not limited to it.

Seven species were limited to inhabiting the litter or soil under Eastern Red Cedar trees, including *Camponotus castaneus*, *Proceratium pergandei*, *Pyramica ornata*, *Strumigenys louisianae, Solenopsis picta*, *Aphaenogaster carolinensis* Wheeler, and *Temnothorax curvispinosus*. Two ant species were limited to other species of trees, *Camponotus decipiens* on *Diospyros virginiana* L. (Ebenaceae) (Persimmon), and *Camponotus mississippiensis* on *Fraxinus americana* L. (Oleaceae) (White Ash). *Crematogaster ashmeadi* occurred on both cedar and ash trees. A single alate queen of *Camponotus impressus*, a species typically associated with trees, was collected in open prairie by J. Trager and J.G. Hill on 3 June 2003. No other specimens of this species were collected, suggesting that this individual was possibly migrating through this habitat.

Exotic ant species reached their highest population densities in remnants that had anthropogenically disturbed areas or were wholly disturbed. In remnants where only a portion of the area is disturbed, exotic ants primarily reached their highest densities in the disturbed areas. An exception to this may be *Brachymyrmex patagonicus,* which is a recent invader to these remnants, due to its range expansion (MacGown et al. 2007). *Brachymyrmex patagonicus* seemingly reached one of the remnants (site 13) during the course of this study. It was likely already established at the other three sites (21, 22, and 23); although it was not found in the initial two surveys of site 22, it was extremely abundant throughout the site on the third survey.

In conclusion, the faunal list produced in this study should provide some baseline data on the ant species composition of prairies for current and future conservation and restoration efforts. Such efforts are important given the endangered status of Black Belt Prairie remnants. Future investigations will focus on relatedness of individual remnants, how various habitat variables (e.g., plant diversity and remnant size) influence ant assemblages, and the relationship of grasslands in the southeastern United States to those of the Great Plains.

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Appendix 1. The following list is arranged by subfamily, tribe, and genus according to Bolton (2003). Names follow Bolton (1995), except *Dorymyrmex*, which follows Snelling (1995); *Pyramica*, which follows Bolton (2000), *Pheidole*, which follows Wilson (2003), and Polyergus, which follows Smith (1947). Following species names is the site number at which they occurred. The superscript [T] denotes a species that is associated with trees, an * denotes that this species was found in the collection of the MEM from pitfall traps run in the early 1990s, and **Exotic** indicates a species not native to the United States based on Deyrup (1992), McGlynn (1999), and Deyrup et al. (2000).

Family Formicidae
- Subfamily Dolichoderinae
  - *Dolichoderus pustulatus* Mayr: Sites 7*, 11*, and 22
  - *Dorymyrmex smithi* McCook: Sites 17 and 21.
  - *Forelius mccooki* (McCook): Sites 2, 3, 4, 5, 6, 7, 10, 11, 12, 14, 15, 16, 17, 18, 20, 21, and 22
  - *Tapinoma sessile* (Say): Sites 3, 8, 10, and 11
- Subfamily Formicinae
  - *Lasius neoniger* Emery: Site 11
  - *Brachymyrmex depilis* Emery: Sites 2, 14, 15, 20, 22
  - *Brachymyrmex patagonicus* Mayr: Sites 13, 21, 22 and 23. **Exotic**
  - *Paratrechina arenivaga* (Wheeler): Sites 5, 7, 11, 12, 14, and 16
  - *Paratrechina vividula* (Nylander): Sites 1, 2, 3, 4, 7, 8, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, and 22
  - *Prenolepis imparis* Emery: Sites 5 and 12
  - *Camponotus castaneus* (Latreille) [T]: Sites 5, 7, and 11
  - *Camponotus decipiens* Emery [T]: Sites 5 and 15
  - *Camponotus impressus* (Roger) [T]: Site 7
  - *Camponotus mississippiensis* Smith [T]: Sites 12, 13, and 19
  - *Formica dolosa* Buren: Sites 1, 2, 4, 5, 12, 13, 15, 16, and 18
  - *Polyergus lucidus montivagus* Wheeler: Site 5
- Subfamily Pseudomyrmecinae
  - *Pseudomyrmex pallidus* (Smith): Sites 17, 20, and 22
  - *Pseudomyrmex seminole* Ward: Sites 20 and 21
- Subfamily Ponerinae
  - *Hypoponera inexorata* (Wheeler): Sites 6, 7, 13, 15, 19, and 20
  - *Hypoponera opaciceps* (Mayr): Sites 1, 11, 15, 16, 19, and 21
  - *Hypoponera opacior* (Forel): Sites 3, 5, 7, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, and 22
  - *Ponera pennsylvanica* Buckley: Sites 2, 4, 5, 7, 8, and 11
- Subfamily Proceratiinae
  - *Proceratium pergandei* (Emery) [T]: Site 7
- Subfamily Myrmicinae
  - *Pyramica bimarginata* (Wesson & Wesson): Site 7*
  - *Pyramica creightoni* (Smith): Sites 11, 12, and 22
  - *Pyramica dietrichi* (Smith): Sites 11, 14, and 17
  - *Pyramica margaritae* (Forel): Site 21. **Exotic**
  - *Pyramica membranifera* (Emery): Site 20. **Exotic**
  - *Pyramica ornata* (Mayr) [T]: Site 7
  - *Pyramica talpa* (Weber): Sites 7, 11, 12, 13, 17, and 22

Strumigenys louisianae Roger[T]: Sites 7, 8, and 11
Cyphomyrmex rimosus (Spinola): Sites 21 and 22. **Exotic**
Trachymyrmex septentrionalis (McCook): Sites 5, 7, 11
Monomorium minimum (Buckley): Sites1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, and 23
Solenopsis invicta Buren: Sites 16, 17, 18, 19, 20, 21, 22, and 23. **Exotic**
Solenopsis invicta x *richteri*: Sites 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15. **Exotic**
Solenopsis c.f. molesta (Say) : Sites 1, 2, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15, 18, 20, 21, and 22
Solenopsis picta Emery[T]: Site 7
Aphaenogaster carolinensis Wheeler[T]: Sites 2 and 11
Aphaenogaster flemingi Smith: Site 5
Aphaenogaster treatae Forel: Sites 5, 7, 11, and 15
Pheidole bicarinata Mayr: Sites 6, 12, 15, and 18
Pheidole dentata Mayr: Sites 1, 2, 5, 6, 7, 8, 11, 12, 15, and 22
Pheidole lamia Wheeler: Site 15
Pheidole pilifera Roger: Sites 5, 7, and 11
Pheidole tysoni Forel: Sites 1, 2, 4, 5, 6, 7, 8, 9, 11, 12, 13, 16, 18, 20, 21, and 22
Crematogaster ashmeadi Mayr[T]: Sites 7 and 13
Crematogaster lineolata (Say): Sites 2, 5, 6, 7, 11, 15, 17, 21, and 22
Crematogaster missuriensis Emery: Sites1, 5, 8, 11, 12, 13, and 17
Crematogaster pilosa Emery: Sites 5, 21, and 22
Temnothorax curvispinosus (Mayr)[T]: Sites 7, 12, and 15
Temnothorax pergandei (Emery): Sites 2, 5, 6, 7, and 11
Myrmecina americana Emery: Sites 5, 7, 11, 13, 18, 20, and 22