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THE NATURAL HISTORY OF THE ANTS OF MICHIGAN'S E. S. GEORGE RESERVE: A 26 YEAR STUDY

MARY TALBOT



MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 202

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ABSTRACT

The results of a 26-summer study of the ants on an 1146 acre (464 ha) natural history preserve in southeastern Michigan are presented. Habitat distribution and nest construction for each of the 87 species are recorded. The sites of collections of each species on the Reserve are shown on maps. In addition, records of colony populations, brood development and nuptial flights of many of the species are presented.

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PREFACE

Shortly before Mary Talbot died on 16 April 1990, she had her final manuscript, "Ants of the Edwin S. George Reserve, Livingston County, Michigan," sent to Professor Francis C. Evans, Emeritus Curator of the George Reserve. Because Professor Evans was no longer affiliated with the Reserve, he forwarded the manuscript to the Museum of Zoology, the administrative unit in which the Reserve is located.

After some time the manuscript was sent to me to evaluate. It was complete except for the content on the species of *Myrmica*, of which no information or records had been provided. In addition, the tables accompanying the manuscript were handwritten and required organization and typing. Mary had previously supplied the Reserve with a set of maps showing the distribution of collections of all species except those of *Myrmica*. She had, however, prepared draft maps of the distributions of three *Myrmica* species (*M. incompleta*, *pinetorum*, and *punctiventris*, species easily recognized). The manuscript had annotations in pencil and needed some editorial adjustments, but it would be publishable if the section on *Myrmica* could be finished.

When Mary Talbot was writing this manuscript in the 1970s and 1980s, she knew that Andre Francoeur of the Universite du Quebec a Chicoutimi was preparing a revision of the genus *Myrmica*. She had sent him samples of her collections in 1975 and again in 1979. Francoeur responded with tentative identifications including four unnamed populations in the *M. spatulata* group. She wrote to him again in October of 1984 asking for clarification of the four populations. He wrote back a month later, reducing the four populations to two. Neither of these was *M. spatulata*; both evidently represented undescribed species. They are recorded herein as *M.* sp. 1 and *M.* sp. 2. Because of the uncertainty of the names of some of the Reserve species, she did not prepare a write-up of any of the *Myrmica* species. Further, she apparently didn't know what to do with the many samples of alate ants that she had collected from nuptial flights. Francoeur had informed her that most of those samples were of mixed species.

I wrote to Professor Francoeur about the names of the Michigan species of *Myrmica* (for another publication) and he readily complied. It was clear that some species were not cleanly separated and that one species, *Myrmica emeryana*, which previously had been reported from the Reserve (Talbot 1975), had been misidentified and was not present in the Reserve or the state of Michigan. Professor Francoeur also provided me with copies of the *Myrmica* records and notes that Mary had sent him to accompany her specimens. These included a list of collection sites (by ESGR grid numbers) with the collection numbers of samples collected in 1975. In addition, I found some other records from other years, mostly from the part of her collection that is at the University of Missouri at St. Louis. It was these notes and records that made it possible for me to extract a little information on each species and incorporate it into the manuscript and the maps.

In the spring of 1997 I had taken the manuscript to my house in Grand Forks, ND to do final editing and writing. Shortly thereafter, my wife and I had to evacuate our house because of a flood. Before leaving the house, I put the manuscript in the attic for safekeeping. Unfortunately, flood waters reached the attic and the manuscript was damaged. Work on the manuscript was then delayed because of the press of other matters.

In the summer of 1999 I returned to the editing of the manuscript. By scanning good pages to my computer and by retyping other pages, I prepared the final version. Bruce D. Worden at the Museum of Zoology revised the old map of the Reserve and prepared a new version on computer. He also carefully transferred the dots from Mary's maps to the proper location on the computer maps. The maps included in this publication are the product of that effort and demonstrate the success of the operation.

Since the time when Mary prepared this manuscript, Barry Bolton (1995) has prepared a listing of the world species of ants. His work has changed the names of several of the species that occur on the Reserve. In such cases, I made the correction. However, he also changed the authors, in some cases giving authorship to the first individual who used the new combination properly, rather than the individual who first described that taxon. Although technically correct by the Rules of Zoological Nomenclature, his changes unnecessarily destroyed easily recognizable connections with the taxonomic past. I have ignored all such changes.

Mary's publication is able to stand alone, but I thought it would be appropriate to have an appraisal of her impact on myrmecology and include it with this publication. I have prepared this, which appears in the appendix.

When I was seeking records from Mary's collection and/or notes, I learned that part of her collection had been retrieved from a dumpster and that Professor James Hunt of the University of Missouri at St. Louis knew the story. I contacted him and he agreed to prepare a short note documenting the recovery of her collection. It, too, appears in the appendix.

The original Talbot manuscript and all records I have obtained for this project have been deposited in the Archives

at Lindenwood University. The binder of original maps detailing the locations of collections of each species has been deposited at the Division of Insects, Museum of Zoology, University of Michigan.

ACKNOWLEDGMENTS

I thank Andre Francoeur, Universite du Quebec a Chicoutimi, for identifying specimens of *Myrmica* and for supplying copies of Mary Talbot's records of collections and notes on *Myrmica*; Theodore J. Cohn, Adjunct Curator of Insects, Museum of Zoology, University of Michigan, for arranging for the preparation of new maps, for information searches in the Museum Library, and for editorial advice; Daniel R. Swanson, Museum of Zoology, University of Michigan, for editing and preparation of the manuscript; Bruce D. Worden, Museum of Zoology, University of Michigan, for preparing the new map and transferring locations of collections to the new maps; Ms. Abigail Alvarez, Museum of Zoology, University of Michigan, for assisting in preparation of the maps; Ms. Virginia Terry, archivist, Lindenwood University, for supplying information about Mary Talbot's activities at Lindenwood and for providing several photographs; Ms. Cara Gilgenbach, archivist, Denison University, for information on the Talbot family; and James H. Hunt, Professor of Biology, University of Missouri at St. Louis, for information on the recovery of the Talbot collection, for providing copies of notes of the old-field studies at the Reserve, and for providing access to the *Myrmica* specimens in the part of the Talbot collection that is housed there.

Paul B. Kannowski Adjunct Curator of Insects Museum of Zoology University of Michigan

PUBLICATIONS OF THE MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 202

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COVER ILLUSTRATION— *Smithistruma pergandei* (Emery), a resident ant species of the Edwin S. George Reserve. Photographed by April Nobile, used with permission, ©Antweb.org. Greenbrier Cove, Sevier Co., Tennessee.

THE NATURAL HISTORY OF THE ANTS OF MICHIGAN'S E. S. GEORGE RESERVE: A 26-YEAR STUDY

Mary Talbot1

INTRODUCTION

Ants are among the most important animal components of terrestrial ecosystems. Their habit of forming colonies in nests connects them to their habitats in very special ways. They are both mobile and fixed. Their nests tie the colonies to specific communities, but the workers' mobility as individuals enables the colonies to utilize resources at a distance. The permanence or semi-permanence of their nests and the longevity of the colonies in the community make ants ideal subjects for ecological and behavioral studies.

I came to the Edwin S. George Reserve in the summer of 1951 to study the ant populations on the old field that was the site of long-term research on community dynamics by Francis C. Evans. From that collaboration came two publications (Talbot 1953, 1954). While carrying out the old-field studies, I also undertook to find and identify all of the species of ants living on the Reserve. Some of the species that I located became the subjects of intensive research on flight behavior and/or colony populations. As my tenure at the Reserve grew, I found that I had accumulated records for a very large number of species for such a relatively small geographical area. I found a total of 87 species (Talbot 1975b) living in habitats ranging from the floating mat of sphagnum moss in the bog surrounding Hidden Lake to the dry sand of the blow-out area in the southeastern corner. It is the great diversity of habitats represented on the Reserve that provides for this unusual abundance of species.

My plan was to prepare a manuscript to document the habitat distribution, populations, and behavior of the species on the Reserve. It would be an extended documentation of what species occurred where and what these species were doing in their habitats.

This publication is the culmination of research during the 26 summers I spent at the Reserve (all but four summers between 1951 and 1980). Most fieldwork was finished by 1975. The first years were concerned primarily with habitat distribution of the species. Soon special interests developed, centering on populations, activities of slave-making ants, and flights of alates. Flights have been seen for 41 of the 87 species and flight dates established for six others.

No collections or observations were made before 2 June or after 3 October. Friends supplied a few records of flights in early spring or late fall. All times cited are Eastern Standard Time (EST). Flight records taken in later years when Michigan had Eastern Daylight Time were changed back to EST to correspond with earlier flight records.

The collecting places of each species have been recorded on grid maps of the Reserve. The originals of these maps have been deposited in the Museum of Zoology at the University of Michigan. Representations of these maps have been appended to this publication.

Material that has been previously published has been condensed and referenced in this report, while previously unpublished material has been presented in more detail.

There have been other studies of ant faunas of regions, such as counties, or of single ecological features, such as peat bogs; however, this study is different because of the length of time involved and of the diversity of habitats represented. It should provide a baseline for future researchers on ant behavior and ecology, not only on the George Reserve, but also elsewhere in the midwestern states and provinces. In addition, it should provide the basis for individuals to determine the effects of habitat changes on the ant fauna of the Reserve. Finally, the maps will enable researchers to quickly locate existing species, especially rare ones.

Study Area

The Edwin S. George Reserve is an area of approximately two square miles in the southwestern corner of Livingston County, Michigan. When established, the Reserve encompassed 1146 acres (464 hectares), and it was this size when I carried out my study. More recently, four small areas have been added to the Reserve bringing its size to 1457 acres (590 hectares). The original lands of the Reserve were purchased by Colonel Edwin S. George of Detroit in 1927 and 1928 and given to the University of Michigan in 1930 for the establishment of a natural history preserve. The Reserve is administered by the Museum of Zoology.

The Reserve is maintained in a natural condition with succession allowed to continue with only one component under control: the white-tailed deer population is reduced annually to maintain a sustainable level. During the study the forest margins have appreciably invaded adjacent fields.

The surface features of the Reserve are glacial in origin. The most prominent of these is the high ridge that extends from the northeast entrance to the center of the Reserve. This esker-like ridge separates the Big Swamp from the Big Woods. There are several prominent kettle holes, one of which is a consolidated bog, Buck Hollow. Much of the surface is gently undulating; many of these areas were cleared in the 1800s and placed in cultivation. The highest elevations (between 975 and

1000 ft. above sea level) are in the north central part and are represented mostly by old fields; the lowest elevations (below 900 ft. above sea level) are in the southeastern part that is occupied by the Big Swamp.

Uplands constitute almost three-fourths of the landscape. The upland soils are predominantly sandy loams. On the low areas the soils are organic, mainly mucks and peats, usually in thick deposits.

Three major types of habitats occur on the Reserve: woodlands, which cover about one-third of the uplands; old-fields, which cover the other two-thirds of the uplands; and wetlands. Woods, occupying the steep slopes and some of the upland, are predominantly of the oak-hickory type, mainly black oak (*Quercus velutina* Lam.) and hickory (*Carya ovalis* (Wang.) Sarg.), but a variety of other trees are scattered through them. Clusters of aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.) occupy some upland borders or more open spaces in the interior, and yellow birch (*Betula lutea* Michx.) and red maple (*Acer rubrum* L.) occur down near swamps. An understory is formed of young trees and shrubs such as dogwood (*Cornus* spp.) and witchhazel (*Hamamelis virginiana* L.). Tall blueberries (*Vaccinium* spp.) grow in low places.

The fields of the Reserve resulted from the clearing of the level to gently sloping areas in the 1800's, which was followed by the planting of crops. According to Cantrall (1943), cultivation ceased about 1900 and the fields reverted to grassland. These old fields are dominated by grasses, mainly Canada bluegrass (Poa compressa L.), poverty oatgrass (Danthonia spicata (L.) Beauv.), arrowfeather three-awn (Aristida purpurascens Poir.), big bluestem (Andropogon gerardii Vitman) and panic-grass (Panicum depauperatum Muhl.). These fields are dotted with many forbs such as goldenrod (Solidago spp.), blazing star (Liatris aspera Michx.), fleabane (Erigeron strigosus Muhl.), bush clover (Lespedeza spp.), wild bergamot (Monarda fistulosa L.) and hawkweed (*Hieraceum* spp.). The more barren spots contain patches of lichens and mosses together with bits of bare soil. Large areas are covered with bramble (Rubus spp.), while hawthorn (Crataegus spp.), red cedar (Juniperus virginiana L.) and common juniper (Juniperus communis L.) are widely spaced. Everywhere woods are invading the fields, forming rich niches for ants.

The wetlands consist of bogs, marshes and swamps. There are two consolidated bogs, Big Cassandra and Buck Hollow, and a bog lake, Hidden Lake, which has a narrow floating mat of sphagnum. The bogs are dominated by leatherleaf (*Chamaedaphne calyculata* var. *angustifolia* (Ait.) Rehd.) and occasional tamarack (*Larix laricina* (DuRoi) K. Koch) trees; the surface is composed of mosses (mainly *Sphagnum* and *Polytrichum* spp.) and cranberries (*Vaccinium oxycoccus* L.). Marshes, characterized by grasses such as blue-joint grass (*Calamagrostis canadensis* (Michx.) Nutt,) and reed canarygrass (*Phalaris arundinacea* L.), sedges (*Carex* spp.), spike-

rushes (*Eleocharis* spp.), bulrushes (*Scirpus* spp.) and diverse forbs, are scattered over the Reserve in kettle holes and other depressions. There are three areas of swamps, two of them small and in the western part of the Reserve. The other one, Big Swamp, fills most of the large depression in the southeast part of the reserve. The Big Swamp is dominated by red maple (*Acer rubrum* L.) and yellow birch (*Betula lutea* Michx.) with poison sumac (*Rhus vernix* L.) and highbush blueberries (*Vaccinium corymbosum* L.) prominent in the understory. Near Hidden Lake the swamp is dominated by tamarack and poison sumac.

SPECIES ACCOUNTS

Subfamilies are presented in the conventional taxonomic sequence. Genera are listed in alphabetical order within subfamilies; species are listed in alphabetical order within genera.

Subfamily Ponerinae

Amblyopone pallipes (Haldeman)

Amblyopone pallipes, an inconspicuous ant because it stays below ground, is fairly common and widely distributed in the oak-hickory woods of the George Reserve, favoring the more moist spots such as oak-hickory-black cherry hollows, sassafras-cherry potholes and hickory-red maple borders of swamps.

Nests occurred most frequently in and under well rotted, moist logs and near the surface of soil where leaf layers were thick enough to provide superficial chambers. They might also be found in soil with sparse leaf cover if it was moist enough, and they sometimes occurred in stumps, under stones and in soil with a moss covering. Nests consisted of one to several neat little excavated cavities. Workers moved slowly and were the color of the rich brown soil, but the long-necked, white larvae or the elongated, yellow pupae were easily seen. When disturbed, workers moved out of sight but generally returned to remove the brood.

Colony size was difficult to determine because often most of the workers were not with the brood, and nests sometimes consisted of two or more chambers separated by several inches. The largest colony (collected September 1) numbered 144 and was made up of 1 queen, 16 workers, 99 larvae, and 28 eggs. The largest group of workers found was 19, and the most larvae and pupae were 112 and 55 respectively. The most alates found in one colony were 11 males and 8 females.

Alate pupae were present from mid-July until the third week of September. No flights were seen, but Haskins (reported by Brown, 1960) indicated that females either fly or walk to an exposed position where actively flying males find them.

Ponera pennsylvanica Buckley

The small colonies of *Ponera* are numerous and widely distributed over the Reserve, occupying a surprising variety of habitats. The species is most abundant in oak-hickory woods, nesting in rather soft logs, in soil under thick leaves or chips of wood and twigs, under stones, or in acorns or hickory nuts.

Nest chambers tended to be small and shallow and it was hard to tell how many belonged to a colony. Isolated workers were often encountered, perhaps foraging underground or in crevices in logs. They rarely came to the surface.

Ponera differed from Amblyopone or Proceratium in that it did not overwinter larvae. Egg-laying started in the spring, and colonies found before June 16 had only eggs; they were not seen after early July. Larvae, first collected on June 22, were present from then until August 25. Production of pupae began about July 5 and a few were still present in a nest on October 3. Alate pupae developed along with worker pupae and some were collected as late as September 24. Males and females were first found on August 1 and a few were still present on September 28.

No flights were seen at the Reserve, but the following fragmentary observations, scattered over several years, indicate that they take place sometime between late morning and late afternoon on warm days where there is not much wind. 1) On August 23 seven males were seen walking on plants above a nest. Two days later a male was in sight here at 12:30 pm. The temperature was 73°F, the sky was faintly overcast and there was a slight wind. At noon on August 28 a female was moving about above this same nest. The temperature was 88°F. Again there was a little wind, which caused her to fall and go below. 2) On September 20 a male was caught in flight at 12:30 pm. The temperature was 75°F and the sky was slightly overcast. 3) On September 28 a male landed beside me and another was found walking on the ground at 3:50 pm (87°F). On September 5 a female was taken while sweeping vegetation in a field at 11:00 am.

Counts to give size of colonies were unsuccessful because workers were often not with the brood and the brood might not all be in one place. Twenty-five was the largest number of workers taken and once 125 pupae were piled together in one chamber.

Proceratium silaceum Roger

Only two colonies and a part of a third of this relatively rare ant have been found on the George Reserve. On July 15 the two colonies were discovered in a rather open oak-hickory woods. They nested 19 inches apart in a large red-rotted oak log. The first had a chamber 7/8th inch long, 3/4th inch wide and 1/4th inch high while the second occupied a chamber 2 inches long, 3/4th inch wide and 3/8th inch high. One colony was made up of a queen, 7 workers, 4 pupae, 11 larvae and 54 eggs. The second consisted of a queen, 12 workers, 41 pupae,

8 larvae and 1 egg.

In another woods four workers were taken in a large hole in the trunk of a hickory tree. The ants were in the loose, chewed wood produced by an *Aphaenogaster tennesseensis* colony that lived further up.

No alates were found in nests, but on August 23 a female was caught flying at 6:30 pm of a warm day.

Previous collecting in other places has shown that this ant usually nests in logs or stumps that lie in fairly moist places and are so thoroughly decayed as to be picked apart with the fingers.

Subfamily Myrmicinae

Aphaenogaster fulva Roger

In 1970 W. L. Brown, Jr. kindly checked 40 collections of *Aphaenogaster* from the Reserve and concluded that there were no *A. picea*, that *A. rudis* was quite variable, and that *A. fulva* was relatively scarce (only 4 collections out of 40). When all the Reserve collections were rechecked, only nine colonies of the typical *A. fulva* were found. These had come from dense to moderately dense woods - typically those of tall oak, hickory and cherry or red maple. One colony lived under and around a stone sunk into the soil and the rest were in moderately- to much-decayed logs or stumps. Most of these had galleries and chambers out into leaves at the logs' sides and down into the soil beneath. Alates were found between August 14 and September 3.

Aphaenogaster picea (Emery)

This species, which I (and W. L. Brown, Jr.) called *A. rudis*, but which has been renamed by Bolton (1995), is common and widespread in almost all the woods of the Reserve, ranging from such low places as sides of potholes and edges of swamps to moderately open upland woods and along their field borders. It, like *A. fulva*, was almost always associated with wood; only occasionally was a colony found in the ground under and around a stone. Commonly, the wood was a much decayed part of a log or stump which might still retain its form or might be reduced to red wood-soil. The nest usually consisted of galleries and chambers in the wood that normally extended down into the soil for a short distance. Brood was sometimes placed among leaves at the sides of logs and once in a while a colony had only leaves or a small chip of wood over the soil entrance.

Pupae of alates were found from June 14 to July 25, alates from July 1 to August 26. On July 27 and again on July 29 groups of alates and workers were found above a nest and it looked as if flights were just over. No alates were seen to fly, but a few males were trying to mate with females there. This was at 7:00 pm (74°F) just after a nearby colony of *Acanthomyops interjectus* had completed flights.

Aphaenogaster tennesseensis (Mayr)

Aphaenogaster tennesseensis was never abundant in any one place but was widely distributed in woods of the Reserve, from the typical, rather dry, black oak-hickory woods to the more moist oak-hickory-cherry. Typically, it nested in rather large logs that were medium to very hard and that were raised somewhat from the ground. However, many lived in softer logs lying on or even sunk into the ground or in stumps and in dead or living standing trees.

Nest structure could be seen only in the softer logs. One such showed a colony whose main galleries and brood were in the center of the log where the wood was beautifully red, had no mold, and could be cut with a hand ax. Brood chambers were enlarged galleries following the grain of the wood. One was 1/2 inch high, 1 inch wide and 6 inches long. Workers did much chewing of wood and sometimes plugged cracks in logs with a plaster of wood granules. At times the first indication of a colony in a standing tree was a pile of sawdust at its base.

Colonies tended to be large, seemingly much more populous than those of other local species of *Aphaenogaster*.

Alate pupae were found from July 14 to August 12 and winged adults from July 14 to September 3. No flights were seen.

Aphaenogaster treatae Forel

At the Reserve *A. treatae* is a widespread and typical field ant, being found all through the dry upland fields and into the oak reproductions at woods edge. In these sandy, sparsely vegetated fields the predominant grasses, Canada bluegrass and arrowfeather three-awn, are mixed with a wide variety of common forbs such as daisy fleabane, lespedeza, wild bergamot, common milkweed and goldenrod.

Colonies were abundant in some fields. In one small plot there was a colony for each 21 square yards (Talbot, 1954) and in one 15-acre field they averaged one colony for each 50 square yards (Talbot, 1953). A count of 30 colonies on the smaller plot gave a mean of 1331 individuals per colony, of which 682 were workers. These colonies averaged 162 pupae, 285 larvae, 181 eggs, 20 alates, and 1 nest queen.

Workers were not seen at midday of hot days, but at favorable temperatures (70-90°F ground temperature) they patrolled the ground constantly, bringing in all sorts of dead or helpless insects. At times they collected grass seeds and other plant parts. They were aggressive in capturing winged ants of other species during their flights.

Colonies always lived in the ground. Some entrances were open and easily seen, but often they were concealed in clumps of grass or other plants. Frequently the entrance was surrounded by a little chimney of dry grass, lichen or moss fragments. Often there was an aboveground chamber covered with dead grass stems and soil particles. A gallery (sometimes

2 or 3) led down into the soil and from this would extend more chambers at different levels. In 30 colonies dug, nests consisted of from 2 to 17 chambers (with a mean of 8.8), and they extended down from 9 to 40 inches (with a mean of 29.5 inches).

Alate pupae were found from June 4 to July 10 and adult alates from June 15 to August 10, although most nests were cleared of winged ants by July 27.

Fourteen flights were watched between June 30 and July 26, and alate or dealate females were seen walking on the ground between June 18 and August 10 (Talbot, 1966). Flights were unusual in that they took place near midday at high temperatures (78 to 88°F at 10 inches above ground) but reduced light. Most of them occurred after the day became too warm for workers or alates to come out of the nest until a cloud came by reducing light and lowering the temperature a bit. Then workers and alates appeared and the winged ants climbed plants and flew quickly. When the cloud passed, the remaining ants retreated into the nest, to appear again if another cloud came over. Flights seen lasted 1 to 25 minutes and were sparse.

Crematogaster cerasi (Fitch)

Crematogaster cerasi is found in open woods, in wood-field ecotones and in sumac clumps. However, it is most abundant in denser woods, and it also nests in swamps and marshes. Occasionally a colony is present in a field, and one lived for several years in the foundation of a building.

Over half of the collections were from colonies nesting inside fairly hard logs or stumps, which they modified extensively into galleries. Sometimes nests were in and under logs and under leaves at their sides. In swamps the ants used tamarack logs if they were available, but they would also form flourishing colonies in hummocks of grass, sedge or sphagnum moss. First-year colonies have been found in acorns, hickory nuts, hollow sedge stems and beneath bits of bark lying under trees. They used carton occasionally to help enclose a nest. Workers were meticulous in following odor trails to foraging areas.

One colony, living under and in pieces of log on a sandy bank, was known for 12 years. It was still producing males and females in 1978, but only a few workers were seen in 1980.

Alate pupae were found between June 15 and August 22 and winged ants from July 21 to September 24. Six flights were recorded between August 27 and September 20. Five involved males and females while the other was of females only. Flights took place at about midday (11:37am to 1:51pm) and began as soon as bits of sunlight raised air temperature to 78°F. Alates flew best between 80 and 86°F. Three complete flights lasted 23, 40 and 70 minutes. Dimming light or a drop in temperature slowed or stopped flying.

Crematogaster lineolata (Say)

Crematogaster lineolata, a common ant on the Reserve, is essentially an ant of wood-field ecotones and of open woods and is especially characteristic of oak reproductions and sumac fringes. It can also extend out into fields but is not found in swamps or bogs, where *C. cerasi* occurs.

It often nested in, under and at the sides of fairly solid logs or bits of wood. Smaller stems of dogbane, meadow-sweet, dogwood and sumac were also used. Sumac provided an especially favorable habitat. Old patches extending out from woods into otherwise open fields often had many dead, but still standing, stems with large, soft pith centers. In these, nests typically began several inches above ground and continued down into the main roots. Brood could be in the root and stem and outside under leaves on the soil surface. A colony could occupy considerable space outside the plant, and there was evidently much moving of brood as temperature and moisture varied. Fallen stems were used in the same way and often contact of stem with ground was sealed with a line of carton. Sometimes a break in a stem was covered with carton except for a small hole left for an entrance.

Colonies of *C. lineolata* might also be completely independent of wood, using clumps of grasses or sedges or simply masses of fallen leaves. Colonies were common on one sandy strip of soil just above a marsh. Here, they lived under a litter of oak leaves that were mixed into the sand. Brood could be scattered out in an irregular line for as much as three yards under a sparse leaf cover. A few openings extending down into the ground ended in chambers just beneath the surface. These ants attended aphids just at the root-stem junction of small oaks (3 to 5 inches tall) and on branches of tiny trembling aspen trees. Sometimes they built carton shelters about the aphids. Like *C. cerasi, lineolata* workers followed odor trails to foraging areas.

Pupae of alates were found between June 20 and September 2 and adult alates from June 27 to September 28. Stray alate females, which had probably just flown, were seen on August 23 and September 28. One flight was seen in which about a hundred males flew at mid-morning of a warm, hazy day (September 16) with the temperature between 82 and 84°F.

Formicoxenus hirticornis (Emery)

Only one colony of this inquilinous species was found. It was nesting 17 inches deep in a *Formica obscuripes* nest when the ants were picked up with a handful of thatch and *F. obscuripes* brood. At this time, June 10, alates were present and the total collection consisted of 11 workers, 4 alate females, 3 ergatomorphic males, a female pupa and 4 worker pupae. The colony was not disturbed further. Samplings of 75 other *F. obscuripes* mounds failed to reveal any more of the inquiline.

This species was listed as *Leptothorax hirticornis* in my list of the George Reserve ants (Talbot 1975b). Buschinger (1979)

transferred this species to the genus Formicoxenus.

Leptothorax ambiguus Emery

Leptothorax ambiguus is quite versatile in its habitats and nesting sites. It favored open places and was apt to be found out on the field side of a wood-field ecotone, in quite open woods or under isolated trees in fields. It also lived in low fields and could penetrate bogs and swamps. It was not present in the exposed middles of high, dry fields nor in deep woods. In low fields nests could be found in the ground among tangled roots. They were also in stems of forbs lying on the ground or even standing upright. Cavities of acorns and hickory nuts were also used.

A count of 10 acorn units that had alates in the nests (July 22 through July 28) gave a mean total population of 113.3 of which 0.2 were queens, 29.6 were workers, 13.2 alates (adults and pupae), 10.2 worker pupae, 18.0 larvae and 42.1 eggs.

Sexuals were produced in mid-summer: alate pupae between June 17 and August 6 and adult alates between July 1 and September 11. Alates were found at lights between July 12 and August 21.

Leptothorax curvispinosus Mayr

This small yellow ant, which is very similar in color and size to *L. ambiguus*, is by far the most common species of the genus on the Reserve. It is widespread and abundant through the oak-hickory woods wherever acorns are found. It also nests in small branches or hollow stems, in logs or bits of wood, in oak galls and hickory nuts. It is not found in open fields or in swamps and marshes where it is replaced by *L. ambiguus*.

Acorn-dwelling colonies are often abundant on slight slopes of the more open woods where leaf litter was light to moderate. Acorns were first occupied by curculionid beetle larvae, which ate out the seeds and then made small exit holes. Suitable acorns were firm (but could be broken with the fingers), dry and not moldy. Numbers of colonies varied enormously from year to year depending upon the previous acorn production of any given tree or the acorn crop in general. Usually every suitable acorn was occupied. Population counts of 525 colonies living in acorns gave a mean of 100.5 individuals (Talbot 1957). The great number of queenless colonies (35.2%) suggested that some colonies occupy more than one acorn for at least part of the summer.

Sexuals were produced a little earlier than those of *L. ambiguus*. Pupae of winged forms were found from June 8 to July 18, while adult alates were in the nests from June 23 to August 10. No flights were seen, but it was common to pick up alates at lights between July 1 and July 27.

Leptothorax duloticus L. G. Wesson

Leptothorax duloticus is an obligatory slavemaker which,

at the Reserve, enslaved *L. curvispinosus* and occasionally *L. ambiguus* or *L. longispinosus*. Since it was discovered in Ohio (Wesson 1937, 1940), it has been found in Illinois, Indiana and Michigan, and in Ontario, Canada. However, distribution has always been spotty, and it remains a rare ant.

At the Reserve it lived in acorns and was taken only where *L. curvispinosus* colonies were numerous. However, it was not found in all places that were occupied by *L. curvispinosus*. It favored gentle slopes of fairly open woods where leaf cover was not heavy.

Colonies were small: a count of 270 collections gave a mean of 11.7 *L. duloticus* workers together with four times that many workers of *L. curvispinosus* (Talbot 1957).

Alate pupae were present from June 26 to August 24 and adult alates from July 21 to September 26.

Slave-making raids were not observed on the Reserve. However, Alloway (1979) has described the raids of laboratory colonies.

Leptothorax longispinosus Mayr

Leptothorax longispinosus is an inhabitant of the more moist woods. It was found in woods of oak and hickory mixed with red maple or black cherry, on slopes of hollows or near swamps, but only occasionally in drier woods or their edges.

The ants often nested under bits of moss-covered or lichencovered bark on trunks of living trees and have been found on black oak, white oak, red maple, hickory, elm and large-leafed poplar, usually within 2 to 16 inches of the tree base. They also lived in logs, small branches on the ground, small stumps, and acorns. Nests usually consisted of one or two chambers and were 1/2 to 2 inches in diameter. Sometimes narrow galleries extended for as much as 4 inches under the bark. Workers usually foraged along tree trunks or logs, rarely on the ground.

One colony (July 26) was composed of 1 queen, 41 workers, 38 males, 34 alate females, 2 male pupae, 8 worker pupae, 3 larvae and 3 eggs.

Alate pupae were found between June 22 and July 26 and adult males between July 19 and August 5.

Leptothorax muscorum (Nylander)

This northern species, which is characteristic of boreal North America, nearly reaches its southern limit in southern Michigan. It has been taken in northeastern Ohio (Headley 1943) but otherwise extends south only in mountains. At the Reserve it seemed tied to the remnants of northern swamps and bogs. It was found most frequently in the large tamarack-poison sumac swamp and at its fern-sedge border or in woods just above the swamp. It was also present in a sphagnum-chamaedaphne bog: in one of its tamarack islands and in some hollow reeds near its border.

Nest sites were usually quite dry. Small twigs sticking up from tamarack logs were favored. Nests were also made in logs of tamarack or other trees, especially under bark or in the more solid wood near the top surface. Logs lying up off the ground were preferred, but even small chunks of wood could be used if they were not constantly wet. None nested under stones as they sometimes do further north.

The ants were not common and workers were hard to trace to nests. Only 15 colonies were found.

Winged pupae were taken between June 27 and July 6 and adult alates from June 22 to July 20.

Leptothorax schaumii Roger

This species was not common but was found in such diverse places as deep woods at swamp edge, higher, moderately open woods, and wood-field ecotone. The type of nesting site was more restricted. In each case it was a fallen tree whose trunk was held up off the ground and was still hard with bark that was solid or only slightly loosened in places.

Colonies were numerous in one elm and two hickory trunks. Most collections were made at one tree. This large hickory had split and one main trunk was hanging so that it sloped from about six feet at the still standing trunk to two to three feet further out where it was held up by numerous branches. For several years these branches still bore green leaves. All the nests were under flakes of bark on the sides or top surface of the sloping main trunk.

Nests were found by feeding cookie crumbs to foraging workers who carried them directly home, sometimes as far as 29 feet. Entrances were tiny round holes at sides of flakes of bark, often at the lower edge of a nest. If any cracks occurred at nest edge, they were sealed with carton. Bark over the nests was so solid that it had to be chipped away with a knife. Usually there was one little, flattened chamber about 1/16th of an inch high and varying in area from 1 3/8th x 1/8th inches to 2 x 3/4th inches. Sometimes there was a little gallery, as much as 3 inches long.

An attempt was made to collect whole colonies and 19 collections that seemed rather complete are listed in Table 1.

Unfortunately, only a few sexuals were discovered. Alate pupae were found between June 22 and July 23, while adult males were seen between July 23 and July 27.

Leptothorax texanus Wheeler

Leptothorax texanus differed from other species of Leptothorax on the Reserve in that it nested exclusively in the soil. It has been found in three places but was common only in one. This was a strip of almost pure sand bordering a marsh and lying at the foot of the south-facing slope of a hill. The strip was quite barren, having only a few scattered small oaks and poplars and a sparse ground vegetation of fine grass or sedge and a few rather stunted forbs. In some places there was a layer of dry leaves, but most of the surface was bare sand. This sand was often dry at the surface but, because of the

Table 1. Populations of Leptothorax schaumii Roger.

		Adults				Pupae		
Date	Queen	Worker	Male	Worker	Male		Eggs	Total
7-1	2	10	0	0	0	9	17	38
7-1	1	15	0	4	0	7	4	31
7-1	2	23	0	9	0	30	14	78
7-3	0	18	0	0	0	44	8	70
7-12	0	10	0	2	0	6	2	20
7-12	1	15	0	13	0	15	18	62
7-16	1	21	0	13	0	30	19	84
7-16	1	17	0	28	0	28	9	83
7-23	2	36	12	11	7	24	19	111
7-23	1	9	0	4	0	15	9	38
7-23	1	2	0	1	0	9	0	13
7-23	1	8	0	7	0	8	9	33
7-27	1	11	3	21	0	19	46	101
7-27	2	14	0	25	0	24	15	80
8-2	2	19	0	35	0	42	30	128
8-3	2	10	0	9	0	18	24	63
8-3	2	73	0	103	0	55	53	286
8-6	2	19	0	8	0	24	12	65
8-8	0	49	0	30	0	25	25	129
Mean	1.3	19.9	0.8	17.0	0.3	22.7	17.5	79.6

marsh, retained moisture beneath. It was a rich place for ants and 20 species have been found there. Over the years the strip has been invaded by trees, but the lower half is essentially the same and *L. texanus* is still common.

Workers foraged along the ground, sometimes singly, sometimes along invisible trails. They were not difficult to see on the pure sand and were not hard to track to nests because they carried cookie crumbs readily. Nest entrances were so small that they were invisible except when ants entered them. Usually there was only one entrance and it could be in a patch of bare sand, at the base of a small plant such as a tuft of grass or in a small bit of moss or lichen. Sometimes an entrance had a small collar of fine carton encircling it.

Trying to determine the size of a nest was frustrating because dry sand shifted and crumbled and because galleries were so small. Digging was successful only when the sand was very wet. Nests averaged three chambers and 3/4th of these were in the first 1/2 to 2 inches. They extended down to between three and six inches. Chambers were smooth-floored

and measured between 1/2 and 5/8th inches in diameter and 1/4th and 1/2 inches high.

It was always difficult to get a good colony count. The four best are given in Table 2.

Alate pupae were taken between June 12 and June 30 and adult alates from June 25 to August 1.

Habitat distribution of *Leptothorax* species:

The following is a brief summary of the habitat distribution that seems most characteristic for each species of *Leptothorax*:

L. ambiguus - Quite open woods, along fencerows and under isolated trees, in low fields and in and around swamps and bogs. In the soil, in acorns lying on the ground, and in hollow twigs and stems lying on the ground or standing upright.

L. curvispinosus - Fairly open woods and woods-edge. In acorns lying on the ground or in crevices above ground.

L. duloticus - Essentially the same distribution as its slave, *L. curvispinosus*, but more restricted. In acorns.

L. longispinosus - Rather deep woods. Small cavities in logs or under bark of standing trees.

L. muscorum - In or near swamps or bogs. In small twigs attached to larger logs.

L. schaumii - Woods. In small cavities under solid bark in fallen tree trunks that are partly off the ground.

L. texanus - Sandy slope just above a marsh. In the ground.

Monomorium minimum (Buckley)

This tiny black ant is widely distributed over the high, dry fields of the Reserve, or among scattered trees at the edges of fields, but it is not found within deep woods or in low, moist fields. In the most barren parts it is restricted to places under overhanging branches of trees. At one place a number of colonies nested in almost pure sand under bits of moss in the shade of a black oak.

A number of colonies were dug in a field, which seemed a typical habitat. Vegetation was not dense and small patches of bare, sandy soil were numerous. Grasses were mostly Canada bluegrass and three-awn, and there were a variety of scattered forbs. Patches of polytrichum moss and red-tipped lichen

Table 2. Populations of Leptothorax texanus Wheeler.

Adults					Pupae						
Date	Queen	Worker	Male	Female	Worker	Male	Female	Larvae	Eggs	Total	
6-12	0	81	0	0	1	55	6	69	26	238	
6-25	1	53	3	2	6	0	14	43	14	136	
6-27	1	71	0	0	2	0	0	31	0	105	
7-7	1	41	0	2	16	0	0	22	0	82	
Mean	0.75	61.5	0.75	1.0	6.25	13.75	5.0	41.25	10.0	140.25	

were characteristic. Nests were large for such a small ant. They extended down into the soil for a depth of 9 to 25 inches (mean depth: 15 inches), and the number of chambers ranged from 5 to 10 (mean of 7.4 chambers). The ants sometimes made small craters of loose soil around nest entrances, and these were most conspicuous when ants were excavating after a rain. Often entrances (1 to 3) were concealed under a moss leaf or bit of lichen. Usually there was a chamber within the first inch of soil, sometimes just under a bit of polytrichum moss or root of a forb. Larvae and pupae could be found in this chamber if the surface soil was not too dry, and usually they were scattered throughout all other chambers. Typically, there was one central, shaft with chambers radiating out from it. They tended to be clustered near the surface -- 44% were between 1/2 and 5 inches. Most often there was a distance of one to two inches between chambers, but occasionally there was as much as 6 to 9 inches separating them. The chambers were small, as would be expected; a very large one measured 3/4th inch in diameter and 1/4th inch high.

Counts of 14 colonies are summarized in Table 3. Some ants were always lost in digging and these were especially difficult, so the result is a definite undercount.

Male and female pupae were recorded from June 15 to July 20 and winged adults from July 7 to August 12. Good flights were not seen, but above-ground activities were witnessed on July 8 and 9. A colony nesting under a bit of moss had made three large (female size) exits in the moss cover. Females began to come out at 8:30 am when the ground temperature was 71°F and the air temperature was 67°F. As the temperature rose (93°F on the ground and 84°F in the air), females moved constantly, their clear wings flashing in the sunlight as they climbed up and down three grass blades, forming clusters that resulted in their being pushed until they fell or moved down, only to move up again. About 35 females were involved and workers seemed responsible for the constant movement and for keeping them within a 6 x 6 inch circle around the nest. Two females were seen to fly, but the rest just kept milling about. Then a male flew into the midst. He seemed to mate with a female but was immediately mobbed by so many females that he could not be seen. Forty minutes later I picked him out of a mass of females and workers. No more males came, but the strenuous activity continued until the ground temperature became too warm (97°F). The females were trying to stay up on the grass blades, but then workers began to force females down into the nest openings. While this was going on, a colony nearby had females out and I picked up a male and female mating. After this disturbance, they retreated into the nest.

Next day (July 9) the original colony had a group of 28 females out repeating the activities. Again one male flew in and was mobbed by females and workers. No females were seen to fly. This day the second colony had females systematically picked off by workers of *Aphaenogaster treatae*, which evaded *Monomorium* workers that were trying to form a protective

ring.

In another year on July 9 at 5:30 pm two alate females were found with a conspicuous number of workers moving about above a nest.

Table 3. Summary of populations of 14 colonies of *Monomorium minimum* (Buckley).

Caste	Smallest colony	Largest colony	Mean
Queens	2	1	1.4
Workers	262	787	526.8
Pupae	8	836	208.2
Larvae	69	757	468.5
Eggs	15	418	172.2
Total	356	2799	1377.1

Monomorium talbotae DuBois

This small, workerless, social parasite was found during a study of populations of Monomorium minimum in a field that is described in the account of that species. The males and females were smaller than those of M. minimum and looked like the latter, except for the genitalia (DuBois 1981). Only three collections were made and these were at the end of the parasite's season for rearing brood. The first collection, made on June 30, consisted of 6 dealate females, 56 winged females, 9 males and 1 male pupa. Most of the alates were in the upper chambers as if they were ready to leave, although a few were in the lower ones, 10 to 13 inches deep. It would seem that some flights had occurred before the other two collections were made, for they were small. They consisted of 4 winged females and 3 males taken on July 4, and 6 dealate females, 1 winged female and 5 males collected on July 13. The M. minimum colony harboring the most parasites had its own queen, but host queens were not found in the other two colonies.

Myrmecina americana Emery

This slow-moving, obscure ant most often nests in deep woods, especially in oak-hickory-black cherry kettle holes or among red maples just above the swamps. The ants are also found in hummocks of both tamarack-poison sumac swamps and sedge marshes. More rarely, they extend into open oak-hickory woods or woods-field ecotones.

This species was found only 39 times at the George Reserve. Nests were usually in or at the side of logs or stumps in the red rot stage when wood is easily picked apart with the fingers. In moist places they also occurred in soil with leaf or moss coverings, at depths ranging from 1/2 inch to 3 or 4 inches. A nest usually consisted of one or two chambers which were well smoothed little cavities 1/2 to 1 inch long and 1/4th to 1/2 inch wide.

9 TALBOT

Colonies were not large. Table 4 gives counts of the 10 best colonies taken. Workers made up a fourth of the population. Colonies averaged 21.3 alates (adults and pupae), of which 11.6 (54.5%) were males and 9.7 (45.5%) were females. Of 17 colonies that produced alates, 11 had males only, 1 had females only and 5 had both.

Alate pupae were present in nests from July 12 to August 18, while adult males and females were first found on August 6 and were still present on September 7 when the last collection was made.

Myrmica americana Weber

The upland grasslands of the Reserve are old fields that have gradually returned to a grass-dominated environment. It is this Kannowski and Kannowski (1957).

Myrmica detritinodis Emery

This ant is an inhabitant of dense, moist woods, especially where the woods contacts a swamp. There, it nests in the soil under moss or in stumps. Kannowski (1970), recording this species as M. emeryana, found it occurring in the swamp forest separating Hidden Lake from the oak-hickory forests. Pupae of alate forms have been collected from late July to late August; alates were found in a nest in late August. No flights were recorded.

In my 1975 list of the Reserve species, I recorded this species as M. monticola.

		Adu	lts							
Date	Queen	Worker	Male	Female	Worker	Male	Female	Larvae	Eggs	Total
7-12	0	27	0	0	29	14	0	17	83	170
7-16	1	54	0	0	3	3	0	71	21	153
7-19	1	44	0	0	40	6	0	40	0	131
7-25	1	22	0	0	27	0	8	8	0	66
7-30	0	67	0	0	68	2	45	14	62	258
8-8	1	103	0	0	30	6	0	41	113	294
8-9	0	20	0	0	34	5	0	4	99	162

5

51

37

32.4

3

4

0

4.3

0

20

0

7.3

Table 4. Populations of Myrmecina americana Emery.

environment that M. americana has effectively colonized. This species is a major component of the ant community of Evans' Field (Talbot 1953) and other grasslands on predominantly sandy soils. Approximately 20% of the ant colonies on Evans' Field are of this species. Nests are in the soil, sometimes at the bases of grasses or forbs. They often have narrow chimneys of soil and plant fragments that may be enlarged to make an above-ground chamber for brood or alates. Workers are active foraging in the daytime for seeds of panic-grass (Panicum spp.). Workers also are occasionally found tending aphids on milkweed and bringing small insects and fragments of larger ones to their nests. Workers forage at temperatures between 60 and 90°F; above 90°, the workers remain in the shade of grasses and forbs and are mostly inactive.

8-10

8-14

9-3

Mean

0

0

0

0.4

42

26

126

53.1

0

0

73

7.3

0

0

24

2.4

Brood are present in the nests throughout the summer months with eggs and larvae still present in early September. Larvae probably occur in the nests throughout the year. Pupae of alates are present in July and August, and males and females are present in nests from late July until early September. Preflight behavior was observed in the vicinity of a nest on 30 August. Flights of this species in Michigan and Ohio, which occurred between late July and mid-October, are described by

Myrmica fracticornis Emery

51

35

130

59.4

47

13

175

43.0

148

149

565

209.6

Marshes at the edges of fields or swamps are the primary habitat of this species; reeds or other dense grasses dominate these marshes. The ant colonies occupy the hummocky soil above the marsh surface. These hummocks are composed of black mucky soil through which roots and stems of grasses grow. Late in the summer one nest had an above-ground chamber formed of soil and plant fragments; the chamber added three inches to the height of the hummock and was filled with brood. Males and females were present in a nest in early September and alates were collected in flight in late August.

Myrmica incompleta Provancher

This ant has the most restricted distribution of the species of Myrmica on the Reserve. It occurs only in the sphagnum moss of the floating mat surrounding Hidden Lake. Colonies form nest chambers in the moss that extends a few inches to a foot or so above the water level of the lake. Colonies may be located by walking on the mat; this depresses the mat below the water level and forces the ants out of their nest. Kannowski (1959a) found alates in nests on the Reserve between late July and mid-August; however, flights have not been observed.

Myrmica lobifrons Pergande

The leatherleaf community of consolidated bogs provides an ideal habitat for this species. The hummocks of living sphagnum and fibrous peat provide a moist but well-drained environment for the colonies. This species also occurs in hummocks of soil in some marshes. Kannowski (1970), recording this species as *M. fracticornis*, provided records of populations for colonies collected on the Reserve. Eggs were present throughout the summer but absent between October and May, during which time larvae were the only form of brood present. Males and females occurred in nests from early July to late August. Flights were observed from late June until early August.

Myrmica pinetorum Wheeler

Uncommon but widely distributed on the Reserve, this species is usually found in sites where a woods meets a grassland or in an open oak-hickory woods. The largest number of colonies found at one site was seven found at Fawn Hill, six of them close together near contact with West Marsh. Nests are located in the soil with a single entrance on the surface of bare ground or under leaves. Sometimes there may be an aboveground chamber for brood development in a clump of moss. Eggs, larvae, worker pupae and males were found in a nest in early September.

Myrmica punctiventris Roger

Found in the more mesic woods on the Reserve, *M. punctiventris* forms nests in the soil with one or several entrances on the surface under leaves or at the edge of stumps or tree trunks.

Myrmica sp. 1

This species is most frequently found in dense oak-hickory woods where the soil is a dark, rich humus, but sometimes also in low, moist fields near marshes. Nests are formed in the soil with evidently only a single entrance in bare soil or under leaf liter. One nest had an elaborate above-ground carton structure and chamber just below a tight tangle of grass roots. Another had a small chimney of carton built among the leaves of a small sedge. A nest in a moist field site had a chimney of carton that enclosed aphids on a plant stem. Males and females were in nests in from late July to mid- September. Flights were observed in mid- to late afternoon on 23 and 25 August.

Myrmica sp. 2

This species is very similar to *Mymica* sp. 1, but tends to occur in more open oak-hickory woods and into the oak reproduction area along old fields. In these sites the soil is more sandy and quite a bit drier than for the other species. Chambers are found in the soil with occasional brood chambers above ground among leaves. Some nests have chimneys of carton surrounding the entrance and extending up the bases of plants. Alates were found in nests between the end of July and late September, but no flights were seen.

Smithistruma pergandei (Emery)

This small, inconspicuous ant often lives near other ants because its food consists almost exclusively of collembolans that may become numerous in ant kitchen chambers (Wesson 1936, Wesson and Wesson 1939). Collections were made in five locations on the Reserve, one in a rather deep oak-hickory woods and the others on slightly drier wooded slopes. Two collections consisted of individual ants.

One of the three colonies taken was in a large oak log lying on a slope characterized by common juniper and oaks. The nest was a little gallery three inches long in wood that could be hacked away with a knife but not broken with the fingers. The second occupied an old stump standing among oaks and black cherries. The Smithistruma inhabited crevices in the outer, firmer wood that was almost dry, while a colony of Lasius umbratus filled the center. The third colony lived in a large stone pile that sheltered eight other species of ants (Ponera pennsylvanica, Aphaenogaster picea, Myrmecina americana, Myrmica sp., Camponotus americanus, Formica nitidiventris, Formica subsericea, and Lasius neoniger). A few workers were found under a stone in a cavity 1/4th x 1/2 inch across. A small root lying just under the ants had a tiny opening and a central cavity 1/2 inch in diameter that was clean and completely blackened. Workers, larvae and pupae were scattered along 10 inches of the horizontal root; then, when it bent abruptly downward, more brood lay five inches down at the end of the cavity.

This latter colony, living among so many ants, presumably had plenty of collembolans and proved to be large, consisting of 522 individuals: 1 queen, 204 workers, 134 worker pupae, 117 larvae and 66 eggs. When collected on September 4, the log colony was made up of 30 workers, 34 worker pupae, 39 larvae, 42 eggs, 77 males and 17 male pupae. The stump colony was not completely counted but had 98 workers and 83 males (August 22).

Male pupae were collected on September 4 and adult males were collected on August 22 and September 4.

Smithistruma pulchella (Emery)

Only one collection of this species was made. It consisted

of 23 workers sifted by berlese funnel from wood-soil found in a dead, standing black oak on a slope of an oak-hickory woods.

Solenopsis molesta (Say)

On the Reserve *Solenopsis molesta* is characteristic of grassy places and is widespread in all types of fields except the very dry and the very moist. It may also be found in open woods or in deeper woods clearings.

Usually colonies nested in the soil without cover, but some have been found under stones or in logs. In most cases they were distinct units living in separate nests but occasionally, under favorable conditions, there would be what seemed like a multitude of colonies intermingling in a restricted space. One such compound was discovered on August 20 in an abandoned *Formica subsericea* mound in a field at woods edge. Here were numerous pockets of workers, larvae and pupae and many females, both alate and dealate. Occasionally a log, in a late stage of decay, might have numerous colonies, especially if there were larger ants living in the same log. *Solenopsis* colonies were found near 15 species of ants of the following genera: *Aphaenogaster*, *Monomorium*, *Myrmica*, *Acanthomyops*, *Camponotus*, *Formica* and *Polyergus*.

Nests seemed rather shallow, and brood and workers were often massed just beneath the surface. Only two nests were dug for depth. One extended down six inches and the other nine inches. The latter had nine chambers with brood in all but the first two (the soil surface was very dry).

A colony collected on July 10 consisted of 1470 individuals: 1 queen, 654 workers, 379 worker pupae, 5 male pupae, 50 female pupae, 373 larvae and 8 eggs. Another colony, counted on September 5, had a total of 2946 individuals: 1 queen, 1869 workers, 472 worker pupae, 498 larvae and 106 eggs.

Pupae of alates were in the nests from June 29 to August 27, while winged adults were obtained from July 21 to September 6. In this species the black males and brown females were huge in comparison with workers. Females were much more numerous than males. In many cases colonies produced only females; some had only males.

Eight flights were seen. They took place in late summer (between August 4 and September 6) in the late afternoon (between 4:30 and 7:00 pm). Favorable temperatures ranged between 72 and 89°F. Once, winged ants retreated from grass blades when the sun brightened and a temperature of 92°F was reached. One flight ended when the temperature dropped to 69°F. Low light seemed to put an end to one flight when, before a storm, temperature remained at 76°F but foot-candle readings decreased from 740 to 460. High humidity, of recent or approaching rain, was favorable.

At flights, blades of grass above nests would be covered with the tiny yellow workers as well as the larger males and females. Winged ants usually climbed to tips of grass blades, fluttered wings a few times and then flew. Once, at 7:00 pm,

a conspicuous number of alates were flying and mating just above head height over a depression in a grassy area.

Stenamma brevicorne (Mayr)

This species is rather restricted in distribution. It was common in one place: a low field bordering a marsh where ground water was often near the surface in the spring. Nests, consisting of one to four chambers, were usually within the first six inches of soil but might extend deeper. A count of 15 colonies gave a mean of 200.3 individuals of which 56.9 were workers (Talbot 1975a). Alate pupae were found from July 9 to August 11 and winged adults from August 10 to September 10. No flights were seen; however, Kannowski (1958) recorded collecting a female in flight at the George Reserve at 6:15 pm on May 30, 1956.

Stenamma diecki Emery

This slow-moving, secretive ant lives in soil in moist places. It was found in the tamarack-poison sumac swamp and along some of its edges that are bordered by low woods. It also occurred near the bottoms of potholes in the oak-hickory woods. The soil in these places tended to be loose and mixed with plant litter, and the ants selected small spots of firmer ground (such as over tree roots) for their nests. Top chambers were just below the leaf-covered soil surface, and nests rarely extended down below five inches. Colonies were small; a count of 15 gave a mean of 234.5 individuals of which 56.0 were workers (Talbot 1975a). Worker pupae were found from June 22 to September 16, alate pupae from July 1 to September 1 and winged adults from July 19 to September 8. No flights were seen.

Stenamma impar Forel and Stenamma schmitti Wheeler

These species were rare on the Reserve. Their distribution, in low, moist woods, was similar to that of *S. diecki*. Adult alates of *S. impar* were found on August 13 and 19. No alates of *S. schmitti* were discovered, but alate pupae were taken on August 6.

Subfamily Dolichoderinae

Dolichoderus mariae Forel

The colonies of *D. mariae* were widely scattered in low places. Low fields at marsh edges were especially favorable. The ants also lived inside bogs and swamps and, in contrast, could sometimes make their nests in rather open dry places, provided they were within foraging distance of water. They nested near small trees, shrubs or tall forbs on which they attended aphids. Permanent, invisible trails extended out from

the nest and these were thickly populated with the shining red and black ants, which touched antennae as they passed each other. Aphid secretions seemed to be their main food, but they have also been found covering a dead earthworm and a dead frog. They were never seen to carry bits of solid food.

They made a nest by excavating a hole in the soil 6 to 10 inches deep, leaving nothing but tangled roots and bases of stems on which brood could be laid. Over this they built a cover, usually raised into an igloo-shaped dome, which, in a moderate-sized nest, was 3 to 4 inches high and 5 to 10 inches in diameter. This dome was made of bits of dry leaves, small stems and grasses. Colonies were huge and the many larvae, pupae, workers and alates filled the nest structure.

In early fall, when most brood had developed and most alates had flown, the fragile domes began to collapse and the colonies moved out. They evidently dug smaller nests in which to overwinter. Sometimes, when the thatch was broken, they also moved during the summer. One colony moved 12 feet, but often the new nest was closer (gaping holes showed where old nests had been). What was thought to be one colony was known for 14 years, in a different place each year but within a 30-foot radius.

Dolichoderus mariae had an exceptionally long period of sexuals in the nest: winged pupae from June 30 to September 16 and adults from June 30 to September 24. Individual colonies did not keep their alates this long, for some colonies in warm places began their development as much as a month before others in shaded positions. Flights were seen between July 4 and September 22, most taking place in August. Some colonies had exhausted their supply of alates by mid-August while others had just begun flights at that time. Flights took place in early morning in response to rising temperature. The alates could come out of the nest and climb grasses at 56°F and begin flights between 58°F and 63°F. Colonies produced a great many alates. It was estimated that 15,000 flew from one colony in 18 flights (Talbot 1956).

Dolichoderus plagiatus (Mayr)

These are primarily upland woods-edge ants, being most common where there are young trees extending out into fields. They are less commonly present in open woods, in low moist fields and occasionally even out in bogs and swamps, but are not found in deep woods or in the middle of dry fields.

Often nests were at the bases of small trees where the workers were attending aphids. It seemed from the commonness of such favorable positions and the fragile nature of the nests that the colonies must move frequently. They could live in acorns, hickory nuts or hollow stems, but by far the most they constructed nests of dry leaves lying on the ground. Sometimes they made a little depression in the ground, but most often the whole colony lived among the leaves. Sometimes one large folded leaf was used, sometimes several were employed. If there were many leaf layers on the ground, they tended to

use the upper, loose, dry layer. Carton was frequently, but not always, used. One colony occupied three touching leaves each of which was folded on itself and sealed around its edges to make a chamber. Carton that formed walls of chambers was smooth on the inside and rough outside. Hickory nut halves could be cemented together leaving only a tiny entrance hole. One colony had its entrance surrounded by a little chimney of carton that extended out for 1/4th inch.

Colonies were small: a count of nine gave a mean total of 184.1, of which 0.9 were queens, 101.3 were workers, 5.8 were alates, 23.6 were worker pupae, 1.4 were alate pupae, 37.7 were larvae and 13.4 eggs.

Alate pupae were found between July 9 and September 2 and adult alates between July 23 and October 3. Parts of three sparse flights were seen between September 1 and 8, in the early morning at temperatures of 65°F to 77°F.

Dolichoderus pustulatus Mayr

Dolichoderus pustulatus was an ant of bogs and swamps and the low fields bordering them. Occasionally it penetrated a little further upland, but it never reached the high field edges where *D. plagiatus* was most common. In low places the two species sometimes occupied the same habitat. They were much alike in their nest structure and they both formed small colonies.

The ants made nests in hollow stems, curled up leaves, in bases of grass stems and among their roots and in cavities near the surface of the soil. Carton was used to some extent but did not seem as common as with *D. plagiatus*.

Kannowski (1967) reported that 41 colonies on the Reserve averaged 445.2 individuals of which 203 were workers. He also found that 10 alate-producing colonies averaged 38 alates per colony. The sparse flights never included more than 20 or 30 in one day (Kannowski 1959a).

Alate pupae were found between June 26 and August 27 and adult alates between July 11 and September 15.

Dolichoderus taschenbergi (Mayr)

The jet black *D. taschenbergi* built nests that were identical with those of *D. mariae* and they formed equally populous colonies. However, colonies were less common (only four were found) and they occupied a different habitat. Nests were at woods edge under or near the bases of large trees and so were shaded most of the time. One was at a woods bordering a low field, but the others were at edges of high woods bordering rather dry fields. In each case the ecotone was taken over by young trembling aspen trees where the ants attended aphids.

Odor trails were made over and through the ground litter of twigs and leaves. The main trails of one colony were uncovered and mapped. Six trails radiated out into the field stopping at six aspens about 36 feet away. Two trails extended to an old nest 48 feet away and two others led back into the woods. One of

these branched to form three trails which faded out 40, 52 and 66 feet from the nest.

In this species flights started earlier in the year than those of *D. mariae* but in other respects were similar. Alate pupae and adults were both present when observations began on June 3. Pupae of alates were found until July 23 and adult alates until August 26. Twenty seven flights were recorded between June 7 and August 21, most taking place in July. Kannowski (1959b) recorded the flights at one nest and found that flights began at temperatures between 58 and 71°F.

Dorymyrmex grandulus (Forel)

This ant, which I recorded in 1975 as *Dorymyrmex pyramicus*, was found at only one place on the Reserve - a sandy, gravelly slope that was an outwash from a small hill behind it. There were no trees and vegetation was sparse, altogether a hot dry place. There were numerous small colonies. Workers were adapted to the heat; they have been seen foraging at a ground temperature of 103°F.

Small, almost flat craters of excavated sand two to three inches across often marked nest entrances, but even when these were blown away, nests were not hard to find because workers carried cookie crumbs directly home. Usually there was a chamber just beneath the soil surface and others were scattered down to as much as 25 inches. Chambers were not necessarily just beneath an entrance and some nests seemed to have several entrances.

Alate pupae were found between June 21 and July 2 and winged ants from June 25 to July 24. On July 9 a flight was seen in the morning when the temperature (10 inches above ground) rose to 81°F. Best flying was at 84°F and flying stopped at 86°F. Workers played an active part in the flight, running around rapidly and seemingly bumping into alates in such a way as to make them fly from the sparce grasses over the nest.

Tapinoma sessile (Say)

Tapinoma sessile lived in every habitat of the Reserve except the dry, open fields. It was very common in bogs and marshes but seemed equally adapted to oak-hickory woods, field edge, old orchards and wet meadows. It was just as versatile in its nesting habits, adjusting to sphagnum mounds, sedges extending up from water, piled up leaves, twigs on the ground, stems of living plants, spaces under loose bark of solid logs, soft wood of well-decayed logs, tops of Formica subsericea and F. ulkei mounds and even bird nests. Almost all the ant nests seemed ill-constructed, messy and fragile. Brood was heaped haphazardly in curled-up leaves or whatever was available, and the ants moved frequently to new sites. Usually the whole nest was above-ground, but in a low field chambers were made at levels of 1/2 to 4 inches in the soil.

Colonies were fairly populous. Smith (1928) estimated that an average colony would consist of from 2000 to 5000

individuals.

Alate pupae were already present on June 2 when observations began and were last seen on June 17. Alates were in the nests from June 9 to July 12. Only two flights were seen, but Kannowski (1959a) gives an account of a series of flights from Reserve bogs. He observed these between June 26 and July 14 between 8:20 am and 1:15 pm at temperatures from 67 to 83°F, under clear to cloudy skies.

Subfamily Formicinae

Genus Acanthomyops

At the Reserve there are five species of these yellow, hypogaeic ants. They vary in abundance, as shown by the number of colonies found: *Acanthomyops latipes*, 56 colonies; *A. claviger*, 28; *A. interjectus*, 13; *A. murphyi*, 11; and *A. subglaber*, 2. They all form large, stable colonies which have been known for long periods of time. One colony of *A. latipes*, known for 26 years, was still producing alates in 1968. A colony of *A. claviger* has been watched for 8 years and one of *A. interjectus* for 19 years. Workers of *A. murphyi* dug out along a road each year for 12 years and those of *A. claviger* beside a stone for 5 years.

In all cases colonies gave little or no evidence of their presence until the flight periods when openings to the surface were made. This digging out varied with time of maturing of males and females and also with the coming of rains which loosened the soil. *Acanthomyops interjectus* made openings earliest, beginning in June, *A. murphyi* came next, in July, followed by *A. latipes* in early August and *A. subglaber* and *A. claviger* in late August.

Acanthomyops claviger (Roger)

Acanthomyops claviger occupied a greater number of habitats than did other species of Acanthomyops. Colonies were distributed in deep woods, woods edge and in fields fairly near trees. Nest sites in the more open places were similar to those of A. latipes while those in woods were more like A. interjectus. Over half the colonies nested in, under and around wood of some sort. A few were found under and around stones and some made nest areas of semi-bare soil or had indistinct, overgrown mounds.

A distinguishing feature of the species was the fact that flights took place late in the year and at low temperatures. Pupae of alates developed between 9 July and 30 August while adults were in the nest by 13 August and were still present on 24 October.

Flights took place in the late afternoon (3:23 to 6:00 pm) when the light was not at its brightest. Hazy days were favorable. Flying did not start until the temperature went down to about 71°F., was best at approximately 68 F., and stopped at 64°F. On the best flight seen (3 October) mass flying took

place at 68°F. and in 20 minutes an estimated 5,000 females flew. The October flight (monitored by Phil Rosen) was also a heavy flight. In every flight some males flew, but they were much fewer in number and small and inconspicuous (Talbot 1963, 1973).

Acanthomyops interjectus (Mayr)

Typically, these ants nested in woods, being found from swamp border to higher dense or open woods or wood-field border, but one large colony lived outside woods edge in a high field behind a pond.

The ants seemed to start their colonies in wood (perhaps beginning as social parasites of *Lasius alienus*). Five lived in old stumps and in the soil around them and two were in and under logs half sunk into the ground. One was a rather indistinct mound of earth which had the remains of a stump buried in it. An elongated, leaf-covered, low ridge seemed to have been formed by soil thrown up over a log as it decayed into the earth. One

colony nested in and around the base of a rather solid stump when first seen, but in later years, as the stump decayed the ants remained in the same place in the soil, making openings for flight among leaves and around small stones.

Mounds developed if digging out took place in the same place year after year and if the loose soil did not blow away. Sometimes a small part would be dug out after a rain but usually mounds were not cared for between flights and became hard and almost deserted. They tended to be low, irregular in shape and vegetation covered. The largest one was in the midst of a blackberry clump which held the soil from being blown away. It grew from year to year and when last measured was 6 feet x 4 feet in diameter and 13 inches high.

Alate pupae were present on 3 June when collection began and were last seen on 9 July. Winged ants were found in the nest from 11 June to 25 August. Flights took place on every suitable day during the flight period and over the years 46 flights have been recorded between 16 June and 22 August.

Flights took place in late afternoon, beginning between 5:05 and 6:30 pm and, under favorable conditions, continuing until dusk. The alates could fly at temperatures between 81 and 66°F. but flew best when temperatures were in the mid- to high 70's. Ordinarily, flights were terminated when temperatures became too low and light too dim, but brightening of light and rise of temperature could also end flight. Wind which moves grasses could delay or stop flights. There were mass flights when, under favorable conditions, hundreds left the nest per minute. At one nest an estimated 55,200 flew in two hours (Talbot 1963, 1973).

Acanthomyops latipes (Walsh)

Acanthomyops latipes colonies favored drier habitats and typically nested in fields near woods edge in places where the

field vegetation was sparse and not leaf-covered. Colonies could also live in the middle of fields around isolated trees, but they were not present in the driest open fields. A few lived inside woods, even under considerable leaf cover.

Some colonies were associated with logs or stones but most simply nested beneath the soil surface. Usually they did not form mounds but a few indistinct ones were made where grasses were thick. They sought bare places for digging out for the flight period and openings were often clustered along centers or sides of roads.

A large colony, which was partly dug, had 40 openings, scattered along 10 x 6 yards just outside woods edge in a sandy upland field. Under the openings were many large chambers connected by numerous galleries. Vertical galleries extended down to deeper chambers which were scattered down to 16 inches. Foraging tunnels stretched out from the nest area among roots of grasses and forbs.

Alate pupae were found between 6 June and 29 August; adult alates between 13 July and 29 September

and flights were seen from 17 August to 27 September. Although they flew later in the year than did *A. interjectus*, flights were similar in all essential ways. The alates flew between 2:45 and 6:15 pm when the day was cooling (81 to 73°F.) and light dimming (2400 to 360 foot candles). Beta females were found in 6 of 24 colonies (Talbot 1963, 1973).

Acanthomyops murphyi (Forel)

Acanthomyops murphyi had essentially the same distribution as did A. latipes but seemed to form smaller colonies. Two colonies were in grassy spots among scattered oaks, eight in open fields fairly near trees or woods edge, while one was in a field at considerable distance from any tree.

One colony nested on a slope under a series of stones set into the soil, but the rest had no special covering. Each of six colonies dug out for flights by making openings along the middle or sides of sunny roads. Those far from roads sought rather barren places. No mounds were found.

Alate pupae have been collected between 19 June and 17 August, and adult males and females from 7 July and 16 September. Twelve flights were recorded between 19 July and 16 September. They took place between 4:35 and 7:35 pm, between temperatures of 81 and 68°F. and light from 3400 to 200 foot candles. As with the other *Acanthomyops*, flights usually ended when light and temperature decreased, but one flight stopped when the temperature rose to 87°F. Wind could delay or stop flights. Females had a distinctive way of standing facing upward with the front legs off the ground. Most ran in a jerky fashion with wings half spread before taking off from the ground.

On one occasion (August 3) many females were seen after a flight attempting to get into *Lasius neoniger* nest openings. *Acanthomyops murphyi* and *A. latipes* are known to start their colonies as social parasites of *L. neoniger* (Talbot 1963, 1973).

Acanthomyops subglaber (Emery)

Only two colonies of this species were found, both on a ridge above a swamp in a fairly dense oak-hickory woods. The first colony, collected only once, nested under and around a stone sunk into the soil and half covered with leaves. The second, known for five years, was found under bits of stone broken from a large immovable rock and galleries were traced for nine feet to a large, well galleried log lying on the slope. Brood was present at the log as well as the stone but the ants dug out for flights only around the stone.

Alate pupae were found between 29 June and 27 August while alates were seen from 24 August to 28 September. On a number of days between 8 September and 22 September males were seen outside the nest attempting to fly but light seemed to decline before temperature dropped sufficiently. On 27 September, an excellent flight day for a number of species, I arrived at the nest in time to see a few males fly at what seemed to be the end of a good flight (Talbot 1973).

Brachymyrmex depilis Emery

These tiny yellow ants are distributed in woods or low fields but are not found in high, dry fields or in swamps. They were most common in open oak-hickory woods, wood-field borders and fence rows, and were most abundant in clay soil. A great many colonies were found in one clayey low field because it was studied intensively by digging yard-square plots. Since the nests were in the soil among plants and had no particular covering or indication of their presence at the surface, they would have been unnoticed otherwise. They favored little raised places of soil and occasionally used sides of mounds of *Lasius minutus*, *Formica subsericea*, and *F. ulkei*. In places where stones were available, colonies had superficial chambers under these. Some lived under clumps of moss or, rarely, under bits of wood, in acorns or under leaf cover.

Beneath the soil the ants built clusters of smooth-walled chambers, three-fourths of which were within the first three inches of soil. Most nests did not extend deeper than 7 or 8 inches. The different stages of brood might be intermingled but sometimes they were segregated in separate chambers.

Alate pupae were found between 24 June and 19 August and adult alates from 12 July to 24 September. Flights took place on warm, sunny days of August and September. They were seen between 21 August and 16 September, at 4:37 to 5:50 pm, temperatures of 86 to 77°F., and light from 2200 to 1800 foot candles. Flying of one alate a minute constituted a good flight. Males and females usually flew from grasses just above the nest (Talbot, 1965).

Camponotus americanus Mayr

This large yellow-brown ant is widespread on the Reserve

in rather dry places. It was not found in the interior of heavily vegetated fields but over half of the colonies recorded were from fields near woods or from fields with scattered trees or shrubs. Others were equally divided between the edges of woods near field border and the interior of open oak-hickory woods.

C. americanus differed from other local *Camponotus* species in that it lived in the soil. Sixty-six colonies were found in open soil without any cover to nest openings. Sixteen had entrances and some chambers under stones. Only three were found in and under logs, and these had galleries extending down into the soil.

Usually nests had multiple entrances which were conspicuous after rains when workers brought out large pellets of coarse, sandy soil. During dry weather the particles dried up and blew away and entrances were often closed. Ants excavated during cool and cloudy weather. One colony had 5 or 6 ants working at an opening during the morning at 77°F. but they stopped at 82° and did not reappear until early evening when the nest was shaded.

Many chambers were near the surface. Some have been found at 4, 6, and 8 inches, but it is not known how much deeper they go. The impression is of rather shallow nests spread over considerable distance. In one place openings were found in a rough line for 6 feet and in another openings were spread over an area 15 x 15 feet. Sometimes chambers just below entrances had a few workers or brood, more often these were empty and brood would be found in chambers scattered underground between entrances. Workers reacted very rapidly to any disturbance and were quick to carry brood from exposed places.

It was easier to explore nests which were partly under stones. One used a stone set four inches into the soil of a hillside that served as a roof for large chambers and galleries. Larvae were piled here according to size and there was one pile of orange colored eggs. One foot uphill another large stone covered chambers with piles of larvae and pupae and another roofed a chamber with alate pupae. Another colony was distributed under a whole pile of small stones set into the top of a similar sparsely wooded hillside. Chambers were large; some measured 3 x 2 inches in diameter and were 1 1/4th inches high. Again, galleries extended back into the hill, and larvae were segregated from worker and alate pupae (usually some segregation of brood took place in this species, but not always).

Most foraging was underground and workers were not common walking on the surface, but sometimes individuals were seen. Once they were found attending aphids on young trembling aspen trees. Usually there was no pathway, but one colony had a visible worn path between two clusters of entrances that were six feet apart. Workers have been seen walking along an invisible trail on a fallen tree trunk.

Alate pupae were found between July 7 and August 22 and adult alates from August 11 to June 15 of the following year.

Camponotus caryae (Fitch)

This is a very rare and elusive ant at the Reserve. It was found 11 times, but each record was for a single worker walking on the bark of a living tree. On each of eight separate dates one ant was taken from the trunk of a partly fallen, but still living hickory at wood-field edge. Another was found on a similar hickory in an open high wood. One was on a living black oak trunk on a high point of an "island" in the swamp and one was on a red maple three feet from swamp edge.

Camponotus nearcticus Emery

C. nearcticus, while not abundant in any one place, was widely distributed in a variety of habitats. Its basic requirement was the presence of trees. About half the collections were made in oak-hickory woods, ranging from deep to open or woods edge. But the species was also found among tamaracks in swamps and bogs and among willows and red maples at their edges, in open groves of large-leafed aspen and in an old orchard of apple and walnut trees.

Favorite nesting places were in small dead branch stubs extending up from logs or in the upper drier rims of stumps. The ants also nested in dead branches of living trees, in large logs (usually at the top) and under loose bark. One small colony occupied the center cavity of a sumac twig. All of these places tended to be dry and the wood was usually hard. In small twigs the center would be hollowed out making a cavity 1/4th to 1/2 inch in diameter and extending for as far as a foot. In larger limbs and in logs the wood might have two or three galleries or it might be so thoroughly galleried that only thin partitions of wood remained. Individual ants were most frequently found walking up and down tree trunks.

Colonies were considerably smaller than those of *C. pennsylvanicus* and *C. noveboracensis*. One taken in July had a population of 1138: one queen, 279 workers, 302 worker pupae, 463 larvae and 93 eggs.

Alate pupae were found from July 8 to August 26. Adult alates were taken only three times; August 8, 18, and 24.

Camponotus noveboracensis (Fitch)

In South Michigan this northern ant is primarily an inhabitant of bogs, swamps and marshes and the low woods and fields around their rims.

Most of the colonies were associated with logs and stumps, larches being most frequently used in the swamps. Often the log was galleried extensively, leaving only thin partitions of wood. Soil beneath the log was also used frequently, and brood could be kept safe in the moist soil if the log became too dry. When stumps were utilized, they were excavated down into the soil. One colony used a dead part at the base of a living aspen tree, and one incipient colony nested in the stem of a milkweed

growing at marsh edge. Colonies could also live without any contact with wood. Black muck hummocks were often used in the swamp. These mounds might be bare or densely covered with moss, grass or sedge. Occasionally a colony was found in the sandy soil just above marsh or swamp edge with nothing to show for its existence except a few openings in the ground.

Workers often made foraging runaways from their nests. These might be shallow grooves cut into the soil or tunnels extending out just below a log or a thick covering of leaves. Workers foraged widely over the ground and sometimes attended aphids on small trees.

One colony was known for 23 years. It lived in a sunny, barren sand area just above the swamp. When found in 1958 it was a large, thriving colony occupying a small log and the soil beneath it. As the years went by and the log began to disintegrate, I put out several small logs that the ants accepted and used. In 1978 the colony was quite small but still produced a few females. In 1980 only a few workers were found.

Like other *Camponotus* species, *C. noveboracensis* overwinters its sexual forms. Alate pupae were found by June 17 and had all emerged as adults by August 21. Adults were found from July 11 to the following June 29, but most colonies were free of males and females by June 20.

A typical male flight took place on June 12 from a nest in two logs in almost complete shade of woods. By 3 p.m. (88°F) males were clustered at openings and workers were keeping them back. Also little gusts of wind kept driving them inside momentarily. At 4 pm (85°F) a cluster of 45 males were beginning to disperse over the log and individuals were shaking their bodies vigorously from side to side or stretching the fore part of their bodies upward. By this time light had dimmed considerably. Males continued to spread and by 4:50 (84°F) 19 had flown. Then suddenly they were shaking more and moving about more rapidly and flight had accelerated until by 5:20 (83°F) 86 had flown, 22 in the last minute. By 5:35 (83°F) 125 had left and there were no more males in sight. This proved to be the last flight of the season for the colony.

Camponotus pennsylvanicus (DeGeer)

C. pennsylvanicus colonies are common in upland oakhickory woods and at their field borders, and they are to be found in almost all wooded parts of the Reserve. This includes fence rows, single trees out in fields, denser woods in valleys and potholes, and willow or red maple borders of marshes and swamps. However, at swamp edge and out in the swamps they usually give way to *C. noveboracensis*.

New colony stages, from lone females to females with their first small workers, have been found in oval shaped chambers under loose bark or in wood. Once two queens with larvae and pupae occupied a cavity together but usually a single queen reared the first brood alone. Older colonies most often nested in large, fairly hard logs, but they sometimes occupied softer logs and smaller branches. They also lived in trunks

of dead, standing trees and dead parts of living trees where their presence was indicated by piles of sawdust at tree bases. Extensive galleries and chambers were carved out of the wood.

Workers foraged on the ground as well as in trees and sometimes wore wide pathways in the soil. Foraging tunnels could extend under logs, leaves and stones and sometimes brood was placed out along these galleries.

Alate pupae were found only once (August 10). Winged ants were present from July 29, throughout the fall and winter and until the end of the flight period next year (July 15). Thus, alates were in the nest for 9 to 11 months.

Only two flights were seen. One of these (June 14) took place from around a window frame of a house. At 3 pm eight females flew while the sky was temporarily overcast, but alternating sun and shade and fast moving clouds kept alates inside until 4:47 pm. During this time temperature and light ranged from 86°F and 600 ft. c. to 76°F and 1000 ft. c. and workers guarded the two openings, keeping females inside. The main flight began when the sun became very weak and the yard was in shade (4:48 pm, 78°F., 1200 ft.c.). At that time about a dozen females were in sight climbing up along the side of the window frame. At first, two to eight flew each minute, but at the height of the flights they averaged nine females flying per minute and 50 others were in sight (4:59 pm, 76°F, 1000 ft.c.). By 5:08 pm (75°F, 1000 ft.c.) flying conditions were less favorable, some females were beginning to drop, and they averaged one flying each two minutes. On the window, alates were clustering at the openings and a few were going inside. When the last female took off at 5:15pm (74°F, 800 ft.c.), 81 females had flown and the rest had retreated into the nest. No males were seen.

In the other flight (June 8) males and females came out of cracks in the solid wood of a large log and flew readily with no preliminary running about and no fluttering of wings. It took place during mid-afternoon (3:15 to 3:40 pm) of a warm day when there was a dim sun and the log was in shade.

Other people reported a number of flights between May 29 and June 22. After flights males and females often came to lights and isolated females could be seen flying or walking on the ground in the late afternoon. Dates for these observations ranged from June 7 to July 15. Thus the flight period seemed to extend from late May to mid July with most flights taking place in June.

Formica aserva Forel

This large, aggressive, northern species, which was formerly known as *Formica subnuda* Emery (Bolton 1995), differs from other sanguinary ants in several ways. It was slightly rarer (16 colonies were found) and lived in more sheltered places: in open to dense woods, often in low woods near water. One colony, known for six years, occupied a log just at the edge of the low ground at a swamp border.

Nests were almost always in and under logs, or more rarely

in stumps, or in leaves piled up beside them. In three cases, nests were in leaves only. Considerable thatch was used (in contrast to other sanguinary ants, which rarely used it) to seal logs to the surrounding leaves or to form chambers in the logs or leaves.

F. aserva enslaved *F. subsericea* but did not keep many slaves. They regularly had fewer slaves than *F. aserva* workers, and in three cases there were none at all. No raids were seen.

Alate pupae were present from June 6 to July 20 and alates from June 16 to July 28. Only two flights were seen(July 15 and 18) and they took place in the morning at slightly lower temperatures than was common for the other *sanguinea* species. Females could fly at 63° to 67° F and flew well in the lower 70's.

Formica creightoni Buren

This ant was described by W.F. Buren from ants found in Iowa, Illinois and the George Reserve in Michigan (Buren 1968). It was collected only 4 times here, three times from colonies and once from a raid.

One colony lived in the shade of an oak-cherry woods with a dense shrub layer and heavy leaf cover. It was in a 4-inch diameter log whose top was fairly solid wood and whose center was wood-soil. A second colony was in a grassy, open woods slope with the nest at the side of a stone. Pupae were scattered in the dry leaves here. The third colony, in a fairly dense woods, was under leaves only. Pupae were piled among the leaves over 15x15 inches, and there were several openings into the soil. This colony was raiding when found at 1:30 p.m. (July 12). On July 11 a raid was seen crossing a woods road at 1:00 pm, but the nest was not found. Slaves were *F. neogagates* and *F. lasioides*.

Alate males were seen once (July 25).

Formica dakotensis Emery

F. dakotensis is easily distinguished from *F. obscuripes* and *F. obscuriventris* by its thick petiolar scale. It is also distinguished by its habitat and nesting habits (Talbot 1971).

Only four colonies have been found on the Reserve, all in fields or field-edge close to water and to a variety of shrubs.

Nests consisted of a series of very small mounds of dried grasses that blended into the background of grasses, blackberries, shrubs, and a variety of field forbs in such a manner that they were not easy to discover. They increased in number as summer progressed and more brood was added.

One colony at wood-field edge had nine such domes spread in a line 30 feet long. Some were touching while others intercommunicated by tunnel runways cut through or just beneath the compact leaf layer on the ground. They were 3 to 9 inches tall and of different shapes, some were rounded while others had extensions built out in one or more directions. Another colony in a low field had 11 mounds spread over an area of 19 x 9 feet. The mounds were 2 to 7 inches high and of irregular shape. The largest was 27 x 24 inches in diameter. One was four feet from its nearest neighbor. All were connected by tunnels and were so constructed that stiff-stemmed plants helped hold the grass structure in place. Inside a mound the soil was excavated for 1/2 to 1 inch to form a floor and the grass thatch filled the interior except for spaces where brood was kept.

Workers were not conspicuous about the nests because, although they worked on the thatch almost constantly, they did this from the inside and because the tunnel runways that connected the domes also extended out for long distances to foraging grounds.

The workers specialized in attending aphids which lived just at the ground level where root and stem meet. They were found on plants such as meadow-sweet, goldenrod, Queen Anne's lace, shrubby dogwood and other small plants. When the aphids were just above soil level, the ants built small collar-like shelters around the stems.

F. dakotensis queens start their colonies by social parasitism and one such mixed colony was found. The single mound nest contained both F. dakotensis and F. subsericea. When found in 1972, the mound was typical of F. dakotensis in structure and F. dakotensis workers outnumbered those of F. subsericea seven to one. The colony had F. dakotensis brood and a few females. Next year the nest site was badly overgrown by high vegetation at the pond's edge, and in September, the ants moved a short distance to a more open spot at the edge of a field. There were then no F. subsericea in the nest. In 1974, the ants had a second mound 8 feet from the first and were thriving.

A distinguishing feature of *F. dakotensis* was that it developed brood very late in the spring. Eggs were present on June 3, but no larvae were found until June 12 and no pupae until June 16. Alate pupae were first found on August 2 and the first alates on August 24. A few males and females were still present on October 7 when observations ceased.

Flights occurred much later in the year than did those of other local *Formica* species. The earliest of 14 flights seen took place on September 5 and most were in late September. Two were seen on October 2 and 3 and evidently some took place later.

Even though the ants flew late in the year, they flew at higher temperature than other local *Formica* spp. Thus, flights did not begin until mid- to late morning (9:34 to 11: 42 am) when the temperature had reached 75°F or above. They flew best at temperatures between 78° and 88°F and did not fly at temperatures above 93°F (Talbot 1971). Passing clouds which reduced light and lowered temperatures would stop flying, and swaying vegetation caused alates to hold on or go down, to climb again and fly when the gust passed. Females tended to linger on the vegetation, and on some flight days this gave rise to a sparse swarm in which males flew back and forth

searching out females and mating with them.

Formica exsectoides Forel

Only one colony of this eastern mound-builder was found. The cone-shaped mound (36 inches in diameter and 10 inches high) was almost bare on top and had an outer layer of sandy, pebbly soil with some bits of leaves and twigs. Sides were covered with grass and the surrounding blackberries were kept back for a foot around its rim. The mound was not distinguishable from that of F. ulkei but the habitat was different. It lay in a sandy field of Canada bluegrass and trailing blackberry and was at some distance from any water.

The colony was found in 1971, and in June of 1972 the mound had deteriorated. Blackberries and grasses were encroaching and only the now-flattened top was bare. Larvae and pupae were being produced and workers were attending aphids on a small trembling aspen tree. In September of 1972, the mound was empty and the colony could not be found.

Formica fusca Linnaeus

F. fusca, F. subsericea and F. glacialis were all combined as F. fusca until A. Francoeur revised the group in 1973. F. fusca (the old subaenescens form) was not especially collected and records are very poor. They lived in woods, usually fairly deep woods, in stumps or logs. Typically, a colony occupied and galleried a fairly soft log placing its brood in and under the log and outside it among leaves at its side or down in the soil for a few inches. Alates were found between July 10 and August 13.

Formica glacialis Wheeler

This ant was confused with *F. subsericea* until its separate identity was determined by Francoeur (1973). It was then found to have a distinct and restricted habitat on the Reserve. All of the colonies formed mounds in low places surrounding (or in) marshes, swamps or ponds. While colonies were scattered in a variety of such places, they were most numerous in two. One was a small water-filled spot bordering a woods at the north fence. The little swamp-marsh had small willows in it and large ferns, grasses and sedges. Eight or more large mounds were here in the grassy border. They were made of loose black muck soil, were cone-shaped or rounded, and had grass growing up their sides. One large, irregular mound (60 x 40 inches across and 14 inches high) was out in the damper parts where very tall grasses grew. Next year the center was filled with water and this mound was gone.

The second region where the ants were common was around two sides of a marshy-edged pond. Here 26 mounds were scattered from just behind the water's edge in very wet soil, back through a narrow strip of low field and part way up a little slope to a higher field where *F. subsericea* took their

place.

The mounds had a mean diameter of 15 inches and a mean height of 7 inches. The largest measured 19 inches across and 10 inches high, and the smallest was 9 inches across and 4 inches high. Those of the lowest places were made of loose, black soil with some roots growing through them and marsh plants growing up their sides (grasses, sedge, scouring rush, shrubby cinquefoil, joe-pye weed etc.). Many had bare tops but some were completely covered. Mounds on the slope were more compact with matted grass growing through them and up their sides; most had bare tops.

Larvae and worker pupae were present all summer, and a large portion of three workers pupae were naked. Covered alate pupae were found from June 13 to July 30 and adult males and females from July 5 to August 18. No flights were seen.

Formica gynocrates Snelling and Buren

Six species of slave-making ants belonging to the *sanguinea* group are present on the George Reserve. *F. gynocrates* was the most carefully studied (Talbot 1985). It was distinguished morphologically from *F. pergandei* by W. F. Buren in 1971 when M. M. Martin had found significant chemical differences between the two. After that it was easy to distinguish the two by habitat preferences and species of slaves captured. Later, this new species was described by Snelling and Buren (1985).

F. gynocrates was an ant of the dry upland fields in places where vegetation was rather sparse and shade minimal. It was most usual where patches of small plants such as red-tipped lichen, polytrichum moss and pussy-toes mingled with a sparse stand of Canada bluegrass.

Workers enslaved *F. vinculans*, a characteristic field ant. Mixed colonies of the two were usually detected because enough soil was deposited on the ground to make a nest area with slightly less vegetation than the surroundings. While both species worked on nest construction, one feature was characteristic of *F. vinculans*. These built small cones of bits of leaves and sand about the bases of forbs which often harbored aphids. The tiny shelters blended so well with the surface litter that they were hard to see unless looked for especially.

Both species were active at high temperatures and both foraged for food. *F. vinculans* workers brought in smaller pieces constantly, while *F. gynocrates* carried larger pieces of insects.

Raids were carried out between June 16 and September 11. Small groups of *F. gynocrates* workers would start out from the nest together. As they progressed, they moved back and forth and spread out until the group dispersed. Other groups, coming along the same invisible trail, would extend it a bit farther. It was thought that the ants used both sight exploration and odor in finding a nest. Once one was found, more ants arrived quickly and attempted to enter. In some cases they

succeeded without opposition and soon emerged with pupae and larvae, but often the F. vinculans workers put up a fight before they were defeated and the brood stolen. Brood was carried back along the same general path that the ants used in coming out. If no nest was discovered, workers gradually went home along this trail. Raids could take place at any time of day since the ants were adapted to high temperatures and could carry out raids when the ground temperatures were as high as $95^{\circ}F$.

Alate pupae were present when collecting began (June 4) and were last seen on July 17. Alates were present between June 21 and August 16 and flights were observed between July 5 and August 14. They began in the morning when air temperature (10 inches above ground) reached 74 or 75°F, and alates flew best in the high 70's. Fifteen complete flights watched lasted a mean of 31 minutes and were sparse. These flights were from six different colonies and three were producing females and three males. The largest numbers seen for a flight were 46 males in one a 21 females in another.

F. gynocrates colonies, like those of others in the *sanguinea* group, moved frequently, although one was found in the same place for 10 years. These moves seemed to take over host colonies that had been raided and subdued. One colony moved to a *F. vinculans* nest 92 feet away.

Formica lasioides Emery

At the George Reserve *F. lasioides* occupies habitats between those of *F. neogagates* and *F. vinculans* and sometimes overlaps with them. Most colonies were found in fields, but not in the driest places. They were at field-wood edge, under scattered trees or under little, moist field depressions.

Openings of nests were often in clumps of dead grass culms, bits of moss or at bases of such forbs as puccoon and everlasting that shed little circles of dry leaves. First chambers tended to be off to one side of entrances (which might be multiple), and chambers were not scattered near the surface as was the case with *F. vinculans*. One large colony was dug. It occurred in a fence row between two fields and workers were tracked with crumbs to three entrances in a yard-long row. First chambers were found 1 to 3 inches below the surface and 7 more were scattered down to depths between 6 and 12 inches. This colony (June 6) had 18 delate females, 593 workers, 511 worker pupae, 588 larvae and 359 eggs.

Alate pupae were found three times: June 18, July 22 and August 3, while adult females were taken 4 times: July 10 and 24, and August 3 and 9.

Formica neogagates Emery

These are dark, timid ants living in small colonies in sheltered places. They are ants of the oak-hickory woods, most often in the denser, more moist parts which include cherry, yellow birch or witch-hazel. They are almost always found in places of heavy leaf cover but can live in more open ground or woods-edge if plants that catch and hold leaves are present. They may also make use of dense sedges or grasses.

Nest entrances were hidden or inconspicuous. Chambers and galleries were made in the more compact lower leaves, and brood was often scattered up in the looser, drier leaves. Characteristically, there were several chambers in the first three to five feet of soil.

Alate pupae were found three times; June 27, July 1 and July 10. Winged ants were recorded only twice; August 1 and September 8.

Twice these ants were found enslaved by the woods-dwelling slavemaker, *F. creightoni*.

Formica neorufibarbis Emery

F. neorufibarbis was found at only one place on the Reserve, in a large chamaedaphnae-sphagnum bog, and it was not common even there. The ants lived in the large hummocks of tough, fibrous, matted stems through which grew sphagnum moss and other bog plants. Workers were elusive and were almost impossible to follow to nests. Only five colonies were found. Chambers were made of bits of dry leaves and were scattered about in the hummock. Tunnels connecting them also ran out into the surrounding mass of stems, root and sphagnum and became foraging trails.

Alate pupae were found twice, June 16 and July 3. Three newly-emerged females were killed in the laboratory on August 3.

Formica nepticula Wheeler

Only two colonies of this *microgyna* group ant were found at the Reserve. One lived in the upper slope of an oak-hickory hillside. The nest was in a trashy layer of leaves under a piece of rusty metal. The ants had runways in the more solid basal leaves and had groups of larvae and pupae in the upper ones.

The second, larger colony was in a place of scattered oaks where the sandy soil was bare in some spots but heavily leaf-layered in others. Workers were first found carrying food to a large area of heavy leaf-layers. They would not carry cookie crumbs, so later I returned with bits of meat and followed workers 54 feet of their nest. This was in a patch of lespedeza which caught and held a thick mat of oak leaves. Several chambers were formed in the first two or three inches of soil, but most of the brood was up in the leaves. Runways and chambers were found in the lower, compact leaves and more larvae and pupae were in the upper, drier leaves. The whole formed an irregular nest area with brood scattered over 12 x 18 inches. In addition to worker larvae and pupae, there were alate pupae and a few males and females (June 29). On July 4 more males and females had emerged in the laboratory.

The nest was virtually destroyed on June 29, and by July 5 the ants had almost completely moved to another place of

thick leaf-layers. A few workers at the old nest were following a loose trail 44 feet to the new one. One male was found here.

These large, red and black ants were conspicuous traveling on the leaves. They foraged for long distances following loose, sparse trails. They were not aggressive but, once on a hand, bit vigorously.

Formica nitidiventris Emery

This beautiful and fast-moving ant is widespread and common on the Reserve. It favored open woods, wood-field ecotones and fields near scattered trees, but some colonies nested in deeper woods and some out in more open fields. Only about 1/4th of the colonies collected had nest entrances that were not concealed. The rest nested under stones, wood or leaves that covered entrances. Many were associated with logs, living in the ground beneath solid logs and also up in the wood of more decayed ones. Nests typically had chambers radiating out from a central shaft that extended down into the soil from a few inches to about two feet.

Alate pupae were found from June 15 to July 19 and alates were in the nest from June 28 to September 4. No flights were seen, but they were undoubtedly of the sparse, slow type described for colonies in Ohio and northern Michigan (Talbot 1945 and 1948).

Formica obscuripes Forel

F. obscuripes, the western thatching ant, reaches almost its eastern limit in Michigan. The Reserve is a favorable place for it, and colonies are numerous on its dry, sandy, upland fields (148 colonies were counted in 1980). They are not present in lower sites near water where mounds of *F. ulkei* occur.

Mounds were rounded heaps of thatch consisting of grass stems, small tree twigs and finer plant material, pebbles and a little soil. Typically, each had a bare top roughly 15 to 37 inches across surrounded by sloping sides that were heavily overgrown with timothy or Canada bluegrass. The total mound diameter varied from 15 to 37 inches and height from 2 to 11 inches.

Often nests were easy to spot in the field because the circle of grass was lush and taller than that of the surroundings. This benefited the ants in two ways. It lengthened the working day when temperatures were high by letting ants work in the shade, and it gave a taking off place for flying ants. Occasionally, a nest was surrounded by trailing blackberries or lay in the partial shade of a tree. If these gave too much shade, the colony moved or died out.

Inside the nest the coarse thatch extended deep into the excavated soil (15 to 24 inches) and had spaces that served as brood chambers. Smaller chambers were evacuated in the soil beneath and around the thatch center. The thatch center was almost impervious to water and was usually dry even when the surface was soaking wet. On some sunny days when the

soil was cold, pupae were brought up and scattered all over the mound surface.

Workers foraged individually, spreading out in any direction from the nest, or they followed one to four definite pathways that led out from the nest to aphid- bearing plants. These runways were usually smooth and bare, 1 to 2 1/2 inches wide and cut into the soil 1/2 to 1 inch. If dense grass fell over them, they became tunnels. One colony had four trails, two going 20 and 35 feet to oaks and two going 105 and 106 feet to trembling aspens. Another had one path which branched to run 25 feet to a young oak and 39 feet to an ash. Spread along the length of the road were eight openings into the soil where workers seemed to be tending root aphids. These openings were typical of trails, and sometimes small thatch structures were thrown up above them. They were also made around such plants as dandelions in places where there were no trails.

Colonies sometimes moved. One, whose immediate foraging area was destroyed when a lawn was cut around the nest, moved brood for 15 days. After colonies move out, the thatch caves in forming a depression that may be evident for several years.

This species matured brood very early in the spring (larvae were not overwintered) and by late May there were larvae, pupae and alates in the nest. Alate pupae had all developed into adults by June 22 and some alates were mature and ready to fly in late May. The first flight seen was on June 1 and the last on July 1. Individual colonies might have 5 to 16 flights. Some produced only males or females while others produced both.

Flights began in the mornings when temperatures reached 69 to 71 F. They stopped when temperature became too high for the alates to come out on the nest or before noon, even if temperatures remained favorable. They could be delayed or stopped by a drop in temperature, swaying grass or passing clouds (Talbot 1959, 1972).

F. obscuripes had well developed and typical ground swarms in which all the flying ants from mounds in a field would meet at one place. The females walked or stood on low vegetation, while males flew back and forth until they found and mated with females.

Formica obscuriventris Mayr

This species forms populous colonies on the Reserve, but it is neither conspicuous nor especially common (30 colonies have been found). Its favorite habitat is at woods edge or along fence rows where young oak and trembling aspen trees are invading a field. Colonies were also present in open woods, clumps of trees in fields and rather open slopes above marshes.

Three-fourths of the nests investigated were associated with wood. Fallen tree trunks with branches still attached were most frequently used, along with logs, stumps, or even bits of bark lying on the ground. In all cases dry leaves were also utilized, banked against the trunk, entangled in small branches

or simply extending out from the wood. Some colonies nested in dry leaves only. In all a moderate amount of thatch was employed, filling holes in logs, sealing openings or outlining brood chambers. Often the best way to find brood was to stir up the leaves banking a log. Nest areas were very irregular, especially for those colonies following several branches extending out from a main trunk and for those using leaves only.

In spite of the fragile nature of such brood chambers, colonies were rather stable. One was known for 19 years. When found in 1954, it was a large and vigorous colony occupying two logs. Ten years later no wood was left and only a fragment of the colony was found among leaves.

F. obscuriventris made even greater use of cut-into-the-ground trailways than did *F. obscuripes*, and these often became tunnels by a covering of leaves. They were permanent pathways to trees or shrubs that harbored aphids, and they usually encircled the bases of such trees. One system of trails extended 45 feet to a cluster of trembling aspen.

One colony occupied the greater part of a fallen tree in a little group of young black oak and black cherry trees lying between two fields. This log also harbored seven other species,* but *F. obscuriventris* clearly dominated the habitat. Much brood was found in and under and at the sides of 16 feet of the main trunk and out along four branches. Covered trails extended out from the branches to a cluster of trembling aspen which harbored aphids.

Alate pupae were found from June 16 to August 6 and males and females were in the nest from July 15 to August 31. Twenty-two flights were seen, over several years, between July 27 and August 31. In 1962 records were kept of 16 flights from one colony (Talbot 1964). The alates began flying at low temperatures (63 to 69°F) in the morning between 7:37 and 8:43 am E.S.T. when rays of sunshine were first striking the nesting logs. They flew best at 68 to 70°F. They did not fly on days of rain, overcast sky or very wet soil.

There was one indication that these ants have swarming areas similar to those of *F. obscuripes*. On August 17, 1975 a friend found about 12 females and 50 males among goldenrod plants in a field. Females were standing on the plants and males were flying about and mating with them.

*[Footnote: This small area proved a good habitat for ants. The seven species living in the log--Formica obscuriventris, Camponotus noveboracensis, Aphaenogaster tennesseensis, A. picea, Ponera pennsylvanica and Lasius neoniger--were augmented by nine species living in the ground--Formica subsericea, Leptothorax curvispinosus, L. ambiguus, Lasius neoniger, Dolichoderus plagiatus, Prenolepis imparis, Ponera pennsylvanica, Aphaenogaster treatae and Myrmica sp.]

Formica pergandei Emery

F. pergandei could not invade centers of dry, open fields where most F. gynocrates colonies lived. Some colonies were

far enough out in field borders so that they received shade for only a small part of the day, but the majority lived just at fieldwood edge or along fence rows, forming large and conspicuous semi-barren nest areas. Several were found in open woods and a few in low fields near marshes.

These ants enslaved F. subsericea, which was abundant at woods edge. A few colonies raided into fields to enslave F. nitidiventris and some mixed colonies consisted of all three species. The slave ants were generally quite docile and did not often resist invasion.

Raids were seen between June 18 and August 16. They were essentially like those of *F. gynocrates* except that they did not take place at high temperatures. Thus, on warm days raiding parties went out in the morning and again in the late afternoon but observed a mid-day lull. Sometimes workers stayed in the captured nest over night. Many raided-colonies were close by, but some were as far as 80 feet away. Once workers of a colony were seen bringing in pupae from successful raids of three different host colonies. There were always more slaves than *F. pergandei* workers in a mixed colony.

Alate pupae were in the nest from June 6 to July 29 and alates from July 1 to August 8. Flights were seen from July 6 to July 27, and took place in the mornings at slightly lower temperatures than those of F. gynocrates. They could begin at 66 to 70^{0} F (ten inches above the ground) and alates flew well in the low 70's. Some flights included both sexes, but many were of males or females only.

Although the location of one colony remained the same for 10 years, most moved occasionally. Probably most such moves were to recently raided *F. subsericea* nests. One such raid was followed. The *F. subsericea* colony had been raided on July 17, 18, and 19, with some fighting. Then on July 20 the *F. pergandei* workers began moving brood into the captured nest and continued to do so for 11 days. On August 3 they raided from the nest. During the moving, female flights took place on five days: July 18, 23, 24, 26, and 27. Most flew from the old nest, but some followed workers along the trail before flying. On three of these days, 108, 84, and 45 females were seen to fly.

Formica rubicunda Emery

Like *F. pergandei* and *F. subintegra* most colonies of *F. rubicunda* were at field edge near woods. Others were just under overhanging tree branches in open woods. Like the other two, they formed nest areas of reduced vegetation, medium-sized ones being about three feet across. Those living where leaf litter covered the ground made tunnels out from the nest and sometimes pupae were brought up and placed there.

Raids were seen between June 18 and September 1 but most took place in June and July. They were like those of *F. pergandei* and *F. subintegra*, taking place in the morning and late afternoon in warm weather.

Alate pupae were found between June 14 and August 14

and alates from July 5 to August 6. Flights, seen between July 12 and August 4, were indistinguishable from those of *F. pergandei* and *F. subintegra* and sometimes flights of all three species were seen on the same days and at the same time of day. All flew in the low to mid 70's.

Formica schaufussi Mayr

F. schaufussi is much like F. nitidiventris but the body is more hairy. It was not so common on the Reserve and was typically an ant of fields. Habitats of the two species overlapped in places of scattered trees or woods- edge, but F. schaufussi was not taken in deep woods. Most nest entrances were open and visible and only a few were found under stones, leaves or clumps of grass. Nest structure was similar to that of F. nitidiventris.

Alate pupae were collected between June 20 and July 11 and alates from July 8 to August 1. Two very poor flights were seen (July 9 and 11) on clear sunny mornings when the temperature ranged from 67 to 78°F 10 inches above the ground and from 81 to 91°F on the ground.

F. schaufussi and *F. nitidiventris* could not be distinguished in the field. Under the microscope most collections were distinct, but some seemed intermediate between the two species.

Formica subintegra Emery

If collecting records are to be relied upon, this is the most common sanguinary ant on the Reserve. Over the years 45 colonies have been found. *F. pergandei* (28 colonies) and *F. rubicunda* (19 colonies) are second and third in abundance.

Most colonies of *F. subintegra* occupied exactly the same habitat as did *F. pergandei* (field-wood border) but some lived successfully in open woods and a few were found in deeper woods. In fields they formed nest areas, but in woods the mixed colonies sometimes followed *F. subsericea* habits, making a nest under logs or stumps. If there was leaf or grass cover at nest edge, the workers often formed tunnels in or under these for a yard or more so that the ants were not conspicuous when leaving the nest. This trait was shared by other sanguinary species.

F. subintegra workers enslaved F. subsericea and 21 raids were seen between July 1 and August 24. These were like those of F. pergandei, with workers going out in small groups over loose, invisible trails 5 to 10 inches across in the morning or late afternoon. They sometimes raided colonies as much as 120 to 140 feet away and most raids were conducted without fighting. One colony was known to remain in one location for seven years, but most moved occasionally, taking over raided nests. A more detailed account of raids has been given (Talbot and Kennedy 1940).

Alate pupae were found between June 10 and July 31 and adult alates from July 1 to August 14. Flights (July 7 to August

8) were like those of *F. pergandei*, taking place in early to mid-morning, usually at temperatures in the mid 70's.

Formica subsericea Say

These ants are conspicuous and abundant on the Reserve and are versatile in their habitats and nesting structures. They are most numerous in fields near woods edge, along fence rows and at clusters of trees in fields. They are also common in some of the more open woods and can penetrate fairly dense places. A few are found in low fields. They do not invade the high, dry, unshaded fields where their place is taken by *F. vinculans*.

Most field colonies live in fairly level places of moderate ground cover, and here the ground surface forms a "nest area," which is a circlular or oblong site recognizable by its sparse vegetation. Some are almost bare, while others are vague because they have low plant cover not much scarcer than the surroundings. Nest areas are often about 24 inches across, but they may vary from a few inches to a huge size. One, along a road, was 110 x 40 inches.

During dry weather the nest surface becomes hard and deserted looking because the ants have openings only around the rim in places of protective coverings of leaves. After a rain the whole surface may have scattered entrances with workers carrying out excavated soil which they drop on the nest area. In places of sparse vegetation it is blown away, leaving the nest area flat or built up only a few inches. However, if nests are in places where grasses are high, in low, moist fields, or on wooded slopes, the soil is held and mounds that are sometimes quite large develop.

Colonies in woods use logs, stumps or bits of bark as nests and brood may be found up in the decaying wood, beneath it or in the leaves at the side. Sometimes, as the wood decays, a mound develops. Sometimes a colony is found in soil under stones or leaves with no sign of a nest at the surface.

Alate pupae were first found on June 20, but they must sometimes be produced earlier because adult alates were once taken on June 23. Alate pupae were last seen on August 15 and adult alates on August 31.

No long series of flight records were made but alates have been found walking or flying outside the nest on July 12, 15, 22, 27, and 30. In August most of three flights were seen. A male flight (August 1) lasted 65 minutes and took place at temperatures between 73° and 76°F. The most males (22 a minute) flew at 75°F, and 677 males were seen to fly. A female nest nearby in the sun had just finished its flight when this one began (10:30 am). Another male flight lasted 40 minutes, taking place between temperatures of 68 and 85°F. Only 2 to 6 males were seen at a time, and this may have been the colonies last flight (August 21).

One fairly good female flight took place (August 5) from a nest near three small elm trees. It occurred between 9:15 and 10:55 am at temperatures between 74 and 76°F under overcast

skies. Most females came out and flew from the trunks or branches of their nests. A year later (August 3) this colony was raided by *F. subintegra* ants in the late morning. While workers fought or spread out from the nest, females also came out and flew quickly from grasses on the ground (temperature 88°F).

A catbird and a red-headed woodpecker picked off some females on the elm trees, and at a male flight a hornet flew low over the grasses and dried leaves to pounce on and carry off a male. It returned three times and caught three more males, even going under some loose leaves to rout one out.

Formica talbotae Wilson

F. talbotae, a small, workerless, social parasite belonging to the *microgyna* group, lives in nests of the prairie mound-builder, F. *obscuripes*. It is a rare ant but has been found in Iowa and North Dakota as well as at the Reserve in Michigan (Wilson 1976).

Only four colonies were found on the Reserve, all living in fairly small nests of the host. The one nest that was dug had many adult males and females of *F. talbotae* all through the thatch, with brood in the deeper thatch and also in chambers in the soil surrounding it. No worker brood of either species was ever found and *F. obscuripes* workers cared for F. *talbotae* brood.

F. talbotae had a long flight period with flights taking place on every favorable morning from mid June to late September (Talbot 1976). They took place in the morning between 69 and 83°F. when the temperature was rising, light was brightening, and vegetation was not swaying. It was estimated that the colony could have produced between 2600 and 2800 alates in a season and that about 42% were females.

Formica ulkei Emery

The large earthen mounds of F. ulkei are common on the Reserve. In a survey of 112 mounds the three largest measured 96 x 84 inches in diameter and 34 inches high, 95 x 75 x 26 inches and 180 x 96 x 30 inches.

Local distribution was governed by three restrictions. The ants needed to be in the open and could not tolerate total shade; they had to be on land that was near water but was not subject to flooding; and they relied on plants harboring aphids or membracids, which provided a great deal of their food. The main plants were several species of shrubby dogwood, clustered on banks around marshes or in fields around permanently wet water holes. Rarely, one was found on a raised place in a marsh.

Mounds were made of soil, and thriving colonies kept the tops bare, although sparse grasses often grew along the sloping sides. A completely grass-covered mound was a sign of a weakened colony. Around a thriving mound there was a ring of grass only, beyond which were the usual forbs and shrubs.

The ants kept these latter from encroaching shrubs in the grass ring. They could not control shade of overhanging branches, and colonies so shaded ultimately died out or moved.

Inside the mound the soil was honeycombed with myriads of galleries which also extended deep into the soil. During dry weather openings over the mound were closed and the surface formed a hard crust. After rains there was much excavation, which added layers of soil to the surface; workers also brought pebbles, twigs and bits of leaves to form a thin outer layer.

Colonization is by two methods. In one, a newly fertilized female invades a colony of *Formica subsericea* and her offspring are cared for by the host workers. Ultimately the host ants die, and a pure colony results. This method of colony formation gives rise to isolated colonies, sometimes in unfavorable habitats. The one mixed colony found on the Reserve was in a low field where ground water sometimes reached the surface.

The second method of expansion is by budding. In this case workers from a well-established colony excavate a new nest and bring larvae and pupae into it. Later a queen is added. This type of colonization was usual on the Reserve and resulted in clusters of colonies. At one place 24 mounds surrounded a series of small, water filled, depressions in a field. At another place colonization of a newly built road was studied between 1953 and 1959 (Talbot 1961). Active colonization resulted in a maximum of 26 mounds in 1956. By 1959 the growth of trees and the spread of dense vegetation reduced the number to 13. In later years checks revealed a steady decline of mounds as shade became more dense and open spots were eliminated. There were six mounds in 1965, one in 1975 and none in 1976. The last colony to die, which seemed to do most of the colonizing, was one that had been known since 1930. At that time it was large enough to be especially noticeable. It seems possible that so called "colonies" formed by budding never loose contact and so make up one huge polydomous supercolony.

Alate pupae were found between June 7 and July 25 and adult alates from June 20 to July 28. Flights were seen between June 26 and July 14. They took place in the early morning (5:20 to 8:40 a.m.) when light was brightening. Males flew from grasses surrounding the mound, while females walked away to fly from trees, shrubs or large, stiff-stemmed forbs (Talbot 1959).

Formica vinculans Wheeler

There was confusion concerning this species for a long time because all *Proformica* without fine hairs on antennal scales keyed to *F. neogagates*. However, there were two distinct groups in two different habitats on the Reserve.

In 1972 William Buren kindly checked a large number of collections and wrote that a few were *F. neogagates* but most were similar to those he had called *F. vinculans* in Iowa. This recognizing of two separate species solved the problem. The

larger, darker, timid ants forming small colonies in sheltered places were *F. neogagates*, while *F. vinculans* were smaller, lighter colored, fast-moving ants forming larger colonies in dry, open fields. In several papers *F. vinculans* was misnamed *F. neogagates* (Talbot 1953, 1965, 1966).

F. vinculans colonies occupy the typical Reserve dry fields where grasses are supplemented by a variety of scattered forbs such as goldenrod, hawkweed, pucoon and lichen. These fields are sandy and the vegetation is sparse enough to leave patches of bare soil without a heavy covering of matted leaves.

The workers are adapted to high temperatures and often forage at temperatures high enough to cause a halt for most other field ants. At these times they run rapidly and climb up off the ground as much as possible.

The ants formed nest areas with several to many openings spread over several inches to several feet. One large nest area measured 8 x 9 feet at flight time. They were rarely conspicuous because there was seldom newly excavated soil, plant growth was not much disturbed and entrances were concealed by bits of living or dry leaves. A distinctive characteristic of the species was the forming of miniature cones or towers. These were built up around the bases of supporting plants and consisted of "pebbly thatch" made of sand grains, bits of grass and small flakes or dried leaves of forbs. The little structures were hard to see because they looked much like natural vegetation. Some were simply built around entrances while others formed small chambers which might harbor aphids on bases of stems and sometimes held pupae or loitering alates. Some were roofs of chambers scooped out of surface soil.

Below ground most of the chambers were spread out close to the surface with only a few extending deep into the soil. One colony had seven chambers scattered over three feet in the first three inches of soil. Two galleries extended down giving off five more chambers at 6, 7, 8, 9 and 12 inches. Another had eight chambers in the upper eight inches of soil and one vertical gallery with chambers at 13 and 18 inches. Five colonies whose populations were counted were chosen because they were of medium size (Table 5).

Alate pupae were found in nests from June 16 to July 14 and alates were seen from June 25 to August 9. The length of the flight season depended on how early flights could start and the number of favorable days. Flights were recorded from July 5 to July 23. In 1961 (a late year) they took place between July 17 and July 23, while in 1962 (an early year) they occurred between July 5 and July 15. Flights began in the morning when temperatures rose to 72°F or above and light was brightening. Colonies in cool morning shade flew later than those in early sun.

Flights ended when the temperature became too high or light darkened. They lasted from 28 to 82 minutes. On one good flight day approximately 600 males and females left a nest while on another day only 14 took off. In all flights seen both males and females were present except the last one in 1962 when only females flew because the nest had been depleted of

males. A more detailed description of flights (in which they are misnamed *F. neogagates*) has been given (Talbot 1966).

F. vinculans ants were actively enslaved by a field-dwelling sanguinary ant (*F. gynocrates*) and large compound colonies were formed. Sometimes the *F. vinculans* workers put up very active resistance and battles ensued. At other times they were intimidated and simply ran out of the nest carrying brood up onto nearby grass stems.

in places to form chambers. Masses of larvae and some pupae would be present in the chambers at or near soil level with more pupae piled in layers of leaves above. Chewed up leaf thatch often outlined these "chambers." Sometimes one large dry leaf would hold several dozen pupae.

The groups of brood scattered among leaves made a nest area of very irregular outline and no constant shape. Such nest areas covered up to 35×30 inches. One colony had a central chamber with larvae and pupae surrounding a trembling aspen

Table	5.	Populations	of Formica	vinculans	Wheeler.
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Date	Queens	Workers	Males	Females	Alate	Worker	Larvae	Eggs	Total
6-17-66	8	2445	0	0	197	670	843	551	4714
6-28-66	2	1145	0	0	67	148	1078	757	3197
7-13-66	1	783	4	4	0	675	435	209	2111
7-26-66	2	1387	0	0	0	624	276	421	2710
8-9-65	1	986	6	0	0	390	556	92	2031
Mean	2.8	1349.2	2.	8	52.8	501.4	637.6	406.0	2952.6

Formica sp. (microgyna group)

These ants were never fully identified. They are definitely of the *microgyna* group and are close to *F. adamsi* or *postoculata* but do not run to either in Creighton's (1950) key.

They were not uncommon on the Reserve (34 colonies were found), but they were elusive ants that made inconspicuous nests. Although workers were large and easily seen foraging on vegetation, they were hard to trace to the nest because they foraged singly, did not form trails, would not take bait and rarely carried solid food (they were found attending aphids for liquid food). Further, they were as apt to walk under leaves as upon them, and they usually moved a colony as soon as it was disturbed.

Most colonies were found at woods edge where there was a broad zone of young oak trees invading a field. Such a habitat often had blackberries or other shrubs, young trembling aspen and a ground cover of grasses, bracken and forbs such as mullein, milkweed and lespedeza. Some colonies nested in more open places where trees were scattered and some were in more sheltered places in woods. The one essential was an accumulation of tree leaves that were dry and loose on top, more compact and moist near the ground and relatively free of mold. Often the leaves were caught in a bush or fallen branch that kept them from blowing.

Nest structure was very simple and involved leaves more than soil. Often a nest center was one or more shallow chambers excavated in the soil and roofed by compact leaves. From there one to several galleries would go down one to six inches into the earth, and they sometimes ended in chambers. From the surface chambers a series of runways would cut 1/4th inch deep into the soil and be roofed by leaves. The compact leaves would be tunneled through and these galleries widened

trunk and groups of pupae scattered out in all directions. Another nest lay in a line 28 inches long and only two inches wide. There was probably a great deal of moving of such colonies since loose leaf layers were easily disturbed and might become too wet or too dry.

Brood was abundant all summer. Larvae and pupae were present when the first collections were made in the first week of June, but all pupae were still larviform at that time. Formed alate pupae were first distinguished by June 19 and were not found after July 22. Larvae were present until September 3 and worker pupae until September 15. Alates were present from July 1 to July 25, with the small females being more numerous than the males. No flights were seen.

Lasius alienus (Foerster)

L. alienus is almost completely confined to woods. It was sparse in the drier oak-hickory highlands but abundant and widespread where black oak mingled with or gave way to black cherry, white oak, aspen, willow or tamarack. These places were on slopes around deep potholes or near and in swamps.

Colonies might nest entirely in the ground, often with chambers under stones, but more typically they nested in stumps and logs of all sizes where the wood was soft and easily galleried. Occasionally they were found under loose bark of harder logs. Sometimes nests extended down into the ground as well as up into the wood. The nearest they came to nesting in fields was in an old apple orchard where well decayed logs were sunk into tall grasses.

L. alienus developed alates earlier than any other Lasius species on the Reserve. Alate pupae were already present when collecting began on June 5 and had all developed by July

16. Winged individuals were found from June 22 to August 12, but most were gone by late July.

Only two flights were seen. One took place on July 17, when at 4:00 pm a large group of alates emerged and flew from an old log. The other, on July 27, also about 4:00 pm lasted about 10 minutes, with males and females flying from the ground. Alates were taken at lights or wandering on the ground from July 11 to August 2.

Lasius flavus (Fabricius)

In most parts of the Reserve *L. flavus* is rare. Except for one low field where it was abundant, it was found only eight times. These eight colonies were in open, grassy woods or in medium-dense woods where leaf cover was sparse. Five had chambers under stones, two under bits of wood and one under a small clump of moss. All had galleries extending down into the ground and out near the soil surface at the sides.

In a low field bordering a marsh colonies were numerous and widely spread. Here 23 colonies were found in 40 square yard plots which were dug at intervals along a strip bordering the marsh (Talbot, 1965). This abundance would not have been discovered by ordinary collecting methods because there were no logs or stones to turn over and the ants made no contact with the soil surface except during flights.

Nests spread out below the surface in irregular shapes which might cover a yard or more. The smooth chambers were very numerous, almost touching, and were connected by short galleries. Some were small but many were as large as 1 1/2 x 1 1/4th inches in diameter and 1/2 inch high. Top chambers had only a light covering of soil and chambers were most common at one to four inches, although some extended down to six or seven inches. Foraging tunnels ran out among plant roots.

Some segregation of brood occurred; often, but not always, eggs, larvae and pupae were in different chambers. Females and female pupae were usually in chambers by themselves, but males and male pupae were mixed with the worker pupae.

Pupae of alates were found from June 12 to August 16 (one sheltered nest had a few male pupae on September 28) and adult alates from July 25 to October 2, although most nests were emptied of winged ants by mid-September. Flights were seen between August 27 and September 7 and must have occurred later.

In getting ready for flights, workers simply broke through the roofs of chambers near the surface, making holes extensive enough for the large females. Two August flights seen were enormous because there were so many colonies taking part. The whole field was dotted with patches of yellow workers, marking places where males and females were flying. September flights were minor because so many colonies had been cleared of alates.

Flights took place in the late afternoon on warm, humid, hazy days. They lasted 25 to 70 minutes. Ants flew between

4:45 and 6:20 pm, E.S.T., between 84 and 70°F, 65 and 85% relative humidity and 3600 and 1,000 foot candles of light. After flights many females dropped, broke off their wings and walked over the ground. Often there were also females of *L. speculiventris*, *L. minutus* and *L. pallitarsis*, which tended to have flights at the same time.

Queens founded colonies independently and usually occupied a single initial chamber, but 2, 3 or 5 queens have been found together. They might have eggs only, or larvae and pupae in all stages plus the first small workers.

Lasius minutus Emery

On the Reserve *L. minutus* is restricted to low, moist places. Nests are numerous in the more open swamps. Kannowski (1959c) found 100 of their mounds in 10 acres of swampmarsh. Some extend into the sphagnum mat of the floating bog and into the denser tamarack-poison sumac areas. They are characteristic of borders of swamps and marshes and are found for short distances in low wet fields or woods skirting these.

L. minutus is a mound-building species. Only one colony was found in wood and this was in a stump so old that all but the rim was wood-soil. Usually the mounds had flat tops lightly overgrown with plants and straight sides which had thick growths of grasses, sedges and other vegetation. If the colony was flourishing, the interior would be completely galleried and soft but sometimes the colony occupied only part of the mound. Mounds were made of whatever type of soil was available. In the swamp they were composed of soft, loose, moist, black muck or the brown, fibrous wood-soil of tamaracks. Those of the floating mat were of finely shredded sphagnum. Along the marsh edge fields they generally consisted of gray or yellow sandy soil, sometimes with a mixture of clay.

Mounds ranged in size from 5 to 26 inches high and from 10 to 45 inches in diameter. Twenty-four that were measured gave a mean height of 14 inches and a mean diameter of 24 inches.

Workers foraged by making tunnels into the moist soil or occasionally in packed layers of wet leaves. They were not seen at the surface except during the flight season and even then they stayed in the shade. At one nest tunnels were traced from the nest to the nearby marsh. Most were 1/2 to 2 inches under the soil surface where there were abundant small roots, but some went deeper into the soil. In several tunnels there were little piles of discarded pupal cases.

Alate pupae were found between June 17 and September 9 and alates from July 25 to October 7. Flights were seen between August 27 and September 27. Workers prepared for flights by making numerous openings on the mound surface and, on days that were not quite right for flying, these were guarded to keep males and females from emerging. In general flights took place between 2:30 and 5:30 pm, when the sky was hazy or the nest was shaded (Talbot, 1965). Temperature

ranged from 88 to 72°F. and light from 5800 to 1000 foot candles. High relative humidity and approaching rain favored good flying. Too bright light, wind or cold prevented flights. A conspicuous characteristic of this species was their mass movements up and down plant stems. Hundred of alates would climb at once and fly readily, but if a slight wind shook the grasses or the light brightened, they all headed down again leaving the plants bare. This mass movement up and down might take place a number of times during a flight.

Lasius nearcticus Wheeler

L. nearcticus looks much like *L. flavus* but differs in habitat preference. While *L. flavus* favors more open areas where soil cover is sparse, *L. nearcticus* is adapted to places where leaf layers accumulate on the ground. It is widespread in oakhickory woods, especially in the deeper, more moist parts.

In about half the collections colonies had chambers under stones. Others were in and under much decayed logs and stumps, under encrusting moss or under layers of leaves. In all cases the nests spread out into the surrounding soil. The presence of scattered stones on a wooded hillside set up ideal conditions for colony abundance. These stones might be large and deep set or they might be small. In any case chambers made under them were favorable places for the hastening of brood development and the loitering of alates before flights. On one wooded hillside colonies seemed as numerous as those of *L. flavus* in the low field.

Alate pupae were found between June 20 and August 29 but were scarce after August 16. Alates were in the nests from July 30 and a few were still present on September 26 when observations ceased.

In 1973 and 1974 the shaded oak-hickory slope where colonies were abundant was watched carefully for flights but the only four seen were not abundant ones. These were on September 8, 9, 12 and 25. Workers made openings from top chambers or at sides of stones when alates were ready to fly. The flight on September 25 took place in spite of discouraging winds because other conditions were good; the sky was hazy and there was a sultry feel of approaching rain in the air. At 5:05 pm (74°F.) a little group of workers came out at the side of a flat stone and climbed slowly to its top, while males gathered 10 inches away on a bit of bare soil. At 5:20pm the females began flying. A check of the hillside showed seven little clusters of ants, five flying from stones and two from under leaves. Back at the original stone a slow flight was continuing with 8 or 10 females and one or two dozen workers in sight at a time. At the small group nearby males were trying to fly, but gusts of wind sometimes picked them up as they spread their wings. Workers were trying to keep them back. The sparse flight continued until 5:35 when workers had succeeded in getting most alates back under ground. By this time the light was dim, the temperature had lowered to 73°F, and the wind was stronger.

The flight seen on September 8 involved even fewer colonies. Only two groups were found; one of females flying from a stone and one of both males and females flying from leaves on the ground. During flight (5:50 to 6:25 pm), the temperature dropped from 76 to 73°F, the light dimmed from 200 to 80 foot candles, the hillside was in full shade and humidity was high.

On September 9 two small groups of males started to fly at 4:55pm (74°F and 190 foot candles) and stopped at 5:07 pm after 35 to 40 males had flown. Seemingly, they stopped because the sky was clearing. Another small group came out at 5:35 pm and a few males flew, but again they went back when the light brightened a little. Another group did not fly because workers of *Aphaenogaster picea* were trying to capture males. This caused larger numbers of *L. nearcticus* workers to come out and the males to go down into the nest.

In none of these instances were environmental conditions quite right for abundant flight and most of the numerous colonies did not take part in them.

Lasius neoniger Emery

L. neoniger is the most common ant on the Reserve. Its small craters of excavated soil are seen in all of the fields, whether barren or thickly vegetated, high and dry or low and moist; but they are most abundant where vegetation is sparse enough to allow small spots of bare soil. Nests are present but less numerous in oak-hickory woods and in the more open places in otherwise deep woods. They are usually not present in dense woods, bogs and swamps.

L. neoniger characteristically nested in soil with no surface covering but if stones were available they sometimes used these to form roofs for superficial chambers where pupal development could be hastened. Colonies sometimes lived in the soil beneath scattered brown leaves or in and under small branches or pieces of wood. In low places they nested among clumps of grass.

The familiar craters were built when excavating was taking place in the nest and soil was being dumped just outside entrances. The moist grains stuck together to form a small circle at each entrance or sometimes even a collar-like structure close around it. When the soil dried, it tended to blow away, thus obliterating the crater.

Trying to ascertain the size of a colony was a baffling problem. On the surface there was a constant opening and closing of entrances (Talbot 1953) so colony boundaries could not be marked by these. Underground, chambers were scattered and foraging tunnels extended out in all directions. In a field thickly dotted with craters it was not known if there were a great many small colonies or fewer large ones. Depth of nests was also unknown. One, dug 18 inches, revealed many chambers with workers and alates but no brood.

Workers made extensive use of secretions of root aphids and did much of their foraging underground. However, they also foraged on the surface, collecting small insects and other bits of food. They were cool weather ants and have been found most abundant on the surface at temperatures below $60^{\circ}F$ (Talbot 1946). They were seldom seen at temperatures above $80^{\circ}F$.

Alate pupae were present from June 23 until August 5 and alates have been found in the nest from July 8 to September 28. Flights began at about the time when all the alates emerged from the pupal stage, and they took place on every suitable afternoon thereafter until all alates were released. Most flights occurred in the latter part of August. Of 55 flights recorded, 2 took place between August 5 and 10, 114 between August 11 and 20, 21 between August 21 and 31, 11 between September 1 and 10, 4 between September 11 and 20, and 3 between September 21 and 27. Usually, during the height of the flight season there were abundant and widespread flights with many colonies taking part so that the air was filled with ants (Talbot 1945). As one Reserve resident put it, "The lawn was awash with ants." By early September many nests were emptied of alates and flights tended to be spotty and sparse.

Worker preparation for flights began, usually after a rain, with the great enlargement of entrances and of chambers just beneath, where males and females could loiter. Entrances were reopened if they were closed by rain and were kept large as long as alates were in the nest. This preparation might begin by the first week of August, and thereafter males might be seen down in openings on most afternoons even when no flights took place. Flights might be delayed by hot, dry weather which made the ground hard. In one extreme case openings were enlarged on August third after three days of rain, but no flights occurred until August 20.

On any favorable afternoon males would begin to push up toward the surface with workers holding them back. If conditions continued to improve males and a few females would push harder and workers would guard less well until they all poured out onto the ground. Soon alates would climb grasses and fly. Some would walk a bit on the ground or plants, spreading out to widen the circle of flying ants. Workers played no farther part until flying conditions became unfavorable again when they would begin urging alates back into the nest. Always many more males than females flew.

Flights have begun as early as 3:30 and as late as 6:00 pm, from 82 to 71°F., and with light intensity as high as 2000 ft.c. to as low as 600 ft.c. Heavy flying most often took place between 4:30 and 5:45 pm and light from 1900 to 1200 ft.c. Flights from individual colonies tended not to be long, from 20 to 30 minutes, but flight over a large area could be much longer because on sunny days colonies in the shade of buildings, trees or tall grasses started earlier (and stopped earlier) than those in sunnier places. Early flights took place when the sky was overcast and temperature was not too high. Late flights started after warm bright days when the sun was sinking, but the temperature had not yet dropped too much. Usually flight ends were brought about by reduced temperature or light.

Occasionally flight would start under a cloudy sky and be stopped when the sun came out. Wind could sometimes prevent a flight. A recent rain or the feel of a coming storm favored flights, but they could not take place under dark clouds.

Mating took place in the air and soon after flight females began dropping to the ground. (I have been on a lake when females were falling like rain drops into the water). Sometimes a female will descend with a male still attached. One such landed on a leaf, twisted to dislodge the male and then immediately broke off all four wings, one at a time, before she moved to the ground and crawled under a chip of wood. First chambers have been found with one or two females in them (Talbot 1965).

Predators, such as toads and spiders, come out during flights and ants such as *Formica nitidiventris*, *Aphaenogaster treatae* and *Myrmica americana* make a business of carrying away males. The first ants may also carry away the larger females, forming groups of two or three to do so.

Lasius pallitarsis (Provancher)

This is a northern forest species that reaches approximately its southern limit at the Reserve (it extends further south in mountains). It is similar to L. neoniger but can be distinguished in the field by its larger size and lighter color and its different habitat preference.

At the Reserve *L. pallitarsis* was confined to bogs, swamps and marshes or to low fields and woods bordering them. In the swamps, colonies occupied hummocks of matted grass and sedge or mounds of loose, black soil overgrown with mosses and sedges. These mounds were sometimes as large as 8 to 10 inches high and 17 to 20 inches across. Those on shore tended to be smaller and were built in thick clumps of grass. Mounds gave a place to escape high water and to keep the pupae out of the moist soil below. In woods, many colonies occupied old, soft stumps and the ants were most often found in parts below the soil level. They also lived in, just under and beside old logs or just under the soil surface and in thick leaf layers if they were well packed and stable. Usually pupae were found in higher chambers and larvae lower in the nest. Chambers with pupae were often distributed horizontally over several feet. This was to be expected since foraging galleries radiated out in all directions and were used by workers attending root aphids and coccids. Some galleries led up to higher ground where brood could be taken during high water. On cool, dull days workers sometimes foraged above ground.

One nest was partly excavated. It lay just at marsh edge and consisted of a six-inch-high mound densely covered with grass and another smaller mound farther inland. Both mounds were made up of labyrinths of galleries and chambers among grass roots. Galleries connected the two mounds and extended out in all directions one or two inches below the soil surface. Chambers were large, averaging 1/2 to 1 1/2 inches in diameter. Brood tended to be segregated, with larvae in

chambers about 6 inches down in the mound and pupae in more superficial chambers in the mound or just under the soil surface nearby. In several places there were blind end galleries filled with discarded pupa cases. Foraging tunnels led out into the field and marsh among grass and sedge roots.

Alate pupae were found between June 19 and August 25 and adult alates from July 22 to September 22. Four flights were seen; August 18, 20, 27 and 28 (Talbot 1965). Flights began when the afternoon light dimmed, either because the sky became overcast, the nest came into the shade of tree branches or because the slanting sun caused grasses to shade the nest. They began as early as 5:00 pm and as late as 5:45 pm, and they stopped between 5:20 and 6:20 pm. Flights could begin when the temperature was as high as 87 or as low as 71°F but they seemed best at about 80°F. High humidity was favorable.

There was no external evidence of "digging out" in preparation for flight; workers and alates simply came up from a trashy layer of twigs and grass stems. There was no massing of ants since they came to the surface over several feet and spread more as they moved about on plants. The large females were more numerous and more conspicuous than the small dark males. They climbed high before flying, usually taking off from sturdy stems of meadow-sweet or goldenrod. Under favorable conditions females walked up stems quickly and flew readily with almost no fluttering of wings. Under unfavorable conditions they fluttered wings more and sometimes dropped.

In general flights followed the *Lasius* pattern; they took place in the afternoon with lessening light, lowering temperatures and little or no wind. On August 28 five species of *Lasius* (*L. pallitarsis*, *L. minutus*, *L. speculiventris*, *L. flavus* and *L. neoniger*) flew from the same field.

Lasius speculiventris Emery

L. speculiventris and L. umbratus are quite similar looking in the field, but the brighter yellow, more shining L. speculiventris was not as common and was more restricted in habitat. Only 15 colonies have been found and all were located in moist places; in the bog and all are located in moist places; in the bog-marsh-swamp complex, in the low fields near the swampy places or in deep woods with much ground cover of leaves and twigs.

One typical swamp-inhabiting colony occupied a large mound of fine black muck, overgrown with plants and penetrated thoroughly with tough fibrous roots. It was 40 inches across and 14 inches high and stood in the inches across and 14 inches high and stood in the almost complete shade of a tamarack-poison sumac-red maple swamp. It was surrounded by dense vegetation of blueberries, ferns, mosses etc. Three other mounds in low wet fields near the marsh edge measured 29 x 14 inches in diameter and 19 inches high, 25 x 25 x 9 inches and 23 x 19 x 3 inches. They were built of gray, sandy soil or of black muck and were all at least partly overgrown with plants such as grasses and sedges and the

shrubby meadow sweet. Smaller mounds might be only 3 to 7 inches high and so overgrown that they seemed part of the uneven soil floor.

Colonies in higher, drier places did not form mounds. (One colony reported (Talbot 1965) as building a large mound near the top of a slope was misidentified. It was *L. umbratus*.) Even in the swamp some colonies nested in wood. One occupied the stump end of a large log lying 8 inches above the swamp and supported by large roots. The main trunk was thoroughly galleried and galleries ran down the roots into the soil. One remarkable structure, built at a swamp edge that had been subjected to high water, consisted of a cone of loose, black muck 8 inches high and 11 inches across at its base and held in place by several stems which it had been built around. Inside the cone were handfuls of workers, pupae and larvae. It looked as if the ants had built a temporary shelter after being flooded out of the soil and wood in which they had lived.

Two colonies, found in dense oak-hickory woods, were nesting in stumps. They were at ground level in the stumps and also in well galleried main roots extending out from them. These structure resembled those of the closely related *L. umbratus*.

Twice workers and larvae were found under small stones and one large colony nested in the soil under and at the side of a large rock sunk into a grassy slope just above a line of trembling aspen which bordered a marsh.

Workers were known to forage in the soil for considerable distances. In a low field they were found as far as 20 feet from a mound, in definite tunnels extending down toward the marsh. They tended to travel one to four inches below the surface and favored making passageways beneath woody roots. At places they were attending root aphids. Empty pupae cases were carried out and discarded in some of these tunnels. In swamps workers have been found foraging in the small space just above the water level and below the soil surface, and during high water they were seen running in files on the wet surface.

One colony has been known since 1962 and in 1980 it was still thriving and producing alates. During these 19 years its low, overgrown mound had been extended out about a foot to maintain its position at the edge of bushes which were encroaching from the marsh into the low field.

Alate pupae were found from June 18 to August 23 and alates from July 14 to September 27. Flights were recorded from August 27 to September 27. They took place in middle to late afternoon starting as early as 2:30 pm on warm, hazy, humid days and as late as 5:30 pm when the sun was bright. Alates flew best at moderate temperatures (83-72°F), in somewhat reduced light (7200 - 2000 foot candles). Bright sun or a breeze could prevent or delay flights (Talbot 1965). They usually ended when the temperature dropped to 71°F. and light dimmed, but might also end if the sun came out bright. On afternoons of bright sun flights might be prevented because it became too cold before light was sufficiently reduced. Flights were conspicuous because the shining yellow workers

accompanied the darker alates as they climbed the tallest and stoutest plants above the nest. Stems of shrubby dogwood and cinquefoil were favored but sturdy grasses and sedges were also used and a few flew from the ground.

Lasius umbratus (Nylander)

Lasius umbratus is not uncommon on the Reserve, and individual colonies are often large and conspicuous. They are most characteristic of old stumps in deep woods but are not restricted to that habitat. Beside the potholes and valleys they also live in more often woods, in swamps and marshes and their edges, and in low or (rarely) high fields. In 43 records of their presence 13% were in marshes and swamps, 15% in fields and 72% in woods.

Of the 43 large nests discovered, 21 were in and under stumps, 16 in and under logs and 6 in mounds. Occupied stumps tended to be in such late stages of decay that they were readily pushed over. Typically the nest was below the ground level and out into the roots, and both stumps and roots were galleried in all directions so thoroughly that only thin, easily crumpled partitions remained. Sometimes handfuls of ants, brood and partitions could be lifted out. The more moist stumps might be half-filled with red wood-soil. Logs in which the ants lived were often firm on top but the lower part, half sunk into the soil, would be galleried into thin partitions or to red wood-soil. In either stump or log the nest extended out into the ground, and brood was sometimes carried into underground runways stretching out as foraging tunnels. The logs and stumps were most often in deep oak-hickory-cherry woods, but some were in more open woods and some at woods-swamp edge or out in the swamp. However, none was found in the chamaedaphne-sphagnum bogs.

In fields where wood was not available, the ants lived in soil and often produced mounds. These were irregular in shape and seemed more the result of digging out for flight in the same place year after year than to an innate tendency to mound-building. Three mounds were found in a low field where water was often high in the spring so they might serve as a raised place for taking brood at such times. One was 15 x 20 inches across and 5 inches high. One mound was in a small wooded strip bordering a swamp and another was at the base of a little grassy slope, not near a marsh. The most unusual one was located on the top of a grassy hill with almost no shade. The mound was grass covered except on top and grew in size over the years from 22 inches in diameter and 10 inches high to 53 inches in diameter and 15 inches high. It was made of clay that became hard and dry. Each year in late summer the whole top would be covered with excavated soil when openings were made for flights. These mounds were not transient; one was checked repeatedly for 20 years and others have been known for 10, 9, and 8 years.

Workers foraged underground and often took brood out along their tunnels. Larvae and pupae have been found scattered in galleries under stones or moss or bits of wood at considerable distance from the main nest. Workers attended root aphids, and in colonies near swamps and marshes, they sometimes foraged into wet soil just above the water level or traveled out on the surface when the ground was soaked.

Alate pupae were present between July 9 and August 25, while alates were found from July 26 to September 27. Preparations for flight began when the workers began to dig out, any time after the first of August, and usually after a rain. On flight afternoons workers and alates gathered at the openings and, after some hesitation, emerged onto the ground. When conditions were right, they climbed grasses on or around the nest and usually flew from these, although they could also fly from the ground. The yellow workers that accompanied the black males and brown females did not interfere with their movements when flying conditions were favorable. When it became too cool or light was too bright, they kept males from flying.

The most favorable flight days were hazy, hot and humid, and under these conditions mass flights could begin in midafternoon. If the sun was bright, they had to wait until later. They were usually stopped by lowering temperature (71°F) and the lessening of light of the sinking sun. (One flight was ended when the sun came out bright and the temperature rose.) Even a very slight wind could prevent or stop a flight. Once, when herds of males were climbing all the grasses, they were repeatedly driven down by little gusts. The mass descent was fast and so was the climbing again after the gust ended. The longest flight seen lasted two hours and the shortest seven minutes. This latter was terminated by a sudden drop in temperature.

Flight activities greatly resembled those of *Lasius* speculiventris and *L. minutus* and conditions were roughly the same for all of the *Lasius* species. On two hot, hazy days (September 6 and 7) there were mass flights of *L. umbratus*, *L. speculiventris*, *L. minutus*, *L. flavus*, and *L. neoniger*. On another afternoon (September 16) all of these flew except *L. flavus* which had run out of alates and, in addition, flight records were made for *Crematogaster lineolata*, *Brachymyrmex depilis* and *Myrmica* sp.

Table 6 gives a summary of flight conditions for L. umbratus.

Paratrechina parvula (Mayr)

These small ants are not conspicuous on the Reserve, but colonies are fairly common in some places. They are most likely to be found in wood-field ecotones, in openings in woods and in fields that are near woods or have scattered trees.

Most nest entrances were simply exposed holes in the ground, so tiny that they were best located by giving the workers crumbs to carry home. Some entrances were concealed in clumps of grass under small stones and acorn cups or beneath sparse leaf cover. Occasionally, when the ants were digging

Table 6. Environmental conditions of six flights of *Lasius umbratus* (Nylander) between August 26 and September 16.*

	Time ^a (p.m.)	Temp. ^b (°F)	Light ^c (foot candles)
Emergence of alates	2:50 - 5:00	88 - 73	4,200 - 1,200
Beginning of flights	3:27 - 5:04	84 - 74	4,000 - 2,200
Peak of flights	3:40 - 5:07	85 - 72	5,000 - 2,000
End of flights	4:48 - 5:28	73 - 71	1,900 - 900

^aTime - Eastern Standard

out after a rain, there would be a little ring of excavated soil. Nests had chambers just below the surface and these might contain brood even in quite dry soil. However, most often the first brood was encountered six inches or more down in the soil, and the chambers could be off to one side, not directly under the entrance. Nests often had several chambers between one and four inches down and then others 6, 7, 11, or 12 inches deep. The small size of galleries and the irregular position of chambers made nest structure hard to define. Brood was also elusive; sometimes a chamber with a few larvae and pupae would be dug and then no more could be found.

Workers on the ground ran rapidly and usually foraged independently, but they have been found following an odor trail while moving their brood to another nest.

Alate pupae were found between July 15 and August 20 and adult alates from July 15 to September 27. They are overwintered and probably fly on the first warm days of spring at approximately the same time and under the same conditions as *Prenolepis imparis*.

Polyergus lucidus Mayr

Forty colonies of the beautiful "shining slave-maker" were found on the Reserve, where their distribution followed that of the slaves, *Formica nitidiventris* and *F. schaufussi*. Thus, it was essentially an upland open field ant that might also be found at woods edge and in openings in oak-hickory woods.

Slave raids were conspicuous because the reddish ants moved rapidly in a compact body to the nest of a colony from which pupae and larvae would be taken. Captured pupae emerged as worker ants to form a mixed colony in which the slave ants did all the work of caring for *Polyergus* brood, enlarging the nest and foraging for food. Raids began in mid-June when *Polyergus* larvae were becoming numerous and needed much food, and the colonies to be raided were developing many pupae. They reached peaks in mid-July and dwindled to an end in early September when pupae to be taken were becoming scarce. During the raiding season *Polyergus*

workers made forays in the mid- to later afternoon on almost all suitable days (Talbot 1967).

Nests were usually in rather open ground and their entrances were inconspicuous unless there was excavated soil around the one to several entrances. Underground structure was characteristic of the slave species; one to three vertical shafts extended downward to as much as 30 or 40 inches and many chambers radiated our from them (Talbot 1948).

Alate pupae were present in colonies over a long period (June 19 to September 2) and adult alates were seen from July 21 to September 26. Flights (from July 31 to September 26) took place in the early afternoon on very warm days (78 to 95°F) when the overhead sun was bright (7000 to 9000 foot candles gave good flying conditions). A passing cloud which reduced light could stop a flight but ordinary wind did not. Clusters of males moved about rapidly on grass blades before flying while females walked on the ground before taking off. After flight delate females invaded colonies of the host species (Talbot 1968).

Prenolepis imparis (Say)

Prenolepis workers and nest openings are not conspicuous in summer when most collecting was done. However, enough colonies were found to ascertain that the species was widespread at the Reserve in a variety of habitats. They seemed most abundant in wood-field ecotones and along roads through woods, but they also occurred inside woods from open oak-hickory and pine to potholes and swamp border. They could be found in low fields of predominately clay soil and in almost pure sand of dune-like open woods.

Studies in Ohio and Missouri (Talbot 1943b) showed that, in contrast to the mid-summer lull, the species was quite conspicuous in spring and fall. In spring the workers foraged any time the temperature was above freezing and reached heights of activity between 45 and 60°F. They also formed distinct circles of excavated soil around nest openings in preparation for mating flights which commenced as soon as mid-day temperatures rose into the 70's. In fall workers foraged on fruit and were especially active after the first frosts when they supplemented their diet by collecting insects killed by the cold. By winter over 75% of the workers were repletes, being so full of honey that their gasters were almost clear and they had difficulty walking. This stored honey seemed to be reserved for use during the summer lull when workers were not foraging but larvae were being fed (Talbot 1943a).

Colonies were not especially large. Twenty colonies dug in Missouri and Ohio averaged 1568.9 individuals of which 1125.6 were workers. Each colony lived in a simple nest in the soil which consisted of a central shaft around which chambers radiated. The shaft might extend as deep as four feet and have as many as 40 chambers, but most nests were considerably smaller than this. In only a few cases were nest openings found under stones. Most were unconcealed and in places

bLight - foot candles, straight up

[°]Temperature - 10 inches above the ground

^{*}Relative humidity between 40 and 90%.

where vegetation was not dense.

At the Reserve alate pupae were found from August 14 to September 17. Adult alates were in the nest from September 5 to the latter part of April of the following spring. No flight was seen but friends reported them from April 14 to April 29. Where colonies were numerous, they formed fairly conspicuous ground swarms in which males flew among the females, which stayed on the ground or on low vegetation (Talbot 1945).

Records were kept of the presence of developmental stages in colonies and of nuptial flights on the Reserve and are presented in Table 7. The dates given are the first and last times that the stage was observed or that flights were seen. The records are more complete for those species that were intensively studied; species that were rare or hard to find have less complete records.

Brood Development and Flight Records

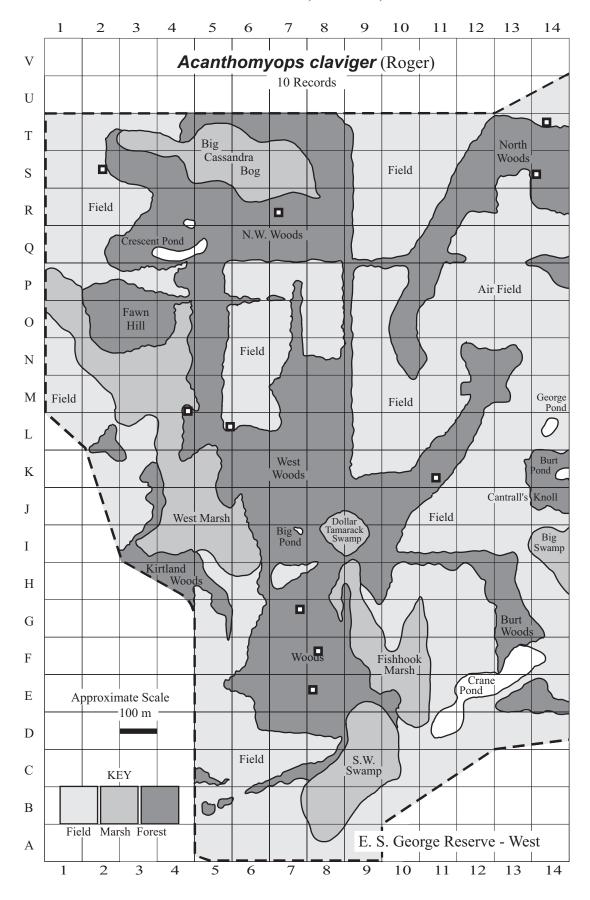
Table 7. Periodicity of immature and alate development and of nuptial flights for all species.

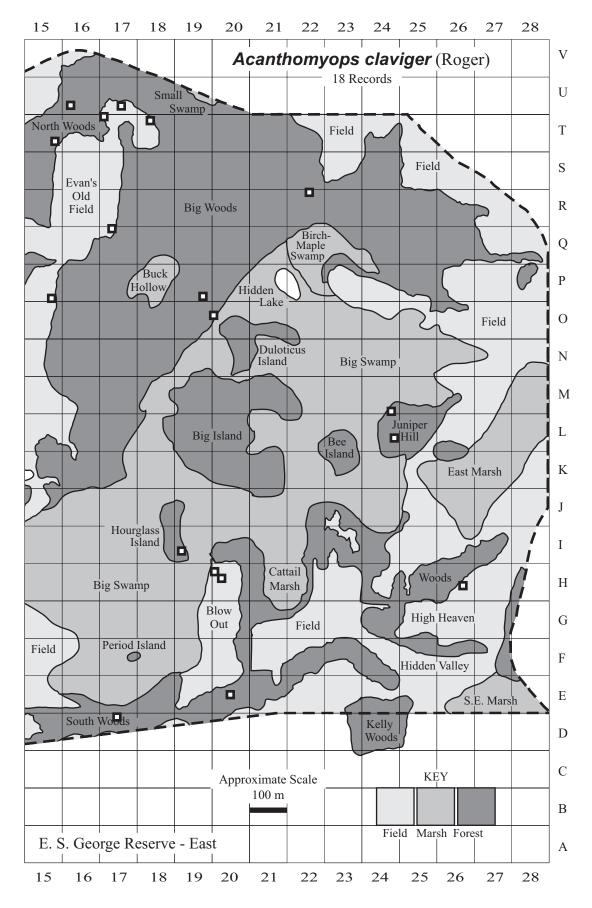
Species	Eggs	Larvae	Worker Pupae	Alate Pupae	Alates	Nuptial Flights
Amblyopone pallipes	June 16 – Sept. 15	June 5 – Sept. 18	June 16 – Sept. 15	July 18 - Sept. 2	Aug. 16 – Sept. 18	
Ponera pennsylvanica	June 18 – Aug. 6	June 5 – Sept. 18	June 6 – Sept. 9	July 16 – Sept. 24	Aug. 1 – Sept. 28	Aug. 23 – Sept. 28
Proceratium silaceum	July 15, 1957	July 15, 1957	July 15 1957		August 23, 1954	August 23, 1954
Aphaenogaster fulva	August 22, 1957	July 6 – Aug. 25	Aug. 14 – Sept. 3	Aug. 14 – Sept. 3	Aug. 14 – Sept. 3	
Aphaenogaster picea	Sept. 14, 1963	June 13 – Sept. 14	July 1 – Sept. 14	June 14 – July 25	July 1 – Aug. 26	July 27-29, 1960
Aphaenogaster tennesseensis	June, 5 1963	June 5 – Sept. 3	June 10 – Sept. 18	July 14 – Aug. 12	July 14 – Sept. 3	
Aphaenogaster treatae	June 3 – Aug. 29	June 3 – Sept. 23	June 9 – Sept. 23	June 4 – July 10	June 15 – Aug. 10	June 30 – July 26
Crematogaster cerasi	July 28 – Aug. 29	June 5 – Aug. 27	June 5 – Sept. 5	June 15 – Aug. 22	July 21 - Sept. 24	Aug. 27 – Sept. 20
Crematogaster lineolata	June 6 – Sept. 17	June 6 – Sept. 28	June 6 – Sept. 16	June 20 – Sept. 2	June 27 – Sept. 18	Sept. 16, 1963
Formicoxenus hirticornis				June 18, 1971	June 18, 1971	
Leptothorax ambiguuus	June 19 - Sept. 10	June 15 – Sept. 28	June 17 – Sept. 10	June 17 – Aug. 6	June 27 – Sept. 11	
Leptothorax curvispinosus	June 6 – Sept. 8	June 3 – Oct. 5	June 6 – Oct. 5	June 8 – July 18	June 23 – Aug. 10	
Leptothorax duloticus	June 8 – Sept. 26	June 8 – Sept. 26	June 8 – Sept. 7	June 26 – Aug. 24	July 21 - Sept. 26	Sept. 17, 1972
Leptothorax longispinosus	June 17 – Aug. 28	June 9 – Sept. 7	June 22 – Aug. 12	June 22 – July 26	July 19 – Aug. 5	
Leptothorax muscorum	June 22 – Aug. 28	June 22 – Sept. 1	June 22 – Sept. 1	June 27 – July 6	June 22 – July 20	
Leptothorax schaumii	July 1 – Aug. 8	June 21 – Aug. 8	June 22 – Aug. 8	June 22 – July 23	July 23 – July 27	
Leptothorax texanus	June 6 – Aug. 10	June 6 – Sept. 15	June 6 – Sept. 15	June 12-30		June 25 – Aug. 1
Monomorium minimum	June 11 – Aug. 24	June 8 – Oct. 3	June 11 – Sept. 14	June 15 – July 20	July 7 – Aug. 12	July 8 & 9
Monomorium talbotae				June 30, 1966	June 30 – July 6	
Myrmecina americana	July 10 – Sept. 3	June 9 – Sept. 3	July 10 - Sept. 3	July 12 – Aug. 14	Aug. 6 – Sept. 7	
Myrmica americana	June 2 – Aug. 5	June 2 – Oct. 2	June 5 – Sept. 28	June 26 – Sept. 4	July 2 – Sept. 27	Aug. 30 - Sept. 27
Myrmica detritinodis					August 8	
Myrmica fracticornis						
Myrmica incompleta	July 19 – Aug. 30	July 19 – July 30	July 19 – July 30	July 20 – July 30	July 20 – Aug. 11	
Myrmica lobifrons						
Myrmica pinetorum	June 17 – Sept. 4	June 17 – Sept. 27	June 17 – Sept. 27	June 25 – Aug. 1	Aug. 1 – Sept. 27	
Myrmica punctiventris	June 2 – Sept. 26	June 2 – Sept. 26	July 6 – Aug. 28	June 19 – Aug. 10	July 20 - Sept. 15	Sept. 14, 1969
Myrmica species 1						
Myrmica species 2						
Smithistruma pergandei	July 15 - Sept. 4	July 15 - Sept. 4	July 15 - Sept. 4	Aug. 22 – Sept. 4	Aug. 22 – Sept. 4	
Smithistruma pulchella						
Solenopsis molesta	June 7 – July 10	June 7 – Sept. 30	June 7 – Sept. 22	June 29 – Aug. 27	July 21 - Sept. 6	Aug. 4 – Sept. 6
Stenamma brevicorne	June 23 – Sept. 10	June 14 – Sept. 10	June 23 – Sept. 10	July 9 – Aug. 11	Aug. 10 – Sept. 10	
Stenamma diecki	June 10 - Sept. 16	June 10 – Sept. 16	June 22 – Sept. 16	July 1 – Sept. 1	July 19 - Sept. 8	
Stenamma impar					Aug. 13 – Aug. 19	
Stenamma schmitti						
Dolichoderus mariae	June 4 – July 3	June 3 – Sept. 9	June 12 – Sept. 17	June 30 – Sept. 16	June 30 – Sept. 24	July 4 – Sept. 22

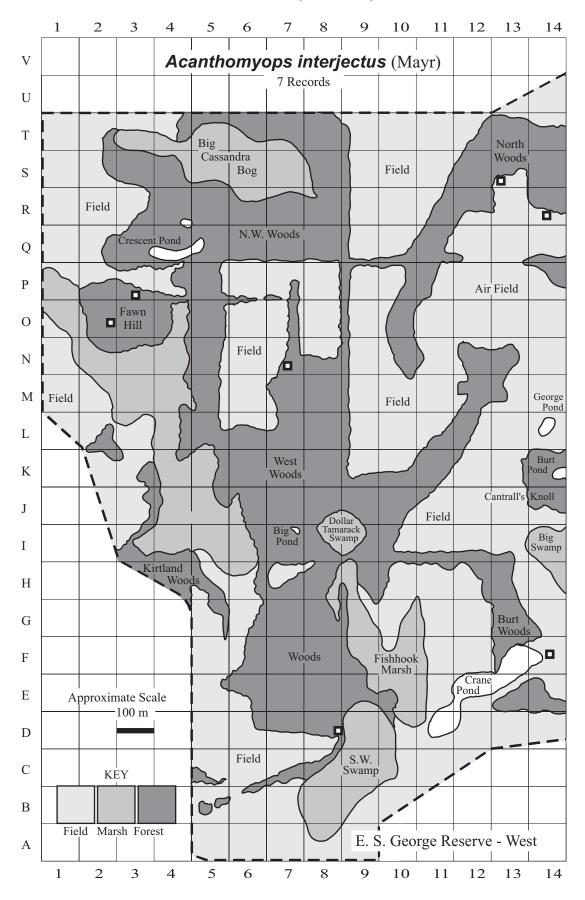
Table 7.	continued.
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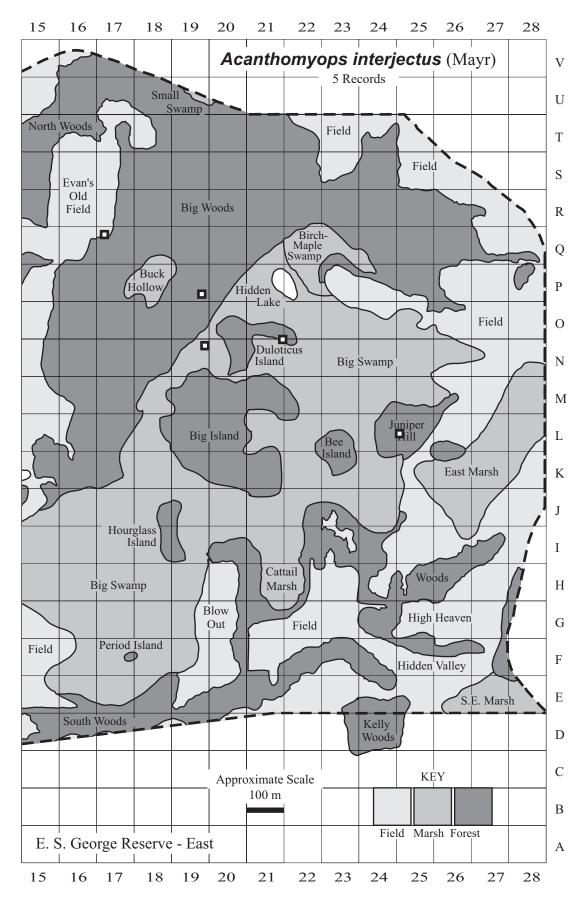
Debelones paraditions Dute 9 - Aug. 12 June 9 - Aug. 12 June 9 - Aug. 12 June 19 - Aug. 14 June 22 - Sept. 15 June 23 - July 23 June 23 - July 24 June 24 - Sept. 21 June 24 - July 2 June 25 - July 24 July 9, 1064							
Designation June 25 - Sept 21 June 4 - Sept 21 June 4 - Sept 22 June 2 - Oct. 2 June 2 - June 17 June 35 - July 24 June 25 - July 37	Dolichoderus pustulatus	June 9 – Aug. 12	June 9 – Aug. 24	June 22 – Sept. 15	June 26 – Aug. 27	July 11 - Sept. 15	Aug. 19 – Sept. 1
Topins	Dolichoderus taschenbergi		June 3 – Aug. 30	June 3 – Sept. 28	June 3 – July 23	June 3 – Aug. 26	June 7 – Aug. 21
Acushomyun claringer June 29 - July 19 June 4 - Sept. 14 July 3 - Sept. 14 July 9 - Aug. 30 Aug. 13 - Oct. 24 Acushomyun caterigerian Acushomyun charger metryeria June 4 - Sept. 22 June 6 - Sept. 20 June 6 - Aug. 22 July 13 - Sept. 18 June 7 - Sept. 4 June 19 - Sept. 21 June 6 - Aug. 22 July 13 - Sept. 28 July 13 - Sept. 28 July 13 - Sept. 28 July 13 - Sept. 29 July 13 - Sept. 29 July 13 - Sept. 29 July 13 - Sept. 20 July 23 - Sept. 22 July 23 - Aug. 21 - Aug. 22 - Aug. 27 Aug. 24 - Sept. 28 Aug. 21 - Sept. 26 July 24 - Aug. 21 July 14 - Sept. 20 Aug. 21 - Sept. 26 July 24 - Aug. 21 July 14 - Sept. 20 Aug. 21 - Sept. 26 Aug. 21 - Sept. 20 July 24 - Aug. 21 July 14 - Sept. 20 Aug. 21 - Sept. 20 Aug. 22 - Sept. 20 Aug. 22 - Sept. 20 Aug. 22 - Sept. 20 Aug. 23 - Sept. 20 Aug. 24 - Aug. 21 Aug. 24 - Aug. 21 Aug. 24 - Aug. 21 Aug. 24 - Aug. 24 Aug.	Dorymyrmex grandulus	June 25 – Sept. 21	June 4 – Sept. 21	June 4 – Sept. 21	June 21 – July 2	June 25 – July 24	July 9, 1964
Acouthonyogo interjectus Aug. 17 – Sept. 18 June 7 – Sept. 19 June 6 – Sept. 20 June 6 – July 9 June 1 – Aug. 25 June 1 6 – Aug. 22 Acouthonyogo interjectus Aug. 17 – Sept. 18 June 7 – Sept. 4 June 19 – Sept. 4 June 19 – Sept. 2 June 19 – Sept. 2 Juny 1 – Sept. 18 July 1 – Sept. 18 Aug. 17 – Sept. 2 June 19 – Sept. 2 June 29 – Aug. 27 Aug. 24 – Sept. 22 Aug. 24 – Sept. 28 Sept. 27, 1971 Componente amystem June 13 – Sept. 24 June 4 – Sept. 28 June 28 – Aug. 28 June 24 – Aug. 19 July 12 – Sept. 24 Aug. 21 – Sept. 28 Aug. 21 – Sept. 18 Componente amystem June 29 – Aug. 26 June 4 – Oct. 3 June 11 – Aug. 23 July 11 – June 29 June 8 A June 18 Componente anystematics June 27 – Aug. 10 June 4 – Oct. 3 June 11 – Aug. 21 July 11 – June 29 June 8 A July 15 Componente anystematics June 27 – Aug. 11 June 4 – Oct. 3 June 11 – Aug. 21 July 11 – June 29 June 8 A July 15 Componente anystematics June 27 – Aug. 24 June 19 – Aug. 21 June 19 – Aug. 21	Tapinoma sessile	June 2 – Oct. 2	June 2 – Oct. 2	June 2 – Oct. 2	June 2 – June 17	June 9 – July 12	June 25 – July 3
Acanthomopous name/nys Anne 2 A	Acanthomyops claviger	June 29 – July 19	June 4 – Sept. 14	July 3 – Sept. 14	July 9 – Aug. 30	Aug. 13 – Oct. 24	Sept. 17 – Oct. 24
Acandomyops marphy	Acanthomyops interjectus		June 7 – Sept. 10	June 3 – Sept. 10	June 3 – July 9	June 11 – Aug. 25	June 16 – Aug. 22
Accordinations June 29, 1954 June 29 - June 29 - Aug. 27 June 29 - Aug. 27 June 24 - Aug. 19 July 12 - Sept. 28 Sept. 27, 1971 Bracklywynec depila	Acanthomyops latipes	Aug. 17 – Sept. 18	June 4 – Sept. 22	June 6 – Sept. 20	June 6 – Aug. 29	July 13 - Sept. 28	Aug. 17 – Sept. 27
Processing supervises June 19	Acanthomyops murphyi		June 7 – Sept. 4	June 19 – Sept. 4	June 19 – Aug. 17	July 3 – Sept. 16	July 19 - Sept. 16
Camponotus americans June 13 - Sept. 24 June 25 - Sept. 24 July 7 - Aug. 22 Aug. 11 - June 15 Value 15 - Camponotus carques Value 29 - Aug. 28 June 5 - Aug. 28 June 9 - Aug. 30 July 8 - Aug. 26 August 8, 1956 Camponotus mercitans June 18 - Aug. 6 June 5 - Sept. 18 June 6 - Sept. 9 Aug. 10, 1974 Aug. 9 - July 11 - June 29 June 8 & June 29 Aug. 10, 1974 Aug. 9 - July 16 May 29 & Aug. 19 July 11 - June 29 July 18 Fornica carcinghtoni July 12, 1957 July 12 - Aug. 28 June 6 - July 20 June 16 - July 28 July 18 Fornica carcinghtoni July 12, 1957 July 19 - Oct. 3 Aug. 2 - Sept. 18 Aug. 24 - Oct. 7 Sept. 5 - Oct. 3 June 18, 1972 June 19 - Aug. 19 June 18, 1972 June 19 - Sept. 14 June 5 - Sept. 14 June 13 - July 30 July 2 - Aug. 6 July 2 - Aug. 18 July 19 - Oct. 3 Aug. 2 - Sept. 15 July 27, 1971 July 10 - Sept. 18 July 10 - Sept. 18 July 10 - Sept. 18 June 10 - Sept. 18 June 10 - Sept. 19 June 18 - Sept. 14 June 13 - July 30 July 2 - Aug. 6 July 2 - Aug. 6 July 2 - Aug. 19 July 10 - Aug. 19 July 1	Acanthomyops subglaber	June 29, 1954	June 7 – June 29	June 29 – Aug. 27	June 29 – Aug. 27	Aug. 24 – Sept. 28	Sept. 27, 1971
Camponotons carryiae June 29 - Aug. 26 June 5 - Aug. 28 June 9 - Aug. 30 July 8 - Aug. 21 July 11 - June 29 June 8 & June 29 Camponotons recurricias June 17 - Aug. 21 July 11 - June 19 June 8 & June 29 Camponotons recording June 18 - Aug. 24 June 5 - Sept. 18 June 6 - Sept. 9 Aug. 10, 1974 Aug. 9 - July 16 May 29 & July 15 July 12 - July 12 July 13 July 14 July 14 July 15 July 12 - July 12 July 15 July 14 July 16 July 18 July 19 July 18 July 19 July 18 July 19 July 18 July 19 Jul	Brachymyrmex depilis	July 3 – Sept. 22	June 2 – Sept. 22	June 12 – Sept. 22	June 24 – Aug. 19	July 12 - Sept. 24	Aug. 21 – Sept. 16
Camponotus neuritius June 29 - Aug. 26 June 5 - Aug. 28 June 9 - Aug. 30 July 8 - Aug. 26 August 8, 1956	Camponotus americanus	June 13 – Sept. 24	June 4 – Sept. 24	June 25 – Sept. 24	July 7 – Aug. 22	Aug. 11 – June 15	
Camponotus noveboraconsis June 27 - Aug. 1 June 4 - Oct. 3 June 11 - Oct. 3 June 17 - Aug. 21 July 11 - June 29 June 8 - July 15	Camponotus caryae						
Camponions pennsylvamicus	Camponotus nearcticus	June 29 – Aug. 26	June 5 – Aug. 28	June 9 – Aug. 30	July 8 – Aug. 26	August 8, 1956	
Formica aserva	Camponotus noveboracensis	June 27 – Aug. 1	June 4 – Oct. 3	June 11 – Oct. 3	June 17 – Aug. 21	July 11 – June 29	June 8 & June 29
Formica descensive	Camponotus pennsylvanicus	June 18 – Aug. 6	June 5 – Sept. 18	June 6 – Sept. 9	Aug. 10, 1974	Aug. 9 – July 16	May 29 & July 15
Formica dastorensis June 4, 1971 June 12 - Aug. 28 July 19 - Oct. 3 Aug. 2 - Sept. 15 Aug. 24 - Oct. 7 Sept. 5 - Oct. 3	Formica aserva		June 4 – Aug. 24	June 5 – Aug. 28	June 6 – July 20	June 16 – July 28	July 15 – July 18
Formica exsectioides	Formica creightoni		July 12, 1957	July 12 – Aug. 9		July 25, 1971	
Formica glacialis	Formica dakotensis	June 4, 1971	June 12 – Aug. 28	July 19 – Oct. 3	Aug. 2 – Sept. 15	Aug. 24 – Oct. 7	Sept. 5 – Oct. 3
Formica glacialis	Formica exsectoides		June 18, 1972	June 18, 1972			
Formica gymocrates	Formica fusca		June 9 – Aug. 15	June 10 – Sept. 15	July 27, 1971	July 10 - Sept. 18	
Formica laxioides	Formica glacialis		June 5 – Sept. 14	June 5 – Sept. 14	June 13 – July 30	July 5 – Aug. 6	
Formica neogagates July 9, 1975 June 9 - Sept. 2 June 10 - Sept. 18 June 27 - July 16 Aug. 1 - Sept. 8	Formica gynocrates		June 4 – Aug. 29	June 18 – Sept. 21	June 4 – July 16	June 22 – Aug. 16	July 7 – Aug. 13
Formica neorufibarbis June 26 - July 22 July 22, 1953 June 26 - July 3 Aug. 1, 1954	Formica lasioides		June 16 – Aug. 24	June 19 – Sept. 23	June 18 – Aug. 3	July 10 – Aug. 9	
Formica nepticula	Formica neogagates	July 9, 1975	June 9 – Sept. 2	June 10 – Sept. 18	June 27 – July 16	Aug. 1 – Sept. 8	
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Formica obscuripes	Formica nepticula		June 29 – Aug. 21	June 29 – Aug. 21	June 29, 1957	June 29 – July 5	
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Formica pergandet	Formica obscuripes		June 4 – Sept. 15	June 4 – Sept. 28	June 3 – June 22	June 1 – July 1	June 1 – July 1
Formica rubicumda June 2 - Aug. 29 June 14 - Sept. 25 June 14 - Aug. 4 July 5 - Aug. 6 July 12 - Aug. 4 Formica schaufiussi June 2 , 1969 June 4 - Aug. 6 June 20 - Sept. 20 June 20 - July 11 July 8 - Aug. 1 July 9, 1975 Formica subintegra June 3 , 1975 June 3 - Sept. 14 June 11 - Sept. 22 June 4 - Aug. 15 June 23 - Sept. 4 July 14 - Aug. 12 Formica subsericea June 3 , 1975 June 5 - Aug. 16 June 11 - Sept. 22 June 4 - Aug. 15 June 23 - Sept. 4 July 8 - Aug. 21 Formica talibotae June 2 - Sept. 20 June 2 - Sept. 18 June 16 - Oct. 1 June 16 - Sept. 25 Formica ulkei June 12 - July 26 June 4 - Sept. 2 June 5 - Sept. 18 June 19 - July 25 June 20 - July 28 June 26 - July 14 Formica (microgyna group) sp. June 4 - July 31 June 5 - Sept. 18 June 19 - July 18 June 28 - July 25 July 2 - July 25 Formica (microgyna group) sp. June 4 - July 31 June 5 - Sept. 14 June 5 - July 16 June 22 - Aug. 12 July 11 - Aug. 2 Lasius flavus June 10 - Sept. 3 June 2 - Sept. 22 June 2 - Sept. 28 June 12 - Sept. 28 July 25 - Oct. 2 Aug. 27 - Sept. 7 Lasius minutus June 2 - Sept. 29 June 2 - Sept. 29 June 10 - Sept. 24 June 17 - Sept. 7 July 25 - Oct. 2 Aug. 27 - Sept. 27 Lasius nearcticus June 6 - Sept. 13 June 5 - Sept. 8 June 20 - Aug. 29 July 30 - Sept. 26 Sept. 8 - Sept. 27 Lasius pallitarsis June 4 - Sept. 24 June 10 - Sept. 26 June 19 - Aug. 25 July 2 - Sept. 28 Aug. 5 - Sept. 27 Lasius umbratus Aug. 14 - Sept. 3 June 2 - Sept. 24 June 11 - Sept. 4 June 18 - Sept. 4 July 14 - Sept. 7 Aug. 27 - Sept. 27 Lasius umbratus Aug. 14 - Sept. 3 June 2 - Sept. 24 June 10 - Sept. 28 July 9 - Aug. 25 July 2 - Sept. 27 Aug. 26 - Sept. 27 Paratrechina parvula June 25 - Aug. 26 June 3 - Sept. 16 June 6 - Sept. 27 July 15 - Sept. 27 Aug. 26 - Sept. 27 Paratrechina parvula June 25 - Aug. 26 June 3 - Sept. 16 June 6 - Sept. 27	Formica obscuriventris	June 10 – July 24	June 5 – Sept. 2	June 16 – Sept. 2	June 17 – Aug. 6	July 15 – Aug. 31	July 27 – Aug. 31
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Formica subintegra	Formica rubicunda		June 3 – Aug. 29	June 14 – Sept. 25	June 14 – Aug. 4	July 5 – Aug. 6	July 12 – Aug. 4
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Paratrechina parvula June 25 – Aug. 26 June 3 – Sept. 16 June 6 – Sept. 22 July 15 – Aug. 20 July 15 – Sept. 27 May 12, 1959 Polyergus lucidus June 7 – Aug. 31 June 22 – Sept. 24 June 19 – Sept. 2 July 21 – Sept. 26 July 31 – Sept. 26	Lasius speculiventris		June 4 – Sept. 24	June 11 – Sept. 4	June 18 – Sept. 4	July 14 – Sept. 27	Aug. 27 – Sept. 27
Polyergus lucidus June 7 – Aug. 31 June 22 – Sept. 24 June 19 – Sept. 2 July 21 – Sept. 26 July 31 – Sept. 26	Lasius umbratus	Aug. 14 – Sept. 3	June 2 – Sept. 24	June 20 - Sept. 28	July 9 – Aug. 25	July 26 - Sept. 27	Aug. 26 – Sept. 27
	Paratrechina parvula	June 25 – Aug. 26	June 3 – Sept. 16	June 6 – Sept. 22	July 15 – Aug. 20	July 15 – Sept. 27	May 12, 1959
Prenolepis imparis June 8 – July 9 June 22 – Aug. 26 July 27 – Sept. 26 Aug. 14 – Sept. 17 Sept. 5 – May 2 April 14 – April 29	Polyergus lucidus		June 7 – Aug. 31	June 22 – Sept. 24	June 19 – Sept. 2	July 21 - Sept. 26	July 31 – Sept. 26
	Prenolepis imparis	June 8 – July 9	June 22 – Aug. 26	July 27 – Sept. 26	Aug. 14 – Sept. 17	Sept. 5 – May 2	April 14 – April 29

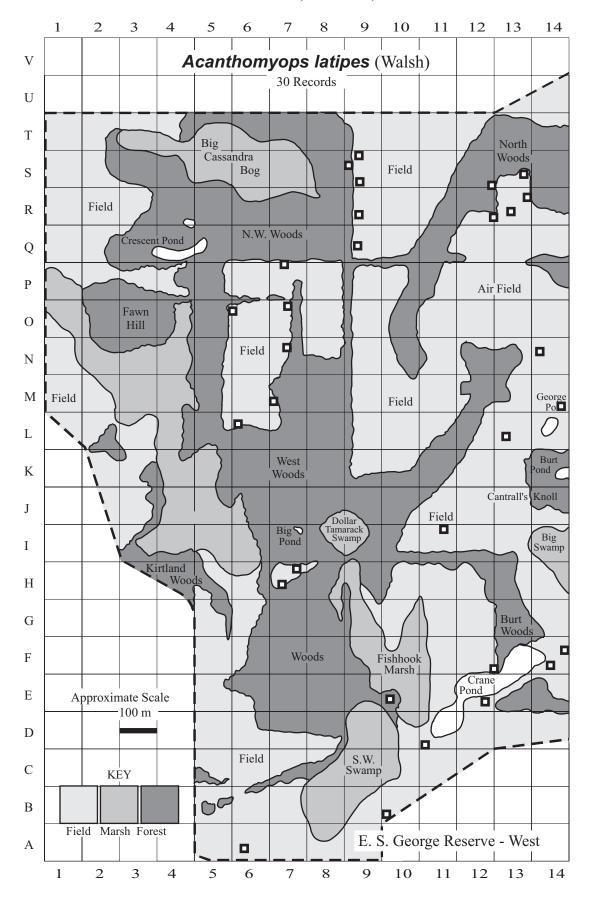
SPECIES DISTRIBUTION MAPS

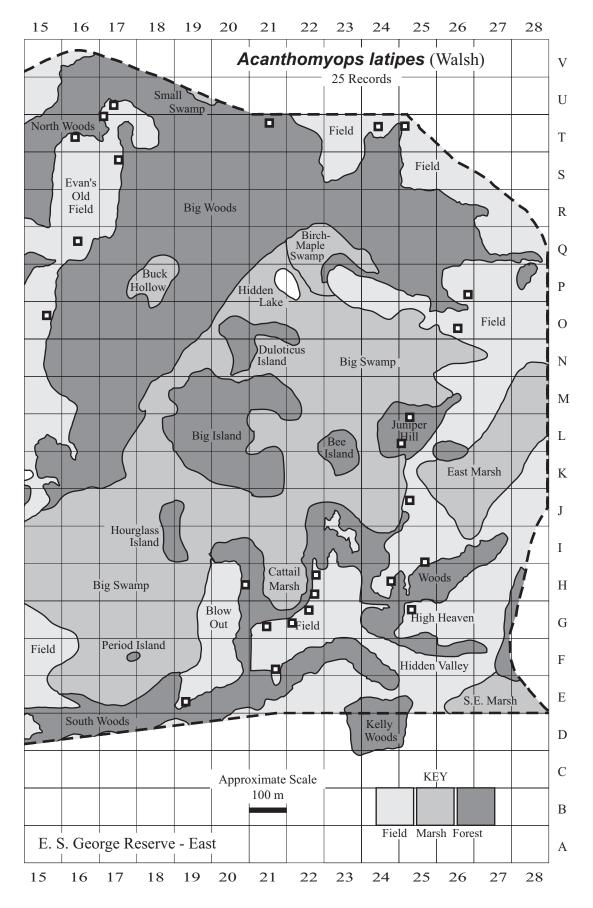


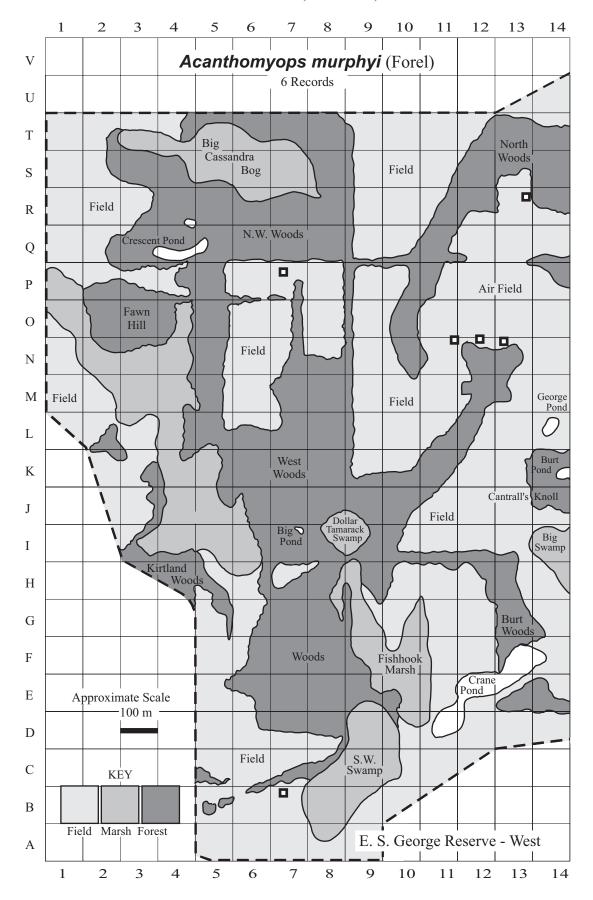


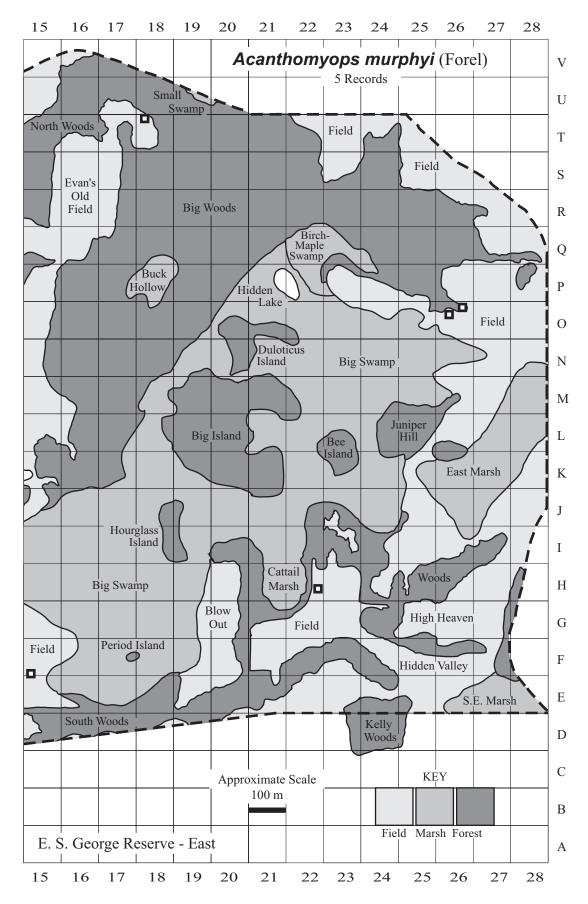




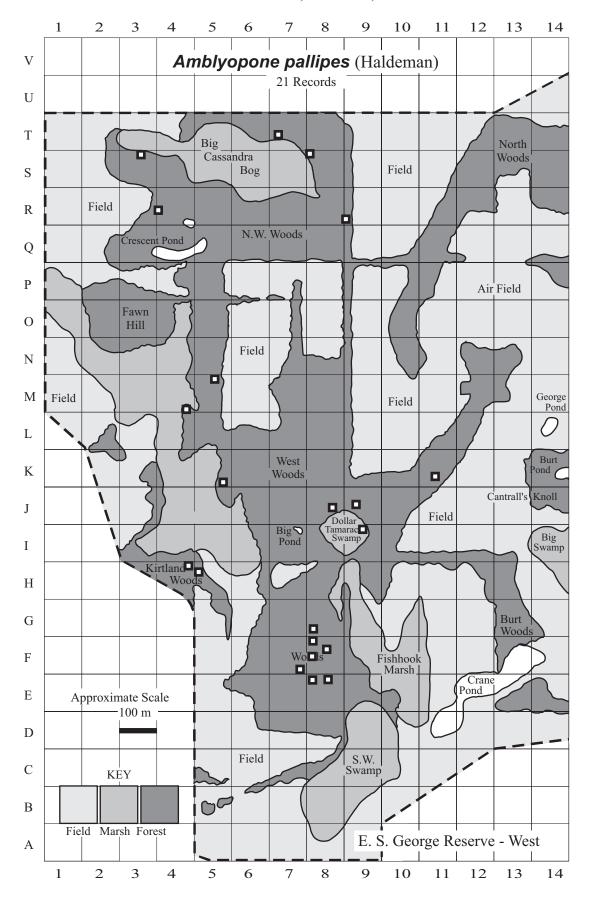


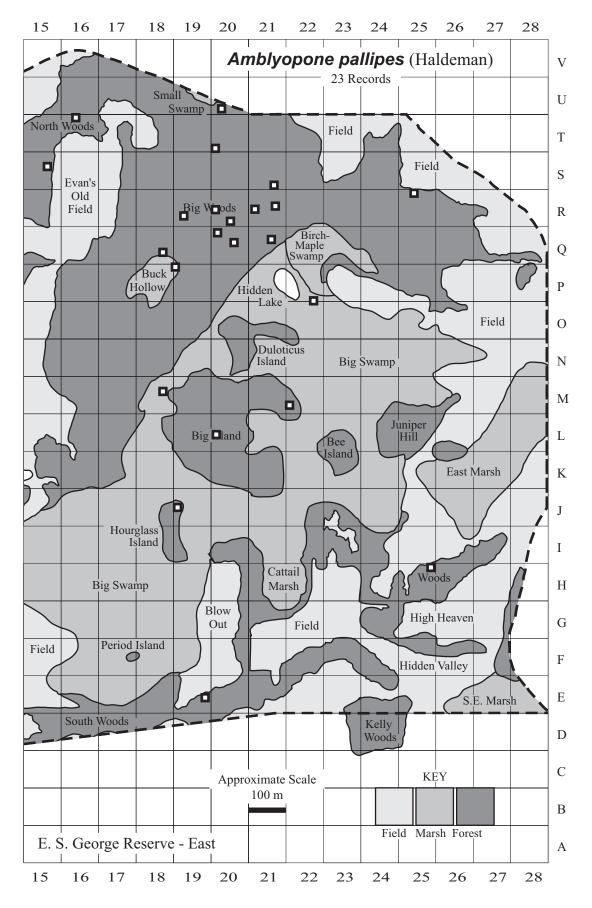


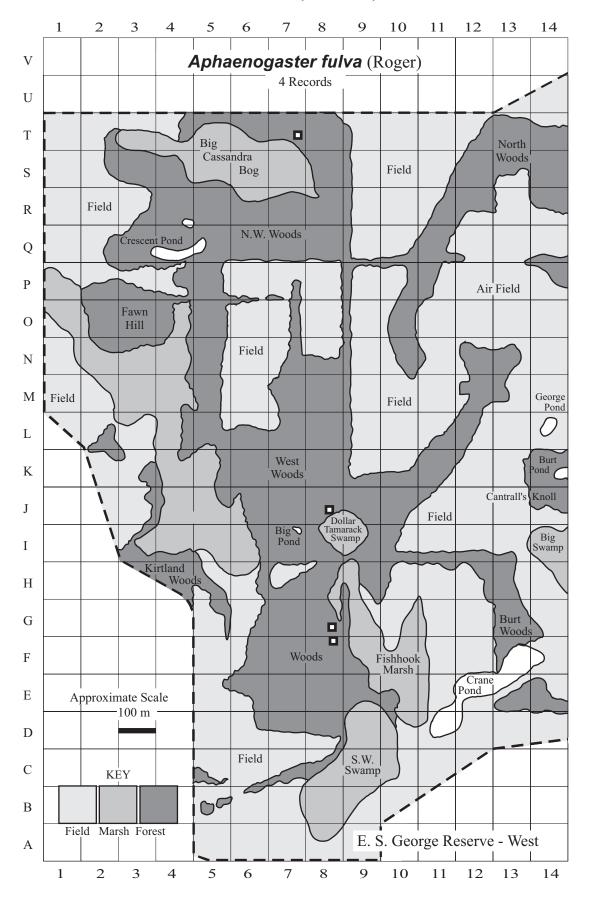


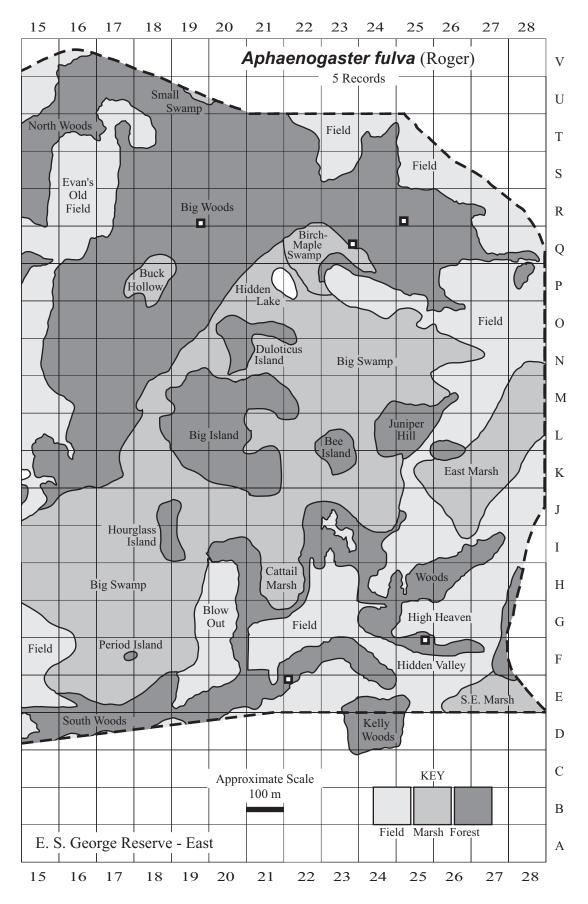


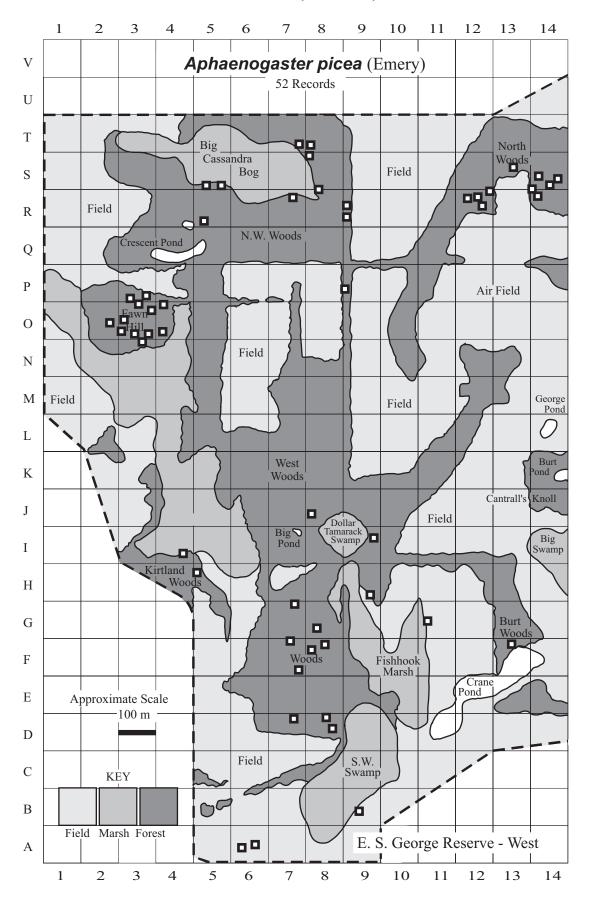


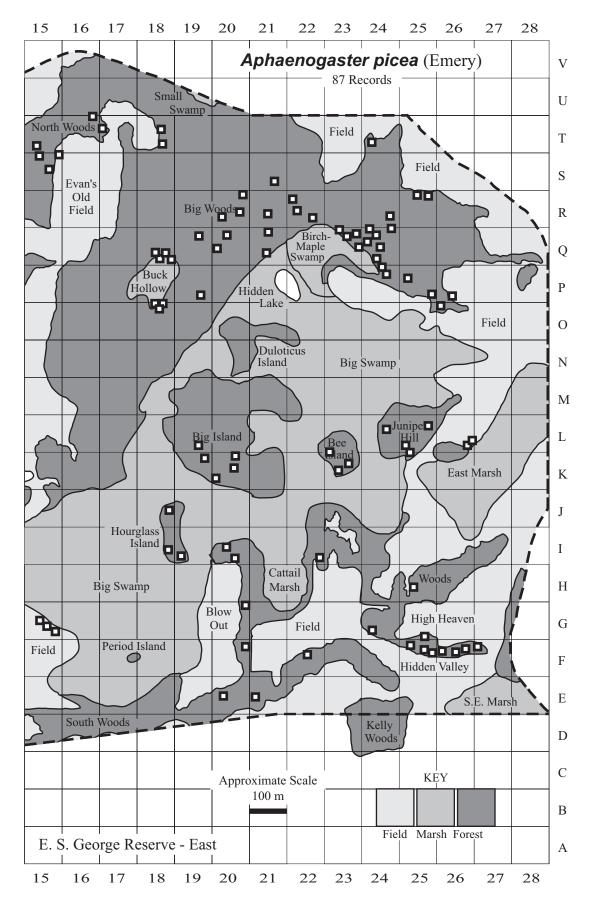


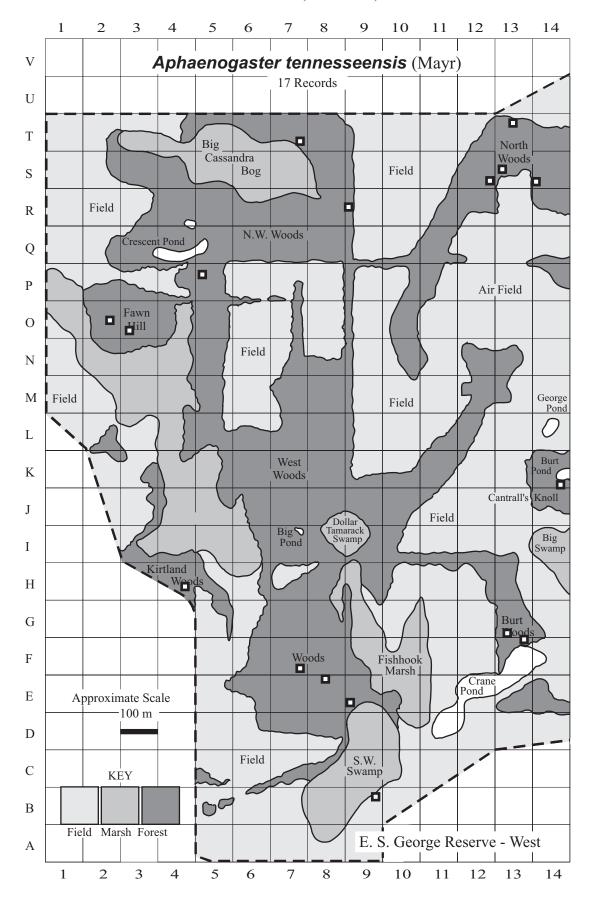


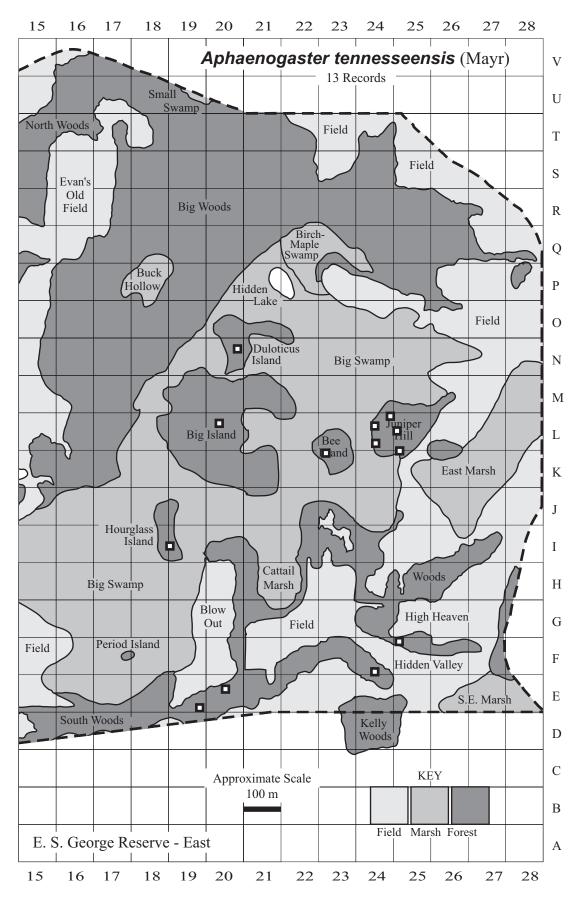


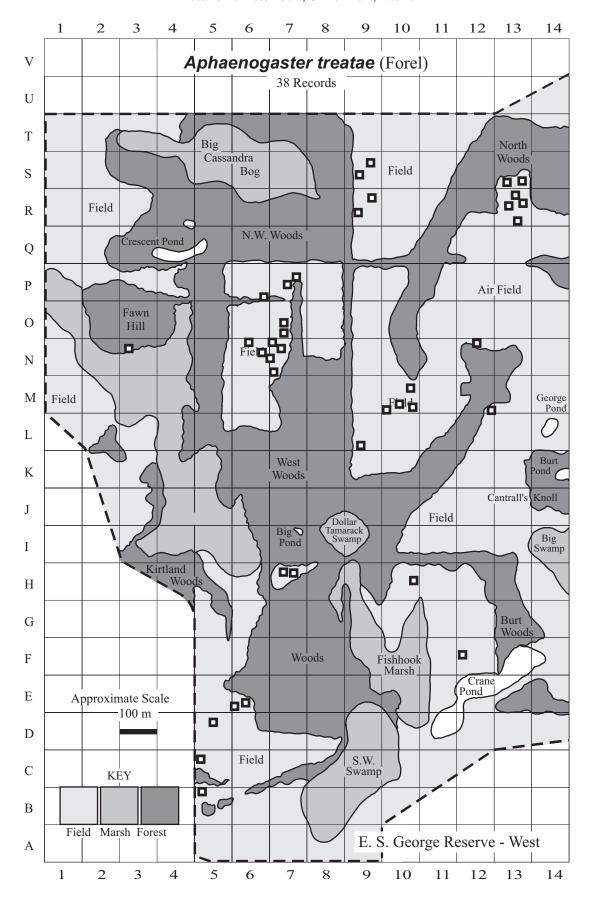


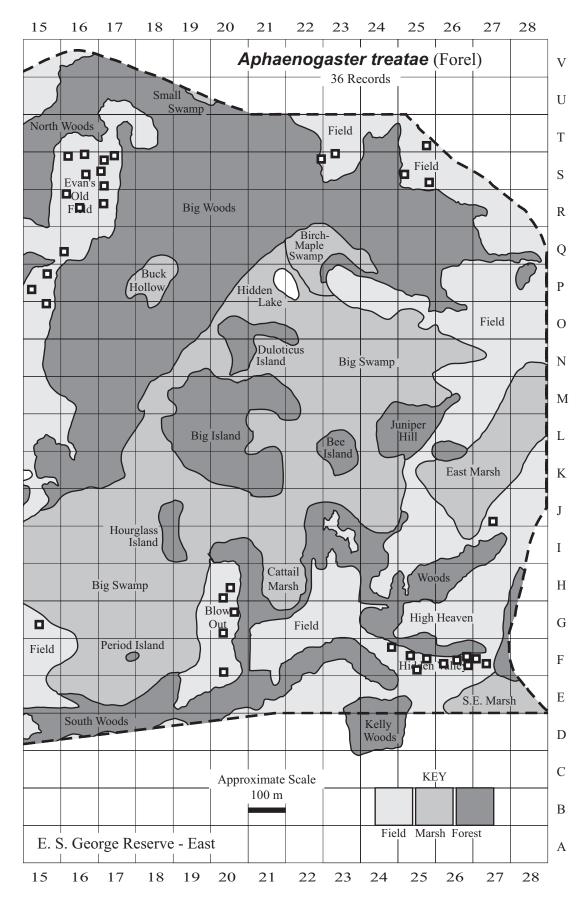


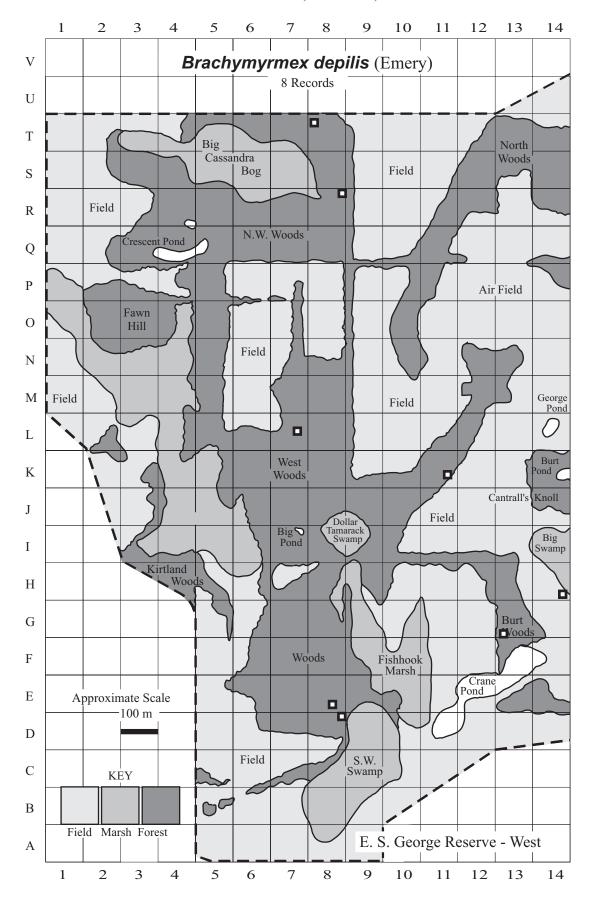


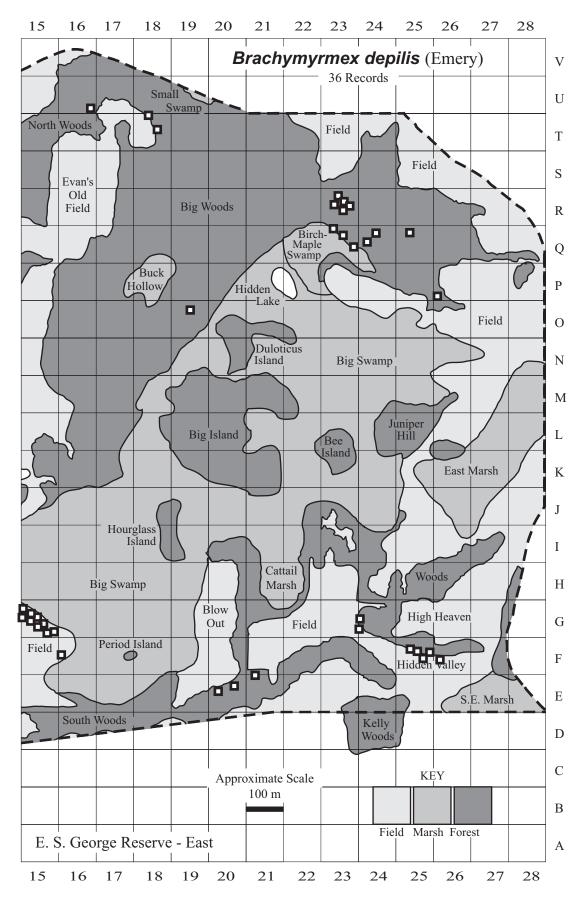


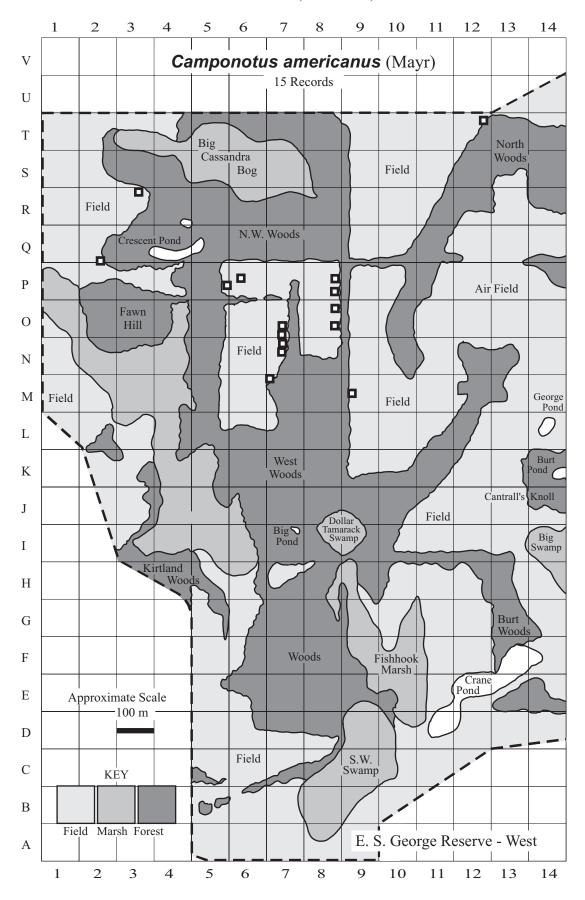


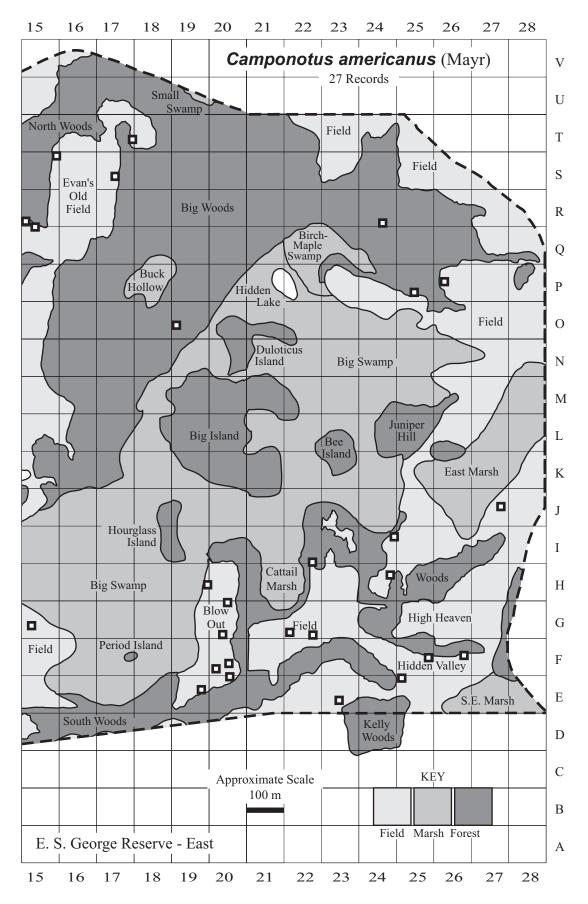


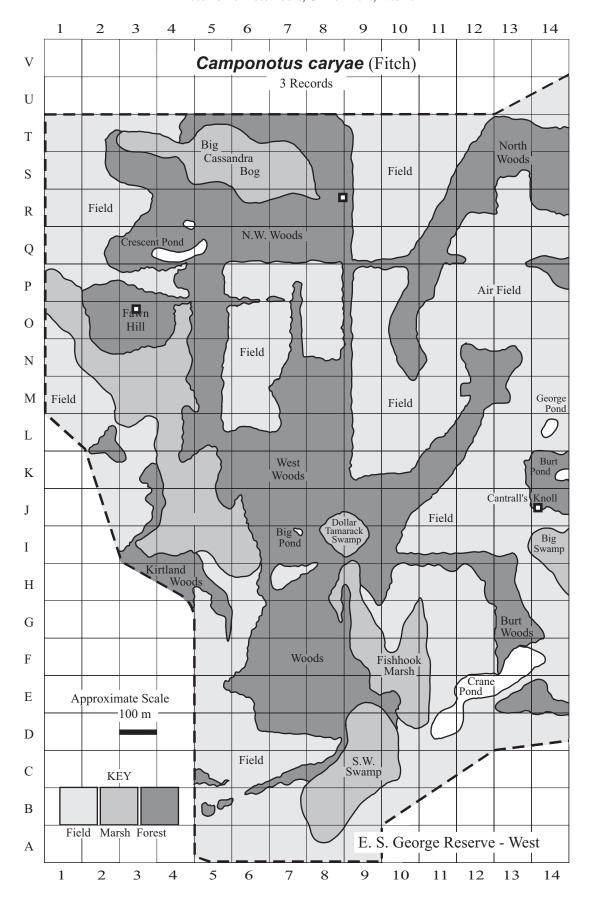


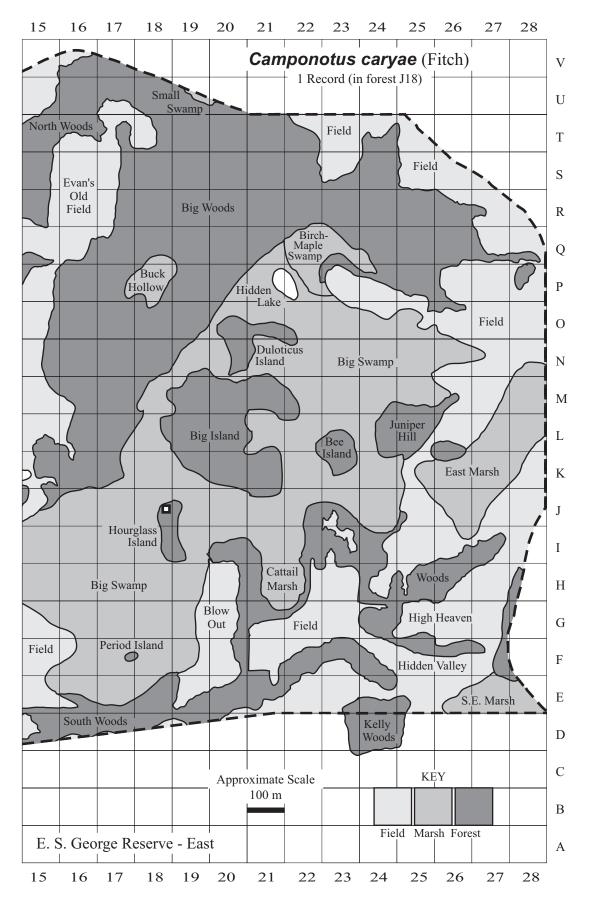


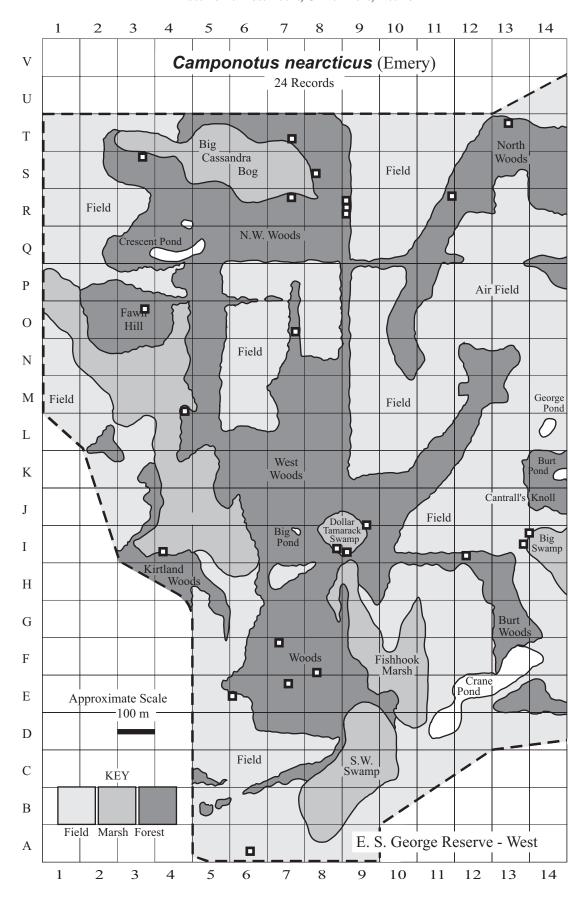


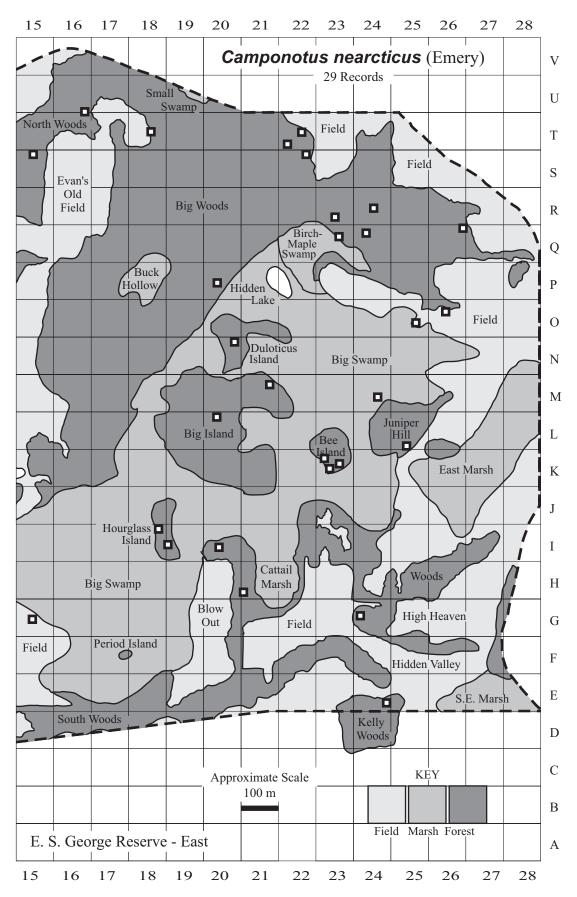


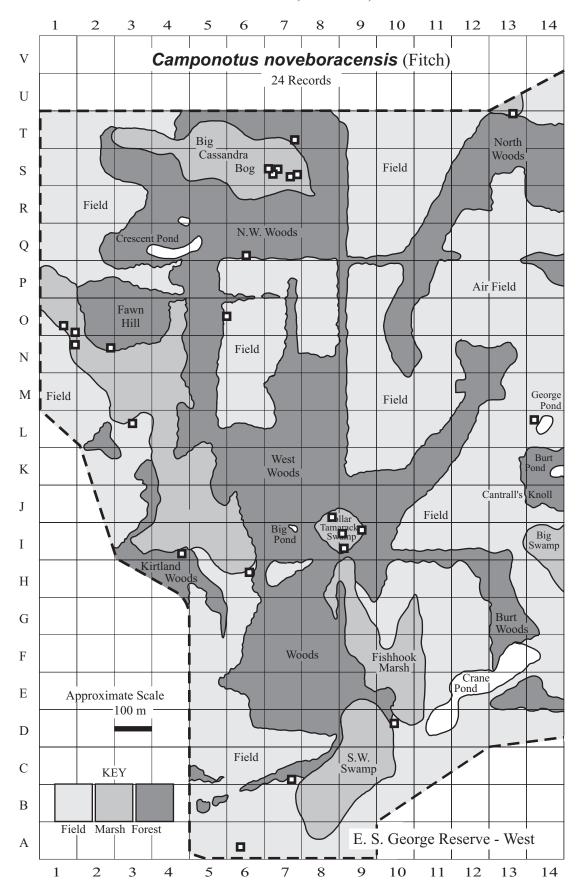


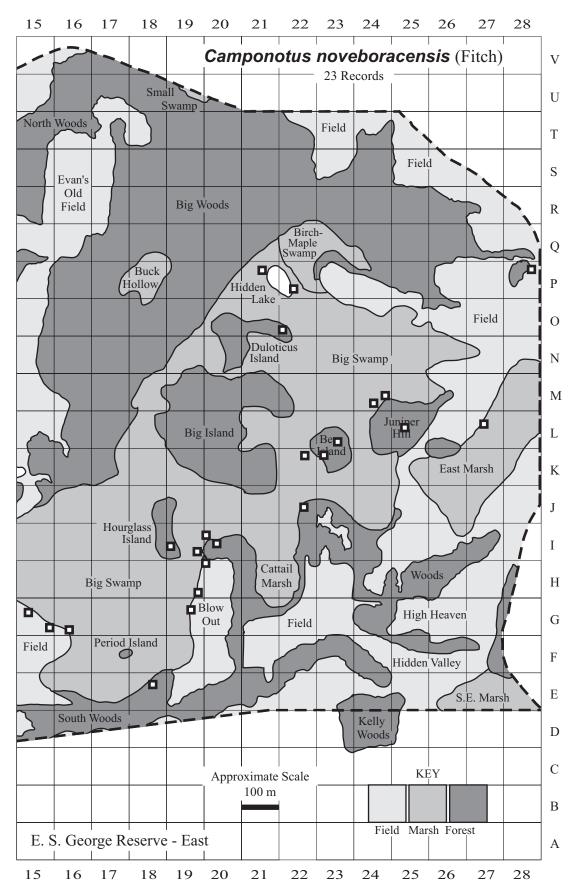


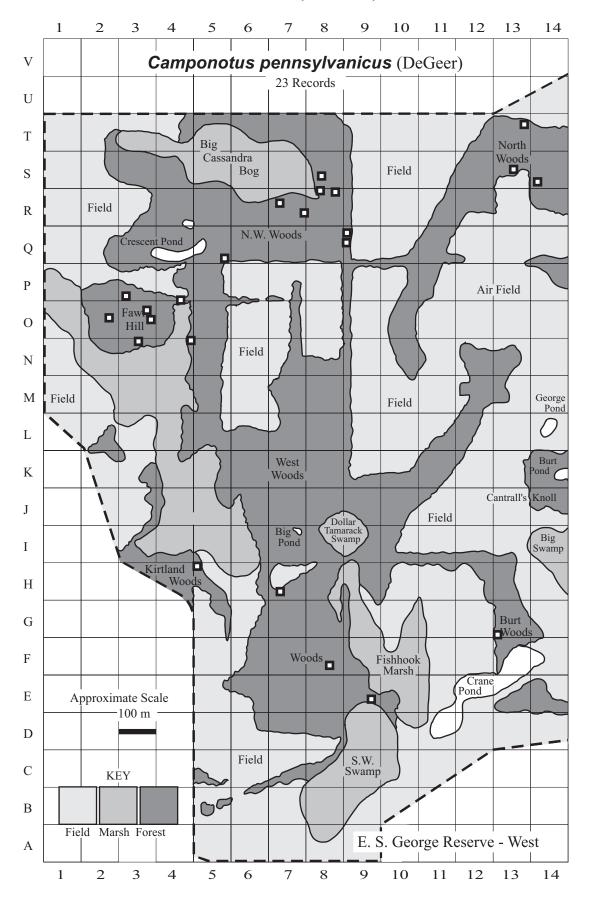


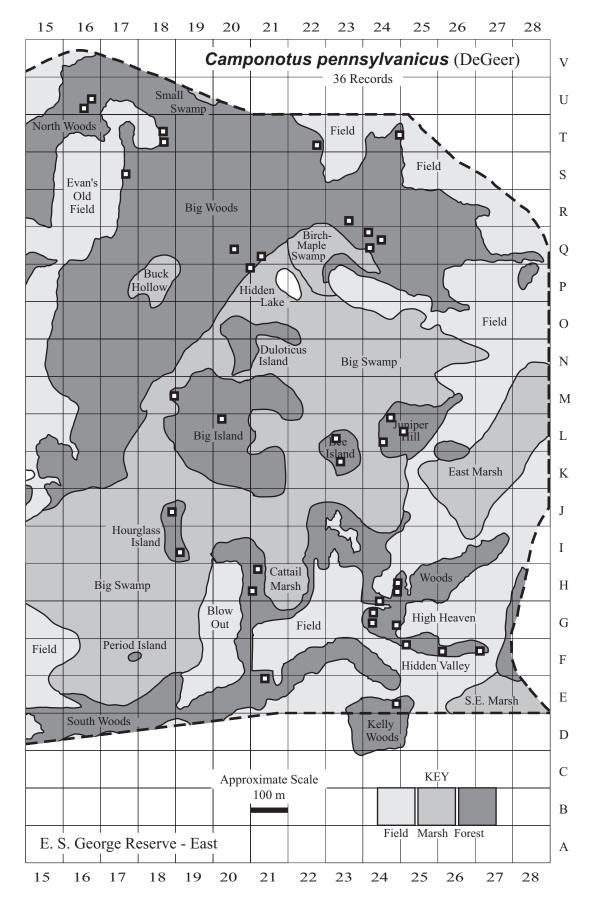


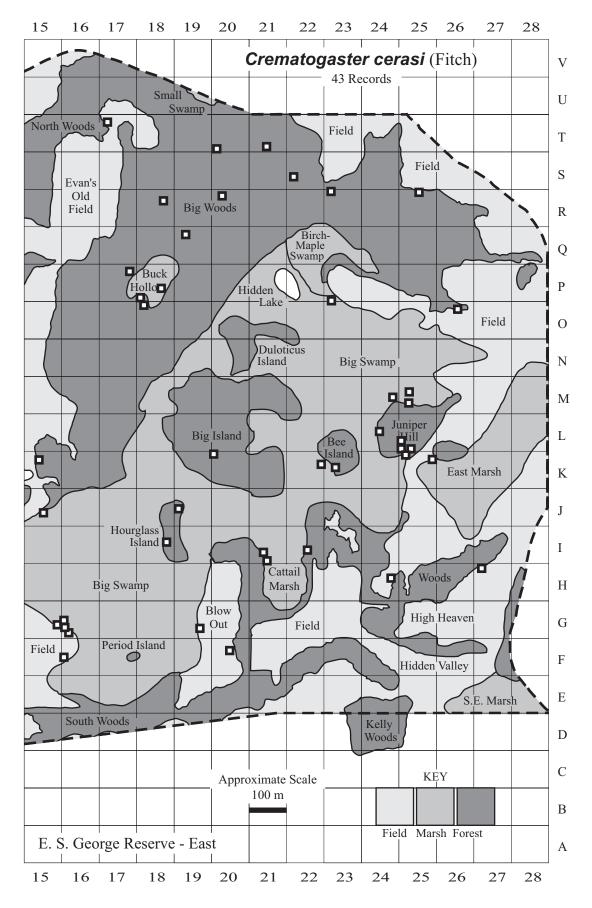


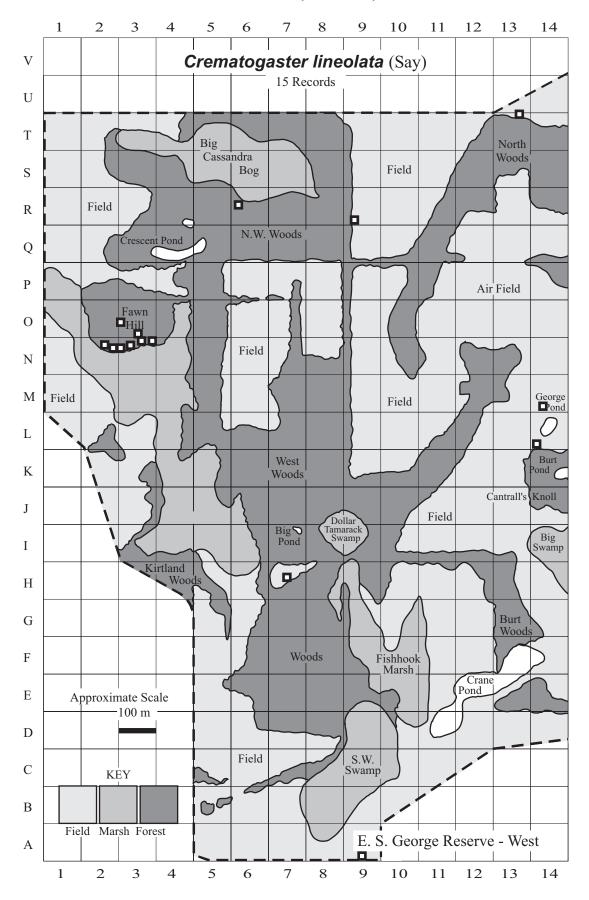


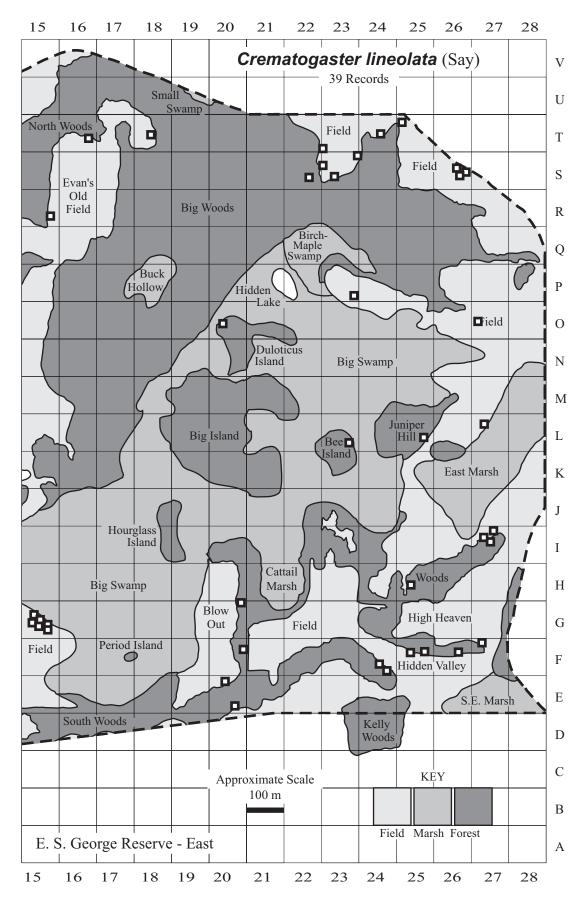


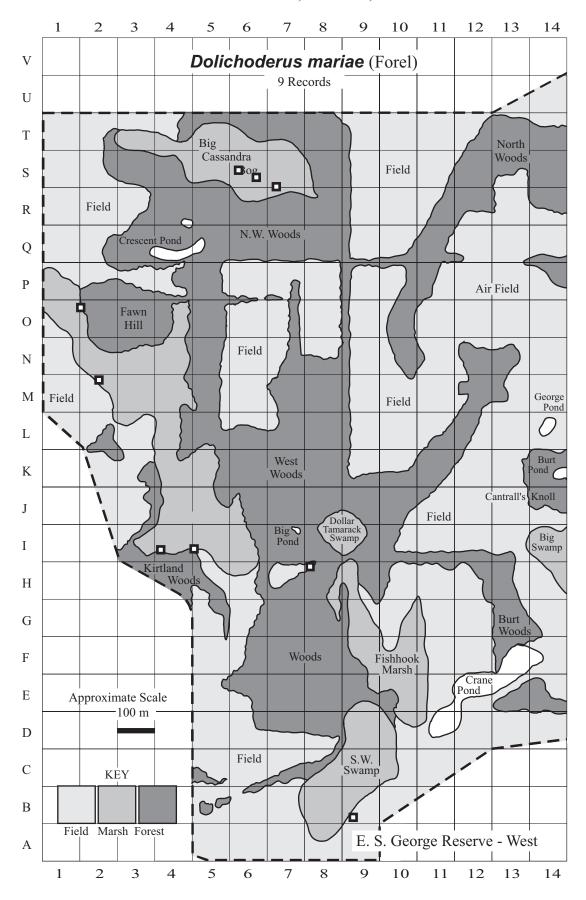




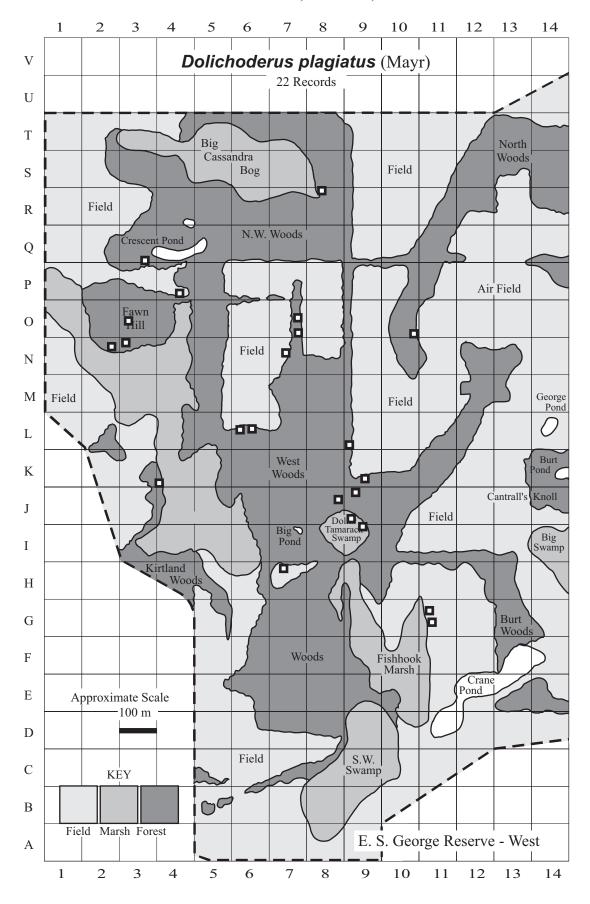


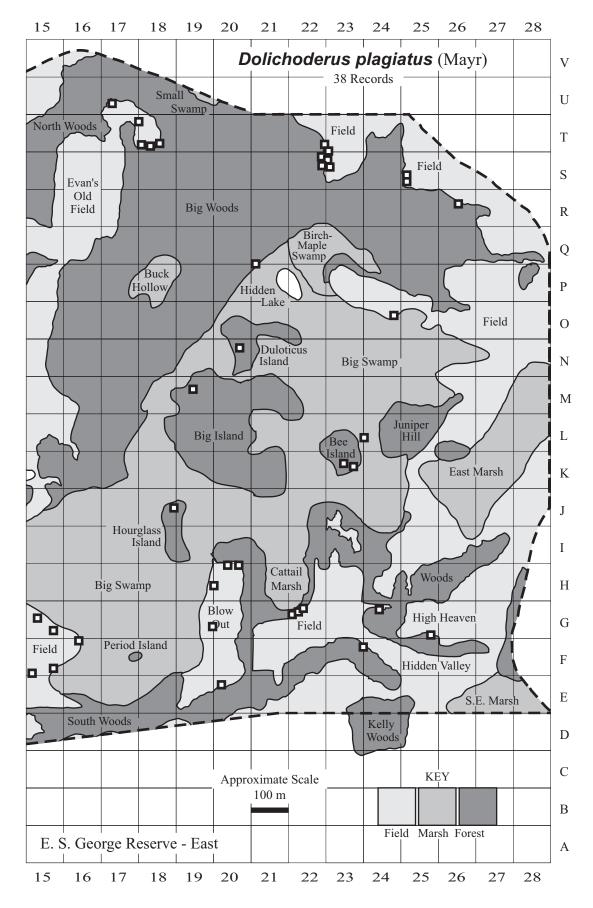


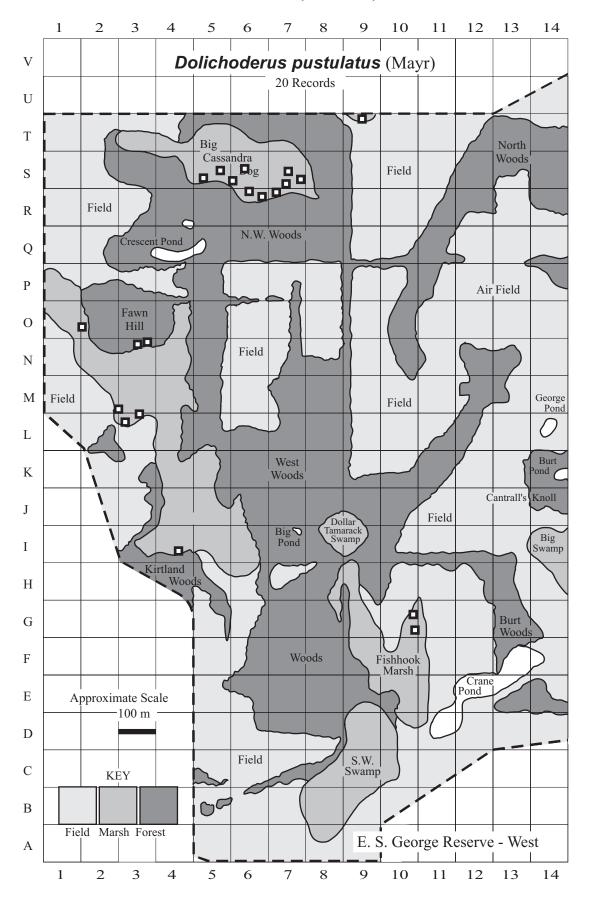




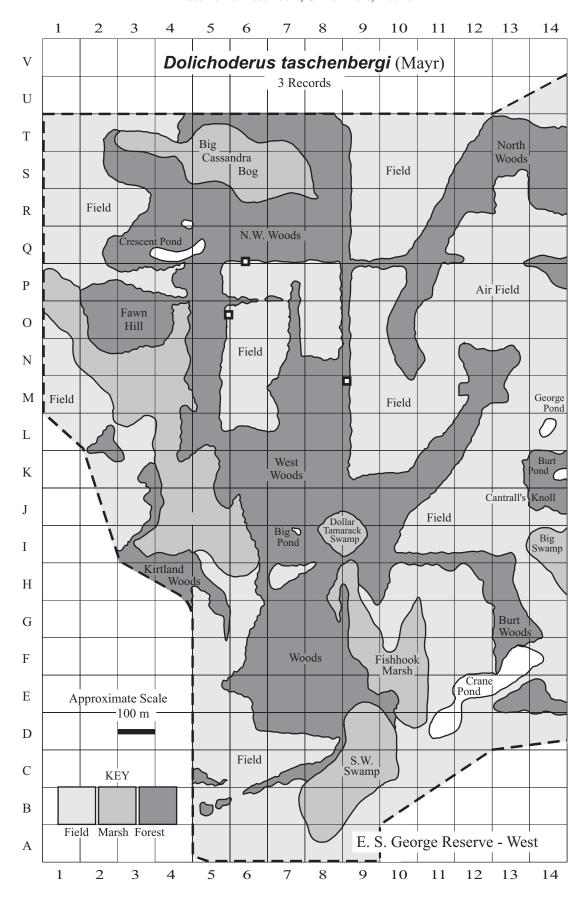


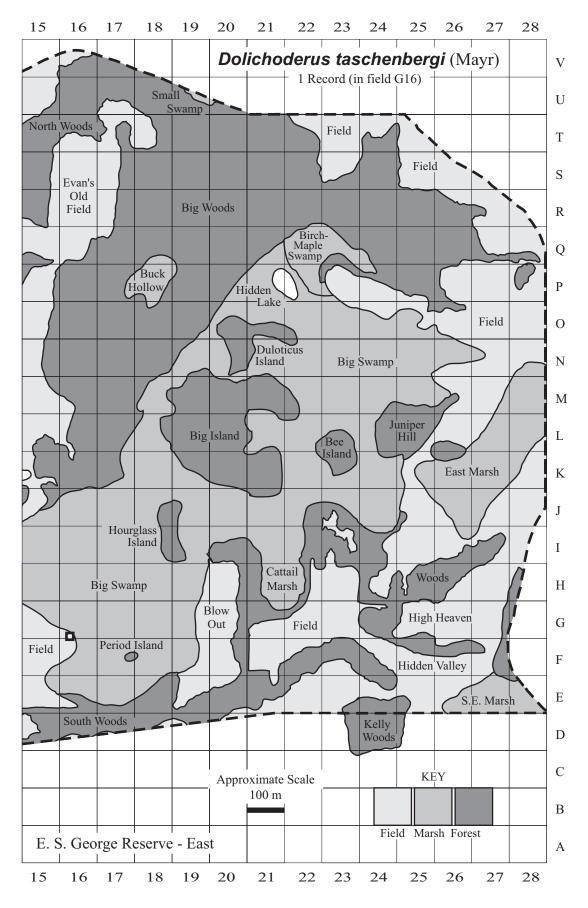




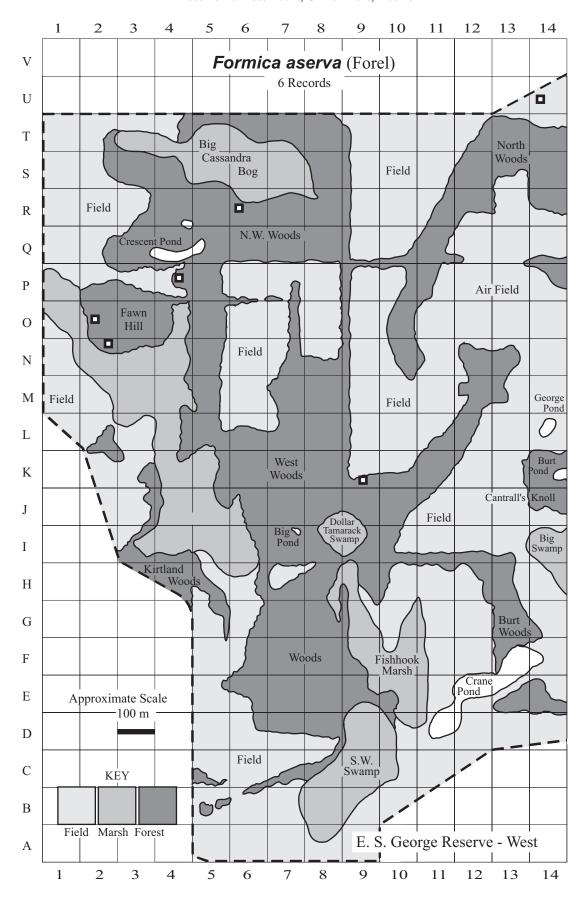


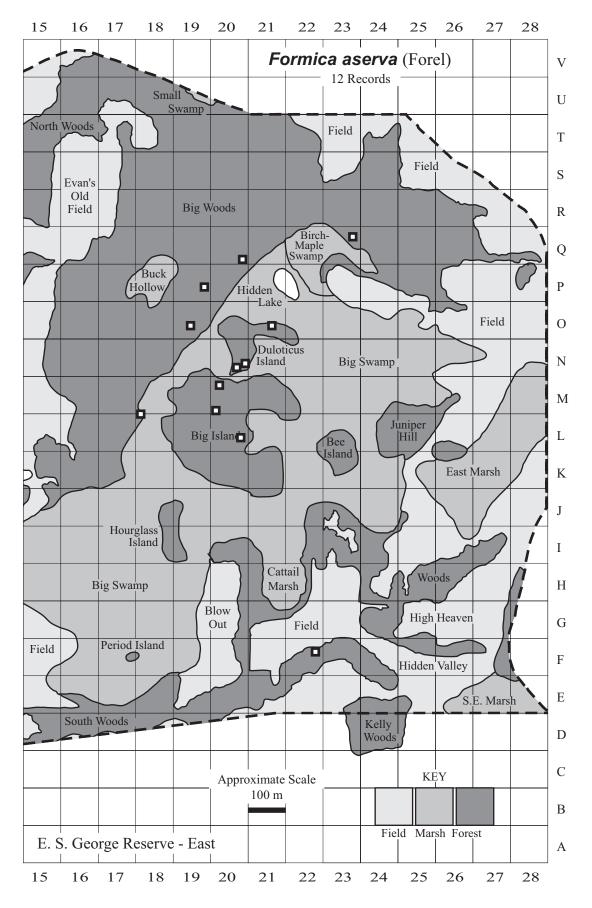


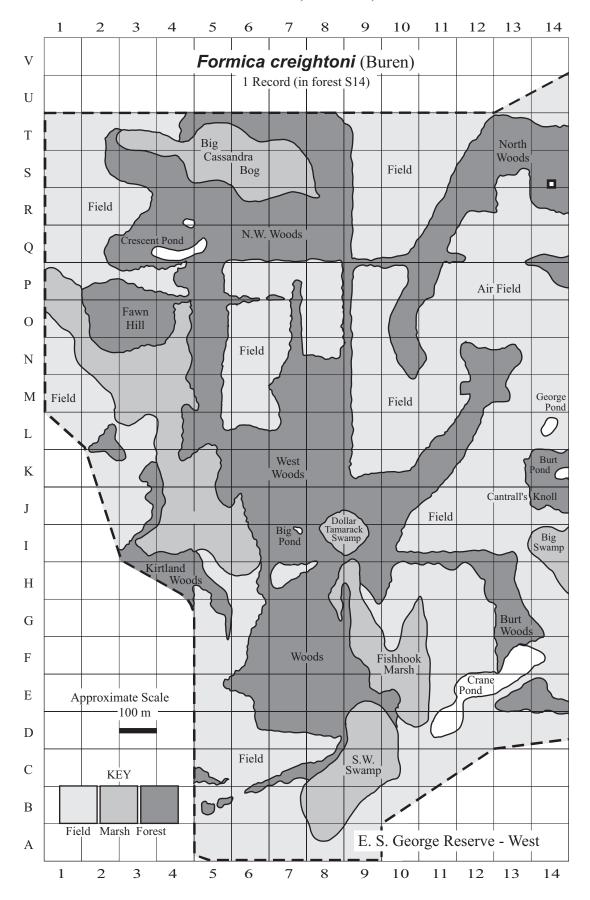


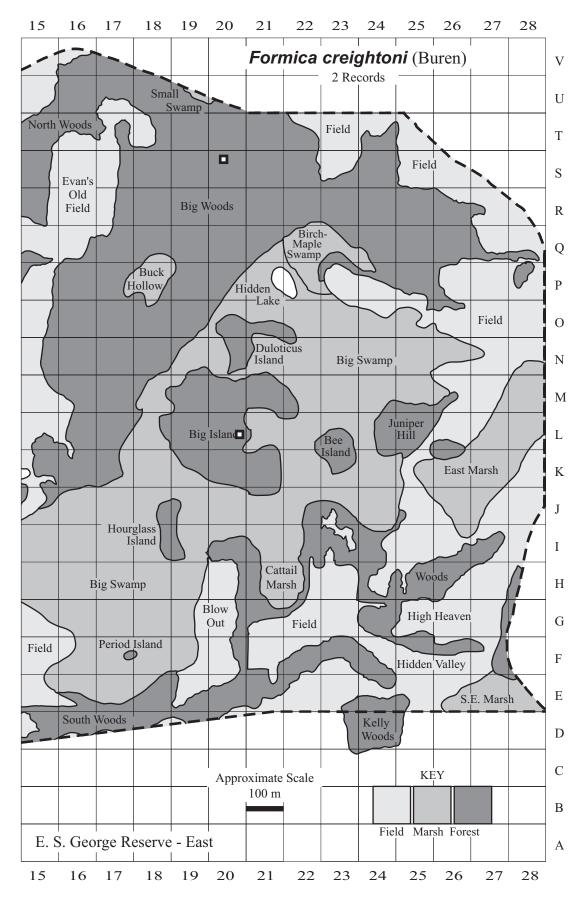


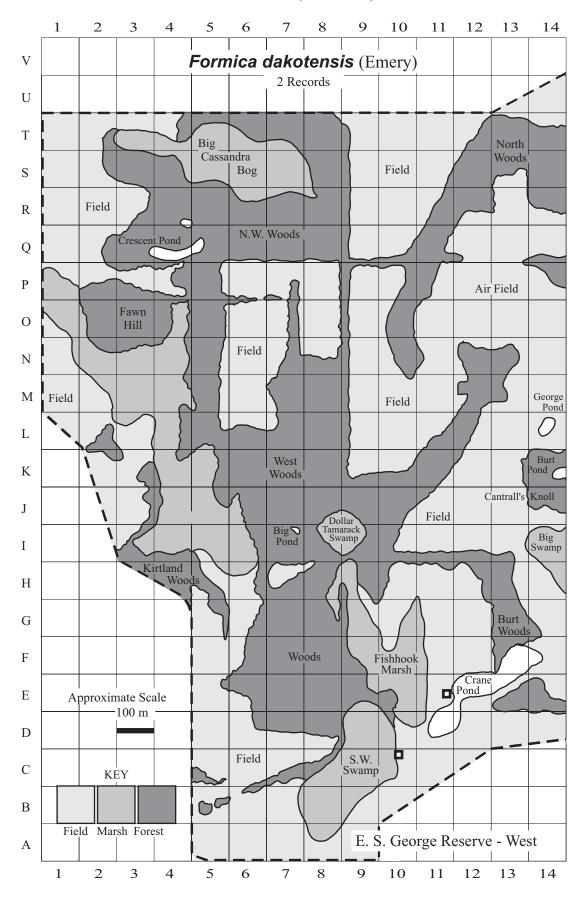




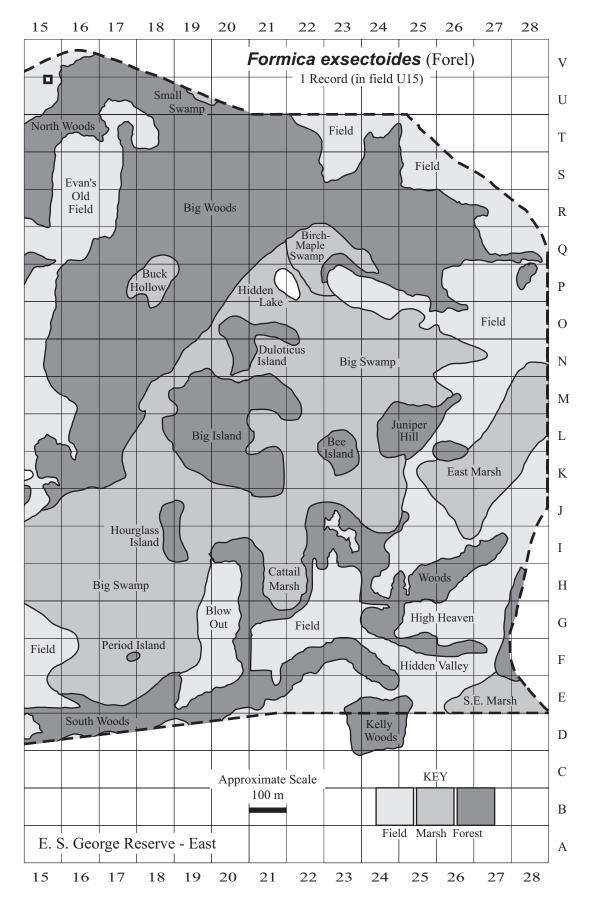


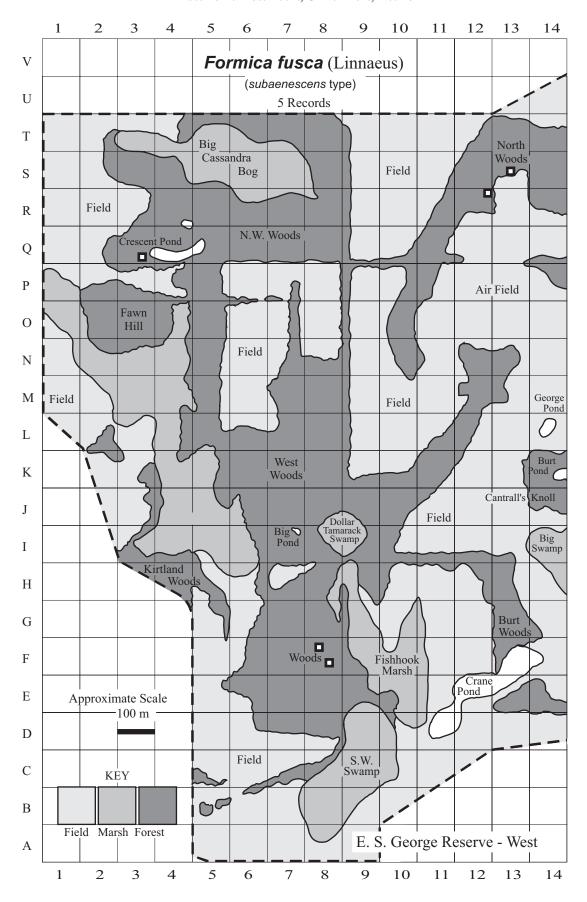


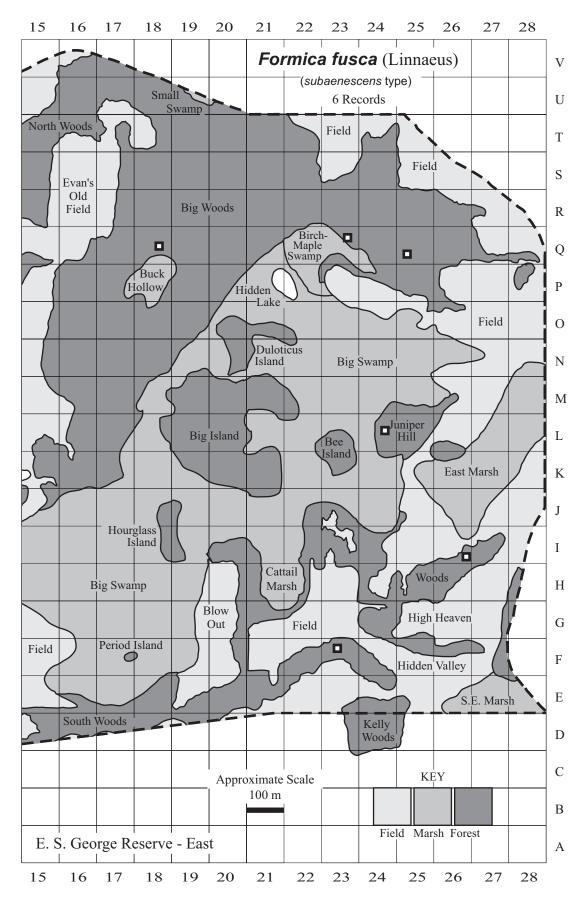


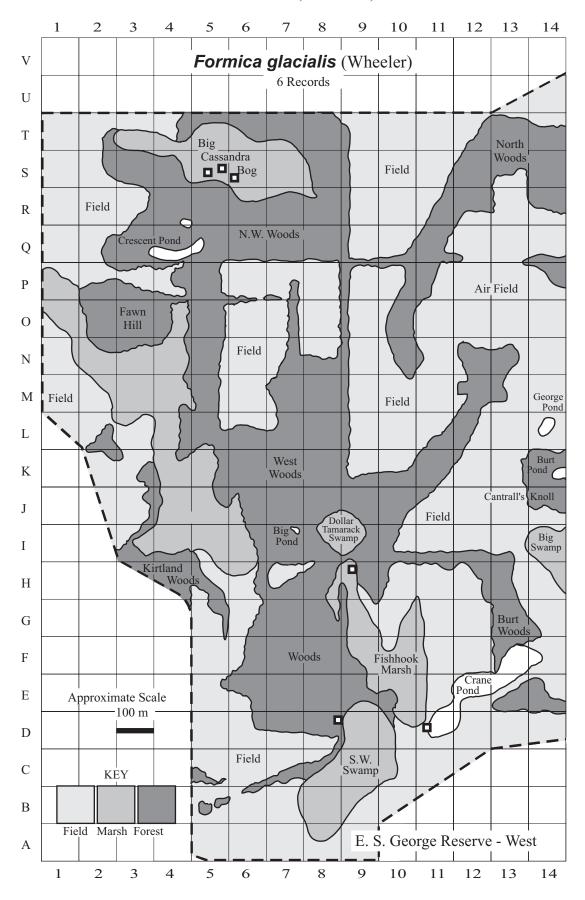


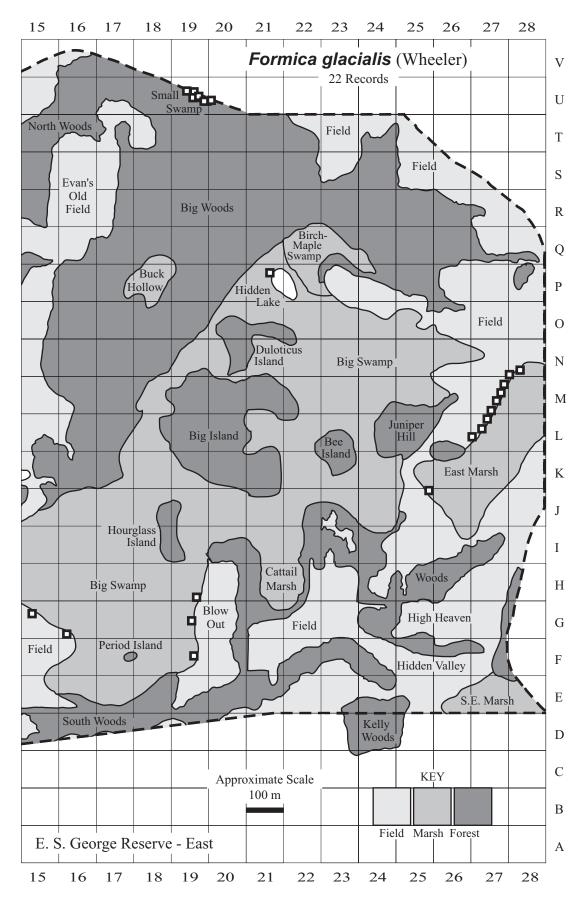


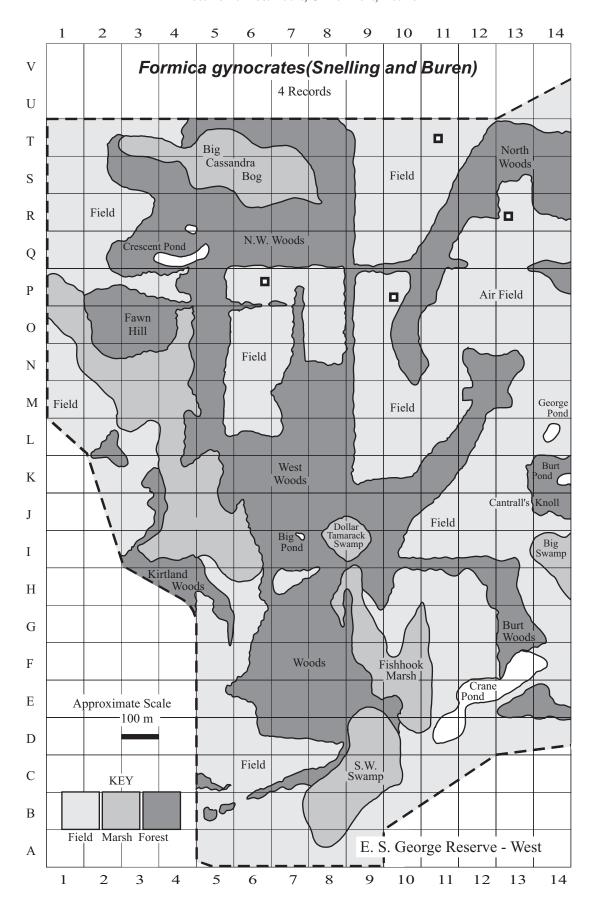


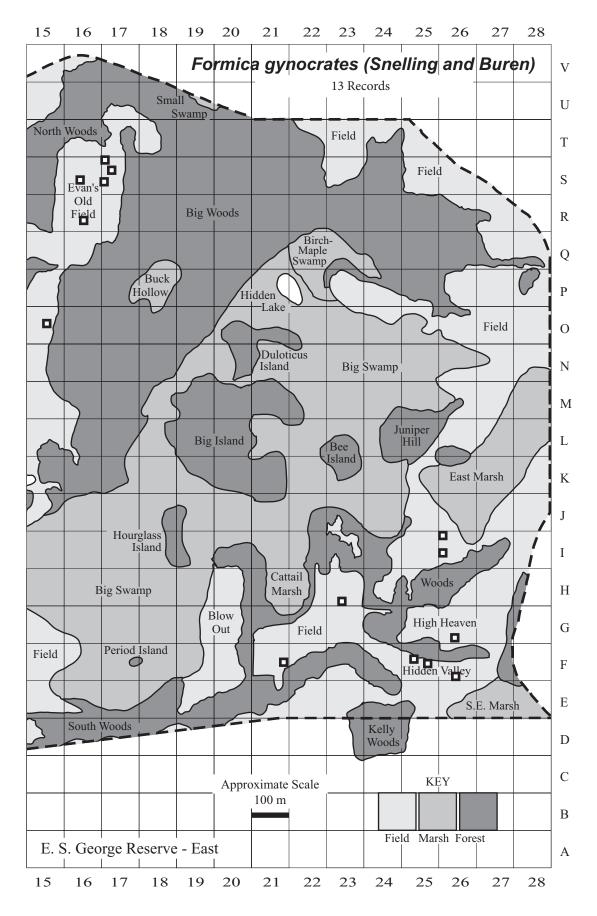


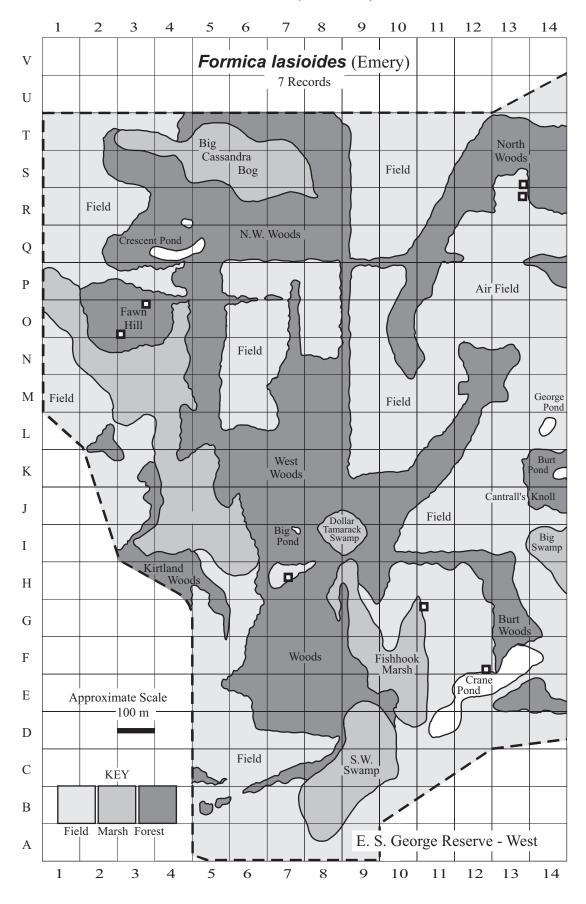


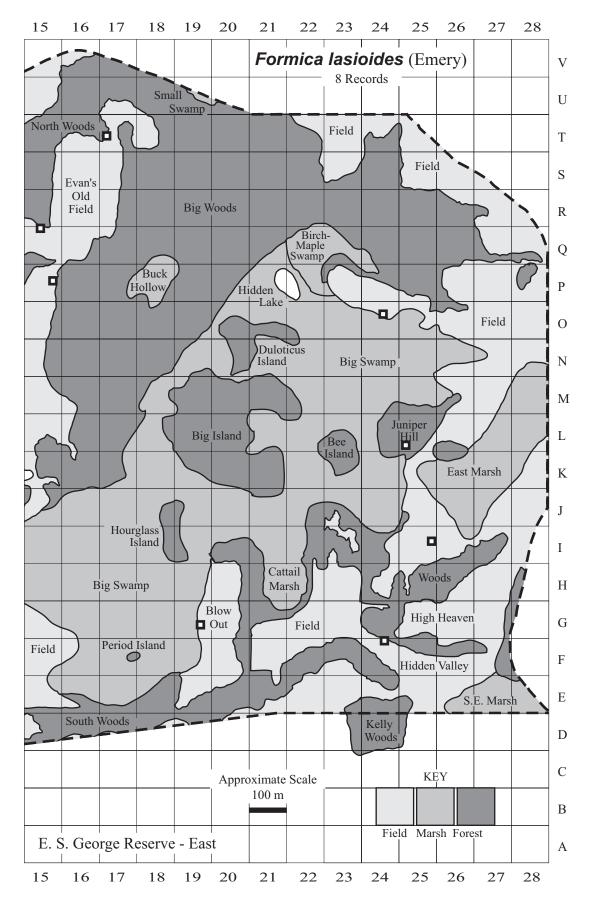


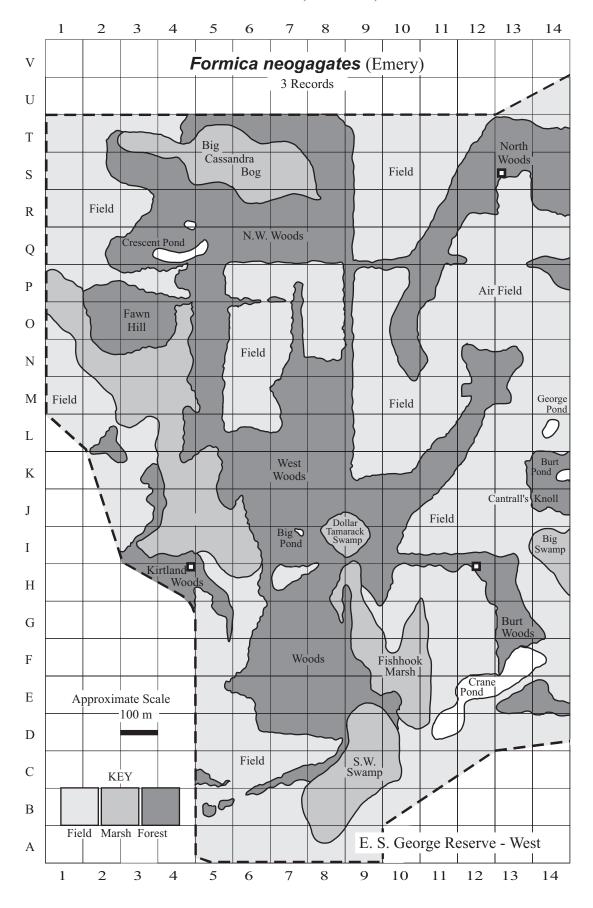


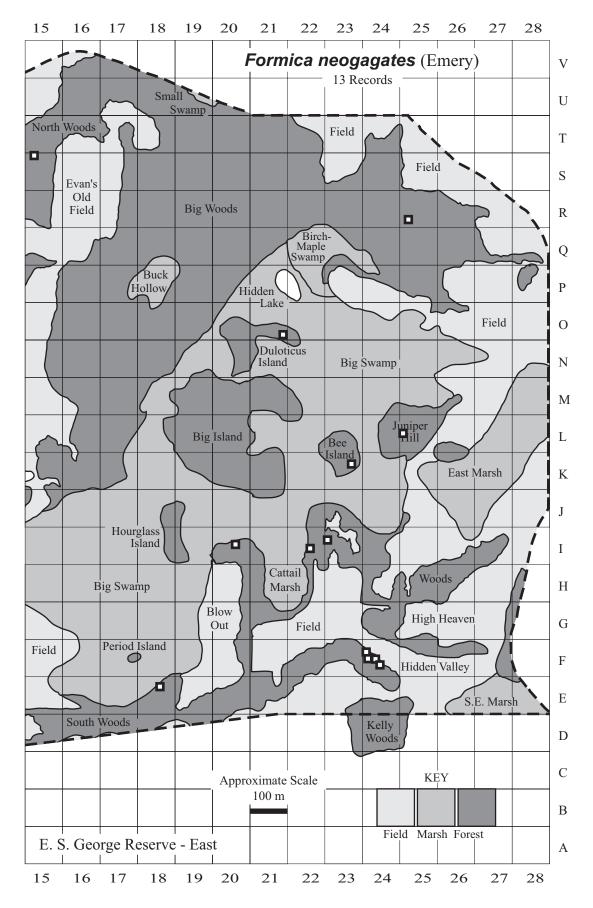


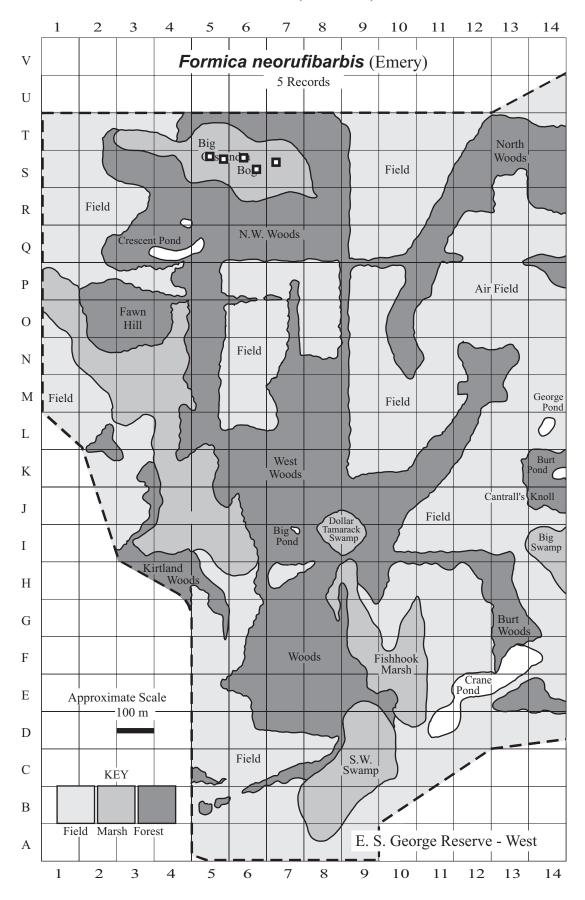


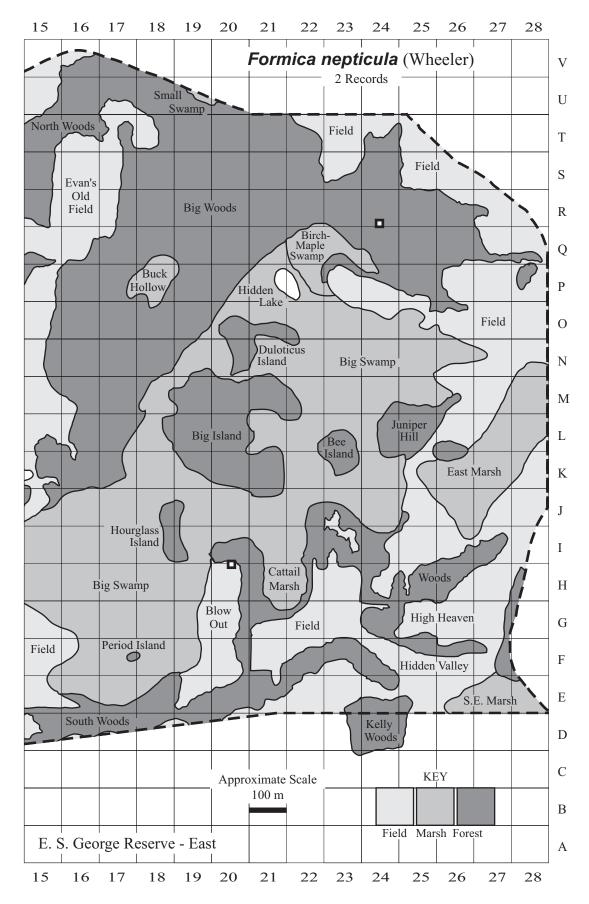


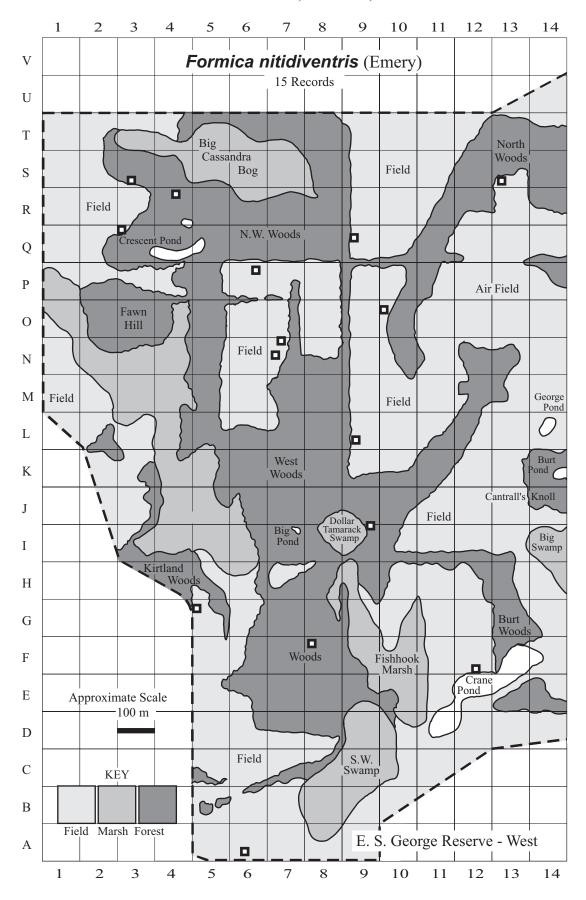


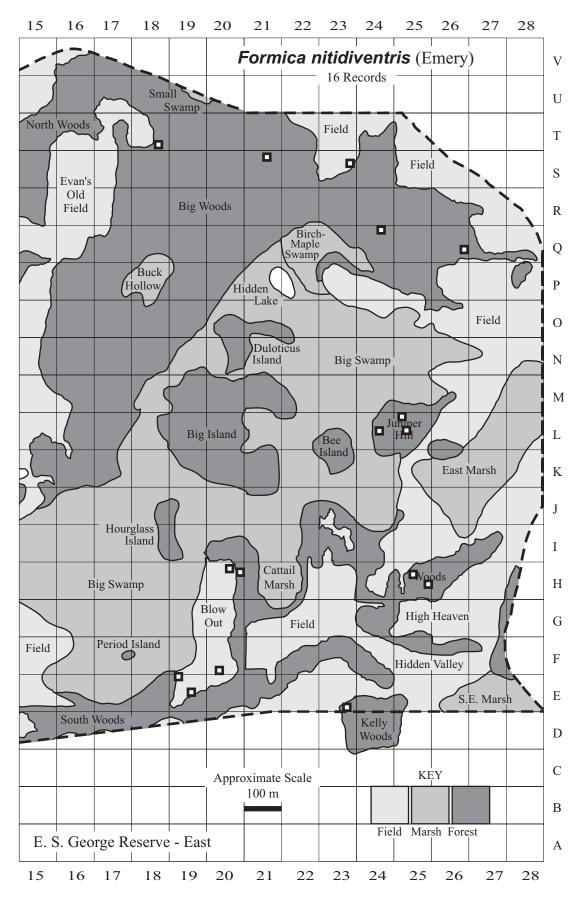


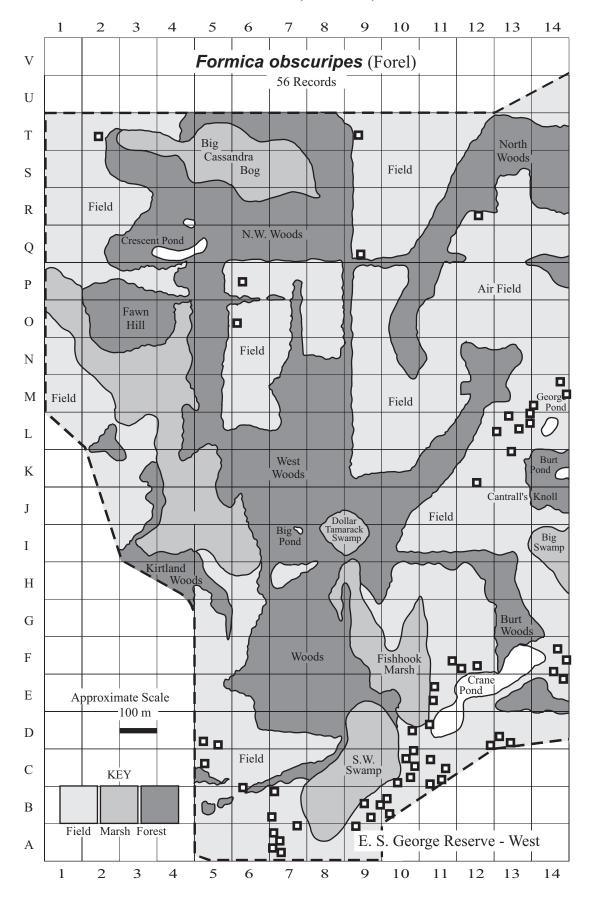


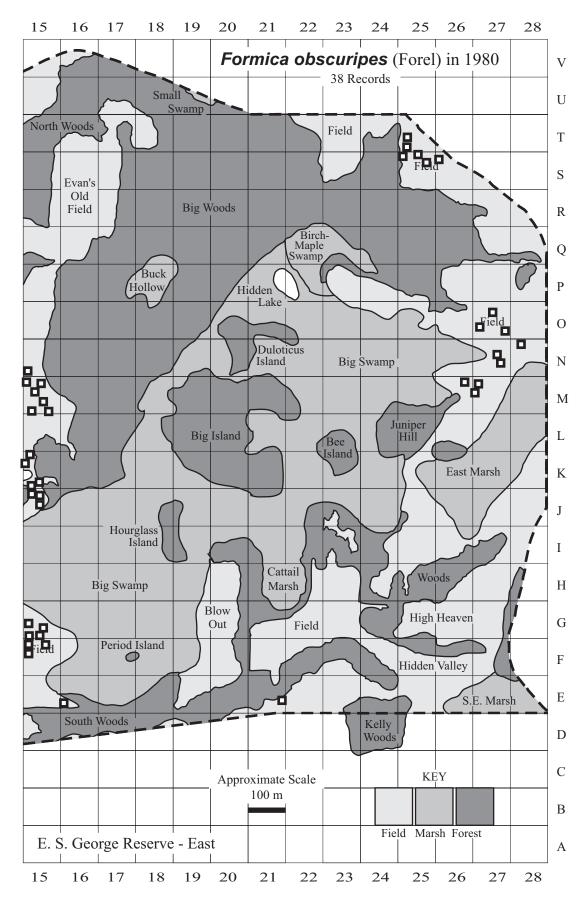


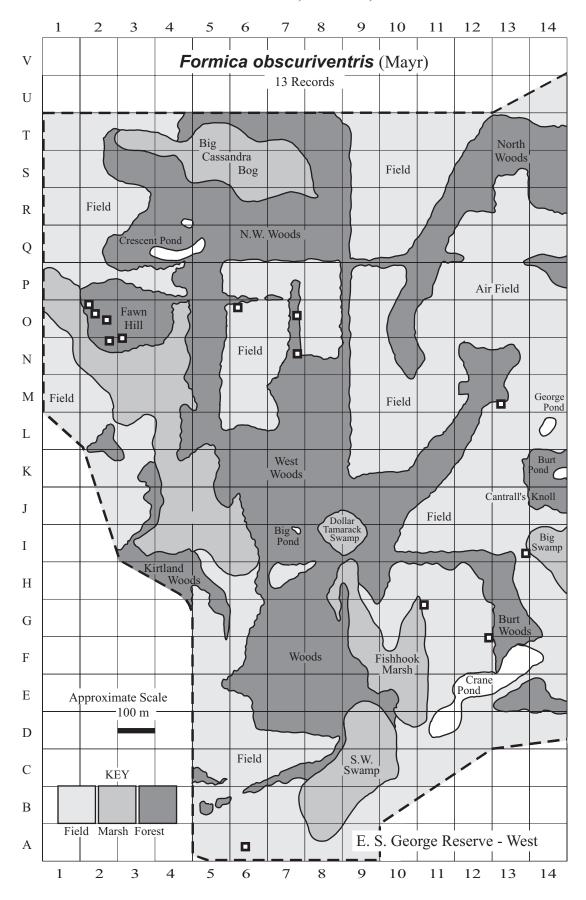


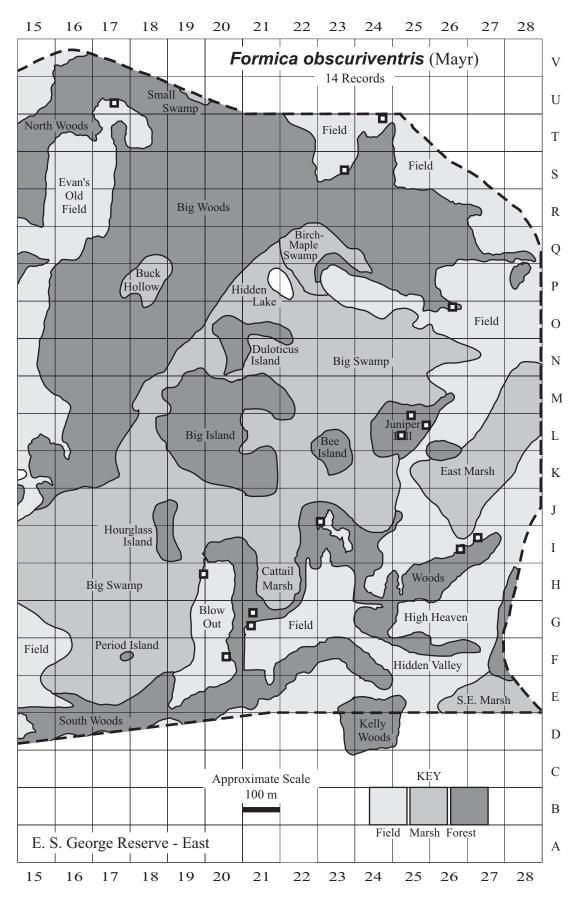


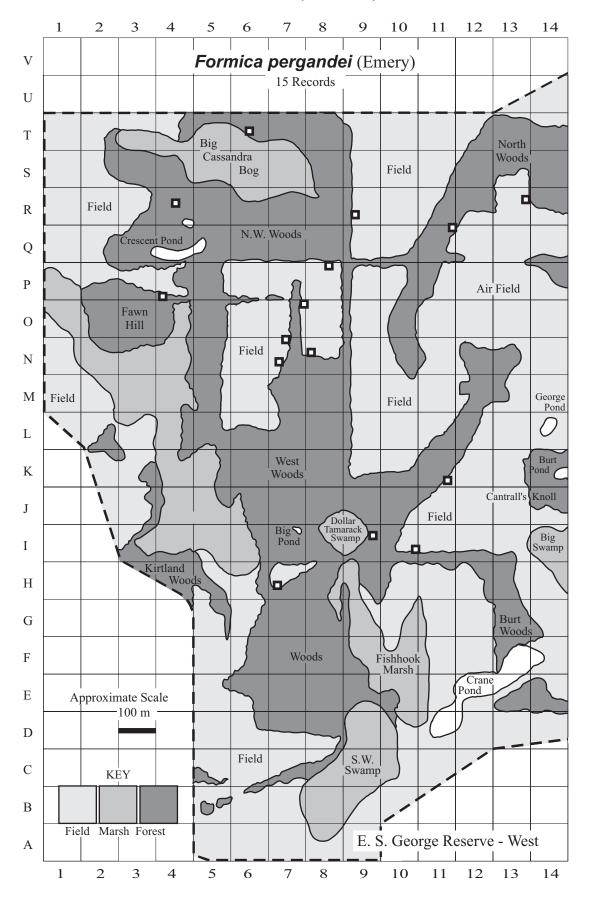




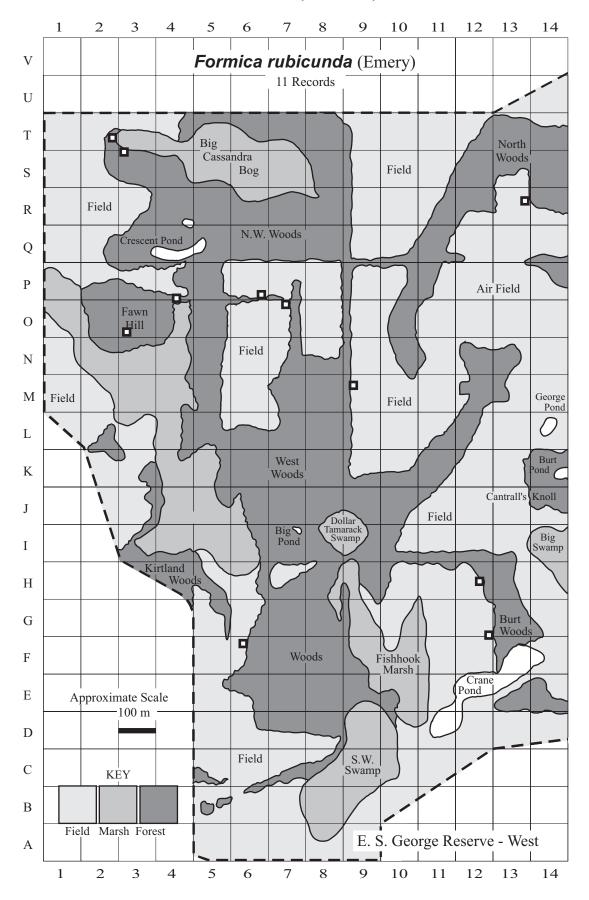


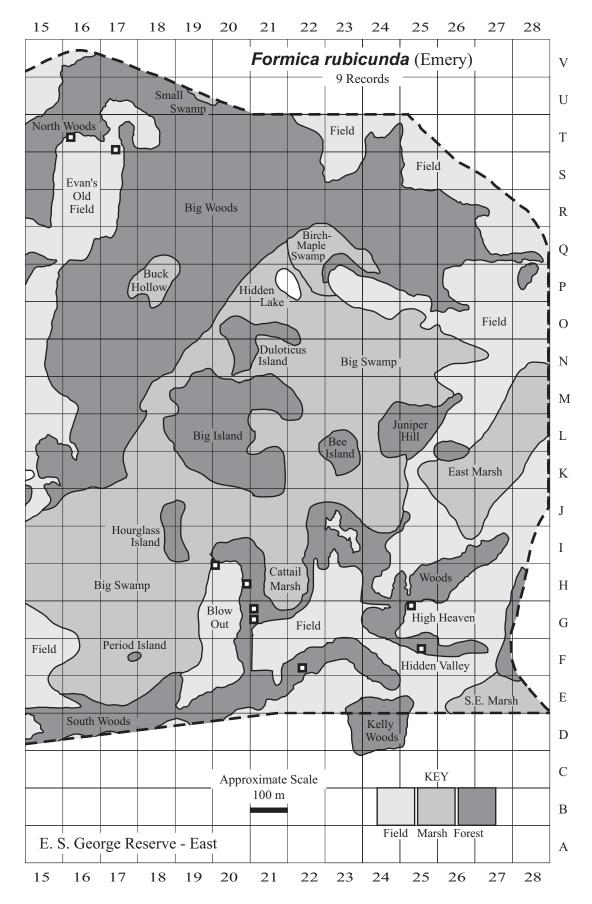


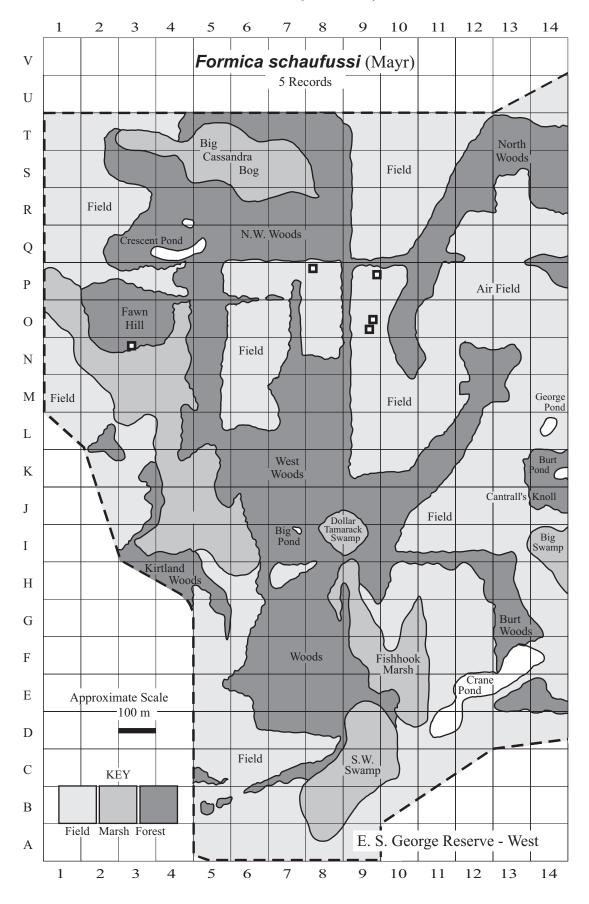




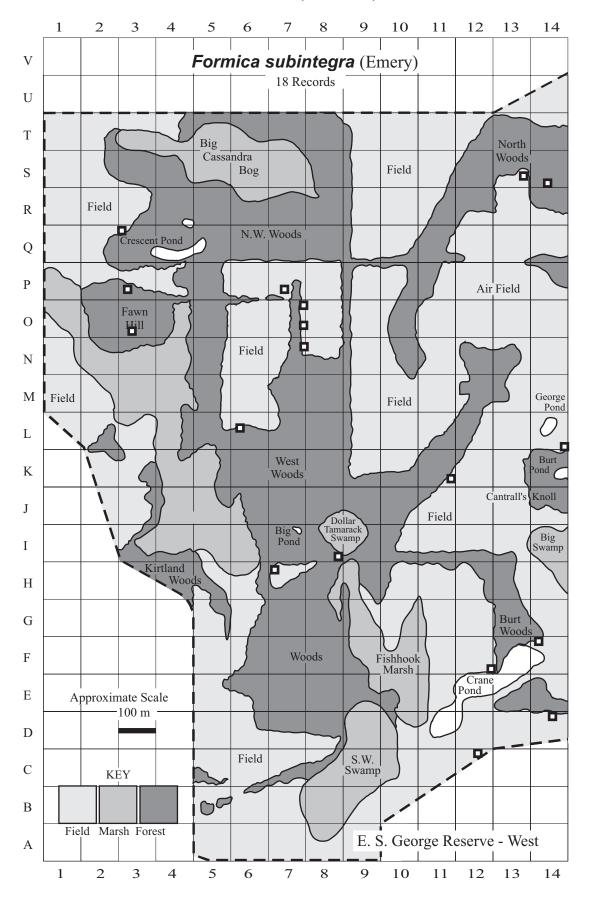


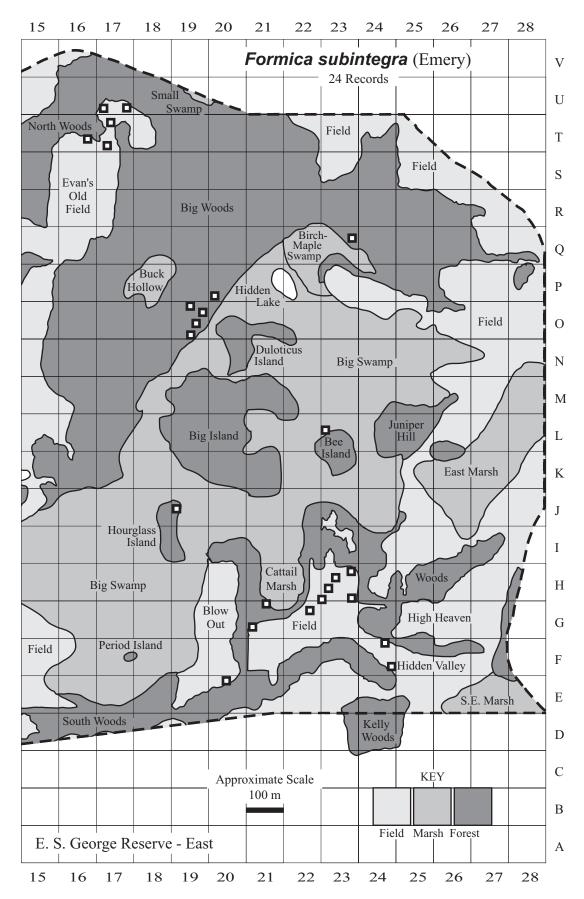


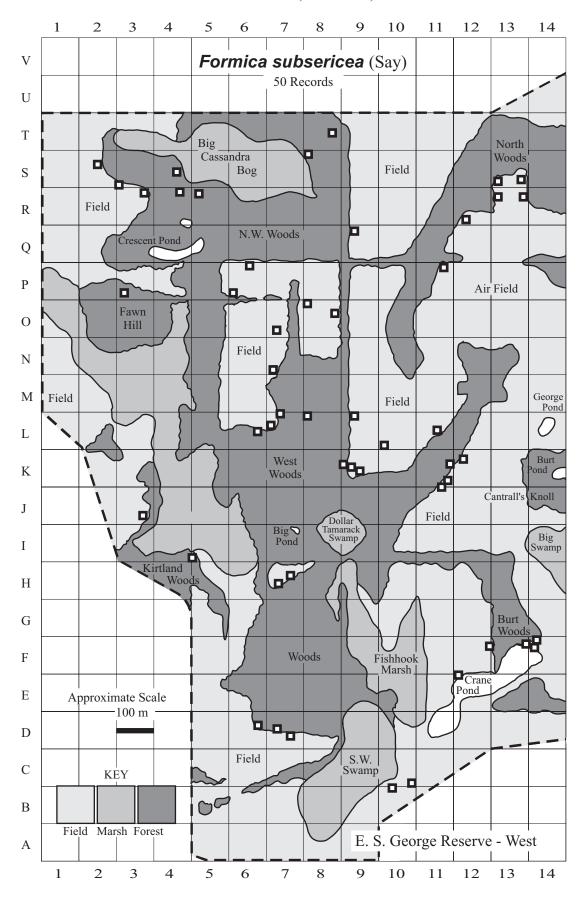


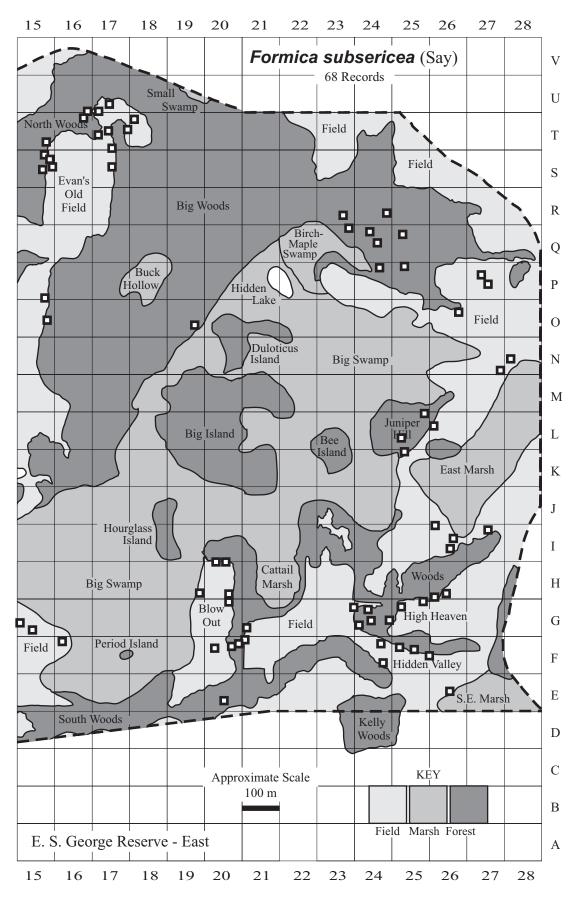


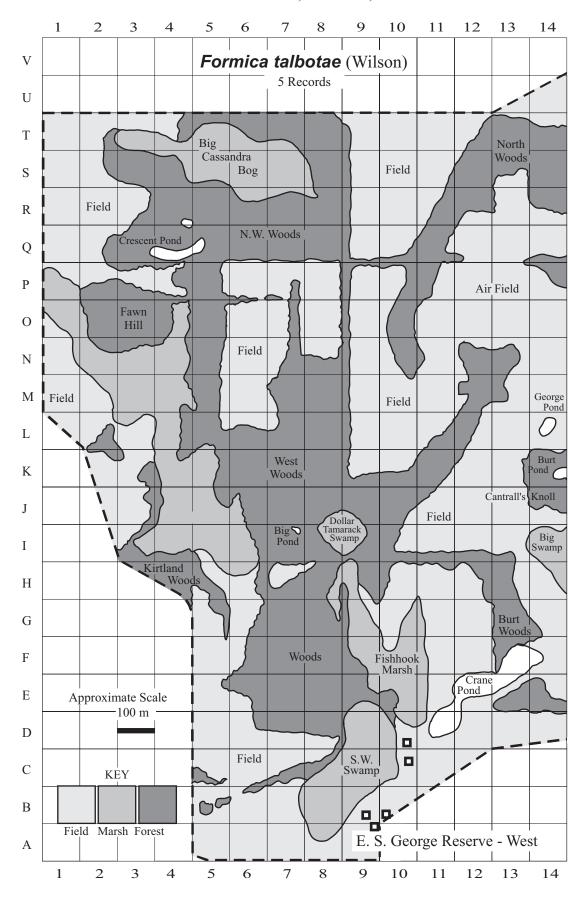


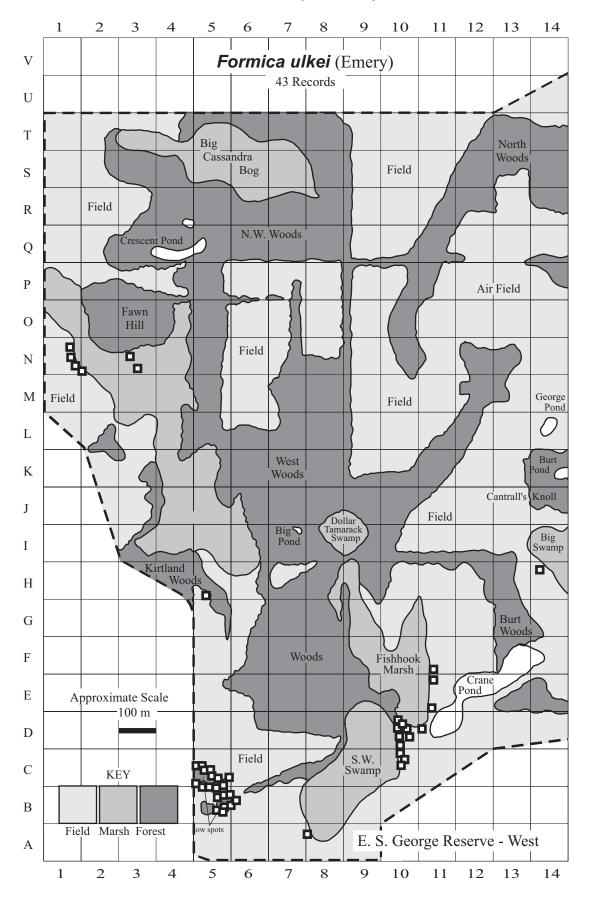


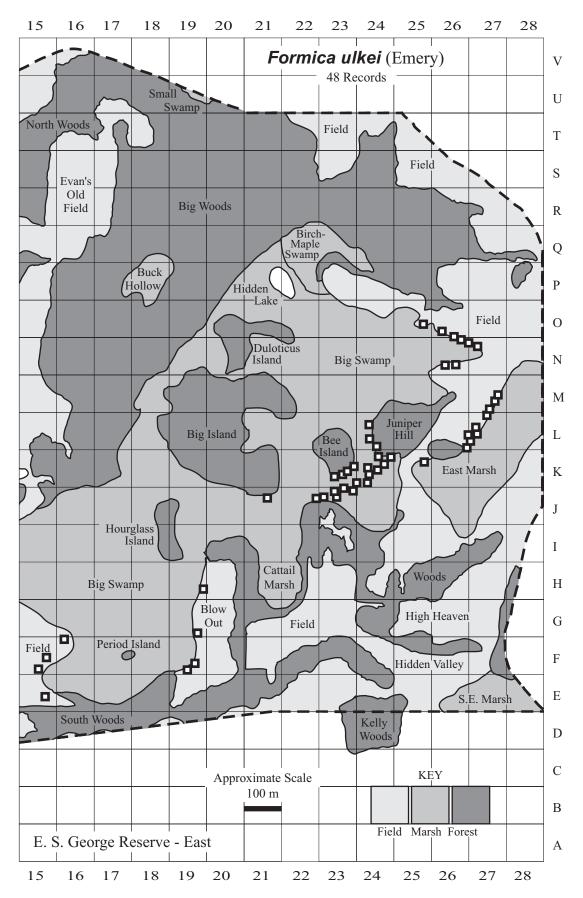


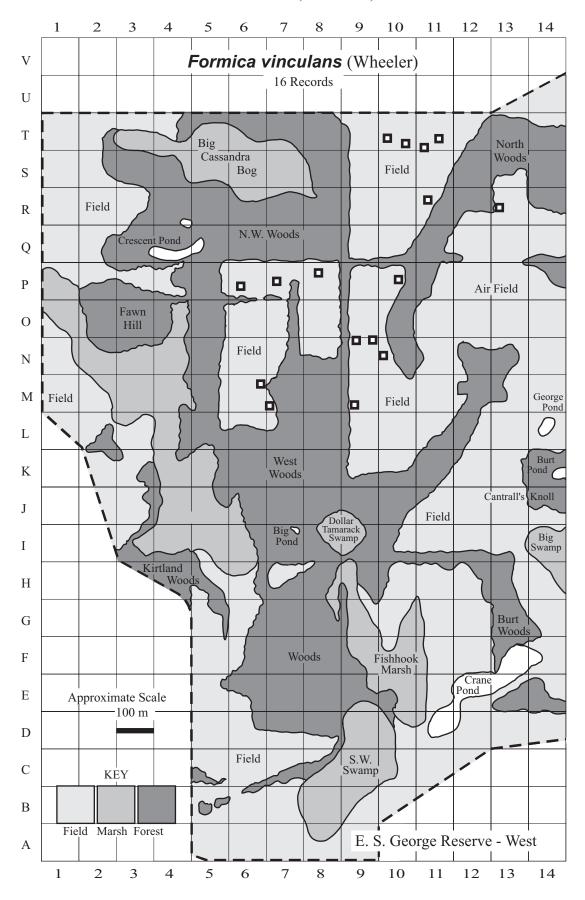


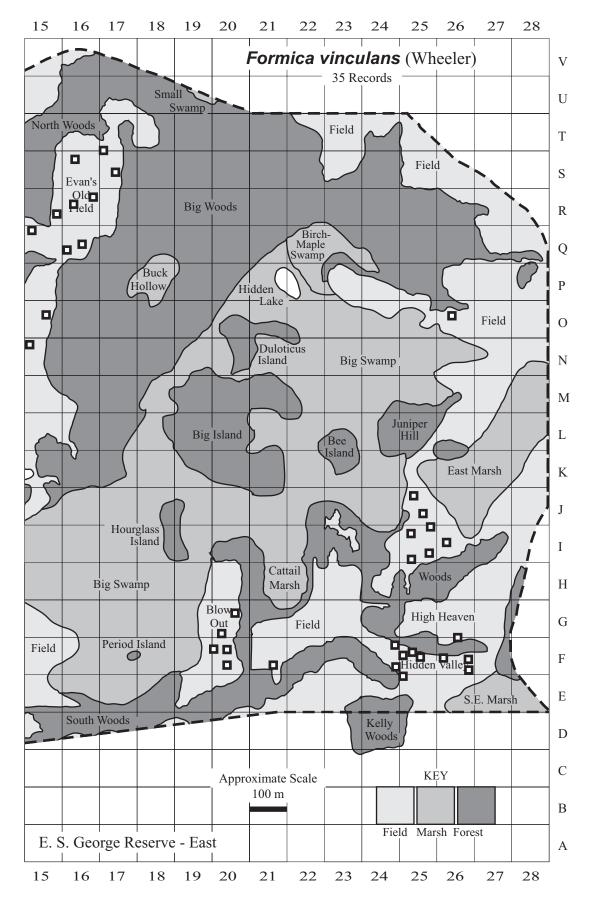


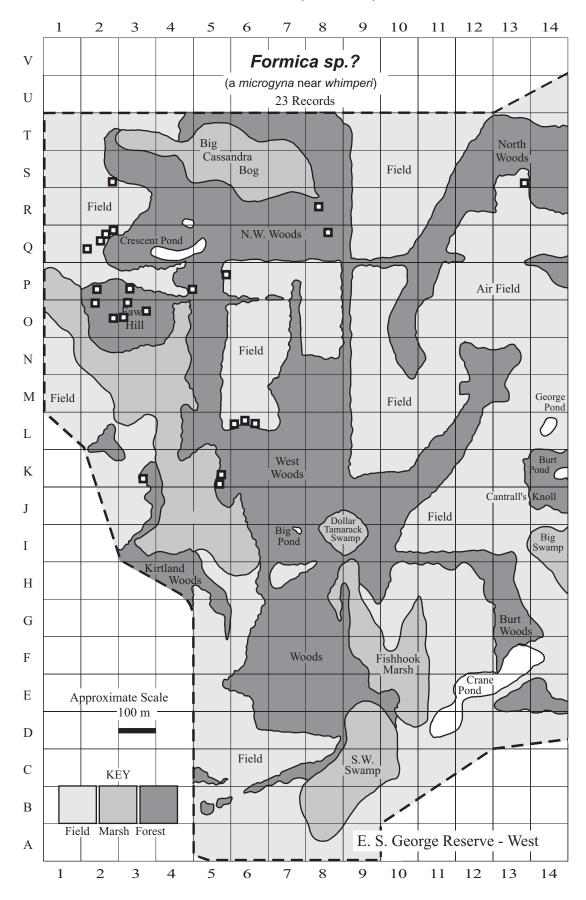




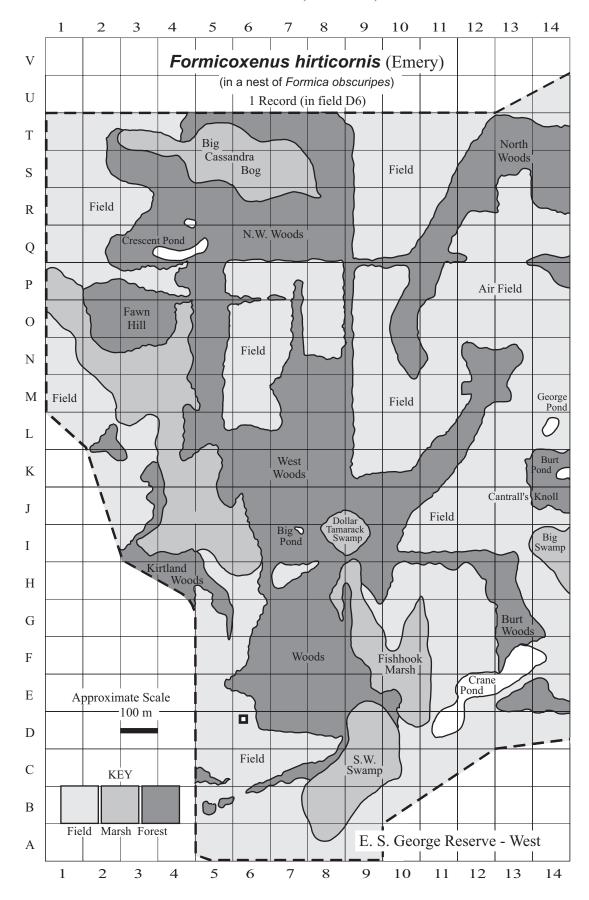


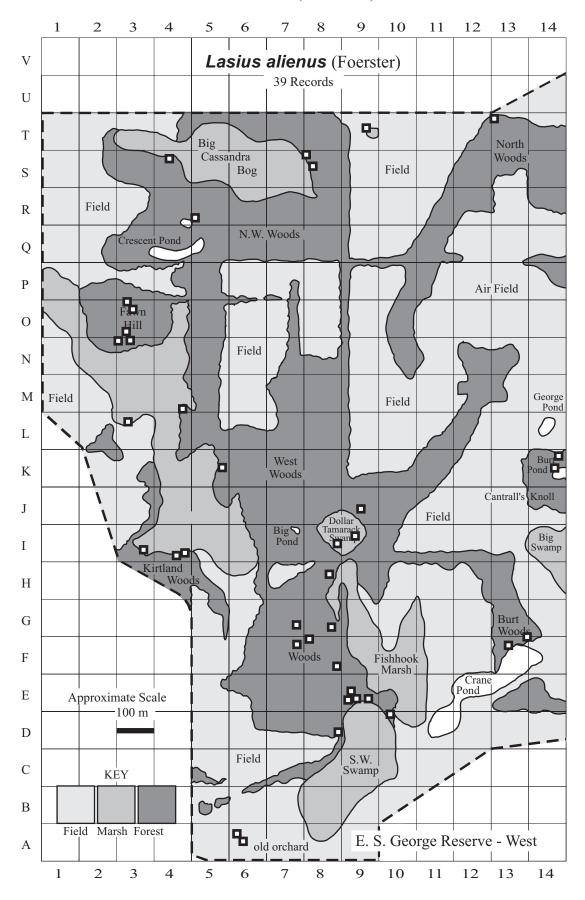


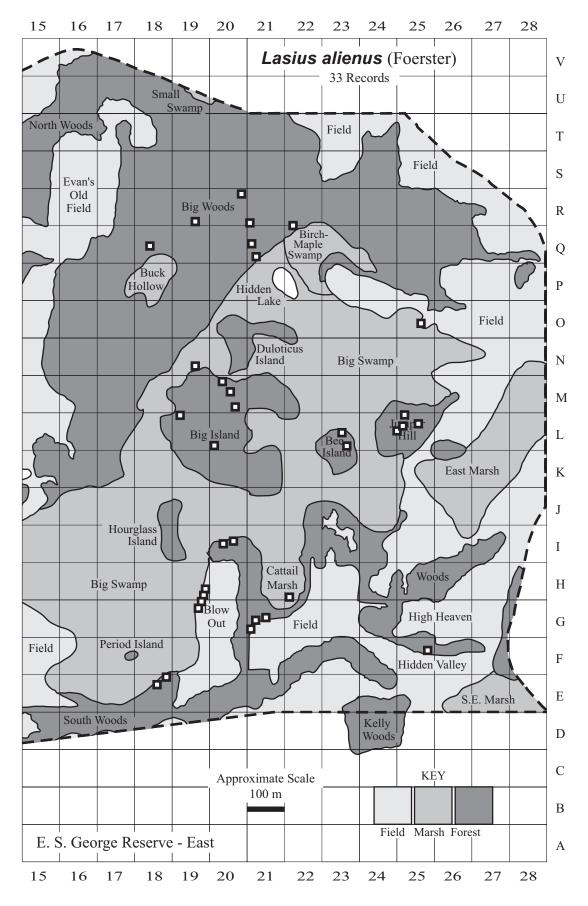


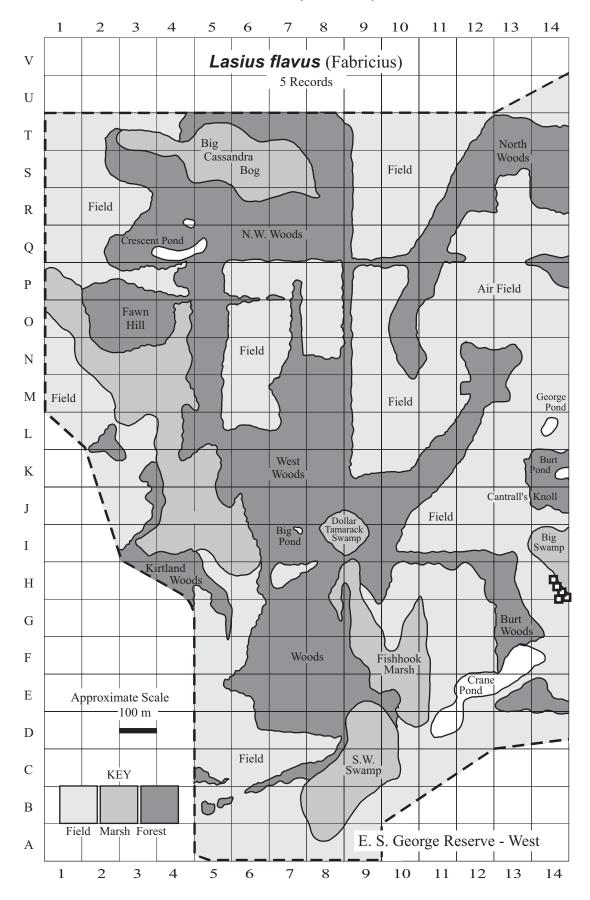




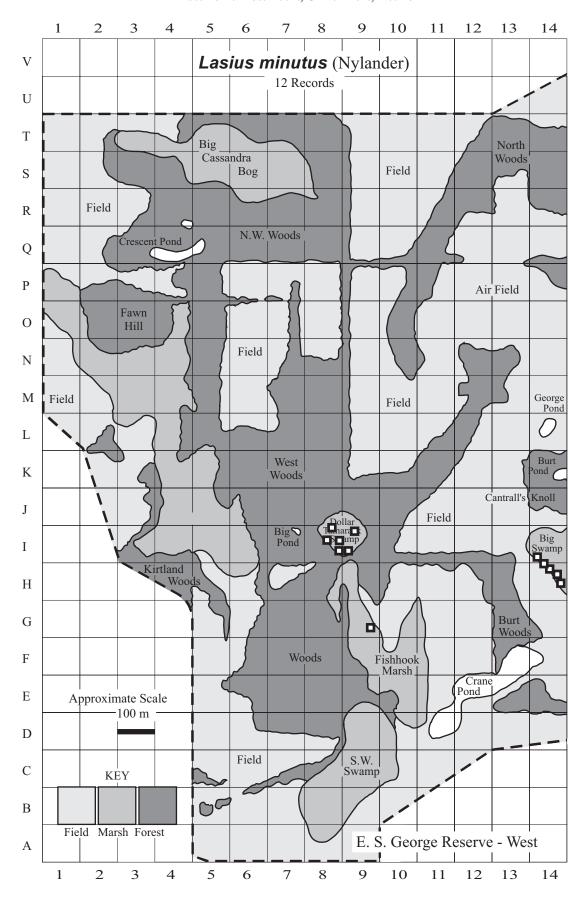




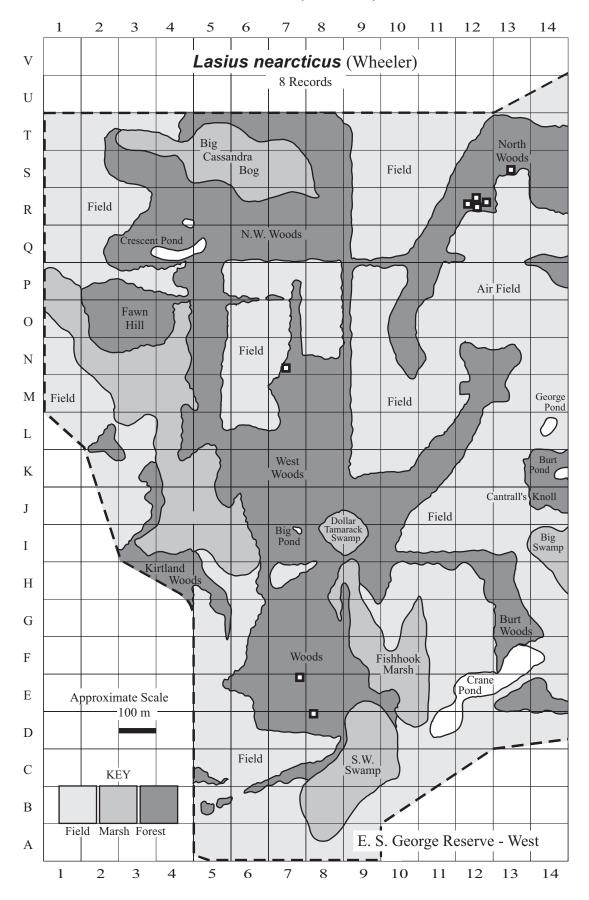


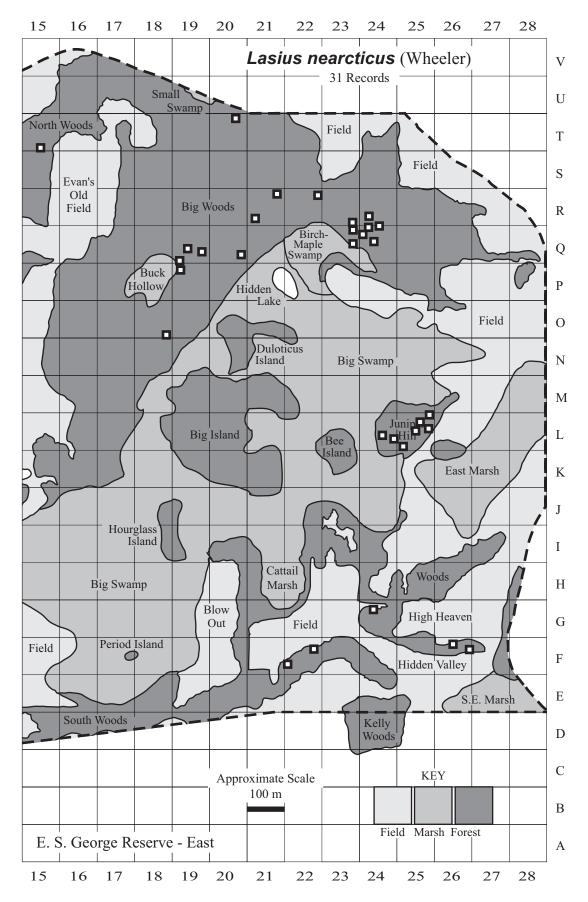


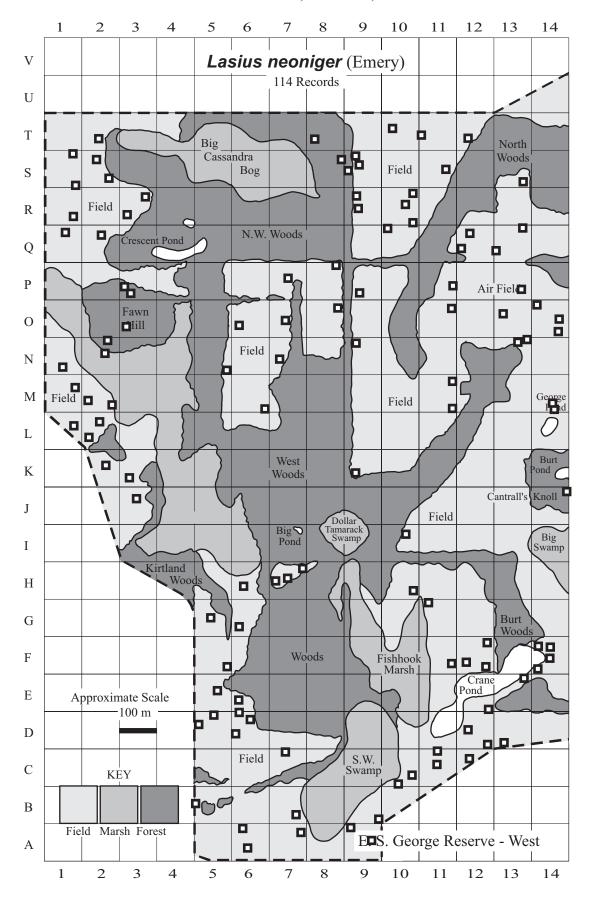




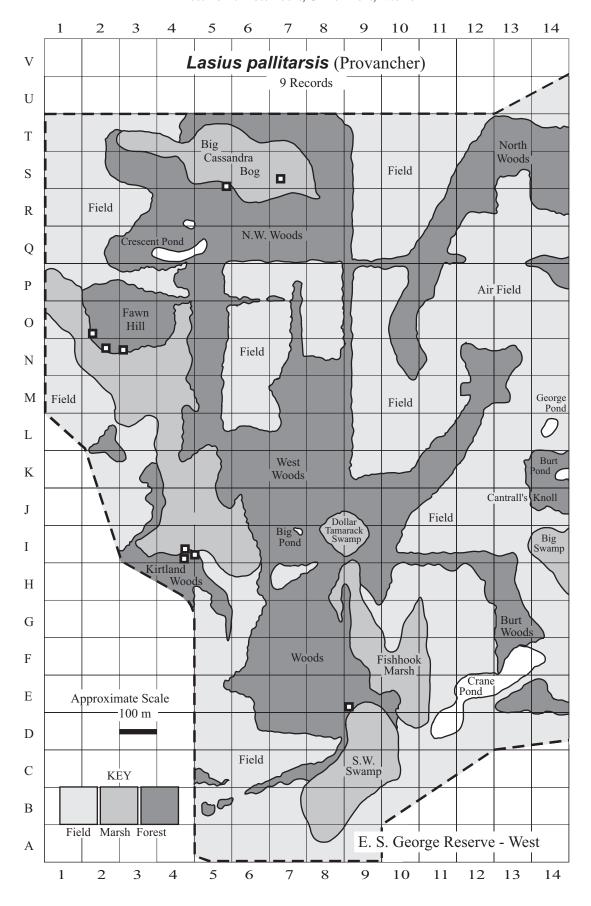


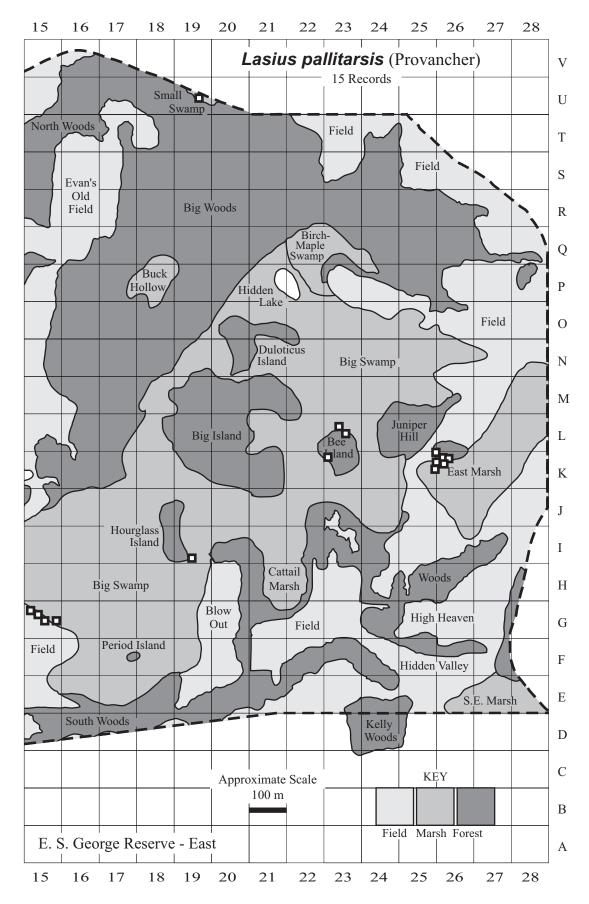


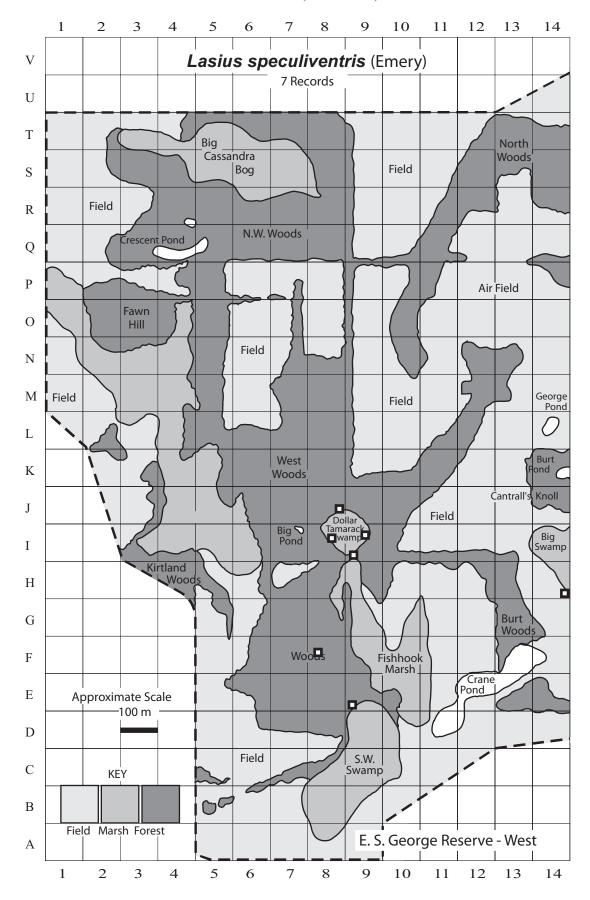




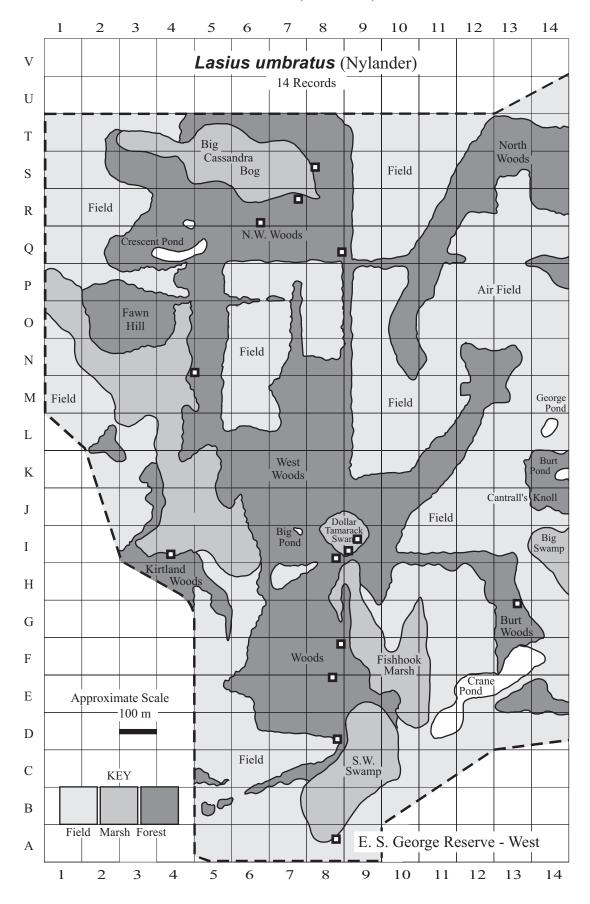


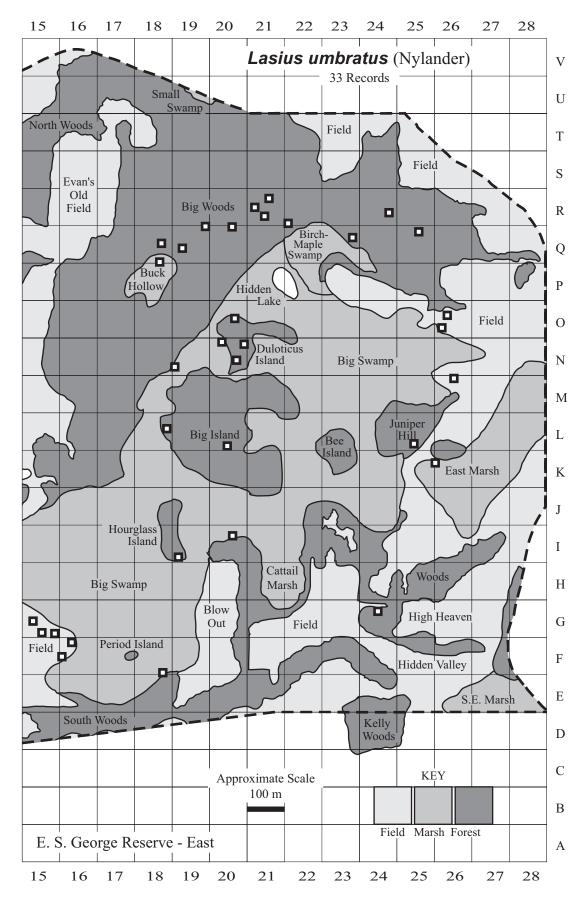


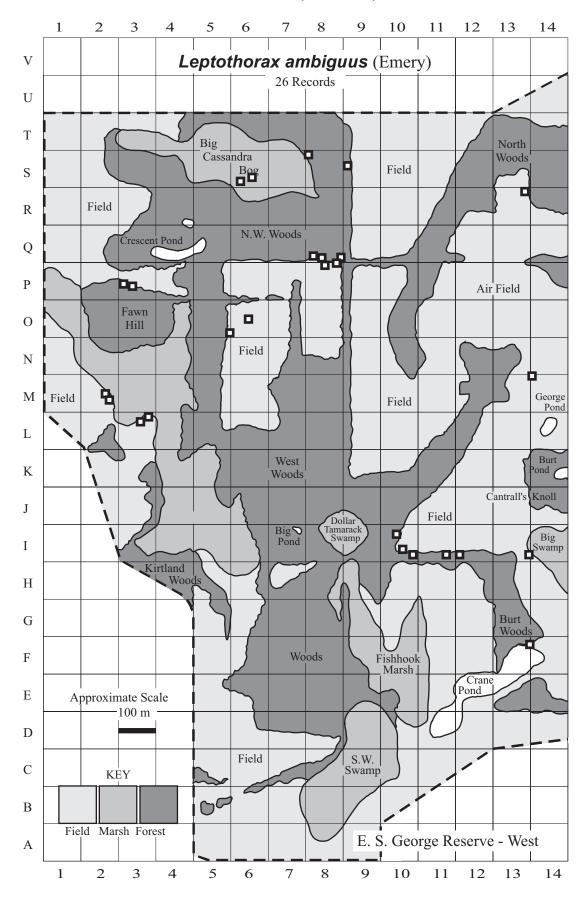


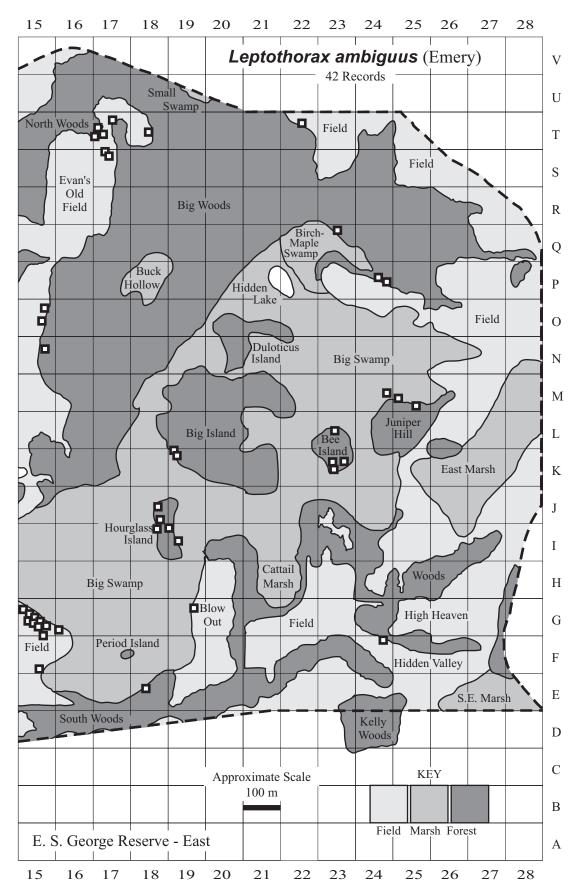


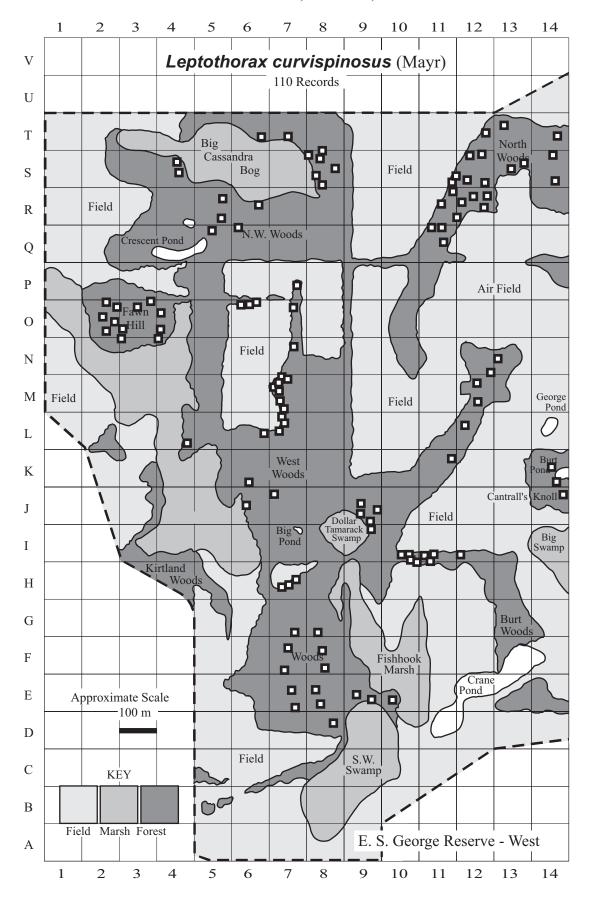


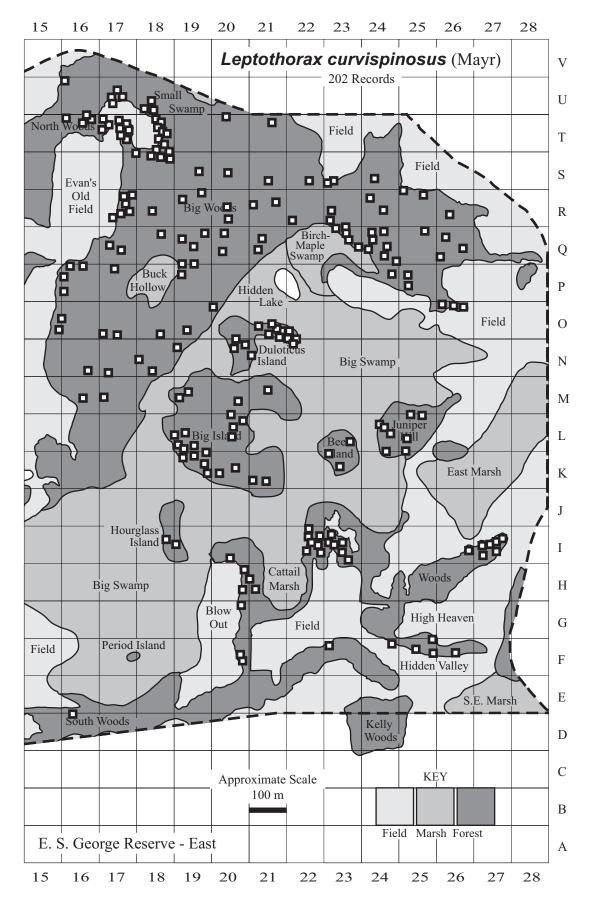


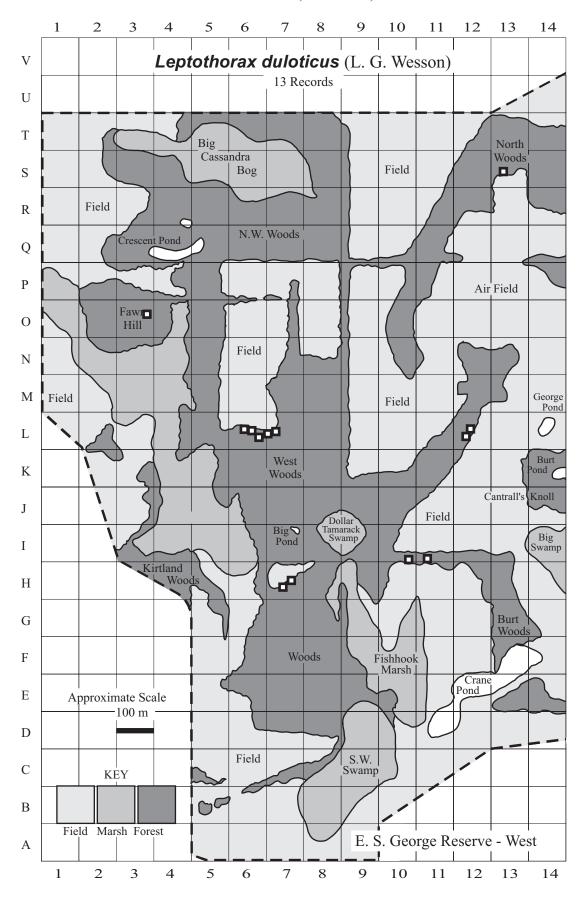


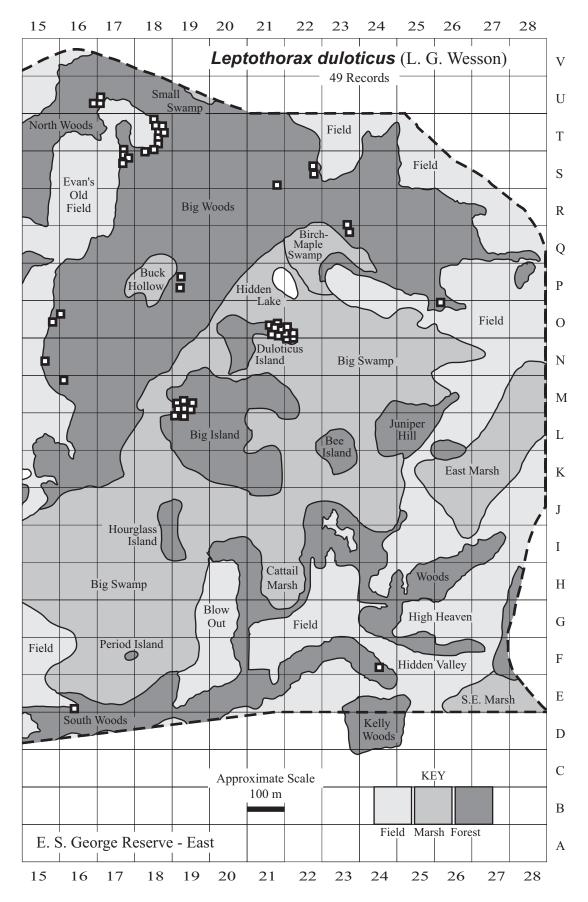


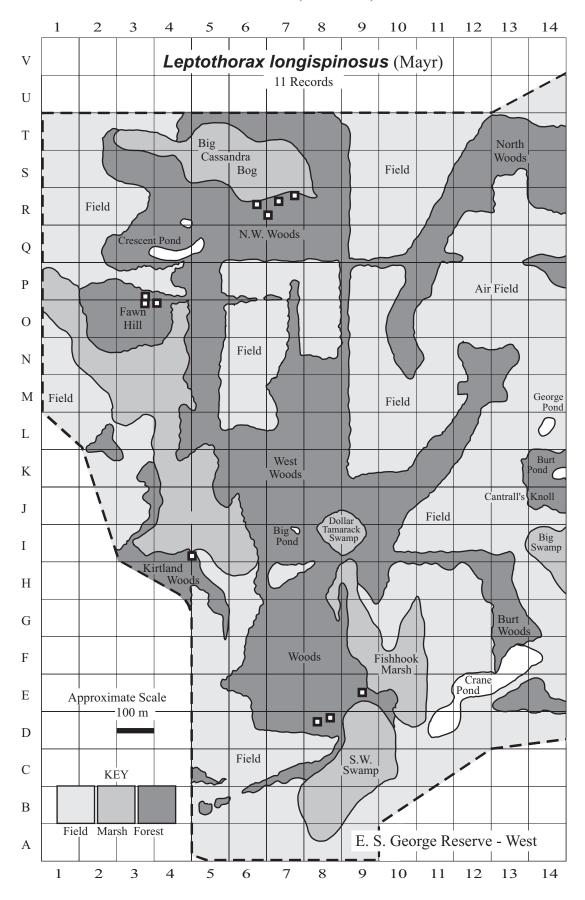


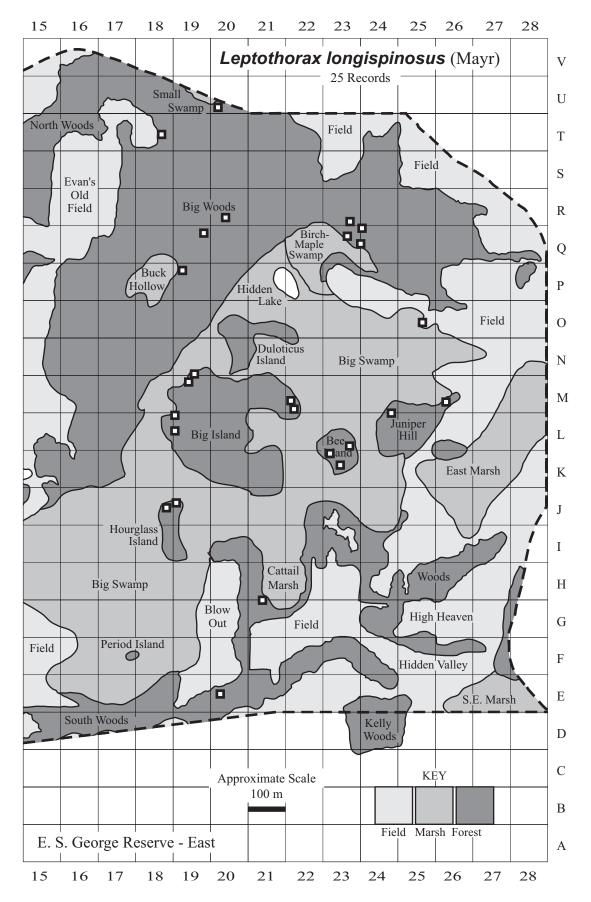


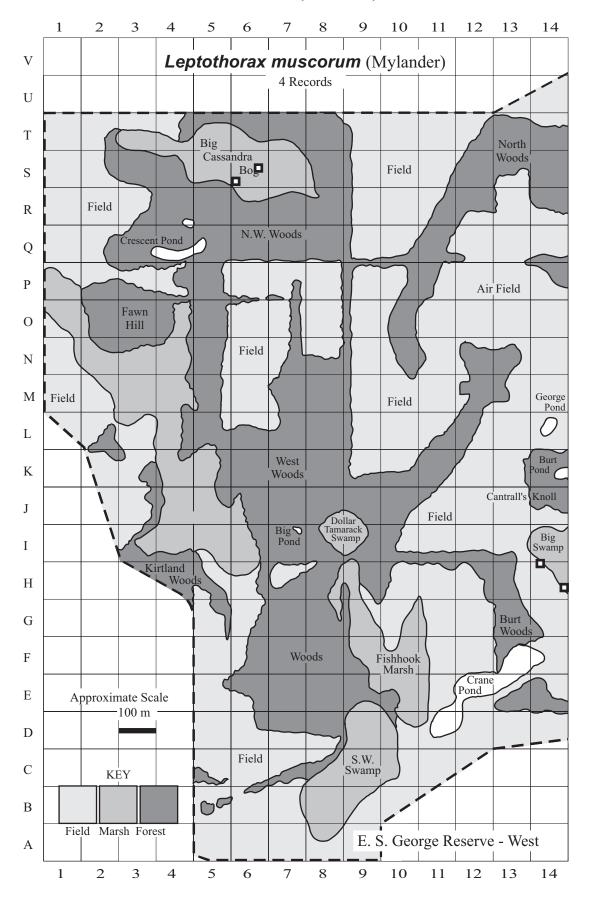




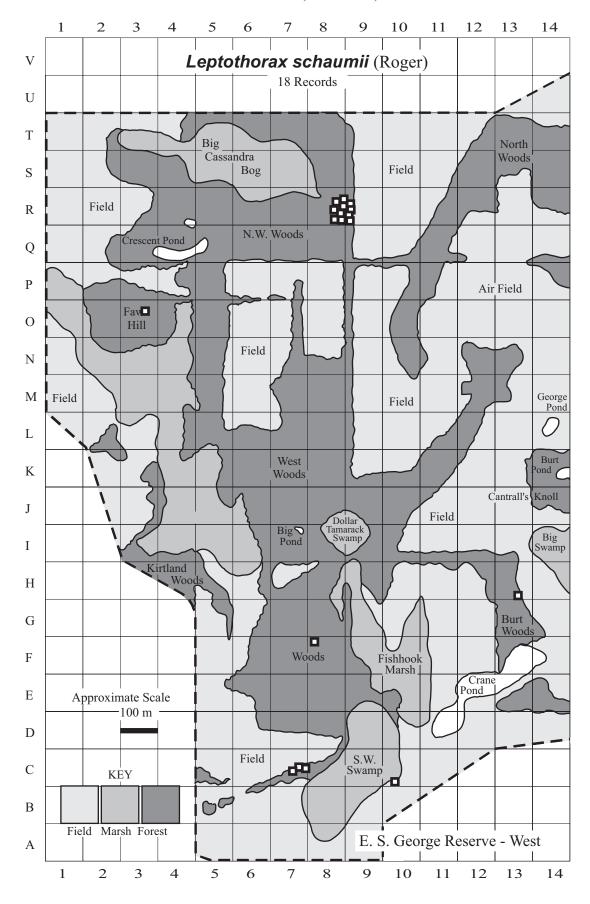


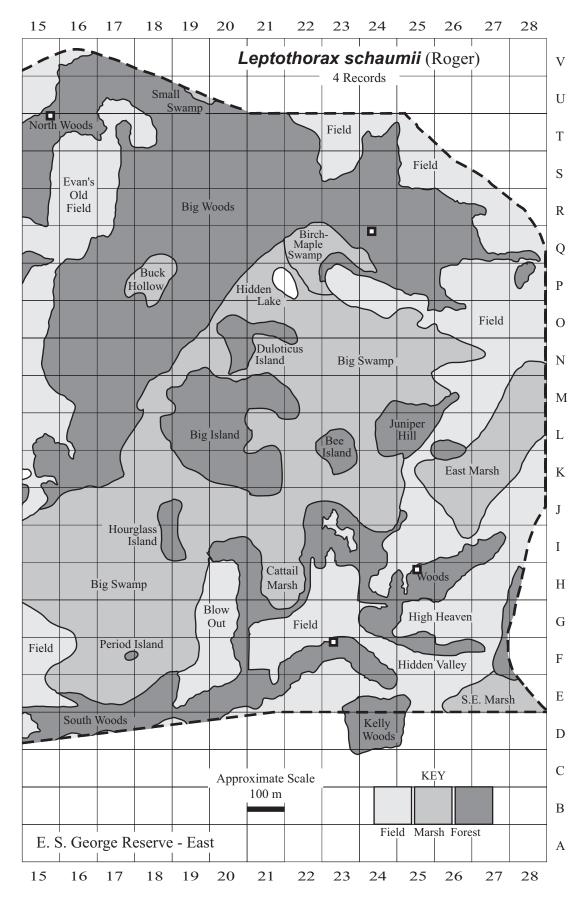


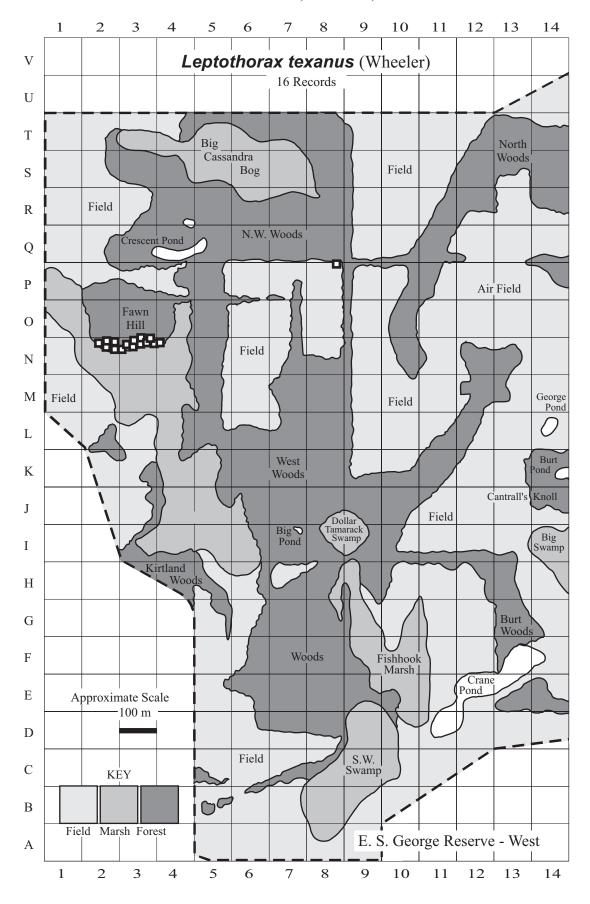


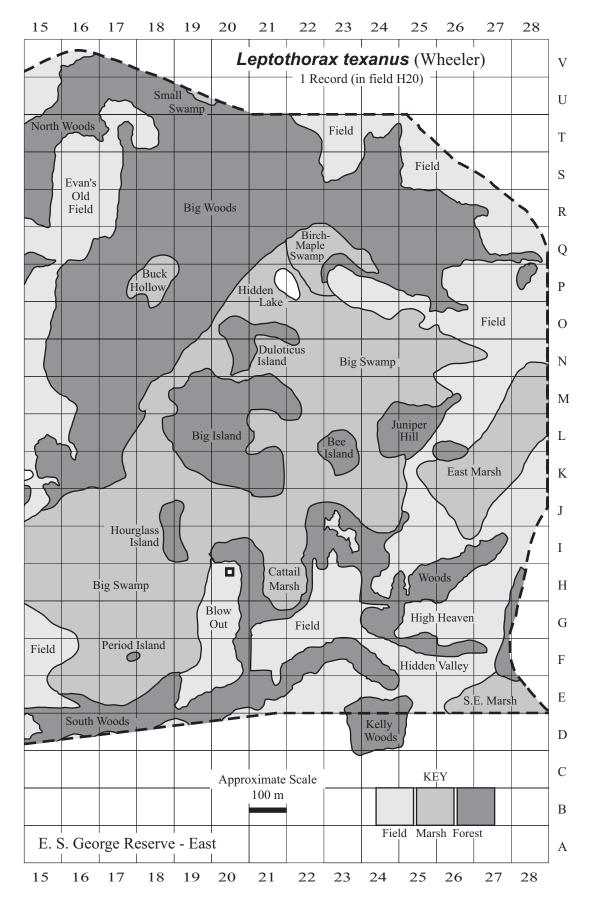


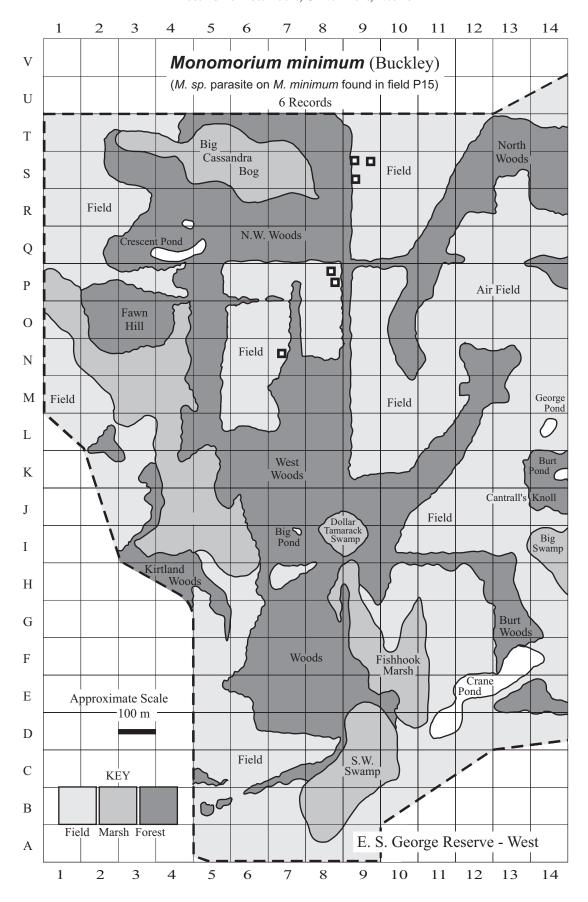


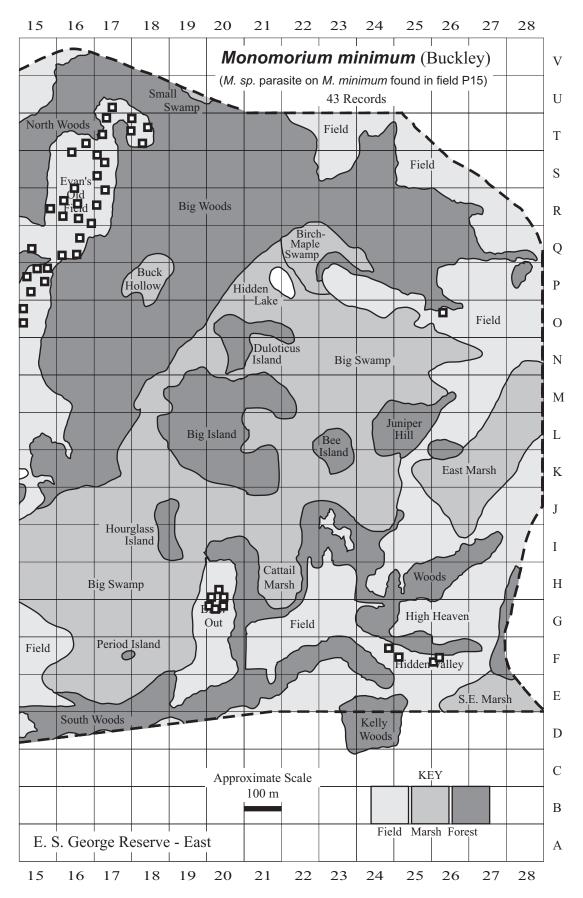




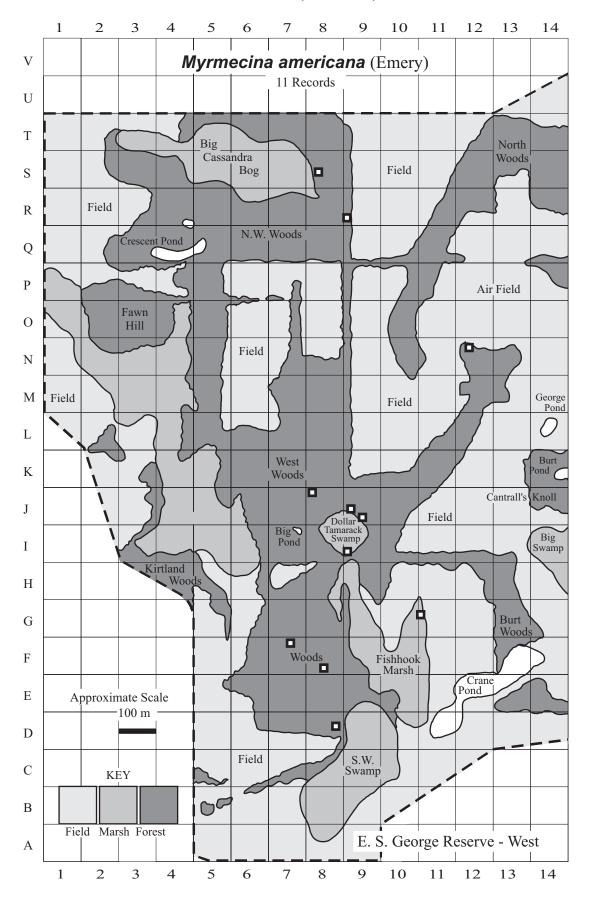


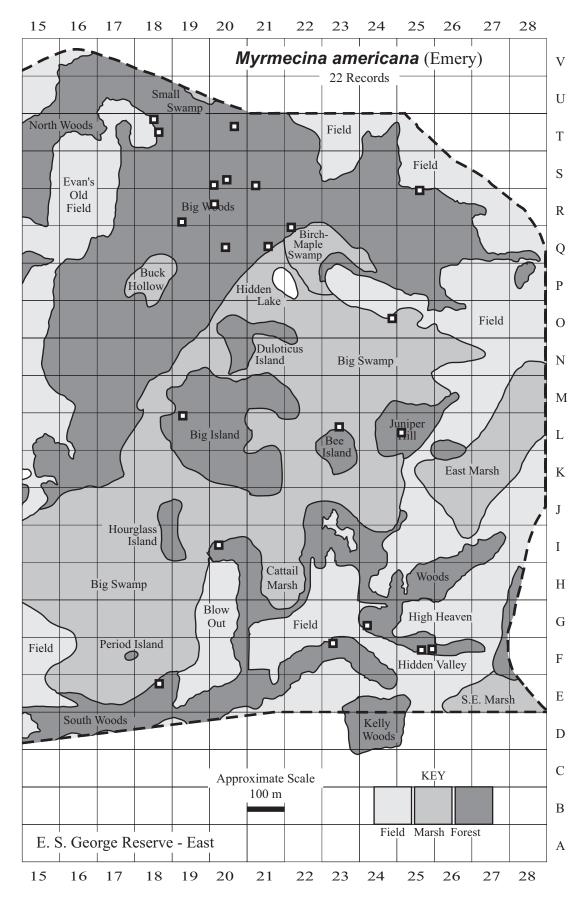


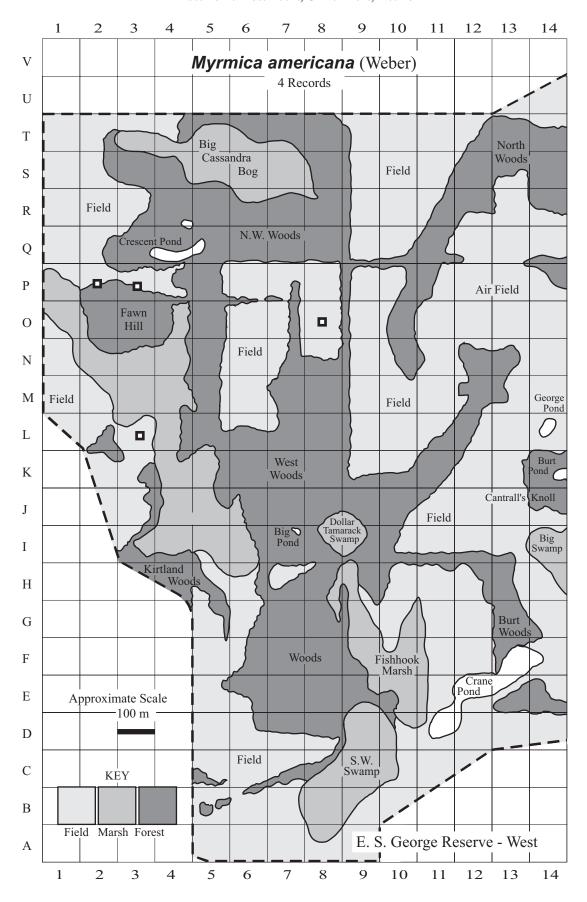


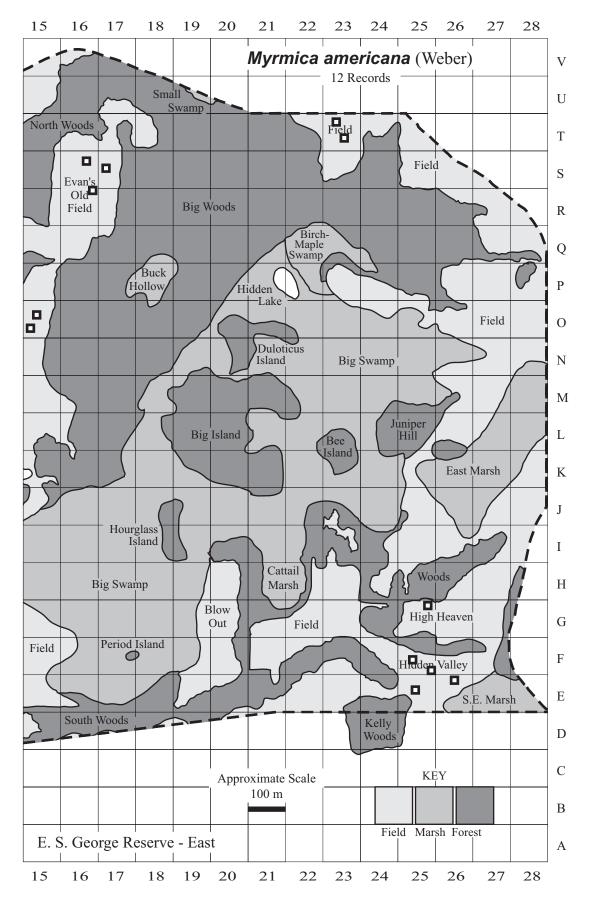


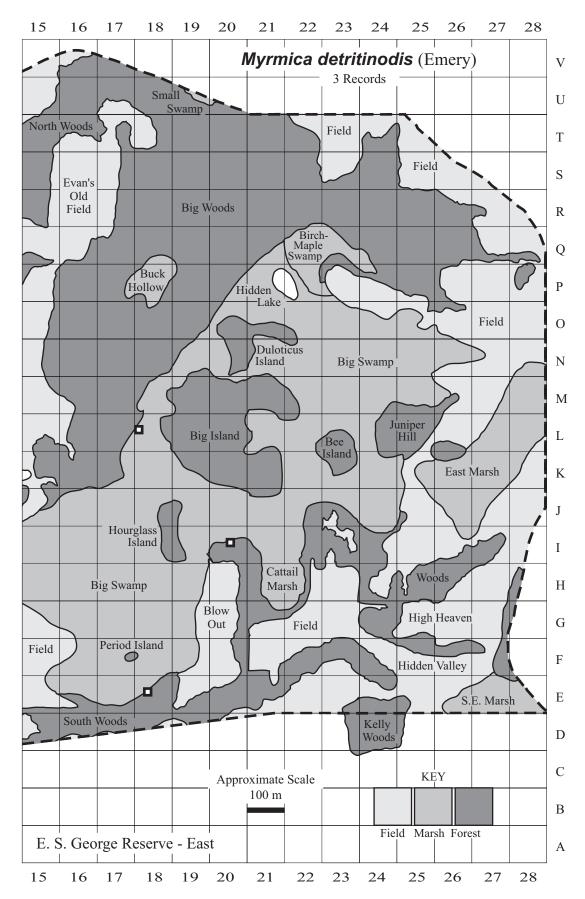


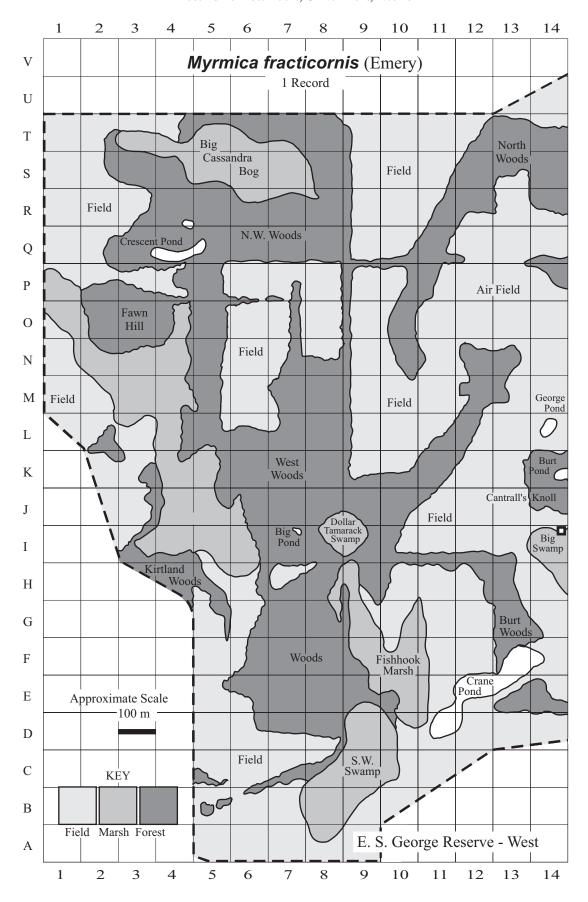


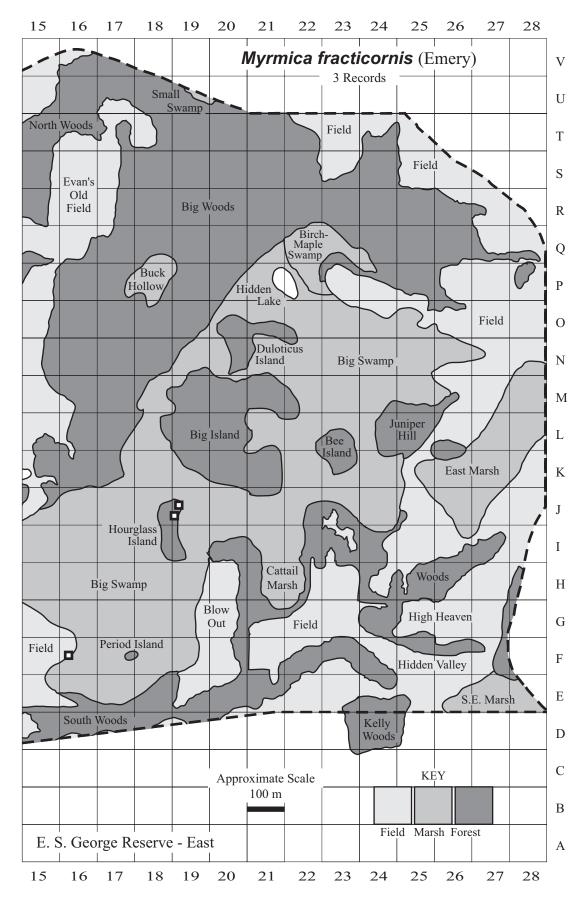


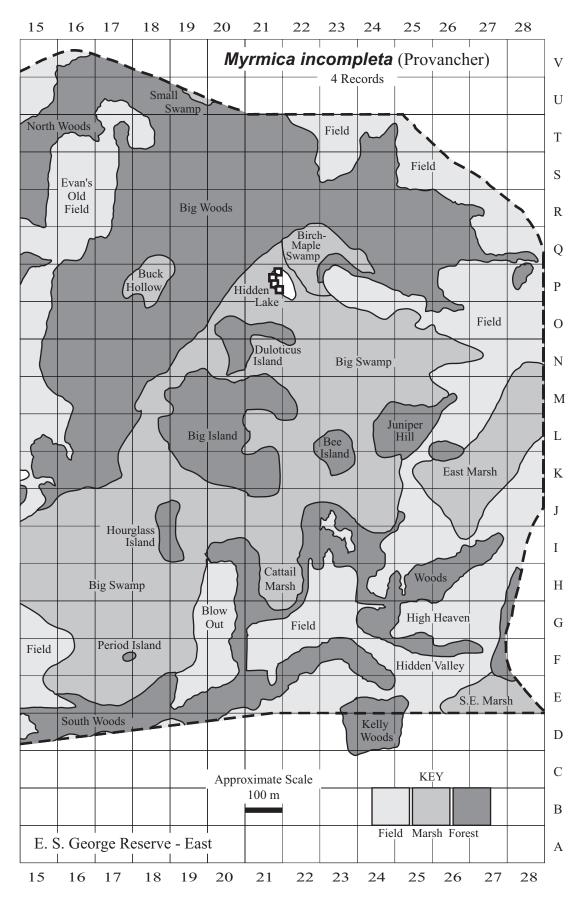


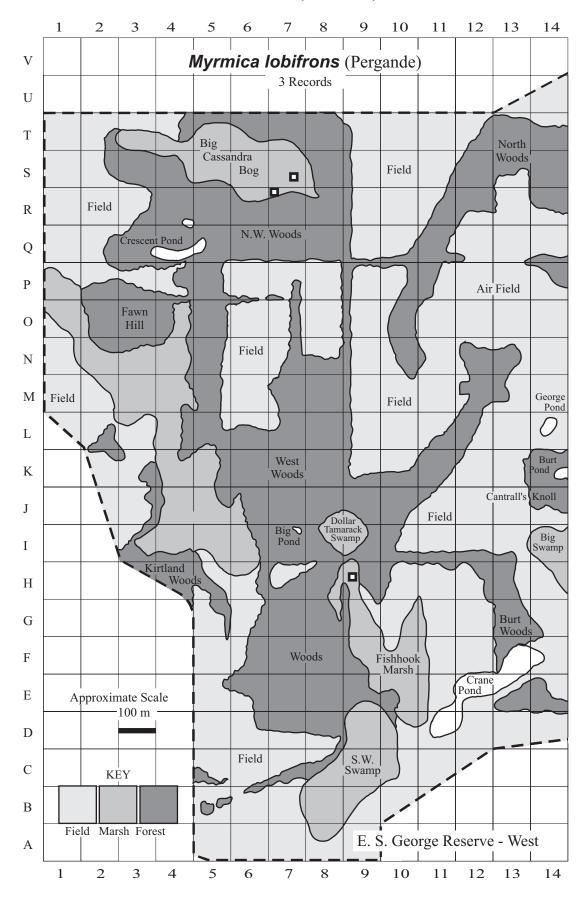


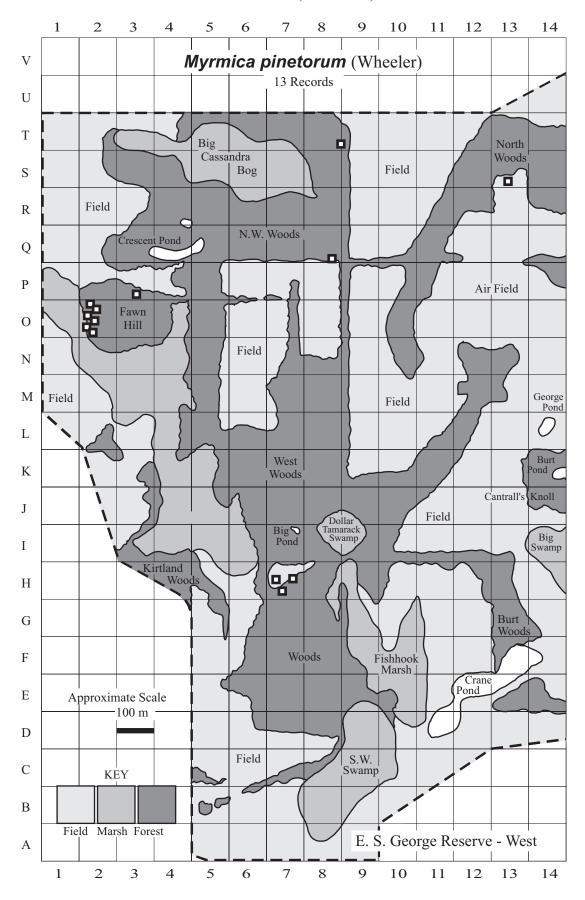


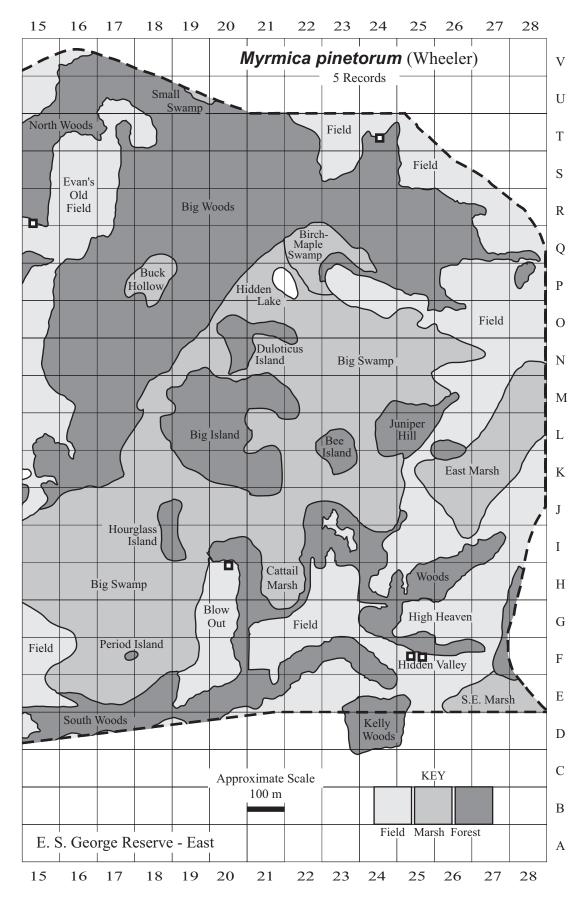


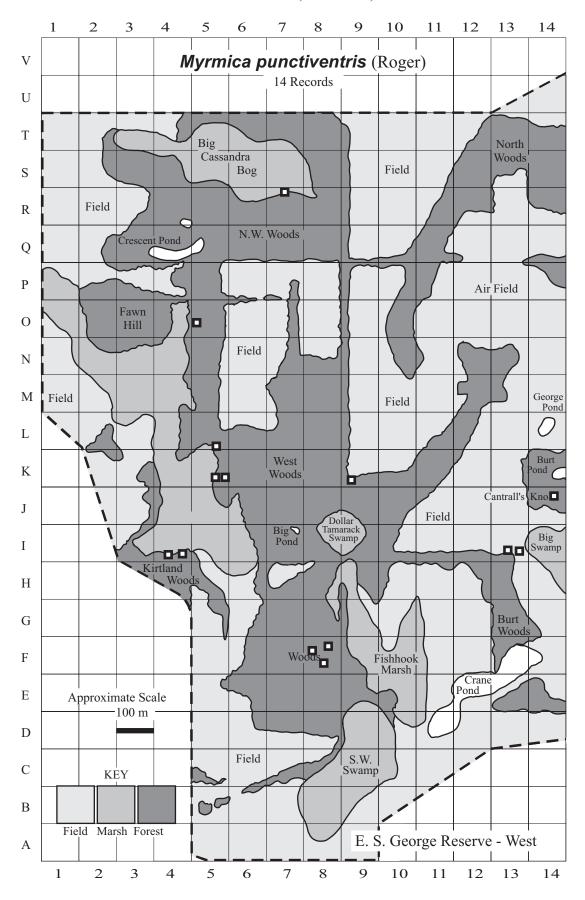




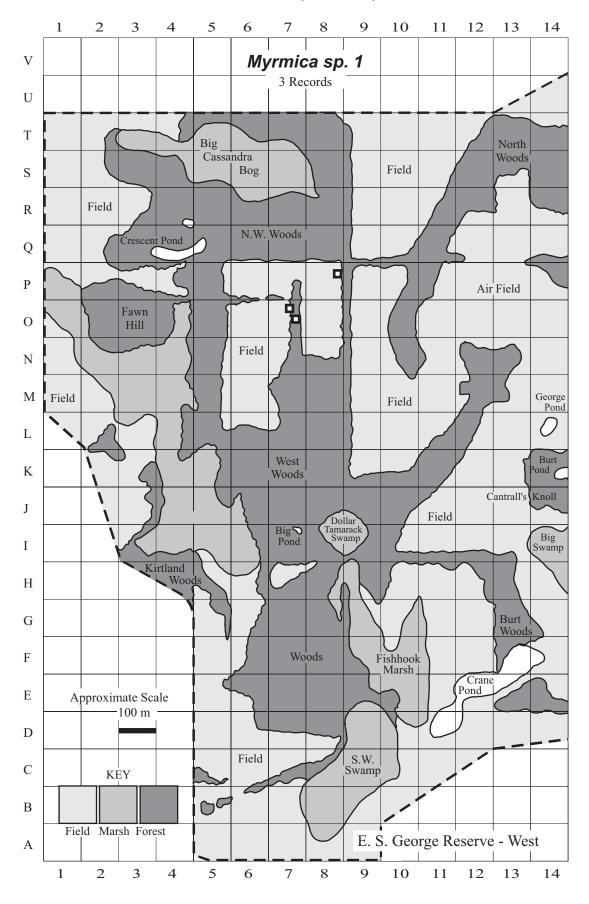


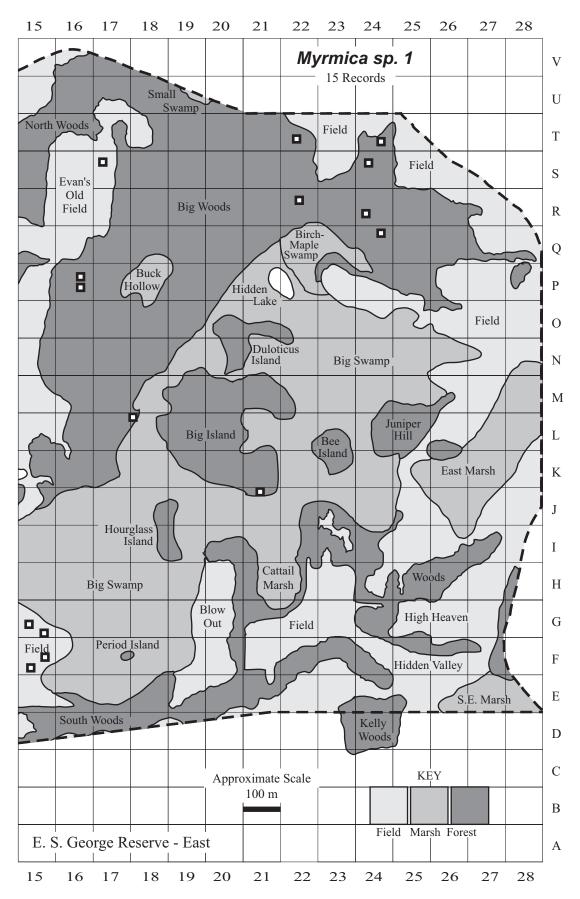


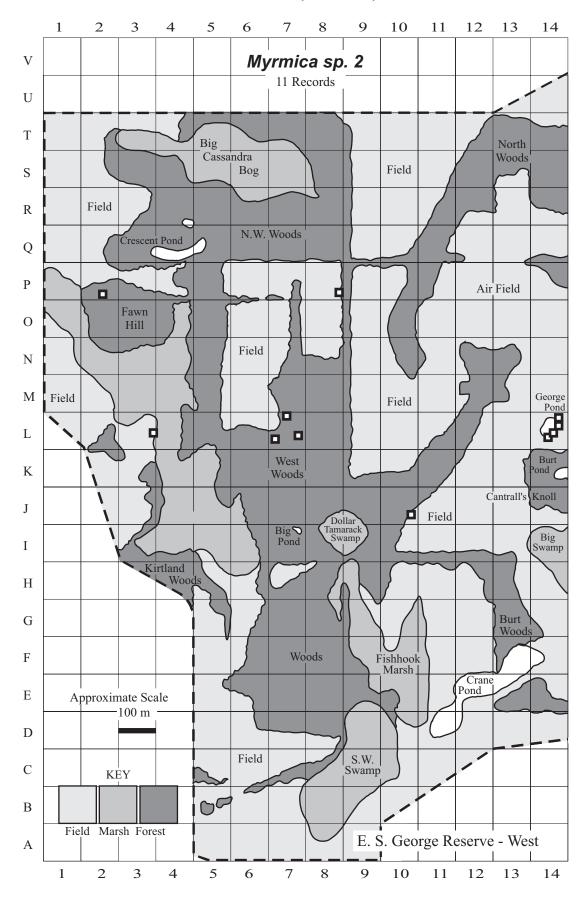


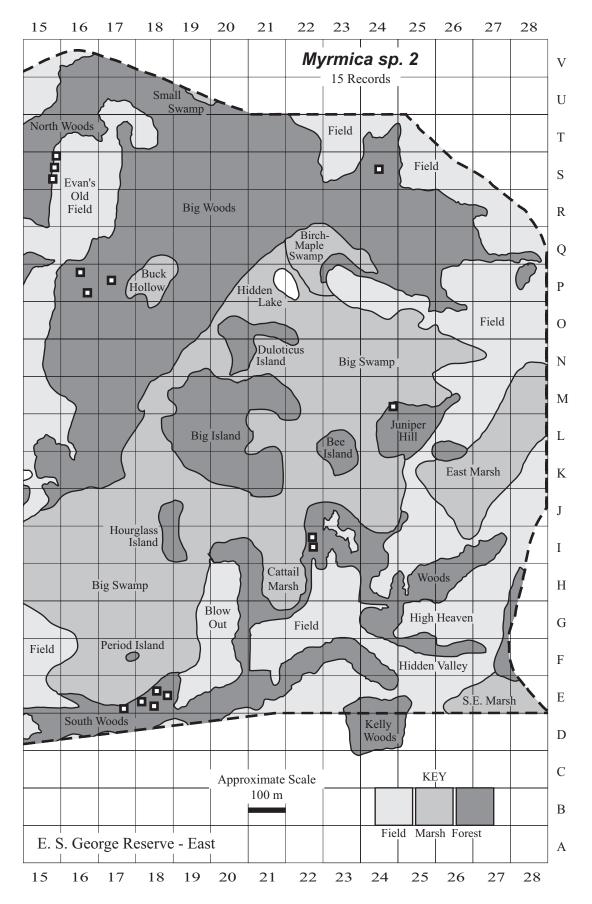


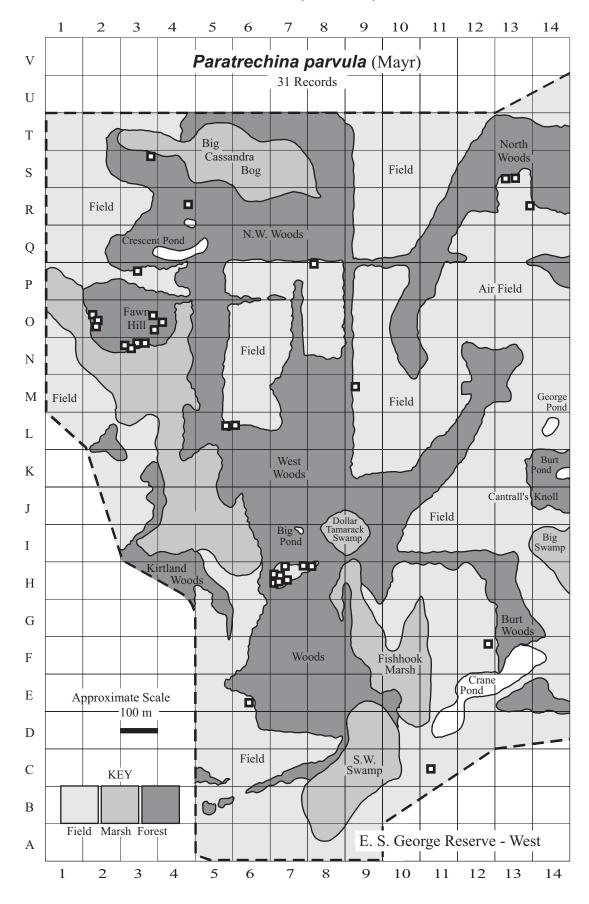




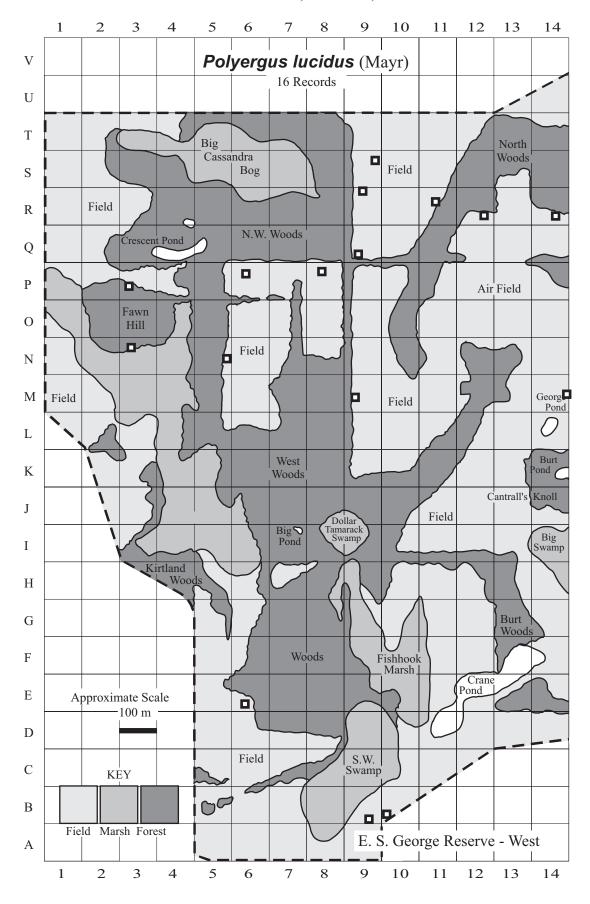




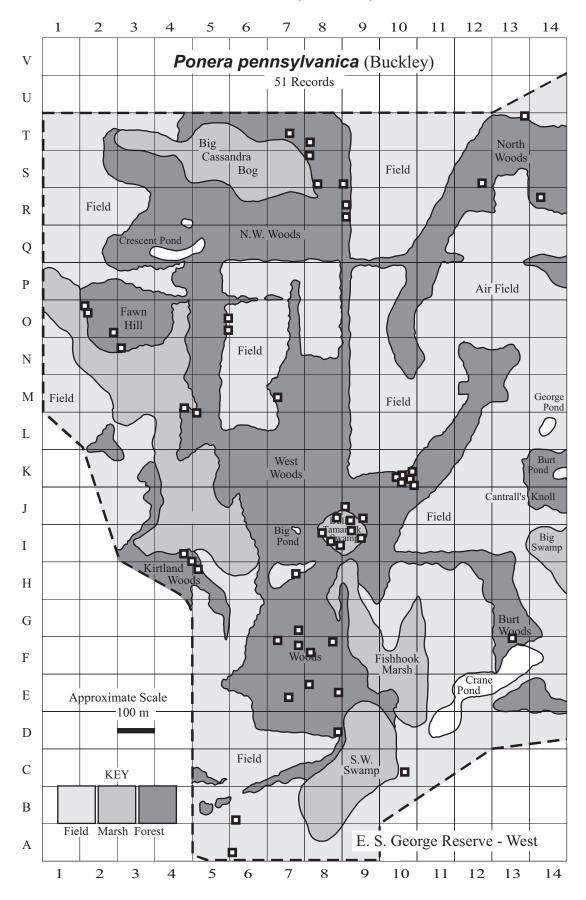


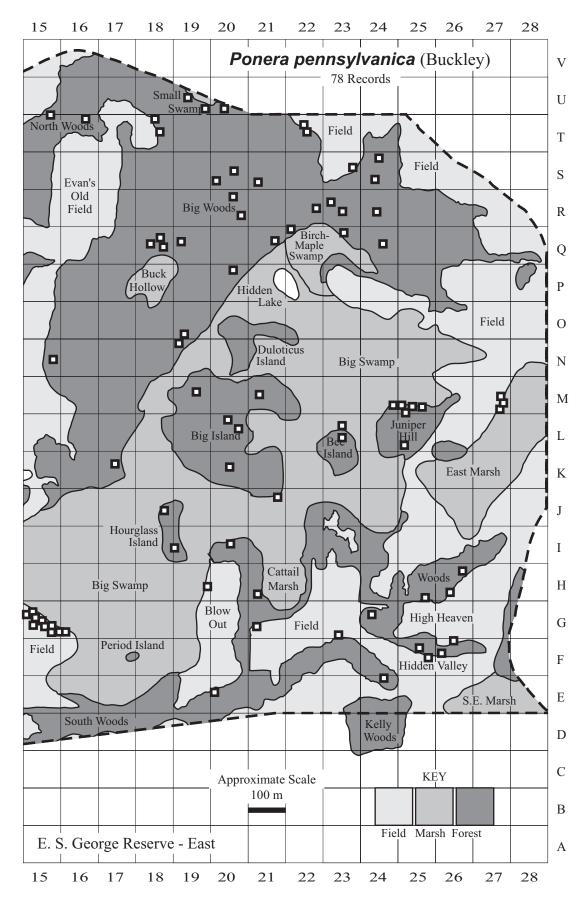


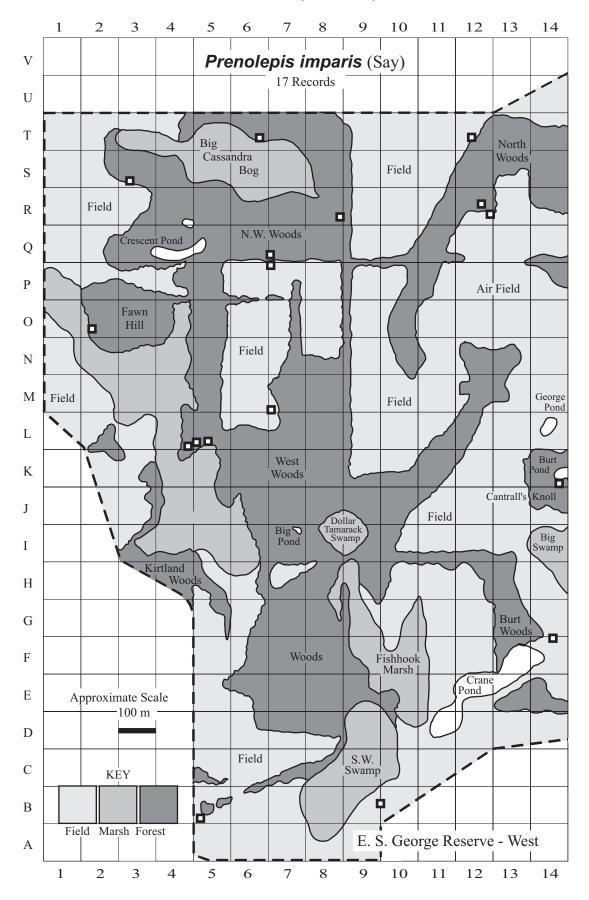


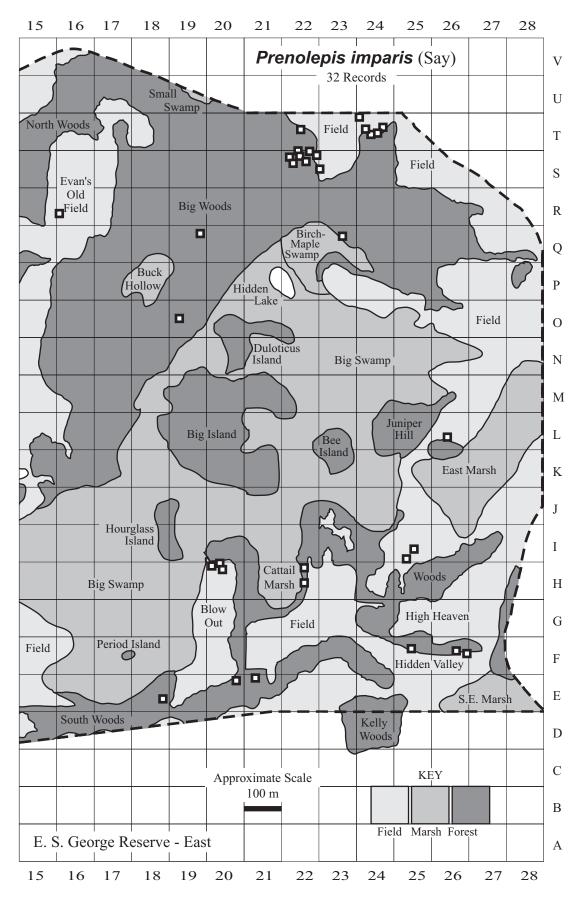


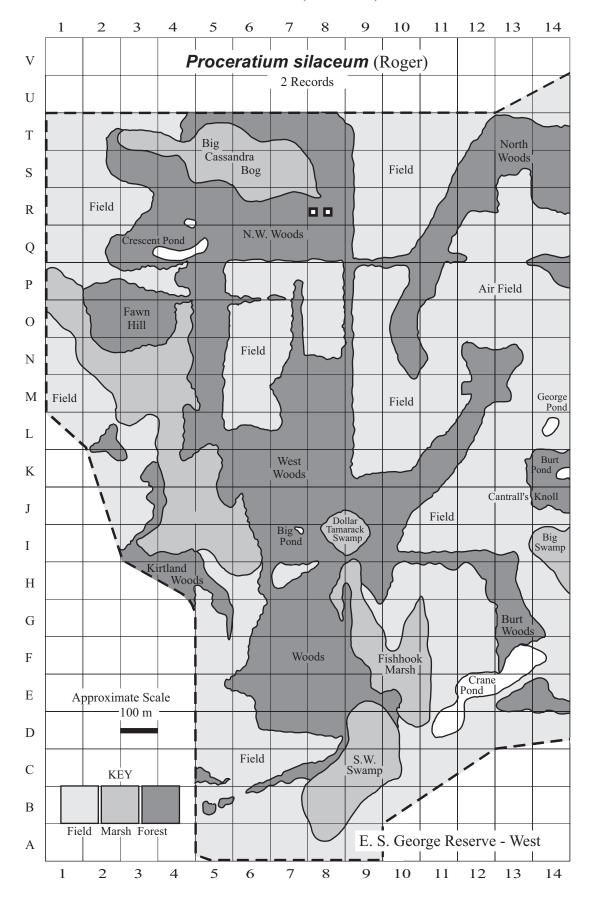


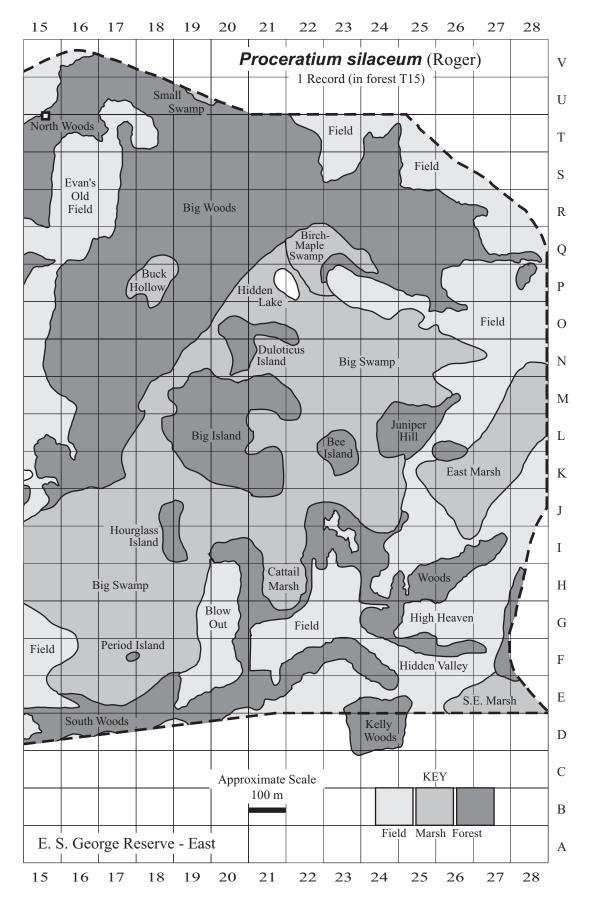


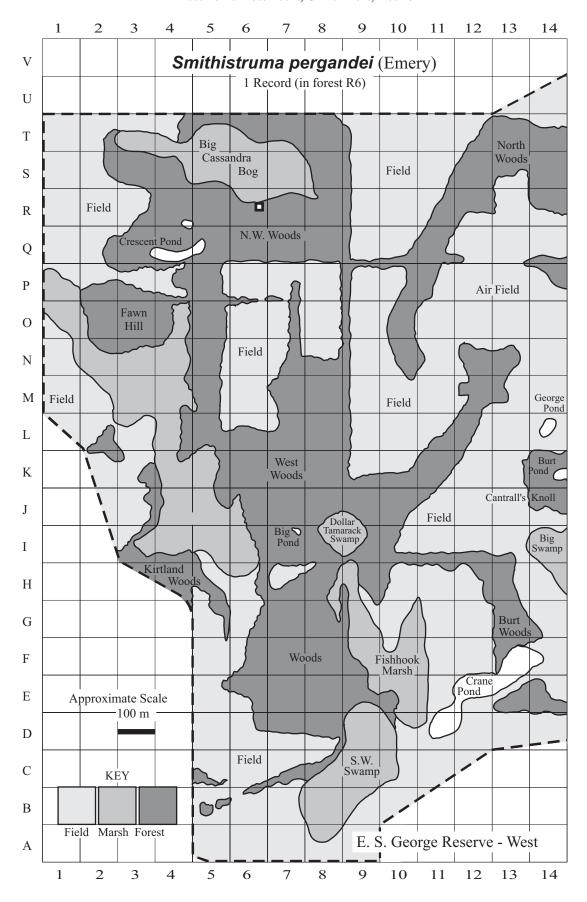


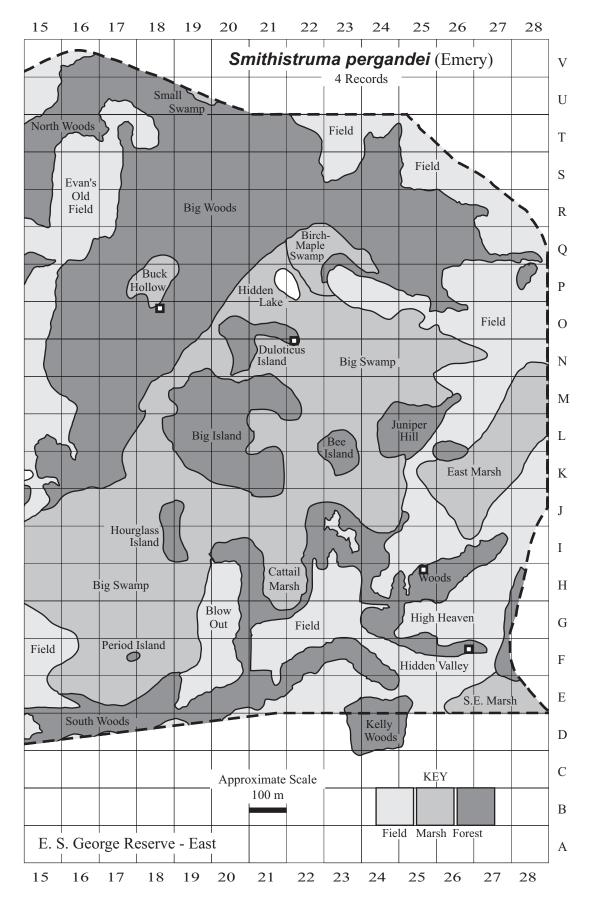




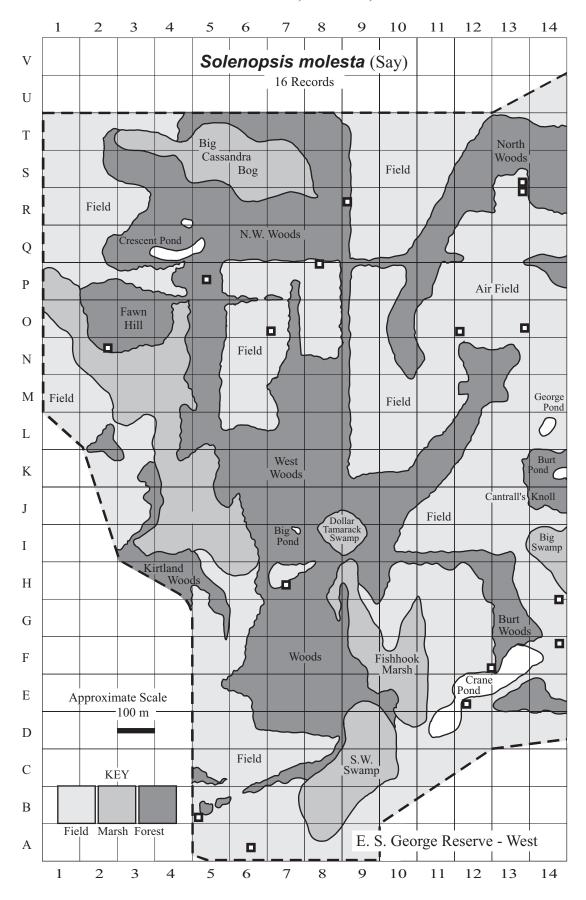


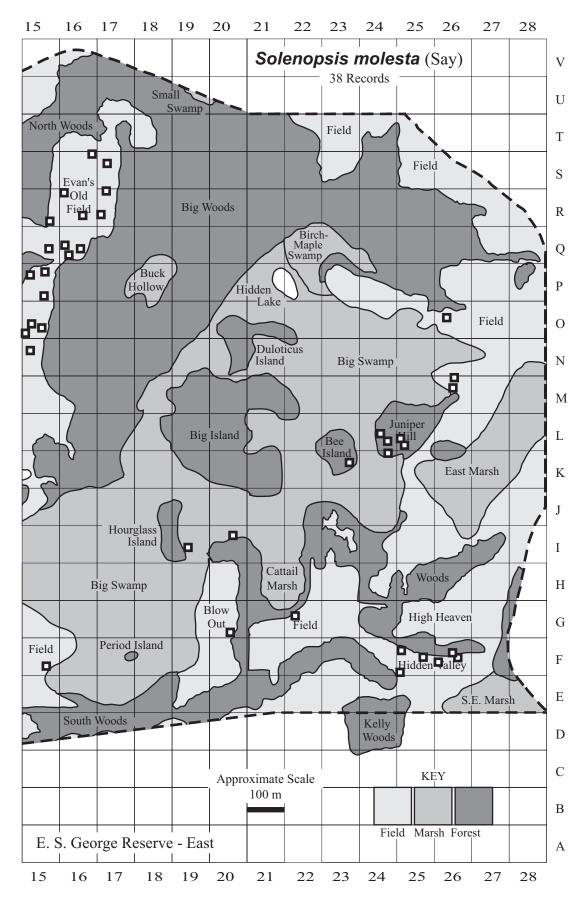


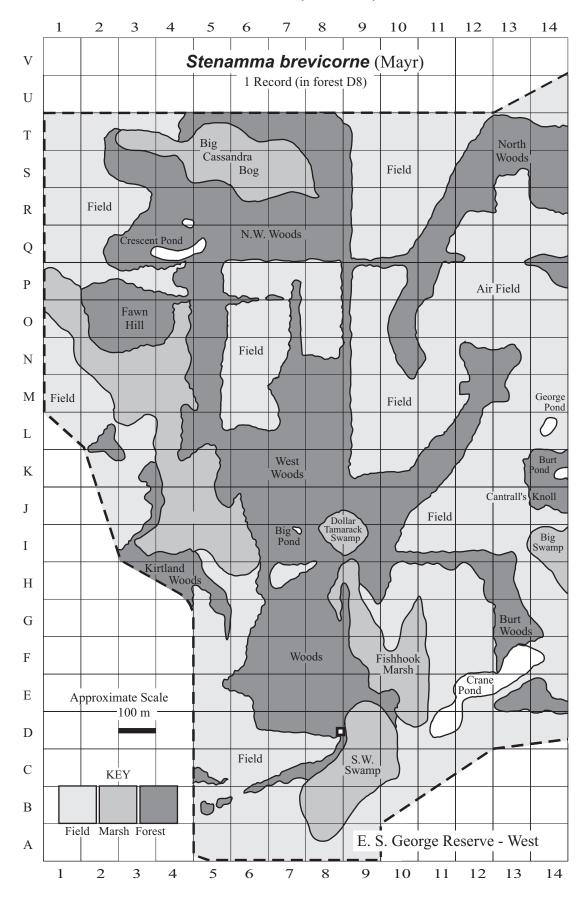




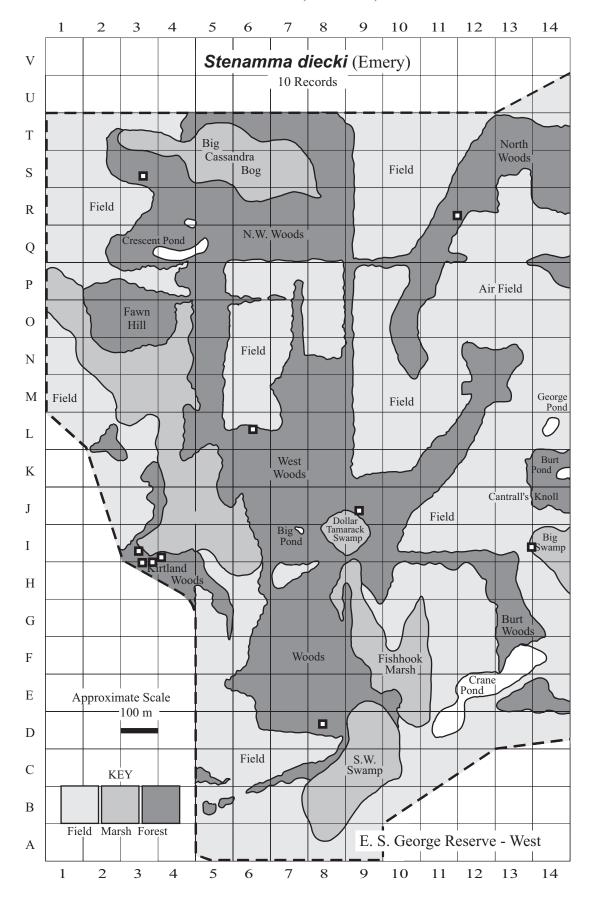


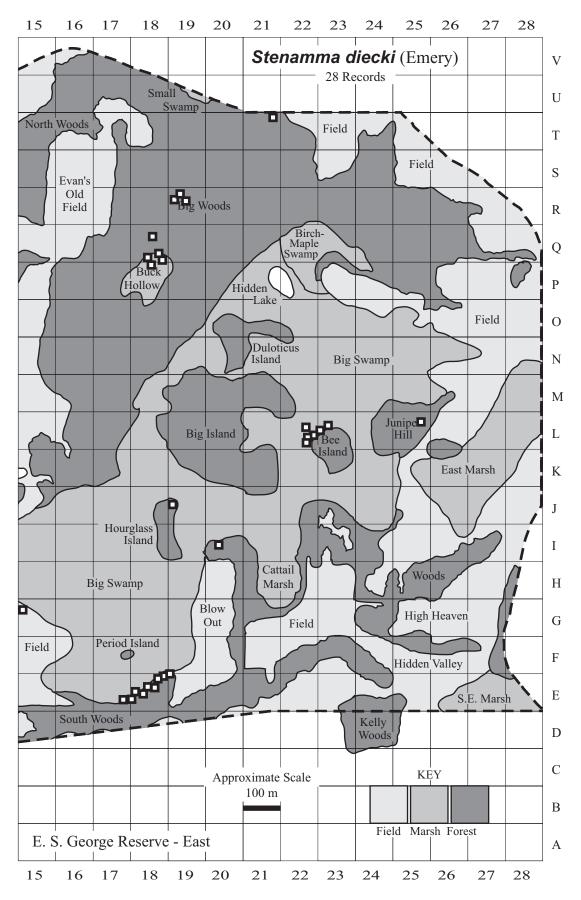


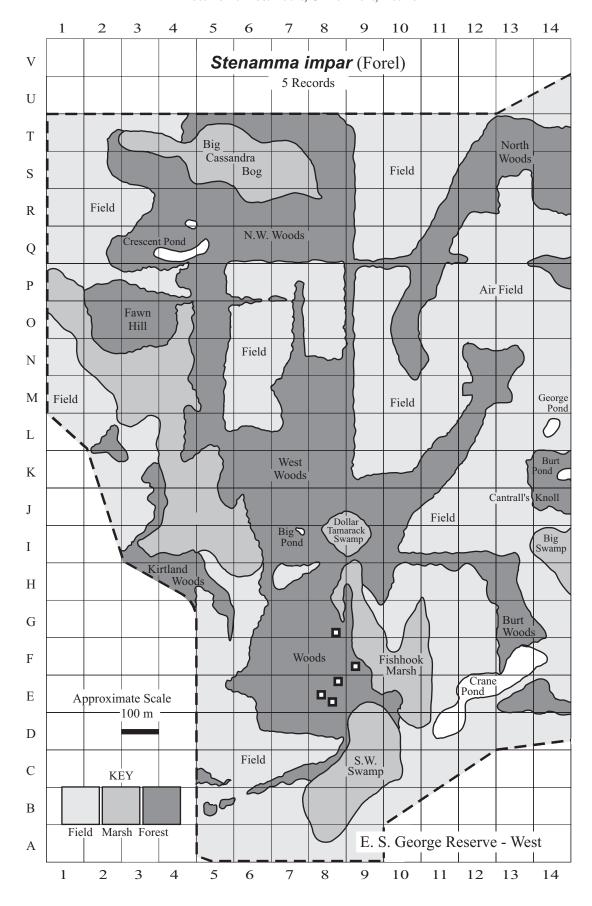


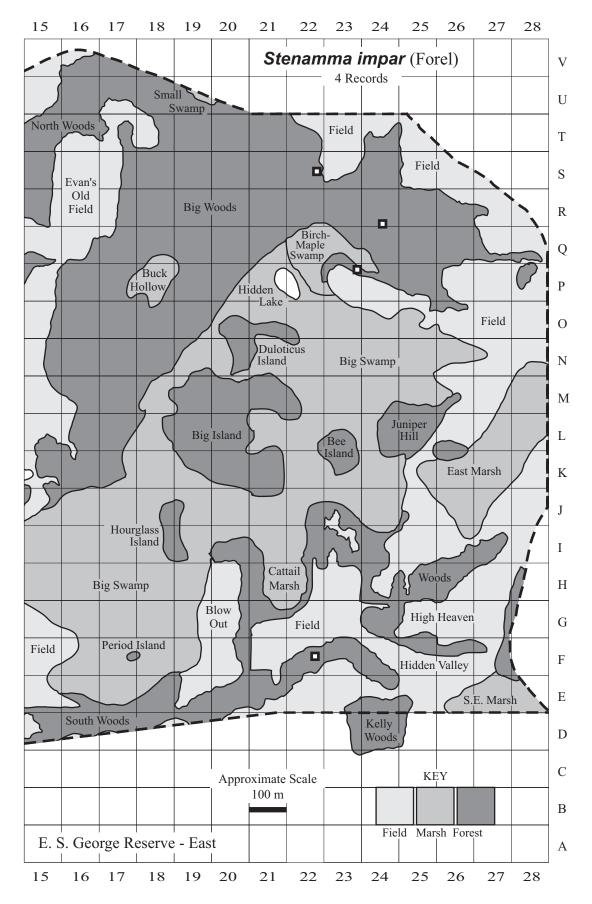


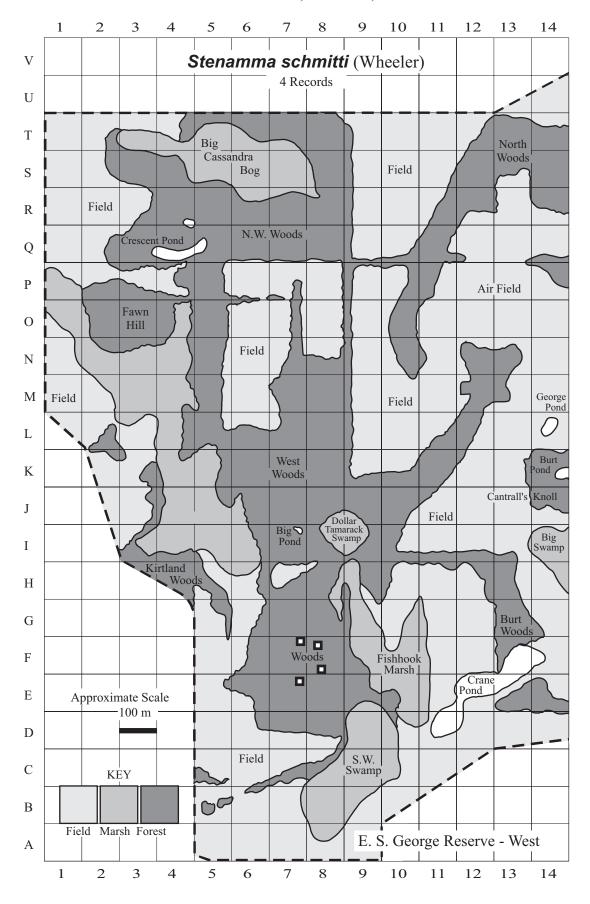


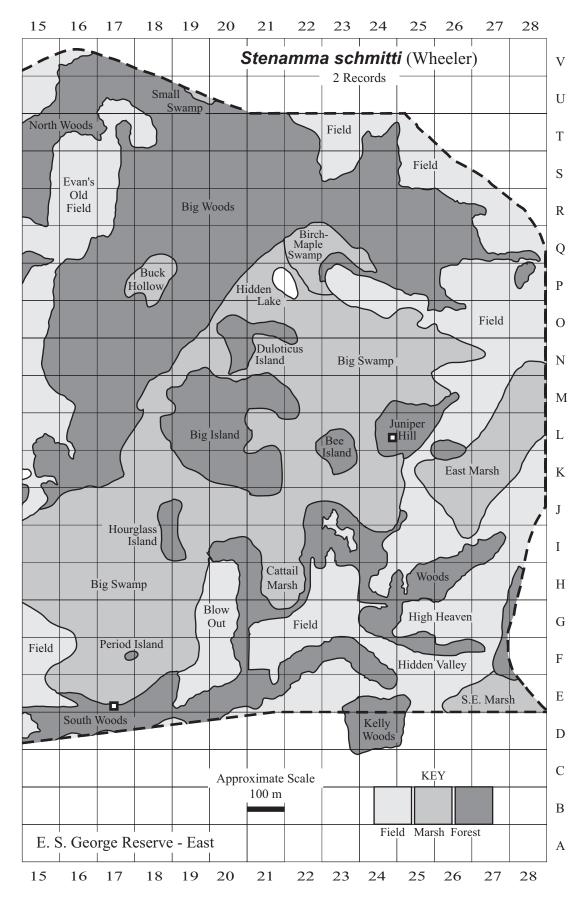


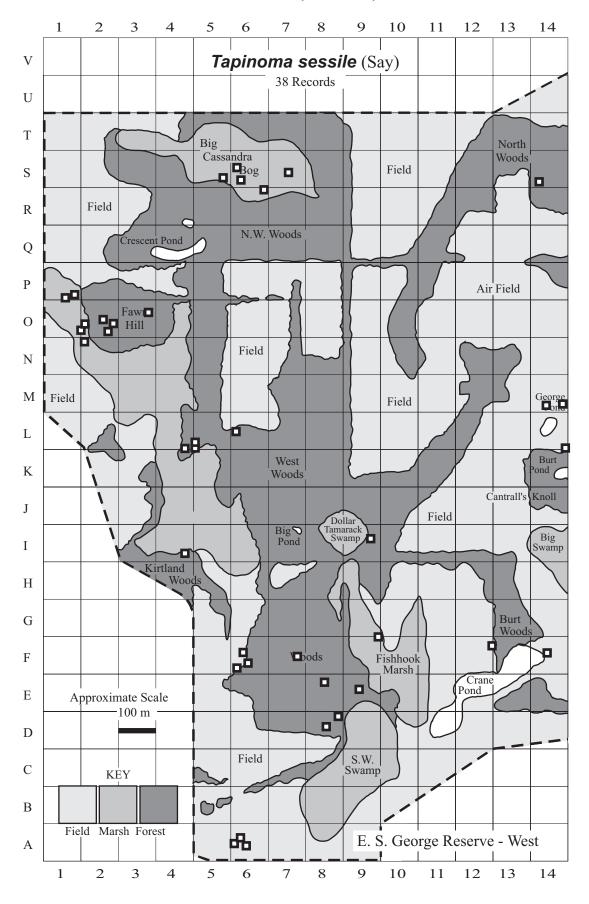


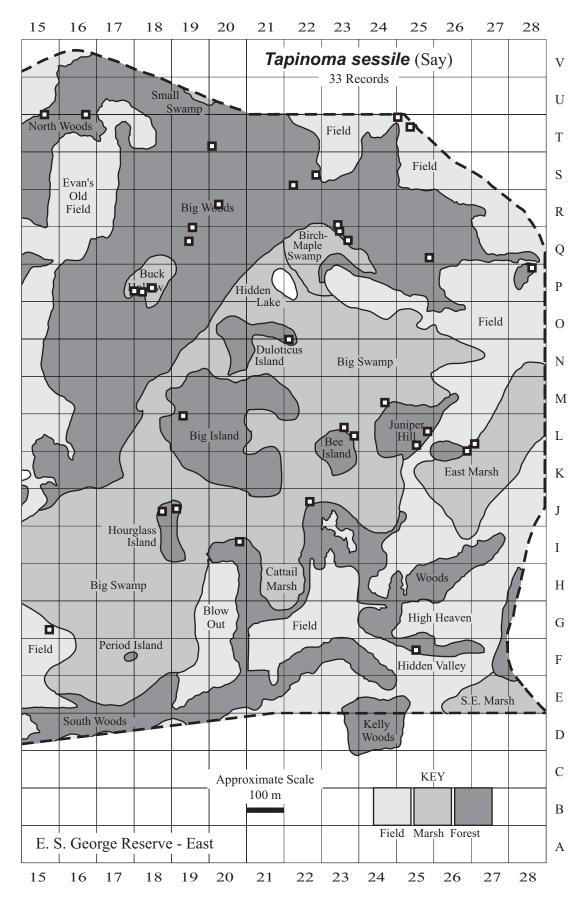












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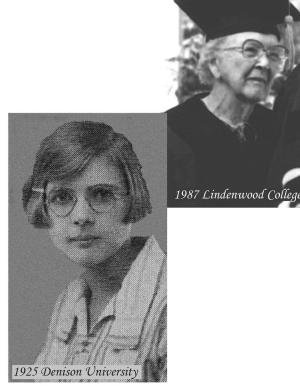
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APPENDIX 1.

A Myrmecologist's Life: An Appreciation of Mary Talbot (with photos)

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The study of ants has interested a number of individuals over the years, especially in the 20th Century in North America. Few have persevered for most of their lifetimes as did Mary Talbot. She devoted more than half a century to the careful analysis of the ecology and behavior of ants, almost all of it at one 1146 acre research center, the Edwin S. George Reserve of the University of Michigan. Braving all kinds of weather, inhospitable habitats such as brambles, barren dunes, and floating bog mats, and attacks by mosquitoes, black flies, horseflies, and other pests, she systematically catalogued the species on the Reserve, documented each species ecological distribution, and recorded behavior patterns for most of the species. The ant fauna of no other biological preserve is as well known as that of the George Reserve, and Mary Talbot is almost solely responsible for it.

Her interest in insects began when she was a young girl who followed her brother, Adolph, around the neighborhood in Tiffin, Ohio while he was collecting insects. Adolph's entomological interests lasted only several years, but he opened a view of the world that was to remain with Mary throughout her life. Her curiosity knew no bounds.

Mary Talbot was born in Columbus, Ohio on 30 November 1903 to Paulina Schmitz and Frank Thresher Talbot. At the time her father was a draftsman for a mining machinery company in Columbus. Later he and his family relocated to Tiffin, Ohio where he was a draftsman for a manufacturing plant. Tiffin was Mary's hometown and it was there that she attended secondary schools. She was graduated from Tiffin High School in June of 1921.

That fall she enrolled in Denison University in Granville, Ohio. Attendance at Denison University was a family tradition. Her grandfather, Samson Talbot, graduated with honors from Denison in 1852. A Baptist minister, he became President of the university in 1863 and served until his death on 10 June 1873. Samson Talbot was a widely respected minister and academician; he was awarded an honorary Doctor of Divinity degree from Colgate University in 1864.

Mary's father and mother also attended Denison; her father was in the class of 1888, and her mother in the class of 1896. She was preceded there by her brother, Adolph, who was in the class of 1922, and followed by her brother John, who graduated in 1932.

While at Denison, Mary was active in the Shepardson Club, a female social club, and the Women's Athletic Association. She played baseball in her sophomore, junior and senior years. She was also active in the Big Sister program at Denison in her senior year. Mary graduated from Denison in June of 1925 with a Bachelor of Science degree, majoring in zoology and minoring in botany.

In September of 1925 Mary entered a master's degree program in entomology at Ohio State University in Columbus. There she studied under Clarence Hamilton Kennedy, a distinguished American entomologist and editor. Kennedy was a specialist in the insects of the Order Odonata, dragonflies and

damselflies. At that time he was developing an interest in the ecology of ants. However, when Mary joined his laboratory, he assigned her to study a rove beetle, *Creophilus villous*. She completed her Master of Science degree in June of 1927 with a thesis entitled: "The Structure of the Digestive System in *Creophilus villosis*." Her thesis was published in the *Ohio Journal of Science* in 1928.

Following graduation Mary started her teaching career. She served as Instructor in Biology at the University of Omaha in 1927-28 and in the same position at Stephens College in Columbia, Missouri in 1928-30. At this time, the beginning of The Depression in the United States, she decided that she needed a doctoral degree to succeed in higher education. She applied to the University of Chicago and was accepted as a student by Alfred E. Emerson, a highly respected ecologist and entomologist. Emerson's specialty was the biology of termites. Mary had become interested in ants through her association with Kennedy, and wanted to do her dissertation on ants. Emerson agreed and she began the study of the ants in the region around Chicago. Her dissertation, entitled "Distribution of ant species in the Chicago region with reference to ecological factors and physiological toleration," was completed in 1933 and published in the journal, Ecology, in 1934.

Mary accepted a temporary position as Instructor of Biology at Mundelein College in Illinois for the first semester of 1935-36. In the spring of 1936 she was appointed to a temporary position as Instructor of Botany at Lindenwood College, a college for females in St. Charles, Missouri. In the fall of 1936 her position was made permanent. She rose in rank to Professor and for a number of years served as chairperson of the Biology Department. She remained at Lindenwood College until May of 1968 when she retired as Professor Emeritus of Biology. (One year later Lindenwood became coeducational. In 1998 the name was changed to Lindenwood University.)

In the summer of 1928 Mary became a research assistant to C. H. Kennedy at the University of Michigan Biological Station at Douglas Lake, Michigan. She also enrolled in Kennedy's entomology course. In the late 1930s she assisted Kennedy in his studies of ants at the Put-In-Bay Biological Laboratory of Ohio State University. While working as his assistant, it was her job to dig the ant nests that Kennedy wanted studied. His admonition to her was always: "Get the queen." Two articles in professional journals, jointly authored with Kennedy, resulted from this research. From the early 1940s until 1951 Kennedy continued his research on ants at the University of Michigan Biological Station. Again, he called on Mary Talbot to be his assistant. Kennedy was an autocratic researcher and he didn't tolerate independence. Mary wanted to carry out some studies that she devised. Kennedy would not agree and he forbade her from doing any work at the Biological Station except on a hillside where Mary had worked before. She continued her studies there on her own, avoiding areas that Kennedy had put off-limits to her.

At the request of Francis C. Evans of the University of

Michigan, she came to the Edwin S. George Reserve of the University of Michigan in the summer of 1952. Evans had undertaken a large-scale ecological study of an old field, now known as "Evans Field" in the late 1940s and wanted someone to study the populations of ants. Mary Talbot was ideally suited for this study, and it developed into a long-term relationship between Mary and the Reserve. After completing the work on Evans project, she returned to the Reserve each summer, with one or two exceptions, for another 26 years.

She received modest support for her work at the George Reserve. Mostly, she used her meager earnings from Lindenwood to support her summer of research. In 1961 she applied to the National Science Foundation for a research grant for a project at the George Reserve on "Flight activities and production of winged individuals in certain Hymenoptera." It was a project on the nuptial flights of ants, but the political climate of the time dictated that "certain Hymenoptera" must be substituted for "of ants." She received a grant of \$6,200. It gave her national recognition for her pioneering work, recognition that forced her administrators at Lindenwood to acknowledge the high achievement of their faculty member.

As if she did not get enough research in the summers at the George Reserve, she spent several winters digging populations of ants in a St. Charles woodland. Her studies of the colony populations of ants are the most complete and exacting of any published. She worked in all kinds of weather and in diverse habitats, including swamps, marshes, floating bogs, barren dunes, even blackberry brambles.

Always desiring to advance her knowledge of biological science so that she could be a better teacher, Mary attended two summer institutes for college teachers that were sponsored by the National Science Foundation. The first was on zoology at Williams College in 1958; the second was a session on plant and animal ecology at the University of Wyoming in the summer of 1959.

What characterized her studies and made her accomplishments so unique was her determination to find and identify each species that occurred on the George Reserve. She did this by studying all habitats yearly, by patiently observing individual behavior, by being observant of everything new and unusual, and by having incredible patience in her observations.

What makes her studies at the George Reserve so unique is the long duration (26 years), the complexity of the habitats, and the diversity of the species. Her ecological and behavioral studies enabled her to discriminate different entities, even though they were classified as the same species. Her studies alone discriminated five taxa of ants that are now recognized as separate species: *Monomorium talbotae, Dorymyrmex grandulus, Formica gynocrates, Formica talbotae,* and *Formica vinculans.* In 1993 Wheeler et al. recognized 113 species of ants as being collected within the state of Michigan. Of those 113 species, 88 were collected by Mary Talbot within the 1146 acres of the George Reserve. Fifteen of those species have been collected in Michigan only at the George Reserve.

Between 1928 and 1985 Mart Talbot published 32 publications in professional journals.

Her honors were few but significant. Two species of ants were named after her: *Formica talbotae* by E. O. Wilson in 1976, and *Monomorium talbotae* by Mark Dubois in 1980. In addition, she was awarded a Doctor of Science degree, Honors Causa, from Lindenwood College at the commencement on 16 May 1987, and the Entomology Department at the Museum of Comparative Zoology at Harvard University recognized her by hanging her portrait in the Museum.

Her ant collections are now at Harvard University and the University of Missouri, St. Louis. A synoptic set of her collections from the George Reserve are in the Division of Insects of the Museum of Zoology at the University of Michigan.

Mary was a reader who always had a book at hand, usually a mystery. She also was a lover of cats, which would be her companions at her home in St. Charles most of her years there.

In early April of 1990 she moved from her home in St. Charles to the Presbyterian Manor in nearby Farmington, Missouri. There she suffered a heart attack; she was taken to the Farmington Regional Medical Center where she died at 9:37 am on 16 April. She was buried on 18 April at Hillview Memorial Gardens in Farmington; there was no visitation. She was preceded in death by her brothers, Adolph and John.

Mary loved to talk ants, even making fun of one of her own studies. In 1948 she had published the results of research at the Michigan Biological Station in the journal *Ecology*. The publication was entitled "A comparison of two ants of the genus *Formica*." In 1950 William Steel Creighton synonymized those two species into one species. From that point on Mary poked fun at herself by referring to her study as "Comparison of two ants of the same species."

Virginia Terry, archivist at Lindenwood University, learned directly of Mary Talbot's influence in the scientific world. She described the experience as follows: "I was a member of an Elderhostel in Alaska in 1995. Some of the group were obviously friends of long standing, because at dinner one evening someone shouted across the room something about the "bug" man. The object of this name-calling responded that he was not a "bug" man, but an "ant" man. Remembering that Mary Talbot had done much research on ants and encountering him after dinner, I asked that, being an "ant" man, did he know of Mary Talbot. His eyebrows went up, and he said spiritedly, "Know Mary Talbot? Of course I know Mary Talbot - everyone in this field knows Mary Talbot." "Well," he added, "I never did really meet her, and that is one of my real regrets. But I have read everything that she wrote. Did you know that she has an ant named after her." I said "Yes." "Did you know that her works are housed at Harvard?" I said "Yes." Then he said with some puzzlement, "Tell me how you know Mary Talbot?" I explained that I was from St. Charles, Missouri, where Lindenwood College is located, and that is where Mary taught for over 30 years and retired from there.

He said, "I can't believe that I am actually talking to someone here in Alaska who personally knew Mary Talbot." (The "ant" man was Murray S. Blum, Professor of Entomology at the University of Georgia.)

She was a quiet, unassuming, humble, and well-mannered lady. Although she had occasion to remember a hurt afflicted by a colleague, I never heard her speak ill of another person. There are many women scientists whose work I have appreciated, but none that I admired and respected more than Mary Talbot.

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APPENDIX 2.

Recovery of the Mary Talbot ant collection

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Sometime around 1987 or 1988 I received a phone call from D. William Tietjen, who was an arachnologist on the faculty of Lindenwood College at that time. He said that a student had brought him some boxes of dried-out shell vials of ants that the student had retrieved from a garbage dumpster outside the Biology Building. The student said that he (she?) wasn't sure but didn't think that the material was something that should have been thrown away. This was about the time that I had been principal investigator on a grant from the Academy of Science of St. Louis to inventory all of the natural history collections in the state. Tietjen therefore called me, recounted the story of the material being found in the trash, and said that he feared for the continued survival of the material at Lindenwood. He asked if I wanted to come and get it, and I said yes. I went over a day or two later and met with Tietjen and with Dr. Darl Anderson, who was Chairman of the Biology Department at Lindenwood. Anderson said that she shared Tietjen's concern about the material if it stayed at Lindenwood and agreed that it would be good if I took it. We were all aware of the significance of the collection. I asked about Mary's interest in the material, and Anderson replied that when Mary retired she had told her that she was through with the collection and that the Biology Department could do with it what they wanted. I was aware at the time (and still am aware) that this was a tenuously slim basis on which to take possession of the collection, but my focus was (and still is) on ensuring that the collection was not lost.

The material consisted of a dozen or more boxes of small shell vials, some wooden trays of shell vials, 3 or 4 Schmitt-type boxes sparsely filled with pinned ants, and a box of files of correspondence and manuscripts. I think that I also brought back a small amount of paraphernalia such as a pinning block, crow quill pen, etc., but most of this material has been scattered in my lab. Here at home I have a glass paperweight that was with the material.

The collection was in extremely bad shape. Eighty percent or more of the shell vials had cork stoppers and had dried out. James Trager had recently arrived in St. Louis and was looking for paid employment, so I took advantage of the coincidence of events and wrote a proposal to the Academy of Science of St. Louis to employ James to curate the collection. The grant was for a bit less than \$14,000, and with that James rehabilitated almost all of the material. I finished the work. Each dried vial was emptied into a tea strainer, rinsed to clean it of the dust, returned to the rinsed vial, filled with alcohol, stoppered with

cotton, and inverted in an alcohol-filled jar together with other vials of the same or related taxa. Today the entire collection of vials is in alcohol and kept in a locked cabinet at U.M.-St. Louis. The pinned material, which includes a number of paratypes, is integrated with our pinned collection (which, for ants, consists almost entirely of vouchers from my graduate work). The box of files is in the locked cabinet with the vials. I believe that the collection is intact as we received it, although there is a possibility that James may have specimens of taxa that were of interest to him. After he completed curation of the collection, there has been no further activity with the material, including no loans. I check it from time to time to make sure the alcohol is topped up; that's all.

The vast majority of the material in alcohol is from three localities: the E. S. George Reserve and vicinity in Michigan, Tiffin Ohio, and St. Charles Missouri. At one time I talked with Roy Snelling about possibly dividing the collection between the Los Angeles County Museum, Harvard and Michigan. The museum at Michigan has told me that they would like to have the material from the E. S. George Reserve. This past week I told Gary Alpert (at Harvard) that I have the collection and would like to talk with him about its disposition. I know that the material would be much better housed somewhere other than its present location. I'm amenable (always have been) to working toward a plan to place the material properly.

My guess, by the way, on who threw out the boxes of vials that began this story is that it was Mary.

pyramicus, 13

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