

POPULATIONS OF ANTS IN A LOW FIELD

By Mary TALBOT

(Lindenwood College, St. Charles, Missouri, U. S. A.)

This study concerns the number of species and abundance of ants nesting in a low wet field, as discovered by the technique of digging yard-square plots of soil (1). It extends two similar studies of populations of ants in woodlands (HEADLEY, 1952; TALBOT, 1957). The Edwin S. George Reserve, where the work was conducted, consists of two square miles of varied contour. Because the soil is largely sandy, drainage tends to be excessive, and consequently the upland fields are dry. The ants of one such upland field (TALBOT, 1953) will be compared with the low field populations of the present study.

The low field lies surrounded to the north, east and south by marsh, and rises to a high field on the west. The small strip selected for study (G 15 on the Reserve map) extends along the north side of the field and is only slightly higher than the marsh beyond it. Along most of the marsh-field border there are clusters of large shrubs (*Cornus obliqua* Raf., *Salix bebbiana* Sarg., and *S. gracilis* Anderss.), but in two low places the field grasses simply merge with and give way to marsh sedge (*Carex rostrata* Stokes). Two large swamp-white oaks (*Quercus bicolor* Willd.) and an elm (*Ulmus americana* L.) serve as landmarks at the marsh edge, and furnish the only shade on the otherwise sunny field.

Vegetation is characterized by the exceedingly large number of forbs mixed with the grasses. From spring to fall the field is bright with flowers. Grasses consist mostly of Kentucky bluegrass (*Poa pratensis* L.), white oat-grass (*Danthonia spicata* (L.) Beauv.), timothy (*Phleum pratense* L.) and black bent grass (*Agrostis gigantea* Roth), with the tall marsh-grass (*Spartina pectinata* Link) making a dense border between field grasses and marsh sedges, wherever shrubs are not present. Of the forbs, goldenrods (mostly *Solidago altissima* L. and *S. juncea* Ait.) are numerous and occupy much space. Asters (*Aster novæangliæ* L., *A. azureus* Lindl., *A. umbellatus* Mill.), Queen Anne's-

(1) The work was carried-out at the Edwin S. George Reserve in southern (Livingston County) Michigan, where facilities were made available by Dr. Francis C. EVANS, assistant director, and Dr. T. H. HUBBELL, director of the Reserve. It was supported by a National Science Foundation grant.

lace (*Daucus carota* L.), Black-eyed Susan (*Rudbeckia serotina* Nutt.), orange hawkweed (*Hieracium aurantiacum* L.), wild bergamot (*Morinda fistulosa* L.) and ironweed (*Vernonia altissima* Nutt.) are widespread. The low spots are marked by Golden Alexanders (*Zizia aurea* (L.) W. D. J. Koch), wild strawberry (*Fragaria virginiana* Duchesne), and mint (*Pycnanthemum virginianum* (L.) Durand and Jackson), with a great variety of smaller and less conspicuous plants growing among the grasses.

In addition to the tall shrubs bordering the marsh, the field is dotted with lesser woody plants. Shrubby cinquefoil (*Potentilla fruticosa* L.) is abundant, and there are scattered clusters of meadow-sweet (*Spiræa alba* Du Roi), trailing blackberry (*Rubus flagellaris* Willd.), common juniper (*Juniperus communis* L.) and small trembling aspen (*Populus tremuloides* Michx.).

To form the study area, the fields north edge was divided into 9 strips, each 20 feet wide, extending north from a base line to the marsh edge. Since the marsh border was irregular, the strips varied in length from 33 to 53 feet, with an average length of 42 feet. The entire area consisted of 870 square yards. In each strip, 4 yard-square plots were dug, and on the 4 longest strips, a fifth was included, making 40 in all. These were spaced at approximately equal distances from base line to marsh edge. Consequently, in each strip, plot number one was highest and driest, and plot number four or five was nearest the marsh. The plots were dug during June through September, 1963.

Usually soil was removed to a depth of 6 to 9 inches, revealing the complete structure of nests which were near the surface and the upper chambers of those which extended deeper into the soil. Occasionally parts of plots were dug to 12 or 14 inches.

Twenty species of ants were found nesting in the 40 plots (Table I). An additional 8 species were present on the strips, but were not in the dug plots (some, like mounds of *Lasius minutus*, were avoided). Twenty-eight was a great number of species for one restricted habitat on the Reserve, which had a total of 68 species. Moreover, there was a dense population of colonies in the field. They ranged from 2 to 28 per plot with a mean of 10.6 colonies per plot. (The number of species per plot ranged from 2 to 9, with a mean of 4.9.)

In general, a field is considered a rather severe habitat, because of its lack of shade and consequent great fluctuations in temperature, high evaporation which may cause intense dryness, and the restricted number of nesting sites. Probably the two most influential factors in accounting for the abundance of ants on this field and in selecting the type of ants found there were the type of soil, and the nearness to the marsh. The soil was not typical of the Reserve as a whole, in that it was solid clay under a layer of clay-loam which formed the upper 4 or 5 inches. The clay held and conserved water, and it allowed the formation of firm-walled, permanent nest chambers. Probably clay accounted for the abundance of *Brachymyrmex depilis*.

Because the field was only a few inches above the marsh, the ground-water level tended to be high. Even in the driest part of the extremely dry summer of 1963, moisture could be found at 14 inches, and often it was much higher. Early spring rains brought the water level almost

TABLE I. — COLONIES OF ANTS IN A LOW FIELD AT THE E. S. GEORGE RESERVE IN SOUTHERN MICHIGAN (Summer 1963)

COLONIES NESTING IN DUG PLOTS	COLONIES IN 40 YD. SQ. PLOTS	PLOTS CONTAINING COLONIES	SQUARE YARDS PER COLONY	NESTING IN SOIL	NESTING AMONG LEAVES	NESTING IN STEMS, NUTS, GALLS OR LOG	FORAGING ABOVEGROUND	FORAGING UNDERGROUND
1. <i>Brachymyrmex depilis</i> Emery	141	36	.28	+				+
2. <i>Ponera coarctata pennsylvanica</i> Buckley	117	35	.34	+		+	+	+
3. <i>Myrmica emeryana</i> Forel (?)	40	24	1.0	+	+		+	
4. <i>Lasius flavus</i> (Fabricius)	23	16	1.7	+				+
5. <i>Stenamma brevicorne</i> (Mayr)	23	18	1.7	+			+	+
6. <i>Leptothorax ambiguus</i> Emery	21	12	1.9	+	+	+	+	
7. <i>Dolichoderus pustulatus</i> Mayr	14	10	2.9	+	+		+	
8. <i>Lasius neoniger</i> Emery	9	8	4.4	+			+	+
9. <i>Formica fusca</i> Linnæus	9	7	4.4	+	+	+	+	
10. <i>Crematogaster lineolata</i> (Say)	7	7	5.7	+	+	+	+	
11. <i>Tapinoma sessile</i> (Say)	6	5	6.7	+	+	+	+	
12. <i>Dolichoderus plagiatus</i> (Mayr)	5	2	8.0	+	+	+	+	
13. <i>Aphænogaster rudis</i> Emery	4	4	10.0	+			+	
14. <i>Prenolepis imparis</i> (Say)	4	4	10.0	+			+	
15. <i>Lasius sitkænsis</i> Pergande	3	3	13.3	+			+	+
16. <i>Formica pallidefulva nitidiventris</i> Emery	2	2	20.0	+			+	
17. <i>Myrmica lobicornis fracticornis</i> Emery	2	1	20.0	+	+		+	
18. <i>Polyergus lucidus</i> Mayr	1	1	40.0	+			+	
19. <i>Camponotus americanus</i> Mayr	1	1	40.0	+			+	
20. <i>Amblyopone pallipes</i> (Haldeman)	1	1	40.0	+			+	+
COLONIES PRESENT BUT NOT ON DUG PLOTS								
21. <i>Dolichoderus mariæ</i> Forel				+			+	
22. <i>Lasius minutus</i> Emery				+				+
23. <i>Lasius speculiventris</i> Emery				+				+
24. <i>Crematogaster cerasi</i> (Fitch)				+	+		+	
25. <i>Camponotus noveboracensis</i> (Fitch)				+		+	+	
26. <i>Formica lasioides</i> Emery				+			+	
27. <i>Lasius umbratus</i> (Nylander)				+		+		+
28. <i>Camponotus nearcticus</i> Emery				+		+	+	

to the surface, and occasionally water stood on the lower parts. This tendency to flooding and constancy of underground water seemed most influential in determining the types of ants nesting there. Those present tended to have ways of getting away from high water. *Formica fusca*, *Lasius minutus*, and *Lasius speculiventris* built mounds. *Dolichoderus mariæ* had small domes of woven grass. Some, such as *Myrmica eme-*

ryana, *Dolichoderus pustulatus* and *Leptothorax ambiguus* could move up among grasses or into hollow stems. Others, like *Lasius sitkænsis*, seemed to transport their brood underground toward or away from the marsh. Near the marsh any raised place was at a premium. Thus any old *Formica fusca* mound might have colonies of *Crematogaster lineolata*, *Dolichoderus pustulatus*, and *Leptothorax ambiguus* in it. Any bit of clay brought to the surface by crayfish could be expected to hold a colony of *Brachymyrmex depilis*.

The nearby marsh also furnished plants that harbored abundant root and stem aphids. *Dolichoderus mariæ*, which sometimes nested rather high in the field, always had trails of workers going to and from the marsh, and forms like *Lasius sitkænsis* and *Lasius umbratus* foraged underground into it.

Because of the constant moisture, forbs were abundant and varied. They offered considerable diversity of food for those using plant parts (aphids) and also for those living on plant-eating insects. In addition, the tall forbs gave some shade, thus prolonging the foraging hours. More important, the mixture of dead grass and forb stems, together with a moderate growth of lichen (mostly *Peltigera polydactyla* and *Cladonia cristatella* var. *vestita*), made a loose litter on the ground surface which was favorable to ants. The litter was not layered and soggy as are accumulations of tree leaves in woods, but it was thick enough to conserve moisture, offer shade and make good construction material for ants such as *Dolichoderus mariæ*, *Dolichoderus pustulatus* and *Myrmica emeryana*, which tended to form aboveground chambers.

In a field the ground is the main nesting-site, and 15 of the species nested in it alone (Table I). Twelve more used both soil and plant parts, and only one species, *Camponotus nearcticus*, was independent of the ground. It was confined to the proximity of the oaks, and nested in their twigs. There were no stones in the field, and the one log was possessed by a colony of *Camponotus noveboracensis*.

Field ants must either forage during the heat of the day, as did *Formica pallidefulva nitidiventris*, or avoid the heat in some way. Forms like *Myrmica emeryana* and *Dolichoderus mariæ* foraged mainly in early morning and late afternoon, while *Lasius neoniger* was especially active during cool moist nights. *Prenolepis imparis* had an almost complete mid-summer lull, at which time it stayed below ground using food stored in the repletes. Another method of avoiding heat is to forage underground, and the low field had 10 species that used this method exclusively or in part (Table I). Four *Lasius* (*L. minutus*, *L. speculiventris*, *L. umbratus*, *L. flavus*) and *Brachymyrmex depilis* almost never appeared aboveground. *Amblyopone* and *Ponera* did occasionally, but mostly stayed below, while *Lasius neoniger*, *Lasius sitkænsis* and *Stenamma brevicorne* seemed to forage both below and above.

Brachymyrmex depilis Emery.

Brachymyrmex depilis was the ant most widely distributed on the study area and the most abundant in colonies and possibly in individuals as well. The low field seemed ideal for *Brachymyrmex* although it was not confined to this habitat and has been found on the Reserve in many places. Although it had previously been collected most frequently in open oak-hickory woods, it was also found from deep woods near the swamp to edges of fields, and it was not strictly confined to clay soil. Nests were often found under stones, but were also present under moss, logs, bits of bark and in the sides of ant mounds. (General collecting tends to favor the discovering of colonies under some kind of cover, and to neglect the finding of nests in soil with no covering.)

The ants were so small and so densely distributed over some plots that it was hard to tell where colonies ended. Groups of ants clustered within a square foot were considered to belong to one colony unless they were clearly isolated. This gave a count of 141 colonies scattered over 36 of the 40 plots. They were most abundant in the middle plots of the strips and less numerous near the marsh where they could survive only if they found projections such as old *Formica fusca* mounds.

The tiny ants constructed numerous chambers which sometimes almost touched each other. Those in the upper crumbly soil were obscure, but in solid clay they were nicely formed, smooth-walled cells which occasionally were as large as $1 \times 3/4 \times 1/2$ inch. Eggs, larvae, and pupae were at times in separate chambers, but often they occurred together. Over half of the chambers were in the first 1/2 to 1 inch of soil; other chambers were common down to 4 inches and were found once in a while to 7 inches. Once, ants were found 8 inches deep, but colonies didn't seem to penetrate to ground water.

Pupae of males and females were found from June 24 to August 19. Adult winged ants were first found July 24, and some were still present on September 16, although most had flown by that time (Table III). Four observed flights took place on August 21, August 22, September 1, and September 16. They occurred in the late afternoon while it was still rather warm, and the sunlight was slanting across the field. The earliest flight began at 4:37 PM, and the latest ended at 5:50 PM. Temperatures ranged from 86° to 77° F., relative humidity from 66 % to 59 %, and light reading from 2,200 to 1,800 foot candles (1). Flight activities were much like those of a *Lasius minutus* on a miniature scale. Workers climbed hurriedly up and down grasses over a little

(1) Temperatures were those 6 to 8 in. above the ground surface. Light readings were obtained by a weston illumination meter which was directed straight overhead. A Bendex psychrometer gave relative humidity 4 in. above the surface, and a hand anemometer measured wind velocity in m. p. h.

patch of about 7 × 9 inches. Males and females climbed to tips of grasses and flew readily. Usually there were only 2 to 10 winged ants in sight at a time, but during good flying they took-off at the rate of about one a minute. The longest flight lasted 25 minutes.

Ponera coarctata pennsylvanica Buckley.

It was not surprising that *Ponera* was widespread on the field, since it can be found in almost every habitat on the Reserve except very dry fields. The large number of colonies (2.9 per plot) did not mean a great total population of individuals, since *Ponera* colonies are very small. However, it indicated that the habitat was a favorable one.

Workers and brood were usually found within the upper loose crumbly inch of soil where chambers are not easily distinguished. In low places, any mounds or lumps of soil were especially favored, and occasionally a colony lived just above the soil line in crevices of woody stems of *Potentilla fruticosa*.

Collections over a number of years indicate that no brood is overwintered and that only one batch of brood is produced. My records show that eggs may be present from June 5 or before to July 2, larvae from June 22 to August 25, worker pupae from July 9 to September 18 or longer, winged pupae from July 16 to September 15 (most gone by August 30), and adult winged ants from August 1 to September 15 or later. After the first of September, males and females were found only in a few colonies living in moist sheltered places, so flights probably occur during late August and early September. Winged ants were seen which had been taken by sweeping on the morning of September 5, 1958, but no flights have been observed at the Reserve. There is some indication that a few alates may overwinter to fly in the spring, since a female flew to the laboratory on June 10, 1954, and one on June 15, 1956. However, no colonies examined in early June have had winged ants in the nest.

Myrmica emeryana Forel (?).

This ant may be *emeryana* if that species is considered to have rather wide variations in structure. It ranked third in abundance of colonies and was widespread over all 9 strips: Workers were conspicuous because they foraged aboveground continually unless midday temperatures were too high.

About one-third of the colonies built superficial chambers of matted grass. Those which did not, had large entrance chambers just beneath the ground surface. Nests were not large; each consisted of a central shaft with 2 to 4 chambers radiating out from it. Eight of the 24 colonies

were incipient ones which would probably not have been found except by the digging technique. Each of these consisted of a nest queen, several small workers and one to several larvae or pupae occupying a single chamber within the first 3 inches of soil.

Eggs, larvae and worker pupae were present in the nests all summer. Records over a number of years show that winged adults may be present after mid-July, and flights take place in late August and early September. Only one flight was seen on the low field. This occurred in the late afternoon of August 28, 1962, when males and females came from a nest and flew from grass tips. The *Myrmica* were not watched closely, because more attention was being given to other species. August 28 was one of the rare days which provided ideal flying conditions, and *Lasius minutus*, *L. sitkænsis*, *L. flavus*, *L. neoniger* and *Brachymyrmex depilis* were filling the air with ants flying toward the setting sun. There was no wind; the sky was slightly hazy and humidity was high (temperature : 84° F. to 78° F.; relative humidity : 65 % to 75 %; light : 2,800 to 940 f. c.).

On September 6, 1963 swarming activities were observed at a tall elm tree at the edge of a field. There had been flights earlier, and at 6 PM thousands of males and females had gathered and were climbing up and down the elm trunk. Males, which greatly outnumbered females, were also flying around the tree like a mass of gnats, returning to it again and again. Females tended to move upward on the trunk and mating occurred there. Many moving females had males attached. After mating, females flew away across the field, but males tended to remain and moved down to the grass and leaf cover as the temperature dropped.

On the low field one of the swamp white oaks evidently served as a gathering point, for on September 10, 1963, twenty-one dealate females were shaken out of surface debris on a plot dug near the oak.

Stenamma brevicorne (Mayr).

Stenamma brevicorne, together with *Lasius flavus*, seemed the most typical ant of the low field habitat. It was common and widespread here (23 colonies on 18 plots), but had been collected only once before on the Reserve (at swamp edge). Three other species of *Stenamma* (*S. impar*, *S. diecki*, *S. schmitti*) present on the Reserve did not live in the field.

Stenamma brevicorne workers foraged over the ground in cool damp weather, and the finding of workers just below the surface indicates that they also foraged below ground in the crumbly topsoil. Nest entrances were simply small openings hidden among leaves and grasses, and were not found unless workers were seen entering them.

An attempt was made to collect whole colonies; therefore nests were dug completely when possible. This was not always a successful pro-

cess, but the general pattern of nest structure seemed clear. Usually there was a chamber within 2 inches of the surface, which might be empty during dry weather. Some nests appeared to have no chambers in the crumbly surface soil but started with a chamber 4 inches down in more solid clay. No colony had more than 4 chambers, and most had only 2. Lowest chambers ranged in depth from 3 to 13 inches, with most at 6 inches. Large colonies dug down to soil moisture, while small colonies did not. Chambers were surprisingly large and were often only partly filled with brood. Those measured ranged from $1/2 \times 1/2 \times 1/4$ in. to $1\ 1/2 \times 1\ 1/2 \times 1$ in. with most being larger than an inch in diameter and a half inch high. The range of size of the 10 most complete population counts is recorded in Table II. Eggs,

TABLE II. — *Stenamma brevicorne*. POPULATIONS OF 10 COLONIES

	RANGE	MEAN
Eggs	7- 52	26.3
Larvae	17-151	59.9
Worker pupae	1-147	50.0
Workers	20-144	69.8
<i>Total</i>	164-331	228.7

larvae and worker pupae were present from before June 23, when the first colonies were dug, through the rest of the summer, although the September 10 colony had only one worker pupa. Twelve colonies which had winged adults or winged pupae averaged 20.6 alates per colony, of which 11.2 were females and 9.4 were males. Winged pupae were found in colonies from July 9 to August 11, and adults from August 10 to September 10 when observations ceased. It is known that *S. brevicorne* has flights in the spring (SMITH, 1957; KANNOVSKI, 1958). It may also fly in the late fall when conditions are right.

Lasius flavus (Fabricius).

Although *Lasius flavus* is listed as only fourth in abundance of colonies, it seemed the most typical (together with *Stenamma brevicorne*) of the low field habitat. Perhaps it was actually the most abundant, since colonies were large and so widely distributed that they almost seemed to form a sub-surface layer over much of the area. They were absent only where the ground was low enough to favor occasional standing water.

Lasius flavus had not been found in other fields on the Reserve, which are usually sandy and well-drained. It had been taken 8 times in oak-hickory woods, always in the soil. Five of these nests were

partly under stones, two were under bits of moss and one was under and up in wood.

On a field where there were no stones, colonies gave no outside indication of their existence. Even at flight-time they did not pile-up excavated soil, but some chambers were so close to the surface that breaking through offered no problem. Workers were not seen above-ground, except when winged forms were out for flights.

Nests of *Lasius flavus* were widespread near the surface, but did not go deep. Larger nests sprawled out in very irregular shapes for a square yard or more. Smaller ones might occupy two or three square feet. Often the ground was honeycombed with chambers of various shapes, so that it looked like a piece of magnified coarse bread. The smooth cavities were almost touching and were connected by several short galleries. They varied greatly in size from tiny cells to those as large as $1\frac{1}{2} \times 1\frac{1}{8} \times \frac{1}{2}$ inch. Chambers began immediately below the surface, but were most plentiful between 1 and 4 inches deep. In 2 colonies brood extended to 5 inches, and in one to 7 inches. Brood was widely distributed among chambers, and some segregation of forms occurred. In one colony where 29 cavities were checked for brood, 4 had masses of eggs; 2 had larvae only; 10 had pupae; and 13 had a mixture of larvae and pupae. The 3 queens of this colony were in separate egg chambers. Males and male pupae were scattered among worker pupae, but females and female pupae were usually isolated.

Eggs were found all summer, but were especially abundant during the first 2 weeks of August when larvae to be over-wintered were being produced. Larvae varied in abundance, but were found at all times. Worker pupae were found from June 11 to September 11, and winged pupae from June 12 to August 16. Adult winged ants were in the nests from July 25 to September 11, and flights were known to occur on August 27, September 1, September 6, September 7, 1963 and on August 28, 1962.

The August flights were both tremendous ones in which ants came up from all over the field until the air was thick with them, flying toward the setting sun. Little pools of yellow workers gathered about inconspicuous openings from which alates emerged. Both males and females flew indiscriminately from the soil, grasses and higher plants. The 1962 flight was long; for 70 minutes ants kept coming out until most colonies were depleted of alates. They flew from 5:10 PM to 6:20 PM at 84° F. to 77° F., 65 % to 77 % r. h. and 2,800 to 560 f. c. of light. There was no wind, and the day had been hot, humid and hazy. By 6:00 PM the ground seemed covered with dealate females, not only of *L. flavus*, but of *L. speculiventris*, *L. sitkænsis* and *L. minutus* as well. August 27, 1963, was a similar day, but flying time was shorter. Flight lasted from 5:20 PM to 5:45 PM at 84° F. to 74° F., 72 % to 77 % r. h. and 2,000 to 1,200 foot candles. *L. speculiventris*, *L. sitkænsis* and *L. neoniger* also flew. This flight

cleared alates from most nests in the open field, but at the far end, where shade caused slower development of brood, there were minor flights on September 1, September 6 and September 7. The September flights took place between 4:45 PM and 5:30 PM at 79° F. to 70° F., 75 % to 85 % r. h. and 3,600 to 1,000 foot candles.

Independent colony founding was abundantly illustrated, and followed the pattern described by DONISTHORPE (1927). Fourteen incipient colonies were found, each in a single chamber 1 to 4 inches below the surface. In 9 cases, there was a single queen, in 3 cases 2 queens together, once 3 queens and once 5 queens. Queens might have eggs only, larvae and pupae, or all stages of brood plus tiny workers. There were 3 examples of incipient colonies in the midst of areas of larger colonies. In one, small workers of the new colony were in a chamber 2 in. down, while large-sized workers foraged an inch above them. This location is not surprising (a number of other ants nested within the bounds of a *Lasius flavus* nest area), but it might well result in the incorporating of the new colony of ants into the older one.

Lasius minutus Emery.

The low field was a typical habitat for this species. Although no colonies were dug on plots, there were 2 large mounds on the first strip, and others bordered the marsh to east and west of the strips. Mounds were located in low places, and most were formed of the black marsh muck. They were large; a typical one was 40 inches in diameter and 12 inches high, with almost flat tops and straight sides. Usually grass was dense on the sides and sparse on top. No workers were seen at the surface until they dug out for flights. Foraging tunnels extended north toward the marsh and were primarily among the thick tangle of roots 1/2 to 2 inches below the surface. Workers attend root aphids (KANNOWSKI, 1959), and ants on these trails often had gasters extended with food. Once when many workers and alates were emerging as adults, a pile of discarded pupae cases was found in a tunnel 7 inches deep and a yard from the mound. Others were scattered along the more superficial foraging tunnels.

On the Reserve *L. minutus* was widely distributed in marshes and tamarack swamps and along their borders. Some mounds in sandy places were made of sand; some in bogs were constructed of sphagnum; but most were composed of the black mucky soil. PAUL KANNOWSKI (1959) plotted the position of approximately 700 mounds in one swamp-marsh region on the Reserve, and by feeding honey mixed with radio-active phosphorus, he showed that a colony may occupy 1 to 8 mounds scattered over as much as 6 meters.

L. minutus had a long flight period and seemed to have difficulty in finding exactly the right flying conditions. In 1963, at mounds on the field, winged ants were present in nests by July 27, and workers began making openings to the surface of mounds after a series of

rains on August 1, August 2 and August 3 and again after a hard rain on August 9. Males and females began appearing on the surface on August 18, but no flights were seen until September 1. Flights also occurred on September 6, September 7 and September 16 and alates were still present when observations ceased on September 20. The best flight (September 7) took place on an overcast day after a rain. Workers began coming out at 3:00 PM; winged ants started flying at 3:12 PM; and flight continued until 5:20 PM. It was a long flight because the sky remained overcast (3,100 to 100 foot candles); temperature changed slowly (79° F. to 72° F.); and relative humidity was high (73 % to 81 %). It was not an abundant flight because little gusts of wind up to 1 mile per hour drove alates down off the grass repeatedly.

These ants were very sensitive to bright light and to wind. Since mounds on the field were not shaded until late afternoon, the ants could fly only when the afternoon sky was overcast or when the sun was setting. This latter time proved poor, for when alates climbed grasses into slanting sun they hurried back or dropped quickly and if nests became shaded by shrubs in late afternoon, the rapidly dropping temperature prevented flight. On 10 days when winged ants came to the surface but could not fly, they were prevented by wind, too bright light or cold. On most bright or windy days they did not come into view.

Flights on the field began at times varying from 3:10 PM to 3:50 PM at temperatures between 73° F. and 88° F., with light in foot candles from 1,000 to 5,800 and relative humidity from 44 % to 79 %. Variations in endings were : time 4:55 PM to 5:35 PM; temperature 72° F. to 76° F.; light 1,600 to 1,200 foot candles; and relative humidity 54 % to 81 %.

An abundant flight in which thousands of ants flew occurred on August 27, 1961 from a mound on another part of the Reserve. There had been rain in the morning, and the afternoon was hazy, humid, warm and still — perfect flying weather. Another colony in full shade had been flying strongly at 2:45 PM, but this one did not become shaded until later and flying began at 3:35 PM (temperature 88° F., light 5,600 foot candles, relative humidity 75 %). Hoards of females and a few males climbed grasses and flew quickly. Soon all the tall grasses were full of alates hurrying up with wing half-spread ready to fly immediately and the black muck mound was covered with yellow workers. Height of flight came at 3:45 PM (85° F., 2,800 foot candles, 76 % r. h.). Twice when the sky became brighter (5,800 and 7,000 foot candles) alates climbed down grasses and milled about on the mound. When light dimmed there was again a sudden movement upward. These mass movements were extremely rapid and included the entire group so that grasses could be cleared very quickly. An approaching rain stopped the flight at 4:15 PM. KANNOVSKI (1959) gives a good account of similar *L. minutus* flights from a nearby bog.

Lasius speculiventris Pergande.

This is another ant typical of the habitat, but because the 2 colonies present formed mounds, they were not included in any dug plots. Workers were found on strips 1, 2, 3 and 4, foraging underground among roots in the first 4 inches of crumbly soil. They had rather extensive, branching tunnels which often ran just beneath woody roots. The workers appeared to travel widely, for some were as far

TABLE III. — EARLIEST AND LATEST DATES ON WHICH PUPAE AND WINGED ADULTS HAVE BEEN FOUND ON ANY PART OF THE E. S. GEORGE RESERVE OVER A PERIOD OF 10 YEARS

	WORKER PUPAE	WINGED PUPAE	WINGED MALES AND FEMALES
1. <i>Amblyopone pallipes</i> . . .	June 16-Sept. 3	July 18-Aug. 31	Aug. 16-Sept. 5
2. <i>Ponera c. pennsylvanica</i> . .	July 9-Sept. 18	July 16-Sept. 15	Aug. 1-Sept. 15
3. <i>Myrmica emeryana</i> (?) . . .	June 11-Sept. 3	June 27-Aug. 11	July 17-Sept. 7
4. <i>Myrmicalobi. fracticornis</i> . .	June 9-Sept. 15	June 27-July 8	June 27-Aug. 10
5. <i>Stenammas brevicorne</i> . . .	June 23-Sept. 10	July 9-Aug. 11	Aug. 10-Sept. 10
6. <i>Aphenogaster rudis</i>	June 14-Sept. 2	June 14-July 25	June 17-Aug. 19
7. <i>Crematogaster lineolata</i> . . .	June 6-Sept. 18	June 24-Sept. 2	June 27-Sept. 18
8. <i>Crematogaster cerasi</i>	June 10-Sept. 5	June 15-Aug. 4	July 21-Sept. 5
9. <i>Leptothorax ambiguus</i>	June 27-Sept. 10	June 17-Aug. 6	June 27-Sept. 11
10. <i>Dolichoderus marie</i>	June 12-Sept. 16	June 30-Sept. 16	June 30-Sept. 22
11. <i>Dolichoderus plagiatus</i> . . .	June 17-Aug. 28	July 9-Sept. 2	July 25-Sept. 2
12. <i>Dolichoderus pustulatus</i> . . .	June 22-Sept. 15	June 26-Sept. 2	July 11-Sept. 15
13. <i>Tapinoma sessile</i>	June 5-Sept. 5	June 5-June 17	June 9-July 12
14. <i>Brachymyrmex depilis</i>	June 12-Sept. 10	June 24-Aug. 19	July 24-Sept. 16
15. <i>Camponotus americanus</i> . . .	July 2-Sept. 6	July 19-Aug. 22	Aug. 11-spring
16. <i>Camponotus noveboracensis</i> . .	June 11-Sept. 5	June 17-Aug. 21	July 11-June 12
17. <i>Camponotus nearcticus</i>	June 26-Aug. 30	July 8-Aug. 26	Aug. 8-spring
18. <i>Prenolepis imparis</i>	July 27-Sept. 17	Aug. 14-Sept. 17	Sept. 5-spring
19. <i>Lasius neoniger</i>	June 5-Sept. 14	July 3-Aug. 5	July 17-Sept. 18
20. <i>Lasius sitkænsis</i>	June 19-Sept. 2	June 19-Aug. 25	July 22-Sept. 2
21. <i>Lasius minutus</i>	June 10-Sept. 1	June 17-Sept. 7	July 26-Sept. 18
22. <i>Lasius speculiventris</i>	July 3-Sept. 11	June 24-Aug. 17	July 24-Sept. 18
23. <i>Lasius umbratus</i>	July 9-Sept. 2	July 9-Aug. 26	July 26-Sept. 7
24. <i>Lasius flavus</i>	June 11-Sept. 11	June 12-Aug. 16	July 25-Sept. 11
25. <i>Formica lasioides</i>	June 19-Aug. 24	June 27-Aug. 3	July 10-Aug. 9
26. <i>Formica fusca</i>	June 4-Sept. 18	June 4-Aug. 4	June 23-Aug. 31
27. <i>Formica pf. nitidiventris</i> . . .	June 5-Sept. 18	June 5-July 19	June 28-Aug. 4
28. <i>Polyergus lucidus</i>	June 29-Sept. 14	June 19-Aug. 24	July 21-Sept. 9

from a known mound as 20 feet. Both mounds were in low ground (on strips 1 and 3) and the larger (25 × 29 × 9 in.) was so overgrown with tall vegetation that it was inconspicuous. The other (23 × 19 × 3 in.) lay at the base of a *Cornis* bush just inland from the marsh and was not so overgrown. Two other colonies nested outside the strips in a bay of low ground which extended further out into the field. One maintained an area of completely bare clay soil (11 × 8 × 1 in.) and the other had a semi-bare area (24 × 17 × 2 in.) penetrated by sparse grass and clover. These were mature colonies which produced winged ants.

On other parts of the Reserve, *L. speculiventris* was quite versatile in its habitats. Colonies were more often in swamps and low woods, but they were also present in open fields and upland woods. The ants made mounds of muck, sandy soil or clay, or lived in much-decayed, thoroughly galleried logs and stumps. One amazing colony nested near the top of a steep slope wooded by *Populus grandidentata* trees. It occupied a huge mound about 4 feet in diameter, and 2 feet high on the downhill side. Sides were straight and covered with a shaggy growth of *Poa compressa* grass. During flight season the flat top was honeycombed with openings and layered with fresh soil.

Flights were essentially as described by KANNOWSKI (1959). Winged ants were present for 3 or 4 weeks before the flying season began (Table III), and colonies began making numerous openings in mounds during the first week in August. In 1963 seven flights were seen on the

TABLE IV. — SUMMARY OF ENVIRONMENTAL CONDITIONS OF 7 FLIGHTS OF THE ANT *Lasius speculiventris* PERGANDE FROM A LOW FIELD BETWEEN AUGUST 27 AND SEPTEMBER 16, 1963

	TIME (PM)	TEMPERATURE (°F.)	LIGHT (foot candles)	RELATIVE HUMIDITY (%)
Emergence of alates	2:50-4:16	88-73	4,200-1,200	40-74
Beginning of flights	3:30-5:04	88-74	6,400-2,300	44-77
Height of flights	3:55-5:07	83-72	7,200-2,000	44-73
End of flights	4:05-5:30	87-71	5,100-1,400	52-81

low field. They took place between August 27 and September 16. Since some colonies were still not cleared of alates, undoubtedly more flights followed (Table IV), gives a summary of environmental variations at flight times. Warm, hazy, humid afternoons favored flights. Brightening sun or a breeze could stop them, but the species was not as sensitive to these as was *Lasius minutus*. The longest flight lasted 2 hours and the shortest 11 minutes. This latter occurred on a sunny afternoon which prevented ants from coming out until 5:00 PM. They began flying almost immediately (5:04 PM), but were cut short when shade reached the nest and temperature and light dropped quickly. Another flight ended abruptly at 4:05 PM when light increased suddenly and the temperature rose.

Flights were conspicuous and colorful, for the bright yellow workers accompanied alates onto the nest and also up on vegetation. Winged ants climbed the tallest plants present, which might be grasses of *Cornis* or *Potentilla* shrubs. They could also fly from the ground. Wind as light as 1 mile per hour could cause them to hurry down from plants, but they returned quickly when the breeze passed and some managed to fly between gusts.

Lasius neoniger Emery.

The 9 colonies found on plots demonstrated various graduations in colony development. Two queens occupied a cavity 1 inch below the surface, and an isolated queen was 1/2 inch down. Four colonies were small, occupying from 1 to 4 chambers and having only worker larvae and pupae. Three larger colonies were producing winged ants. The largest spread over 3 square feet and had formed a honeycomb of many chambers down to 8 inches. Eggs and larvae tended to be segregated from pupae and were in lower chambers. Female pupae were found in only 5 chambers, but male and worker pupae were widely distributed.

All colonies were found in the higher parts of the strips. This was to be expected, since *L. neoniger* was predominantly a field ant which could thrive in the most barren, sandy places. It penetrated open woods, but was replaced by *L. alienus* in deep woods and swamps. It nested mainly in open soil with only entrances or craters to indicate nests, but it also occurred under stones, under logs, in clumps of grass or among matted leaves. In cool damp weather workers foraged on the surface. At other times they stayed among leaf layers and in the crumbly surface soil.

On the low field *L. neoniger* flights took place on approximately the same dates as those of the yellow *Lasius*. In 1963, 9 flights or parts of flights were seen between August 20 and September 18. (The earliest and latest flights recorded for other years were August 5 and September 20.) Usually *L. neoniger* began flying a little later in the day than did the yellow *Lasius*. They have been seen to start flights between 4:30 PM and 6:00 PM and to stop between 5:00 PM and 6:45 PM, depending on whether the day was hazy or clear and whether the colony became shaded or received the last sun rays. Flights occurred during temperature variations from 82° F. to 71° F. Hazy, warm afternoons of high humidity favored flights. As with other *Lasius*, flights might be widespread and abundant on certain evenings, so that the whole place seemed flooded with ants, or ants might fly from one crater only while many nearby showed no activity. Any breeze prevented or retarded flight.

Lasius sitkaensis Pergande.

On the field, *L. sitkaensis* was found in 3 plots, and was known to occur in 2 other places. It was definitely associated with the marsh; workers foraged into it, and moved brood toward it in dry weather. The colony on strip 1 had only part of its nest on plot 4; the rest extended for 2 yards down to marsh edge and probably continued into it.

The part dug occupied a low, indistinct, densely overgrown mound (which may have been made by *F. fusca*). Chambers occurred down to 6 inches, but most were within the first 2 1/2 inches. Here the soil was labyrinthed with chambers which ranged in size from 1 × 3/4 × 1/2 inches to 3 1/4 × 1/2 × 1/2 inches. Galleries connecting them were numerous and wide, often 1/4 in. in diameter. Larvae and pupae were segregated in separate chambers, and empty pupae cases were discarded at ends of galleries just off the mound.

The second colony consisted of a queen, a few workers, worker pupae and larvae nesting 2 inches deep in thickly overgrown soil a yard from the marsh. The third « colony » was an isolated queen in a chamber 1 inch below the surface. Usually workers foraged in tunnels among roots just below the surface, but on damp cool days they also foraged aboveground.

On the Reserve, *L. sitkænsis* has been found in swamps and marshes and in woods and fields bordering them. Woods colonies were most numerous, and they were most often in well-galleried stumps, with brood down in the wood-soil of roots. Usually the colony was not confined to the stump, but might have brood spread out from it under leaf layers. One colony had brood scattered under leaves alone over an area roughly 2 feet in diameter, and another had pupae spread along a line for 2 yards. In swamps and marshes colonies might occupy large black muck mounds (one was 16 × 17 × 10 in.) or might be beneath rather tough clumps of grass.

Flights were recorded on August 18, August 20, and August 28, 1962, and August 27, 1963 from the colony nesting on strip 1. Since the best records were obtained on August 20, this flight will be described. There was no evidence of digging out to the surface; workers and alates came out of a trashy layer of twigs and grass stems which covered the soil for 1 or 2 inches. This layer had been hollowed-out in spots to provide loitering place. Just after the nest area had come into shade, males began coming up (5:40 PM; 84° F.; 80 % r. h.). Five minutes later the large females began climbing, and flying started at 5:48 PM (82° F.; 80 % r. h.; weak sun with light at 2400 ft. candles). Females climbed steadily but quietly. Usually wings were folded, but sometimes they were half open and were fluttered briefly before the take-off. The heavy females selected woody stems of *Cornus* or *Potentilla* and climbed high into the weak sunshine. The tiny males climbed grasses and flew from lower places. There was no massing of ants because they came out of the ground over a large area. Thirty-six females and a few males were the most seen at any one time. This was 5:50 PM when flight conditions seemed best (81° F.; 80 % r. h.; 1300 ft. candles). Soon after this, a cloud covered the sun; thunder was heard; and little gusts of wind began. Females began having difficulty in flying; they had to flutter wings more vigorously and were more apt to drop when taking-off. When the wind shook

stems, females started down or simply held on until stems were still again. By 6:10 PM the few remaining females had gone back into the nest and the last male flew (76° F., 84 % r. h., 460 ft. c.); it began to rain soon after. The ants were out for 30 minutes, and the flight lasted 22 minutes.

Lasius umbratus (Nylander).

On strip 8 many workers were gathered inside a natural-looking irregular mound (12 × 15 × 7 in.) near the marsh. Another group was found in a different irregular mound 10 feet away on strip 9. No brood was present, and an intense search in the tall vegetation of the field and marsh nearby failed to reveal the nest. It is possible that the mounds may harbor brood when the water level is high.

At other places on the Reserve, *L. umbratus* nested most often in and beneath stumps and logs. Nests in large stumps were typical for the species. Often the stump was decayed inside and easily pushed over, because large colonies completely galleried the stump base at ground level and below, and made chambers in the red wood-soil that resulted. Colonies sometimes extended out into soil and under leaves for several yards from stump or log and foraging tunnels stretched even farther. Workers usually foraged through soil or leaf layers, but sometimes came to the surface on damp days or in wet places. They were most often found at edges of swamps and marshes, and in low woods near them.

Leptothorax ambiguus Emery.

Nine of the 21 colonies of this species lived in the ground while 12 were entirely aboveground. Those beneath the surface were in the upper 2 inches, and were often in clumps of grasses and forbs, or on sides of old mounds. Those on the surface favored places of dense vegetation; living down in the surface litter in curled-up leaves, bits of small hollow stems, goldenrod galls and the crevices and flaky bark of *Potentilla fruticosa* stems. One colony had an especially neat little nest consisting of a hollow stem 3/8 in. wide and 2 inches long, with one end completely plugged with carton, and the other end covered except for a small circular opening.

Leptothorax ambiguus had been found in other habitats on the Reserve; in bog or swamp, in oak-hickory woods, and woods-field edge. In general, it favored slightly more exposed places than did *Leptothorax curvispinosus*. It was typical that along one fence row of large oaks, *L. curvispinosus* were plentiful in acorns beneath the trees, but were replaced by *L. ambiguus* in the field just outside the overhanging branches.

Usually all brood was piled together. Larvae were over-wintered and were constantly present. Eggs were being laid from spring to September. Worker pupae were gone by the middle of September. Although winged pupae have been found from mid-June to August 6, they were most plentiful during July. Adult alates were present from June 27 to September 11, but were most numerous from mid-July to late August.

Colonies on the plots were not collected for counting, but previous collections from acorns gave the record found in Table V. Most of these

TABLE V. — *Leptothorax ambiguus*. 50 COLONIES FROM ACORNS
(Collected between June 22 and August 24.)

	RANGE	MEAN
Eggs	1-236	31.2
Larvae	3-180	40.6
Worker pupae	0-78	14.4
Workers	6-106	37.3
<i>Total</i>	21-320	128.0

colonies had 1 queen; several had 2 or 3; and 1, during flight time, had 6 dealate females. Twelve collections made between July 7 and July 28, which included males and females, averaged 13.6 alates per colony, of which 6.3 were males and 7.3 females.

This may be an under-count, since colonies might have had some brood outside the acorn. The 2 colonies counted on the low field fell within the range recorded here, having 53 and 143 individuals respectively, of which 13 and 30 were workers.

Dolichoderus mariaë Forel.

The low field was a good habitat for ants of the genus *Dolichoderus*. Three of the 4 North American species lived on the strips, while a colony of the fourth (*D. taschenbergi*) had a nest about 40 feet to the southeast at the edge of a little wooded area.

D. mariaë was not included in any of the dug plots, and only one colony actually nested in the study area; nevertheless, it was an important ant in the environment. The colony on strip 6 and another just up-field from strip 9 maintained lines of workers which foraged to the marsh across strips 6, 7, 8 and 9. Other colonies were found to the east and west of the study area in the same habitat.

In the field, the igloo-shaped domes characteristic of this species were made mostly of grasses, with only a few dried leaves. They varied

in size from small domes $3 \times 5 \times 2$ inches to huge stacks $12 \times 15 \times 4$ inches. Beneath the dome, soil was excavated around grass roots to form a large cavity extending 6 or more inches into the ground. This space was criss-crossed by roots among which brood was kept.

From numerous openings in the domes, lines of ants foraged toward the marsh. They attended aphids on small trembling aspen trees, ironweed, boneset and *Spirea alba*. Trails to feeding grounds were quite permanent, sometimes even cut into the soil. One colony, which moved its nest site, went out of its way to continue on an old trail. Colonies seemed to move rather frequently, leaving behind deep holes partly filled with wisps of grass thatch to show where they had been. One colony was seen to move 23 feet, but more frequently they moved only a foot or two.

Eggs and larvae were already present on June 4. Worker pupae were first collected on June 12, and winged pupae June 30. Both were still present on September 16 although larvae were not seen after September 9. The first adult winged ants were found June 30, but some colonies still had only pupae of alates on July 24. Alates were still present in some colonies on September 22.

Flights have been described (KANNOWSKI, 1959; TALBOT, 1956). They were abundant and occurred regularly each morning unless weather conditions were quite unfavorable.

Colonies of *D. marix* offer a beautiful example of the way in which flight periods may vary from colony to colony, depending chiefly upon the position of the nest. A colony on a barren sunny slope of sand matured its brood very early. A flight was seen from here on July 4, 1962, and by July 25, 1962, no more winged ants were in the nest. On the low field 3 colonies were watched in 1963. The first had flights from late July to mid-August. The second still had no adult alates on July 29, but had begun flights by August 4. By September 16 no more winged pupae were present, although there were still males and females in the nest. The third nest, located in a shaded place, was very slow in maturing its brood, and did not begin flights until the first week in September. On September 16, there were still winged pupae in the nest and a good flight took place on September 22. Thus, the exposed nest on sand had its flights through July; one colony on the field began flights in late July, a second in August and a third in early September.

Dolichoderus pustulatus Mayr.

This species differed from *D. marix* in that it formed small colonies in obscure places. Fourteen colonies were found on 10 plots, and workers foraged on 25 plots scattered over the entire 9 strips. This ant was common in or near marshes, bogs and swamps of the Reserve, but was not taken in the higher woods and fields.

Usually colonies nested in the trashy layer of grass culms and twigs, heaping brood upon bits of curled-up oak, willow or *Potentilla fruticosa* leaves, or on the overlapping leaf-like lobes of a lichen (*Peltigera polydactyla*). Sometimes carton made the nest more secure, but more often it was not used. Other nests were in hollow stems, or circled small clumps of grass and extended down among their roots, and a few consisted of cavities in the upper 2 inches of soil.

Eggs and larvae were already present in early June. Worker pupae were first found June 22, winged pupae June 26 and adult winged July 11. Eggs have not been discovered after August 12, nor larvae after August 19. Worker and winged pupae became scarce after the first of September.

Flights took place during August and early September, and 1 male was found as late as September 15. PAUL KANNOVSKI (1959) has seen 6 flights from Big Cassandra Bog on the Reserve. They occurred between August 8 and August 20, and alates flew from 7 : 15 to 9 : 30 AM at temperatures between 63° and 75° F. No good flights were seen on the low field, but on August 19, 1963, 2 males and a female flew from a *Cornus* bush at 64° F., and on August 22 and August 30 dealate females were found walking on the ground.

Dolichoderus plagiatus (Mayr).

This ant nested on only 2 plots (5 colonies), both near the marsh side of the strips. On the Reserve *D. plagiatus* was not so common as *D. pustulatus*, but it was much more widely distributed, being found in open high woods and wood-field ecotones as well as in marshes and bogs. Its nests and habits were much like those of *D. pustulatus*, and records from other years show that it matured brood on about the same schedule. Alates have been taken in the nest from July 25 to September 2, and KANNOVSKI (1959) reported a flight on August 11 which was similar to those of *D. pustulatus*.

Formica lasioides Emery.

The field was not a favorable habitat for the genus *Formica*. Only 3 of the 12 species of the Reserve lived there. *Formica lasioides* was rare and was not found nesting on any plot. However, a colony lived near the field edge of strip 6, and a few workers foraged into strip 8.

On the Reserve, *F. lasioides* was most often found in open woods or in fields at woods' borders. It favored more sheltered places than did *F. neogagates* and was replaced by the latter in drier fields. It tolerated

rather heavy leaf layers, and sometimes hollowed out chambers in them. Most colonies nested within the first 5 or 6 inches of soil, but some formed chambers as deep as 12 inches. No flights have been observed.

Formica fusca Linnaeus.

In contrast, *Formica fusca* was a conspicuous ant which adapted to the low ground by building mounds. Ten earthen mounds of thriving colonies averaged 18 inches in diameter and 8 inches in height. These were not included in any dug plot. One small decadent colony occupied only the center of the overgrown remains of a mound which was reduced to 6 inches on one side, and 2 inches on the other. This mound illustrated clearly the importance of slightly raised places, for 6 species of ants nested on it (*Leptothorax ambiguus*, *Ponera coarctata pennsylvanica*, *Dolichoderus plagiatus*, *Myrmica emeryana*, *Brachymyrmex depilis*, *Crematogaster cerasi*).

All of the colonies without mounds were incipient ones, consisting of a queen and a few larvae, pupae and stunted workers or merely a queen alone in a chamber 2 or 3 inches below the surface.

On the Reserve, *F. fusca* built mounds only in low places. It could be found in any habitat, except very dry fields, and it adapted nesting habits to the surroundings. In higher fields and open woods there were often nest areas of excavated soil which tended to keep vegetation sparse but which did not pile up. In woods, nests were often under and in logs and stumps.

Collection records over a 10-year period give the impression that winged pupae and winged adults were in the nests for a long time. Actually, this inference resulted from the great variation in time of brood development in colonies situated in dry sunny places and those in moist cool ones. Flight periods also fluctuated greatly from colony to colony. Parts of flights have occurred from July 9 to August 21 over the years, and they must have taken place still later in the season.

Three whole flights were recorded on the Reserve. That of August 21, 1961 seemed typical. The day was overcast and warmed slowly. The all male flight took place between 10:05 AM and 10:50 AM at temperatures between 68° F. and 85° F. Relative humidity varied from 69% to 52%, and light from 2100 to 8000 foot candles. Males came out from under leaves around the nest area, climbed grasses or small (6 inch) oak trees, and flew quickly. Often only 2 to 6 were in sight, but as many as 5 flew a minute, and 72 were seen to fly in the 40 minute flight period. During this time a small black and yellow hornet kept coming back at about 10 minute intervals to carry off males. Once when none were in sight, it went under the leaves where males had been emerging, routed-out 2 and captured 1 of them.

On August 1, 1956 a female flight from a nest in the sun stopped at 10:28 AM at 78° F., while a male flight in the shade continued until 11:35 AM at temperatures varying from 73° F. to 76° F. and back again to 73° F. as the sky became overcast. An estimated 266 males flew in 65 minutes, with as many as 22 a minute at the height of flight. On August 5 a flight was seen in which most males and females climbed high into a group of elm trees before taking-off. This was between 9:15 AM and 10:10 AM at 74° F. to 77° F. On August 3, 1956 an abnormal flight occurred as a result of a nest being raided by *F. subintegra*. Workers and females were driven from the nest, and females flew hastily from grasses and also from the ground. This was unusually late (between 11:00 AM and 12 noon) and at a very high temperature (88° F.).

Formica pallidefulva nitidiventris Emery.

This ant is most characteristic of open dry fields, but it has been found in almost every habitat on the Reserve, and was represented on plots of the low field by 2 colonies. However, it was much more abundant than the count indicated, for workers foraged over the entire field, and were especially conspicuous during midday when temperatures were too high for other species to be out.

No flights were seen on the Reserve, but they must have occurred in July and early August. At Tiffin, Ohio, about 135 miles south, flights were recorded between July 12 and July 24, 1942 (TALBOT, 1945). They took place in the mornings at temperatures between 76° F. and 85° F. Near Cheboygan, Michigan, flights occurred from July 15 to August 4, 1945, between 6:10 AM and 10:40 AM at temperatures which varied from 61° F. to 87° F. (TALBOT, 1948).

Polyergus lucidus Mayr.

A thriving mixed colony of *Polyergus lucidus* and *Formica pallidefulva nitidiventris* moved into the bare soil of a plot on strip 7 two weeks after it had been dug. They remained there for the rest of the summer, the *Formica* workers doing much excavating, while *Polyergus* workers loitered about the entrance.

On strip 4 a *Polyergus* female with no workers was discovered in a *Formica pallidefulva nitidiventris* nest. Because some of the pupae present were those of *Polyergus*, this was evidently an early stage in colony founding by a female.

At the Reserve *Polyergus* was a field ant. Raids and flight activities of this species have been studied, and will be reported in a later paper. Flights that took place at midday have been recorded from July 31 to September 9.

CreMATogaster lineolata Say.

The 7 colonies found on plots all had most of their brood above the soil surface in layers of oak leaves, dead stubs of grasses and in the trashy layer of stems and leaves. Typically they made chamber-like depressions in the soil, sometimes lined with carton. A number of other colonies nested in old mounds of *F. fusca* and *L. speculiventris*. One of these, dug on September 17, 1963, had a few eggs and small larvae among leaves caught in grass at the surface, more in a cavity 2 inches down and great masses of eggs in large chambers 8 inches deep in the mound.

CreMATogaster lineolata was a common ant on the Reserve; its preferred habitats being dry, shrubby fields and open woods. Often nests were in logs or twigs and bases of sumac stems. Frequently they were among leaves and other debris. Carton might be used to seal the end of a branch or to complete the enclosure of a chamber beneath a log or among grasses. Openings extended down into the soil, and there seemed to be much moving of brood to favorable spots.

Time of production of sexual forms varied greatly from colony to colony. Winged ants have been found from June 27 to September 18. Evidently most flights occurred in late August and early September. Only one flight was seen in the field. It took place on September 16, 1963, from a colony nesting on the side of a low overgrown *L. speculiventris* mound beside the marsh. The sparse, all male flight was probably a late one for the colony. It occurred between 10:05 AM and 10:42 AM on a warm hazy morning when the temperature was 82° F. to 84° F., relative humidity 51 % to 41 % and light 6200 to 7200 foot candles. A little wind of 1 mile an hour retarded but did not stop flying. Only about 100 males flew. Workers climbed grasses and at flight's end carried a few males back into the nest.

CreMATogaster cerasi Fitch.

For some unexplained reason *CreMATogaster lineolata* workers foraged over the western 5 strips, but were replaced completely by workers of *C. cerasi* over the entire eastern 4 strips. No *C. cerasi* colonies were found in the dug plots, nor did an extensive hunt reveal any. It was possible that they were foraging in from the marsh, for *C. cerasi* was a common ant of the swamps and marshes. Here it sometimes nested in sphagnum hummocks, and among stems of *Chamadæphne*. In higher places it was usually found in logs, or under them and among leaves at their side. It was common in woods and did not invade drier places as successfully as did *C. lineolata*.

One flight was seen on August 27, 1959, from a colony occupying a solid elm log lying in a grassy woods. There had been a rain the day before and the morning was rapidly becoming hot and humid. Flight took place between 11:45 AM and 12:45 PM, and reached its height as the sky became less overcast and spots of sunlight hit the log. (Colonies in the open had been flying earlier because a winged female was found at 11:30 AM.). Temperature was 84° F. to 85° F., and relative humidity 75 % to 76 %. Workers and females (there were no males) covered the whole end of the log, but there was no flurry of activity. Females walked about or stood still. Occasionally one raised her wings or fluttered them briefly. Usually they simply opened their wings and flew. Some fell and climbed grasses to fly again. An estimated 400 females left the colony in the 40 minutes of flight.

Tapinoma sessile (Say).

This species was common but not abundant on the field. Nests were found 6 times on 5 plots, and workers walked over 23 plots. Colonies used matted grass, layers of leaves and bases of woody stems for nests. They also dug into the soil as deep as 4 inches during the dry summer. At other places on the Reserve, they nested in acorns, twigs, logs, sedges, sphagnum, and soil, forming temporary nesting sites from which the colonies moved easily. They are widespread in bogs, swamps, marshes and woods, usually preferring the damper places. Pupae of sexual forms were already present in early June, and adult alates have been found from June 9 to July 12. KANNOVSKI (1959) gives an excellent account of flight activities, reporting flights from June 26 to July 7 which occurred in the mornings at temperatures between 67° F. and 79° F.

Aphaenogaster rudis Emery.

This ant was abundant and widespread on the Reserve, being found in all types of woods and extending into the edges of upland fields, but it was not common nor conspicuous on the low field. Although one small colony lived on a raised place near the marsh, the 3 large colonies were on the drier edges. *A. rudis* was versatile in its use of nesting materials, but on the field it was restricted to the soil and the loose layer above it. One colony constructed a large superficial chamber of grasses held together by carton and a second piled brood among overlapping lobes of lichen. The other two had no aboveground structure. Chambers in the soil were large and well formed. They varied in number from 1 to 7, and extended as deep as 8 inches.

Records from other years show that larvae are constantly present during the summer and are over-wintered. Worker and winged pupae were first found June 14. No winged pupae were taken after July 25, but some worker pupae were still present in early September. Adult alates have been found from June 17 to August 19. Twice, July 27 and July 29, 1960, winged ants were seen upon plants in the late afternoon, but no actual flights were observed.

Prenolepis imparis (Say).

This species appeared able to tolerate the wet field because of clay soil present. Four colonies were found, all in plots farthest from the marsh. Nests had 5 or more chambers, and probably extended to standing ground water. Workers seldom foraged during midsummer, so the species played little part in field activities at this time.

Prenolepis imparis over-winter winged ants, but no larvae, and previous records from the Reserve show no eggs after July 9. Adult alates were not seen before September 5. Reports from other people indicate that flights took place during mid-April. They probably followed the same pattern of flight activities as do the ants in Missouri (TALBOT, 1945), flying on the first warm days of spring when the temperature went above 70° F.

Myrmica lobicornis fracticornis Emery.

Although this species was abundant in the nearby marsh it was found on only 1 plot and was represented by 2 small colonies which had chambers within the first 4 inches of soil on an old overgrown mound. The plot was almost at marsh edge, and was in the shade of an oak. No winged ants were present, but other records show them to mature early in the summer (June 27 - August 10). KANNOVSKI (1959) has given an excellent account of 10 flights which took place in Big Cassandra bog on the Reserve between July 17 and August 6.

Camponotus noveboracensis (Fitch).

A mature colony of this species was in possession of the only large pieces of wood in the field — 3 remnants of a tree trunk lying among the tall grasses at marsh edge. At times, workers, alates and brood were under and up in the logs, but during the dry summer they stayed down in the moist mucky soil of the dried up marsh. In August an

incipient colony was found which consisted of a queen and 5 worker pupae. These occupied a chamber just under the surface of a large mound completely covered with marsh grass.

On the Reserve, *C. noveboracensis* was typically found in swamps or marshes or in woods and fields near them. The ants could live in quite barren places if they were close to water. Nests were most often in logs and down in the soil beneath them, but 2 flourishing colonies have been discovered in soil alone. One nest was indicated simply by openings into a sandy bank above a swamp, and the other was in a large overgrown mound of muck which may have been constructed by *Lasius minutus*.

Brood development of the species could be followed easily, because one colony, nesting on a sandy slope, was never disrupted when its log was lifted. In fact, it adopted 2 new logs which were placed beside the original one. This colony produced its first bright-colored callow females on July 11, 1962, and still had a straggling of males and females on June 12, 1963. Thus it harbored alates for 11 months of the year.

Flights of the species probably began in May and they continued until mid or late June. Only one flight has been recorded, and it was the final flight of the season for the colony. This all male flight took place on June 12, 1961, from a log lying on an oak-covered hillside. At 3:10 PM, when spots of shade started coming over the log, workers gathered at 3 exit holes and males began looking out. At first workers kept them from emerging, but as shade increased, males began to move out onto the log (4:00 PM). They moved slowly, often standing quietly. A little wind was blowing, and any gust sent them back into the shelter of the log. By 4:30 PM more than 30 males were on the log and workers were no longer holding them back. They were now ignoring the breeze, and occasionally one shook his body vigorously from side to side. Flying began at 4:36 PM, but in the next 44 minutes only 37 flew. By this time approximately 60 had gathered on the log, moving about more and often shaking vigorously, but not opening their wings until the instant of flying. In the 12 minutes between 5:20 PM and 5:32 PM, 81 males flew. This almost cleared the log and at 5:35 PM the last (125th) male took off. No more were present in the nest. (The log was watched for the next 4 afternoons, and then was opened.) The flight afternoon had been warm and the temperature was 88° F. when males began to emerge. It was 85° F. at 4:00 PM and 84.5° F. when flight started, so temperature difference did not trigger flying. Shading of the log and the gradual dimming of light did seem to be critical. Flight ended when all males flew, so the 83° F. temperature here was not significant. The colony had been unsuccessful in flying on the day before. Males had attempted to emerge as soon as the entrances were in the shade, but workers kept them back by touching them with jaws and antennae. They began pushing out at

2:45 PM (87° F.). The high humidity and darkening sky of an approaching storm favored activity, but gusts of wind kept sending all back into the log and no flying had taken place when rain began at 4:15 PM.

Camponotus americanus Mayr.

Only one colony was found on the plots. It was a small one, consisting of a queen, a few workers and some larvae and pupae. They were found 6 and 8 inches down in the hard clay in 3 large chambers (one was $2\frac{3}{4} \times 1\frac{3}{4} \times 1$ inches) spaced 2 inches from each other. There was no indication of the nest at the surface, nor were workers found at any other place on the strips. This was evidently not a good habitat for the species, for at other places on the Reserve it was found in high sandy fields, wood-field ecotones and open woods. Nests were most often in the ground with no indication of their presence except for scattered large openings and a little excavated soil. Sometimes the ants used a stone as a partial covering of the nest area, and more rarely they nested in, as well as under, a log. Chambers and galleries were large and widespread under the surface. Males and females were present from early August, and were evidently overwintered to fly the next spring.

Camponotus nearcticus Emery.

Only one ant of this species was found. It was near one of the oak trees and probably came from a colony in an oak twig. *C. nearcticus* has never been found nesting in the soil on the Reserve. Colonies were most often in twigs extending from logs on the ground or still attached to living or dead trees, but sometimes they nested in stumps or under bark of larger logs. The species was widespread wherever nesting sites were available. Alates were produced in August and probably were overwintered.

Amblyopone pallipes (Haldeman).

Only a single ant was found on the study area. It was common on the Reserve in the more moist parts of woods, nesting just beneath the soil surface or under and in decayed logs. Previous records show larvae present all summer; worker pupae from June 16 to September 3; winged pupae from July 18 to August 31; and males and females from August 16 to September 5. No flights have been seen.

Comparison with other habitats.

Although each of the low field ants except *Stenamamma brevicorne* had also been found in some other habitat on the Reserve, they overlapped

TABLE VI. — COMPARISON OF SPECIES OF ANTS IN FOUR RESTRICTED HABITATS (2)

	LOW FIELD MICHIGAN	HIGH FIELD MICHIGAN	LOCUST WOOD WOOD, OHIO (1)	BEECH MAPLE OHIO (1)
1. <i>Amblyopone pallipes</i> (Haldeman)	+		+	+
2. <i>Ponera coarctata pennsylvanica</i> Buckley	+	++	+	+
3. <i>Myrmica americana</i> Weber		+		
4. <i>Myrmica emeryana</i> Forel (?)	+			
5. <i>Myrmica lobicornis fracticornis</i> Emery	++			
6. <i>Stenamamma brevicorne</i> (Mayr)	+		+	
7. <i>Aphænogaster rudis</i> Emery	+	+	+	+
8. <i>Aphænogaster tennesseensis</i> (Mayr)			+	+
9. <i>Aphænogaster treatæ</i> Forel		+		
10. <i>Crematogaster lineolata</i> (Say)	+		+	+
11. <i>Crematogaster cerasi</i> (Fitch)	+			
12. <i>Monomorium minimum</i> (Buckley)		+		
13. <i>Solenopsis molesta</i> (Say)		+		
14. <i>Myrmecina americana</i> Emery			+	+
15. <i>Leptothorax ambiguus</i> Emery	+			
16. <i>Leptothorax curvispinosus</i> Mayr			+	+
17. <i>Leptothorax longispinosus</i> Roger				+
18. <i>Dolichoderus mariæ</i> Forel	+			
19. <i>Dolichoderus plagiatus</i> (Mayr)	+			
20. <i>Dolichoderus pustulatus</i> Mayr	+			
21. <i>Tapinoma sessile</i> (Say)	+		+	+
22. <i>Brachymyrmex depilis</i> Emery	+		+	
23. <i>Camponotus americanus</i> Mayr	+			
24. <i>Camponotus pennsylvanicus</i> (DeGeer)		+	+	+
25. <i>Camponotus noveboracensis</i> (Fitch)	+			
26. <i>Camponotus ferruginea</i> (Fabricius)				+
27. <i>Camponotus nearcticus</i> Emery	+		+	+
28. <i>Prenolepis imparis</i> (Say)	+	+	+	+
29. <i>Lasius sitkænsis</i> Pergande	+			+
30. <i>Lasius alienus</i> (Foerster)			+	
31. <i>Lasius neoniger</i> Emery	+	+		
32. <i>Lasius flavus</i> (Fabricius)	+			+
33. <i>Lasius umbratus</i> (Nylander)	+		+	
34. <i>Lasius speculiventris</i> Emery	+			
35. <i>Lasius minutus</i> Emery	+			
36. <i>Acanthomyops latipes</i> (Walsh)		+		
37. <i>Acanthomyops claviger</i> (Roger)			+	
38. <i>Formica lasioides</i> Emery	+	+		
39. <i>Formica neogugates</i> Emery		++		
40. <i>Formica subintegra</i> Emery		++		
41. <i>Formica fusca</i> Linnaeus	+	++	+	+
42. <i>Formica pallidefulva nitidiventris</i> Emery	+	++		+
43. <i>Polyergus lucidus</i> Mayr	+	+		

(1) From *Colonies of ants in a locust woods*, by A. E. HEADLEY, 1952.
(2) Names of the ants follow Creighton's *Ants of North America* except in the following cases: in Creighton No. 1 is *Stigmatomma*; No. 2 runs to *C. lineolata subopaca*; No. 11 runs to *C. lineolata*; No. 26 is *C. pennsylvanicus ferruginea*; No. 29 is in synonymy under *L. niger neoniger*; No. 32 is *L. brevicornis*; No. 33 is *L. umbratus aphidicola*; No. 35 is *L. bicornis minutus*.

very little with species characteristic of higher, drier fields (Table VI). One such field (TALBOT, 1957) had 9 species which were the same as those of the low field, but only 2 of its duplicates (*L. neoniger* and *F. pallidefulva nitidiventris*) were listed as being widespread and numerous. Three others (*F. lasioides*, *Prenolepis imparis* and *Polyergus lucidus*) were given as « field or border ants — not numerous, » and the remaining four (*Ponera coarctata pennsylvanica*, *Myrmica emeryana*, *Aphaenogaster rudis* and *Formica fusca*) were invading the field border from adjoining woods. This leaves 19 species of the low field which were not found on the drier one.

It seemed possible that the low field was more closely related to a woods habitat. No similar intensive study has been made of any woods on the Reserve, but A. E. HEADLEY (1952) has listed ants from 2 types of woods — locust and beech-maple — in northern Ohio (Table VI). Eleven of the 17 locust woods' ants and 9 of the beech-maple climax were duplicated on the low field, indicating that the 2 habitats are more nearly alike than were the 2 types of fields. However, 13 low field ants were not found in either woods. The low field therefore seems a rather complex habitat with distinct characteristics of its own, which resulted from a combination of influences from the surrounding marshes, fields, and woods.

Summary.

Populations of ants of a low field in southern Michigan were studied and 28 species were found in an area of 870 square yards which bordered a marsh. Abundance of colonies was determined by digging 40 yard-square plots. *Brachymyrmex depilis* and *Ponera coarctata pennsylvanica* were widely distributed and had the greatest number of colonies but the yellow *Lasius* seemed the most typical of the habitat. *Lasius flavus* formed large colonies, widely spread just beneath the soil while *L. minutus* and *L. speculiventris* built mounds. The genus *Dolichoderus* was also typical of the habitat. Three of the 4 North American species nested on the study area, while the fourth occurred nearby.

Flights of the *Lasius* species, which took place in the late afternoon of August and September were abundant and conspicuous.

Résumé.

On étudia les populations de fourmis qui habitaient un champ d'altitude basse dans le sud de l'état de Michigan. On en trouva 28 espèces dans une étendue de 727 m² qui bordait un marais. On détermina l'abondance des colonies en creusant de petits terrains carrés de 36,5 mètres de chaque côté. *Brachymyrmex depilis* et *Ponera coarctata*

pennsylvanica étaient largement distribués et avaient le plus grand nombre de colonies, mais le *Lasius* jaune semblait être l'espèce la plus typique de l'habitat. *Lasius flavus* formait de grandes colonies, largement étendues juste au-dessous du sol, tandis que *L. minutus* et *L. speculiventris* construisaient des tas. Le genre *Dolichoderus* était également typique de l'habitat. Trois sur les quatre espèces nord-américaines nichaient sur le terrain étudié tandis que la quatrième nichait tout près.

Les vols de l'espèce *Lasius*, qui avaient lieu tard dans l'après-midi aux mois d'août et de septembre, étaient abondants et bien visibles.

REFERENCES CITED

- CREIGHTON (W. S.), 1950. — The ants of North America. *Bull. Mus. Comp. Zool.*, **104**, p. 1-585, 57 pl.
- DONISTHORPE (H.), 1927. — *British ants, their life-history and classification*, 2nd Ed. (Routledge and Sons, London, 436 p., 18 pl.).
- HEADLEY (A. E.), 1952. — Colonies of ants in a locust woods. *Ann. Ent. Soc. Amer.*, **45**, p. 435-442.
- KANNOVSKI (P. B.), 1958. — Swarming of the ant *Stenamma brevicorne* (Mayr). *Ent. News*, **69**, p. 231-233. — 1959. The use of radioactive phosphorus in the study of colony distribution of the ant *Lasius minutus*. *Ecology*, **40**, p. 162-165. — 1959. The flight activities and colony-founding behavior of bog ants in southeastern Michigan. *Insect. Soc.*, **6**, p. 115-162.
- SMITH (M. R.), 1957. — Revision of the genus *Stenamma* Westwood in America north of Mexico (*Hymenoptera, Formicidæ*). *Amer. Mid.-Nat.*, **57**, p. 133-174.
- TALBOT (M. T.), 1945. — A comparison of flights of four species of ants. *Amer. Mid. Nat.*, **34**, p. 504-510. — 1953. Ants of an old field community on the Edwin S. George Reserve, Livingston County, Michigan. *Cont. Lab. Vert. Biol.*, n° 63, p. 1-13. — 1957. Populations of ants in a Missouri woodland. *Insectes Sociaux*, **4**, p. 375-384.
- WILSON (E. O.), 1955. — A monographic revision of the ants of the genus *Lasius*. *Bull. Mus. Comp. Zool.*, **113**, p. 1-199, 2 pl.
-