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ANTS OF AN OLD-FIELD COMMUNITY ON THE EDWIN S. GEORGE RESERVE, LIVINGSTON COUNTY, MICHIGAN

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INTRODUCTION

A STUDY of community dynamics has been initiated by the Institute of Human Biology, University of Michigan, with a long-term investigation of an old-field community on the Edwin S. George Reserve in southeastern Michigan. This program, begun in 1948, seeks to ascertain "the complete biota and the organization and operation of a natural community" (Evans and Cain, 1952). The present paper is a report of preliminary studies of the ants of that field made to find out what species are present and, as far as possible, what part they play in the life of the community. The work was done during the summer of 1951 and was assisted by a grant from the Edwin S. George Fund for Visiting Naturalists. Facilities of the Reserve were made available by J. Speed Rogers, Director, and Irving J. Cantrall, Curator of the Reserve. Francis C. Evans provided the necessary background knowledge of plants in the field and made many helpful suggestions for carrying out the work.

DESCRIPTION OF THE HABITAT

The field under study is a 15-acre tract in the central part of the Reserve and is bordered on the east and west by oak-hickory woods. Detailed studies of the vegetation (Evans and Cain, 1952; Cain and Evans, 1952) show that the field is essentially a Poa compressa-Aristida purpurascens grassland community. These grasses are mixed with a variety of other plants which are distributed unevenly in such a way as to give the field a mosaic appearance. In some places the panic grasses form circles of light green, in others dry heads of Lespedeza rise several feet, and in still others flowers of Asclepias, Liatris, Monarda, Solidago, or Potentilla are conspicuous in their season.

The topography consists of ridges and miniature plateaus alternating with shallow depressions which in some places are as much as 5.5 feet deep. These low swales collect enough organic matter and hold enough moisture to maintain a thick growth of Kentucky bluegrass (Poa pratensis). Over most of the field, however, sterile soil and rapid drainage allow only the relatively sparse growth of the upland vegetation.

The field has a barren aspect in certain places where grasses are almost completely replaced by plants which grow close to the ground. These consist chiefly of large clones of mosses (mainly Polytrichum and Ceratodon), lichens (primarily species of Cladonia), or the composite Antennaria. The aspect of barrenness is increased by scattered patches of soil, many of which are the result of rodent and ant digging.

Major succession of the field back to oak-hickory forest seems to be slow. Evans and Cain (1952) have pointed out that this is probably due to the sterility of the soil and the effects of overbrowsing by a herd of deer. Small hickories, oaks, and cherries, and scattered junipers and hawthorns suggest, however, that in time the field will revert to a deciduous forest.

Short-term vegetational changes within the field itself, called "micro-successional cycles" by Evans and Cain (1952), are of more immediate interest because of the part ants play in their development. The progress of one of these cycles is essentially as follows: colonies of such mosses as Ceratodon and Polytrichum, or of the close-growing Antennaria, or of certain grasses invade any patch of bare soil and form a pioneer stand of low, dense-growing vegetation. Soon these patches are taken over by Poa compressa and scattered representatives of other grasses and forbs. After these have flourished for a time, the accumulation of dead culms retards further growth of grass and produces conditions favorable for lichens such as Cladonia. The lichens do not seem to prevent erosion by rain, wind, frost, or animal activity and they are frequently covered in a short time by fresh soil, thus preparing the way for a repetition of the cycle. Ant digging was found to be responsible in many cases for the small areas of bare soil on which these cycles are initiated.

METHODS OF STUDY

In a field entrances to ant nests are often thoroughly concealed. In order to find colonies, cake crumbs were scattered, and ants were followed as they carried them to the nests. Each nest so found was marked with a stake and recorded on squared paper. This technique was quite accurate for Myrmica, Aphaenogaster, and Formica, but not so successful for Lasius, Solenopsis, and Monomorium. The last two are small and often did not forage aboveground; their colonies were hunted by removing small stones or by bending plants to one side. It is probable that the number of Solenopsis and of Monomorium colonies recorded represents an undercount. In contrast, Lasius figures doubtless represent an overcount because of the difficulty in distinguishing limits of colonies. For this study each crater of soil which had ants going in and out of its entrances was recorded as a separate colony. Although it is known that a single colony may have more than one such active crater, no one has determined how extensive a Lasius colony is (Headley, 1941).

The abundance and distribution of ant colonies were determined by two principal methods. The first concerned the location of colonies in each of 25 staked plots selected to include as many types of plant associations as possible. The area of each plot was 10 square meters. This method provided information about the comparative densities of the various ant species in the several plots. The second method consisted of locating colonies throughout somewhat larger areas selected for their particular topographic positions. To determine the influence of swales or shallow depressions in the field upon ant distribution, colonies were staked along a transect through a swale and up its slopes to nearby ridges. Another group of colonies was studied at the west edge of the field, in order to evaluate the influence of a bordering woods. This second method yielded information about the factors affecting local distribution patterns.

GENERAL DISTRIBUTION OF THE ANT FAUNA

The 16 species of ants listed in Table I were found nesting in the field. Detailed studies centered around the first seven because they were common and typical species of field ants which affected the field relationships to the greatest extent. Of these, Lasius niger neoniger[1] was perhaps the most widespread. It did not maintain colonies in the thickly grassed swales and was less abundant in shaded areas but was the most conspicuous ant in every other part of the field. It seemed especially well adapted to the driest, most barren parts. Myrmica

[1]These are the Lasius with erect or suberect hairs on their antennal scapes which run to neoniger in Creighton's (1950) keys. They have been examined by E. O. Wilson who is revising the forms of Lasius (Lasius) and who states that they are americanus Em.

americana, Solenopsis molesta, and Monomorium minimum were almost as widely distributed but they were not so well adapted to the driest areas and thus flourished in the moister places, being found even in the bottom of swales. Aphaenogaster treatae, Formica neogagates, and F. pallidefulva nitidiventris (= F. p. schaufussi incerta before Creighton, 1950), also typical field ants, were widespread on the slopes and ridges covered with sparse stands of Poa compressa which spread over most of the field but did not thrive in the driest or in the most moist places.

The other nine species found in the field seemed to be of minor importance. Prenolepis imparis was found several times in June but then disappeared to stay below ground and was not seen again until apples began to ripen near the field late in August. This is a cold-weather ant, and it may play a more active part in the field ecosystem in early spring and late autumn. Formica lasioides was found several times but certainly was not numerous. Six colonies of the blood-red slave maker, Formica rubicunda, were known to exist on the field, and these

TABLE I

Ants of an Old-field Community on the Edwin S. George Reserve, from a Study Made in the Summer of 1951

Typical field ants — widespread and numerous:

1. Lasius niger neoniger Emery
2. Myrmica americana Weber
3. Aphaenogaster (Attomyrma) treatae Forel
4. Formica (Proformica) neogagates Emery
5. Formica (Neoformica) pallidefulva nitidiventris Emery
6. Solenopsis (Diplorhoptrum) molesta (Say)
7. Monomorium minimum (Say)

Field or border ants —not numerous:

8. Prenolepis imparis (Say)
9. Formica (Proformica) lasioides Emery
10. Formica (Raptiformica) rubicunda Emery
11. Polyergus lucidus Mayr

Ants invading the field border — of local distribution and limited abundance:

12. Formica fusca Linne
13. Camponotus pennsylvanicus (DeGeer)
14. Aphaenogaster (Attomyrma) rudis Emery
15. Myrmica emeryana Emery
16. Ponera coarctata pennsylvanica Buckley

made conspicuous raids on F. neogagates. The one colony of the shining slave maker, Polyergus lucidus, enslaved F. p. nitidiventris.

Ants of the field border seemed to require shade for at least part of the day and prospered under a leaf covering. Consequently, the three large hickory trees left by the settlers who cleared the field formed islands for these forms. The following border ants can be expected to increase in number as the field reverts to woods: Myrmica emeryana will replace M. americana, Aphaenogaster rudis will increase as A. treatae dies out, and Formica fusca will take the place of F. neogagates and F. p. nitidiventris. Camponotus pennsylvanicus will nest wherever logs are present, and Ponera coarctata pennsylvanica will live in decaying wood or under leaves in soil.

ABUNDANCE

The results of the examination of 25 selected 10-square-meter plots are shown in Table II. The most widely distributed species were also the most abundant in numbers of colonies found. Lasius niger neoniger is undoubtedly the most abundant species on the field although the 125 active craters recorded for it probably represent an overcount of colonies; its circles of bare soil certainly made it the most conspicuous. Myrmica americana, with 58 distinct colonies, was second in abundance. Aboveground, Myrmica workers were more numerous and widespread than those of Lasius; the former foraged continuously as long as temperature permitted, but the surface activity of the latter was largely confined to bringing up more soil.

The importance of Aphaenogaster treatae in the field seemed greater than the figures indicate. Individuals of this species foraged for fairly long distances (9 to 12 feet) from the nest, gathering a great variety of food, and colonies were never close together. Formica neogagates and F. p. nitidiventris displayed patterns of distribution and habits much like those of Aphaenogaster. F. p. nitidiventris workers were very conspicuous foragers, especially in hot weather when all other species were below ground. This habit of long-distance foraging enabled a single colony to patrol a large surface area, and it is not surprising that colonies of these species were not clustered together.

When the entire ant fauna is considered, there is a mean of approximately one colony per square yard for the 299 square yards (250 square meters) studied in the 25 plots. Average areas for single colonies of each species ranged from 2 square yards for L. n. neoniger and 5 square yards for M. americana to 23 square yards for F. neogagates, 50 square yards for A. treatae, and 60 square yards for F. p. nitidiventris.

Calculations of actual numbers of ants in the field presented greater difficulties, for there was much variation in the size of colony populations, not only among species but also among the colonies of any one species. The most practical attack on the problem of total population would seem to be to determine average populations for each species.

No direct determination of numbers was attempted on the field, and no colonies were dug since it was desired to avoid any disturbance of the soil. The only population figures available are for F. p. nitidiventris and A. treatae. Individuals of F. p. nitidiventris were not counted at the Reserve, but 24 colonies dug at the University of Michigan Biological Station (Talbot, 1948) were probably similar in size. They were found to average 2352 individuals (eggs, larvae, pupae, adults), of which 855 were workers. If, at the Reserve, there is a general distribution of one colony for each 60 square yards, then the field should support a population of approximately 1320 colonies of this species and consequently 3,000,000 individuals of which over 1,000,000 are workers. Several A. treatae colonies were dug at the Reserve during the summer of 1952 in an area directly adjoining the study field. Colonies averaged 1331 individuals, 682 of which were workers. If there is a general distribution of one colony for each 50 square yards, there are, in the field, 1584 colonies comprised of approximately 2,100,000 individuals, of which 1,000,000 are workers.

LOCAL DISTRIBUTION PATTERNS

To determine whether or not there were differences in vertical distribution shown by the various species, ant colonies were staked through a moist swale and up its slopes to the drier ridges above. The selected swale consisted of an oval area supporting a thick stand of Kentucky bluegrass about 16 yards long and 9 yards wide from which the ground rose on all sides to form ridges 4.4 to 5.4 feet high and 20 to 30 yards away from the swale. On the slopes Poa compressa was the dominant plant, interspersed with a variety of other grasses, forbs, mosses, and lichens, all distributed sparsely enough to allow the bare sandy loam to be seen.

For this study four species were considered (M. americana, F. neogagates, F. pallidefulva nitidiventris, and A. treatae), and their nests were staked on the east, west, and north slopes. In all, 125 colonies were found in an area of about 800 square yards. M. americana was most abundant with 78 colonies, or one colony every 10 square yards; F. neogagates had 20 colonies, or one colony for each 40 square yards; A. treatae was more sparsely distributed with 14 colonies, or one for each 57 square yards; and F. p. nitidiventris had 13 colonies, one for each 61 square yards. This agrees with the plot survey in relative abundance of colonies of the four species, but shows a less dense distribution.

There was some evidence of differential vertical distribution, as indicated in Table III. Myrmica colonies were most abundant on the lower parts of the slopes, whereas the other three species flourished higher up. The dense matted grass of the swale bottom proved unfavorable for ant nests; a survey of 10 square meters in its center revealed only four M. americana colonies and two of Solenopsis molesta. Myrmica colonies were most abundant in a ring just above the bottom of the swale; evidently soil and vegetation conditions in the sparser grass

TABLE II

Summary of Active Ant Colonies Found on 25 Selected Plots in an Old-field Community, Edwin S. George Reserve, 1951

Area of each plot = 10 sq. m.

Species	Plot Number																									Colonies in 25 Plots	Density of Colonies (per Plot)	Plots in Which Species Occurred
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25			
Lasius niger neoniger .	33	17	5	6	1	7	7	...	6	1	3	6	10	2	3	...	5	4	3	2	...	...	...	4	...	125	5.00	19
Myrmica americana. .	...	...	1	1	9	5	4	1	...	5	3	2	...	5	...	2	1	2	3	1	9	4	...	...	...	58	2.32	17
Solenopsis molesta . .	...	...	1	3	2	...	3	1	1	1	4	4	6	...	1	9	3	1	...	1	...	2	...	...	2	45	1.80	17
Monomorium minimum	...	...	...	1	3	...	...	...	2	3	...	...	1	...	2	1	1	1	...	...	...	...	...	...	...	15	0.60	9
Formica neogagates .	...	...	...	...	1	2	4	1	3	...	...	...	...	...	2	...	...	...	...	...	...	...	...	...	...	13	0.52	6
Aphaenogaster treatae	...	...	...	1	...	...	...	1	...	...	...	...	...	...	1	...	...	1	...	...	1	...	1	...	...	6	0.24	6
Formica pallidefulva nitidiventris	...	...	1	1	...	...	...	...	...	1	...	1	...	...	...	...	1	...	...	...	...	...	...	...	...	5	0.20	5
Formica rubicunda . .	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	0.04	1
Polyergus lucidus . .	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1	0.04	1
Formica lasioides . .	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	1	0.04	1
Aphaenogaster rudis .	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	1	0.04	1
Ponera coarctata pennsylvanica	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	...	2	0.08	1
Myrmica emeryana . .	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	4	5	9	0.36	2
Formica fusca	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	1	0.04	1
Total . .	33	17	8	13	16	14	18	4	13	11	10	13	17	7	9	12	12	9	6	5	9	6	3	10	8	283	11.32	
Principal Plants of Plot	Antennaria - Aristida - Polytrichum	Aristida - Cladonia - Ceratodon	Aristida - Cyperus - Cladonia	Panicum - Ceratodon	Poa compressa - Aristida - Ceratodon	Poa compressa - Cladonia	Poa compressa - Cladonia	Poa compressa - Cladonia	Poa compressa - Aristida - Cladonia	Poa compressa - Aristida - Polytrichum	Poa compressa - Aristida	Poa compressa - Aristida	Poa compressa - Aristida	Poa compressa - Aristida - Panicum	Poa compressa - Aristida - Panicum	Poa compressa - Panicum	Poa compressa - Lespedeza - Antennaria	Lespedeza - Aristida - Panicum	Lespedeza - Poa compressa	Rumex - Poa compressa - Poa pratensis	Poa compressa - (swale border)	Poa pratensis (swale)	Poa compressa (border near woods)	Poa compressa (woods border)	Hickory shade - island of border ants			
	Open Field Sites																					Special Sites						

were better for their nests. The two F. neogagates colonies listed for the lowest level were also not in the swale itself but were about a foot above it. No Lasius craters were found at this level or in the swale, but they were numerous in all parts at higher levels.

The abundance and variety of food available within the swale may have influenced nest locations. Ants were seen to carry spiders, crickets, beetles, leaf hoppers, larvae of various kinds, and parts of grasshoppers. Aphids were numerous on the leaves of milkweed (Asclepias syriaca). M. americana was particularly conspicuous as a forager here; it was joined by F. p. nitidiventris, which came down the slopes from longer distances, some as much as 18 yards. In addition to a plentiful food supply, temperature conditions in the swale were

TABLE III

Differential Vertical Distribution of Ant Colonies from a Swale to a Ridge - a Rise of 5 Feet 5 Inches, E. S. George Reserve, Summer of 1951

Species	Height of Level Above Bottom of Swale		
	0'-1'5"	1'5"-3'5"	3'5"-5'5"
Myrmica americana . . .	40	24	14
Formica neogagates . . .	2	8	10
Aphaenogaster treatae . .	0	6	8
Formica pallidefulva nitidiventris	0	6	7

ideal for foraging because the thick stand of grass retained the night's coolness and cut off the sun's rays. At 11:30 A.M. on July 19, for example, temperature in the sun on the ridge was 98° F., when in the swale it was only 78° F.

Studies of the field border nearest the woods showed that woodland ants were invading the field concomitantly with woodland plants. Camponotus pennsylvanicus, which requires wood for its nests, was found foraging on the field's edge, and one small colony was discovered nesting in a branch under a hickory tree in the center of the field. A Formica fusca mound was found under the same tree, and several others occurred just off the field at the wood's edge.

Aphaenogaster rudis and Ponera coarctata pennsylvanica, abundant in the woods, were able to maintain themselves at the field's west border where there was a rather permanent ground covering of oak leaves. Myrmica emeryana seemed the most successful of the border ants; a group of colonies was found at the northwest corner of the field and another group on the west side of a hickory tree, both in the shade of overhanging branches and in an area of thick grass, mixed with a layer of dead grass stems, tree leaves, and twigs.

The west border of the field proved best for ant invasion because it afforded three conditions not common to the field proper: (1) a scattering of little oak trees, (2) a sparse but distinct covering of oak leaves blown in by a prevailing northwest wind, and (3) afternoon shade from the nearby woods supplemented by little areas of moving shade from the small trees. The hickory trees in the field's center duplicated conditions of shade and ground cover.

THE ROLE OF ANTS IN THE FIELD COMMUNITY

Nest building and its effects. — Soil was the only habitat available for ant nests. Not only were there no sizable logs, but the extreme fluctuations of surface temperature prevented ants from nesting in matted or upright stems. Thus, the typical field ants were all soil-dwelling forms.

Lasius niger neoniger nest entrances were by far the most easily located, for although workers spent most of their time underground, they were constantly bringing soil to the surface, so that each nest entrance was surrounded by a crater of bare soil. Their nest-building activity seemed to play an important part in microsuccession. As pellets of soil were piled up to form craters around nest entrances, lichens and mosses were buried and often killed. Lasius seems, therefore, to shorten the declining or lichen stage and to retard the development of the pioneer stage, thus prolonging the bare soil period of microsuccession. The piles of bare soil also contribute to the process of leveling the field. During rains the soil was washed down, and as it dried it was blown by the wind. Soil was deposited in depressions, which were thereby raised at the same time that the ridges were being lowered.

The soil of 20 Lasius craters observed in the plot survey was collected to learn how much was brought to the surface. The average crater was 13 cm. long and 11 cm. wide, with a center 2 cm. high. The average volume of soil per crater was 164 cubic cm., and the average weight was 171 grams. These data, together with a mean crater density of 5.00 per 10-square-meter plot, show an estimated average soil displacement of 82 cubic cm. or 85.5 grams per square meter of surface area. If these figures are applicable to the entire field, Lasius is responsible for the displacement on each acre of approximately 12 cubic feet of soil weighing 750 pounds.

The ants were continually abandoning entrances and making new ones; they excavated soil all through the summer except in extremely dry weather. To illustrate this, one plot was studied four times during the summer. On June 23, after a rain and at moderate temperature which allowed full surface activity, there were 17 active craters and 8 inactive ones. A week later, after another hard rain, there were again 17 active craters but only 12 of them were those staked the week before. Later (August 8), after a dry period, 5 old craters were still in use, 7 had been abandoned, and there were 5 new ones, making a total of 10 active craters. The dryness continued, and a week later only 6 active craters were found, although the count had been taken early in the morning at favorable temperature (66° F.). Thus, the number of craters in this plot varied from 6 to 17, depending on the amount of excavating the ants were doing. Excavating activity, in turn, was conditioned by moisture and temperature. Any rain after a dry period caused new craters to be thrown up.

In contrast to entrances of Lasius nests, those of Aphaenogaster treatae were quite inconspicuous. This ant was most abundant in areas of sparsely growing grasses, such as Poa compressa, Aristida purpurascens, and Panicum depauperatum, and could not tolerate heavy swale stands of Poa pratensis. Nest entrances were large, often 1 to 1.5 cm. across, but they were usually so thoroughly concealed by blades of dead grass or overhanging lichen that they were found only when the ants entered carrying crumbs. Entrances usually slanted under roots of grasses; sometimes there were two, one on each side of a grass clump. Frequently, before the entrance there was a little depressed runway of more or less cleared soil beyond which might be a heap of excavated soil pellets or perhaps the discarded seeds of Panicum depauperatum or of mullein flowers if the workers happened to be collecting these. The entrances usually led to a large superficial chamber, sometimes entirely aboveground and roofed by upright or matted grass blades plastered together by soil pellets, sometimes sunk into the soil for as much as 5 cm., but still covered by the light, compact thatch roof or by a crust of lichen or moss. These chambers were usually not distinguishable from the common litter of dead grass stems lying on the ground. Chambers varied in floor area from 3 by 5 cm. to 3 by 15 cm., and from 2 to 5 cm. in height, and were usually irregular in shape. They were interlaced by grass stems and roots from around which the soil had been removed. From the superficial chamber 2, 3, or 4 large galleries led down to another large chamber from which descended one or more galleries. The impression was always that of large spaces around the grass roots, a condition which tended to increase the rapidity of drainage and thus to prevent the growth of thick stands of grass, and which during dry weather must have hastened the death of the vegetation. The effect of Aphaenogaster nests on the development of microsuccessional changes seems, therefore, to be one of terminating the grass stage and of including the degenerative lichen stage.

Myrmica americana nests seemed quite similar to those of A. treatae with respect to their influence on microsuccession. Surface chambers again made large spaces around the roots and resulted in increased drainage and drying. Myrmica entrances were unique in that most of the colonies built chimneys 0.5 to 1 cm. high, of woven grass blades or bits of lichen stuck together with soil pellets.

Formica neogagates nest entrances were even more inconspicuous and were never found until ants were seen entering them. They consisted of openings of 0.5 cm. or less, concealed under bits of lichen or grass. Small galleries sloped directly into the soil with no surface chambers. In contrast, compound colonies of F. neogagates and F. rubicunda were conspicuous. One small colony had thrown up a circle of soil 13 by 15 cm. and 0.5 to 2 cm. high, bare except for six stalks of

P. compressa and one of Rumex Acetosella. A larger colony had formed a bare area 35 by 30 cm. pierced only by several P. compressa and stunted, withered Rumex. The crater of this colony had four openings at its center, which was 3 cm. high, and three other openings about its rim. The bare soil seemed much hollowed out by chambers just below the surface, and Rumex roots growing through them were covered with root aphids. These nests also seemed to have the effect of eliminating the microsuccessional grass stage.

A nest of Formica pallidefulva nitidiventris usually had one entrance, often partly concealed by vegetation, with a small mound of excavated soil near by, sometimes as far as 15 cm. away. Previous study at the University of Michigan Biological Station showed that nests of this species may have from 2 to 5 galleries extending as deep as 30 to 40 inches.

Food and foraging habits. — The ants were primarily scavengers and patrolled the ground so thoroughly that dead animals were never allowed to litter it. Insects were the most abundant source of food and formed the main part of the diet, but spiders were also frequently collected, and one dead ground squirrel was found covered with Solenopsis molesta. Sometimes injured or slow-moving insects were collected alive.

Secretions of root and stem aphids formed a second important source of food. Lasius niger neoniger depended on root aphids for their main food and were found foraging at the surface only during cool, damp weather; Myrmica americana and Formica neogagates were seen frequently on stem aphids of milkweeds. Flower nectar formed a third source of food, and milkweed flowers were especially attractive to M. americana, F. neogagates, F. p. nitidiventris, F. lasioides, L. n. neoniger, and Prenolepis imparis. F. p. nitidiventris also seemed to collect milkweed juice from breaks in the stem.

At the time when mullein (Verbascum thapsus) was in bloom, A. treatae collected petals by pulling them from the flowers. These were found fresh and intact on the refuse piles, and it is not known whether any were used for food. During the first half of July, when seeds of Panicum depauperatum were ripening, certain colonies of M. americana and A. treatae appeared to make harvesting of the seeds their main activity. Members of one colony were observed to be bringing in one or two seeds a minute. Curiously enough, other workers of the colony were carrying seeds out of the nest at about the same rate and depositing them on discard heaps a few inches away. Under the microscope these seeds seemed to be just as whole and good as those being brought in by foraging ants. Many colonies in the P. depauperatum areas accumulated little mounds of seeds outside the nests. Later, after rains, some of the seeds sprouted, so perhaps in this instance the ants were favoring growth of the panic grass. Seed harvesting and flower attending were seasonal, but the collecting of dead insects went on day after day during the entire summer.

The foraging activities of the various species of field ants resulted in a 24-hour patrol of the ground surface. L. n. neoniger workers did most of their surface foraging during the night. In the early morning and late afternoon the field was predominantly populated by M. americana and A. treatae, but at midday F. p. nitidiventris and F. neogagates were often the only ants seen. This division of time for labor was dependent on reaction of the species to fluctuations in temperature, which were especially marked on the open field, there being little to form a shield against the direct rays of the sun. L. n. neoniger workers did not forage much aboveground except when temperature was low and humidity high. Consequently, they could forage during many nights but were kept below ground during all but cool, cloudy days. M. americana and A. treatae foraged at medium temperatures, but F. p. nitidiventris and F. neogagates did not reach full foraging force until temperatures were high.

Surface temperature readings were taken to determine the critical temperatures for some species. The following examples seem typical. M. americana were being watched one afternoon when moving clouds made alternate sun and shade, and temperatures fluctuated above and below the ants' critical range. At 84° F. Myrmica workers foraged actively and at 88° F. they could still walk across the sunny patches to the nest, but at 92° F. they were unable to traverse the hot soil and kept circling in the shade or climbing grass blades. At 94° F. no ants were in sight. Approximately 90° F. seemed, therefore, to be the limiting temperature. Ants trapped out of the nest during the heat of the day clustered just below the soil surface among the roots of grasses or forbs. A. treatae reacted in a similar manner but could tolerate slightly higher temperatures.

F. p. nitidiventris and F. neogagates did little foraging until the ground temperature reached 80 F. Observation on an afternoon when sun temperature on the ground was 96 F. and shade temperature was 82 F. showed that F. neogagates workers were proceeding normally to and from their nests, whereas M. americana individuals were immobilized, apparently trapped by the heat of any spot of bare sunny soil. One hour later, when surface temperatures had risen to 106° F. in the sun and 86° F. in the shade, even the F. neogagates workers were unable to reach home.

These variations in reaction to temperature illustrate differences in adaptation to field life and offer a partial explanation for the coexistence of so many different species. L. n. neoniger has become essentially independent of the ground surface through its cultivation of root aphids and is rarely exposed to extreme heat. M. americana and A. treatae are ground surface foragers but confine their activity to periods of moderate temperatures; such periods are long enough and occur frequently enough for these species to maintain themselves. F. p. nitidiventris and F. neogagates are adapted to withstanding higher temperatures, and their foraging time was cut by even a moderate drop in temperature.

Parasitism and predation. — Parasitic orange mites infected all four species of Formica. Spiders captured some ants, and a tiger beetle (Cicindela sp.) was watched as it pounced upon an ant and ate it. Flickers (Colaptes auratus) were found opening Myrmica nests in other parts of the Reserve but were not observed on this field.

SUMMARY

A survey of the ant fauna of an old-field community on the Edwin S. George Reserve revealed the presence of 16 species. Seven of these were common and typical field forms, four were less numerous and were found sparingly in both open-field and field-border situations, and five were present only in the proximity of adjacent woods or under the shade of large isolated hickory trees. The border species appear to be gradually replacing the typical field forms as the field reverts to oak-hickory woodland.

Examination of 25 selected 10-square-meter plots indicated that Lasius niger neoniger was the most widespread and numerous species, with an average density of five colonies (active craters) per plot. Comparable densities for the other typical field ants were as follows: Myrmica americana, 2.32; Solenopsis molesta, 1.80; Monomorium minimum, 0.60; Formica neogagates, 0.52; Aphaenogaster treatae, 0.24; Formica pallidefulva nitidiventris, 0.20.

The distribution patterns of several species were studied by local surveys. The dense growth of Poa pratensis in shallow depressions or swales was unfavorable for ant nests. Myrmica colonies were most abundant on the lower parts of the slopes of these swales, whereas Aphaenogaster and Formica flourished higher up. The west border of the field provided the most favorable conditions of shade and cover for the invasion of woodland ants.

The craters of soil brought to the surface during the construction of Lasius nests were estimated to represent an average displacement of 82 cubic centimeters or 85.5 grams per square meter of surface area. One of the principal effects of this activity was apparently to encourage and prolong the development of the more barren stages of microsuccession. Subsurface chambers formed by the nest building of Aphaenogaster, Myrmica, and Formica produced large drainage spaces around the roots of grasses and forbs and tended to prevent the growth of dense stands of vegetation.

Foraging by ants kept the field clear of dead animals. Insects and the secretions of root and stem aphids were the principal foods. Plant materials collected included seeds, nectar, and parts of flowers.

Variations in temperature seemed to control the foraging hours of the different ant species. Lasius foraged only during cool, damp weather; Myrmica and Aphaenogaster confined their hunting to periods of moderate temperatures; the typical field Formicas are evidently adapted to withstanding higher temperatures. The differences in reaction exhibited by the various species resulted in a constant patrol of the field.

Mites were found on all four species of Formica. Ant predators included spiders, tiger beetles, and the flicker.

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