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# Nest Morphogenesis and Population Ecology of Two Species of Formica

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NEST MORPHOGENESIS AND POPULATION ECOLOGY  
OF TWO SPECIES OF FORMICA

by  
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Bachelor of Science, University of North Dakota 1954

Master of Science, University of North Dakota 1956

A Dissertation  
Submitted to the Faculty  
of the  
University of North Dakota  
in partial fulfillment of the requirements  
for the degree of  
Doctor of Philosophy

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Permission

Title NEST MORPHOGENESIS AND POPULATION ECOLOGY OF TWO SPECIES  
OF FORMICA

Department Biology

Degree Doctor of Philosophy

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Signature Donald A. Sather

Date May 4, 1972

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## ABSTRACT

Two species of thatching ants (Formica obscuripes and F. oreas comptula) are common to the ecotone and woodland habitats of the Forest River Biology Station near Inkster, Grand Forks County, North Dakota. The general ecology for each species was determined with emphasis on mound morphogenesis, colony-founding and population characteristics. For each species the following samples and data were collected: random samples of each population, thatch sample, external and internal mound measurements, and field maps of distribution patterns.

The morphogenesis of F. obscuripes mounds was found to follow a predictable pattern with three well defined but transitional nest forms: (1) Stage I, characterized by a thatched dome without excavation, (2) Stage II, characterized by a raised, thatched dome, earthen embankment and an excavated pocket containing thatch, and (3) Stage III, characterized by a depressed dome of deteriorating thatch producing a crater-like effect.

Random samples of workers taken from selected mounds in various stages of growth indicated that the ratio of minors to majors increased with growth and aging of colonies. Minors made up a larger percentage of the sample taken from Stage III mounds as compared to Stages I and II.

Annual measurements of mounds over a seven-year period showed that the growth of mounds and population followed a predictable growth

curve. Stage I mounds were typically geometric in their rate of growth whereas Stage II mounds had an arithmetic growth rate. Stage III mounds showed a negative growth rate.

The distribution patterns of colonies were found to be isolated and random (prairie and woodland habitats), uniform (prairie habitat), and clumped (woodland habitat).

The means by which new colonies were established varied with the habitat. Indirect evidence indicates that isolated prairie and woodland colonies are probably founded by solitary queens following the marriage flight, while mounds within clusters were founded by the process of colony division. A relatively rare process, colony translocation, resulted in the abandonment of one nest in favor of another of recent origin.

Individual F. *oreas comptula* nests were, for the most part, asymmetrical in shape with little change in morphology (except size) between Stage I and Stage III nests. No relationship was noted between major/minor ratios and nest size. The sequence of events leading to colony senescence as observed in F. *obscuripes* was not found to apply to this species.

Clusters of F. *oreas comptula* nests, usually associated with dense stands of Kentucky blue grass, were not found to be composed of discrete colonies but were parts of a complex of interconnected nests. The movement of tagged workers and the transfer of brood between nests indicated that such clusters were polydomous. Isolated and randomly dispersed colonies were rare.

The establishment of new colonies was through the process of colony budding. Spatial separation occasionally resulted in the establishment of secondary polydomous clusters.

## INTRODUCTION

Two species of thatching ants (Formica obscuripes Forel and F. oreas comptula Wheeler) are common to the ecotone and woodland habitats of the University of North Dakota Forest River Biology Station near Inkster, Grand Forks County, North Dakota. While the typical nest structure of both species is well known, the manner of mound construction and colony founding is not.

One of the earliest accounts of the nesting habit of F. obscuripes was made by McCook (1884). Although not referred to by specific name, he undoubtedly was describing the above species, which has since become known as the "thatching ant". A detailed account of the nesting behavior of F. obscuripes was reported by Weber (1935); additional notes on the biology of this species were given by Cole (1932). King and Sallee (1953, 1956) determined the half-life of F. obscuripes colonies. Wheeler (1910) and Creighton (1950) discussed the possibility of temporary social parasitism as a means of establishing new colonies, whereas King and Sallee (1953) noted that F. obscuripes may at times form new colonies by the process of budding.

The stage through which a nest may pass and the relationship of the population to this stage is not known, although tentative conclusions concerning the growth of colonies of social insects were proposed by Bodenheimer (1937).

A search of the literature has revealed little information concerning the ecology of F. oreas comptula. References to nest structure and the

nature of the material used in its construction were made by Cole (1932) and Wheeler and Wheeler (1963). No evidence has been cited concerning the founding of new colonies nor is the sequence of nest or mound construction known. No data are available as to the nature of distribution patterns or population characteristics.

The following study is an attempt to gain some insight into the nature of mound morphogenesis, mode of colony founding, and population characteristics for each species.

Field investigation was carried out during the summers of 1964 through 1970 with the majority of the field work conducted at the Forest River Biology Station.

## MATERIALS AND METHODS

Following selection of sites and mounds, numbers were assigned and stakes placed to insure the accuracy of future reference. The date, specific locality, general habitat, measurements of mounds, and type of sample were entered on each card.

Bulb aspirator and tweezers were used in collecting workers. An effort was made to insure that majors, medias, and minors were included, but no attempt was made initially to obtain a random selection. However, samples collected for determination of population characteristics were random and obtained from each mound in the following way: mounds were selected on the basis of size from the smallest to the largest. All collections were made within a  $\frac{1}{2}$ -hour period in order to lessen the possibility of changes in the surface activities of the workers between the times of the first and last collections. Sampling consisted of removing a portion of thatch, measuring 15 cm in diameter by 2.5 cm in depth, from the surface of the mound. This material and the ants contained therein were placed in a field bag and an anesthetic applied.

Selected mounds were also dissected in detail in order to determine the number of queens present. Since queens may move into soil chambers when disturbed, two methods were used to insure as little movement as possible. Mounds less than 12 cm in thatch diameter were quickly anesthetized by saturating the surface with chloroform and covering with a plastic sheet for a period of 15 minutes. When all activity appeared to have ceased, the thatch material was removed with a trowel or by hand and

spread on a tarpaulin for careful examination. Small mounds were examined in about 1 hour whereas the largest took 5 hours.

Larger mounds proved to be too deep and massive for the quick penetration of chloroform. Rapid anesthetizing was carried out by utilizing a 1.5 cm by 90 cm copper tube near one end of which were placed ten 3 mm holes. The end of the tube was sealed by flattening to a point and then inserted into the mound to a depth marked by the contact between thatch and soil (Figure 1). The tube was left in place several days. Chloroform was then poured through the exposed opening and a plastic sheet placed over the mound. Dissection of the mound proceeded as before.

Mounds in various stages of development were dissected for the purposes of measurement, sampling of thatch, photographing the exposed lateral surface, and the determination of interior morphology. When permitted by local conditions, mounds were dissected along an east-west plane providing a southern vertical exposure of thatch, soil embankment, brood chamber (if present), and soil chambers. With the exception of small nests, no attempt was made to follow soil chambers to their limits.

Determination of the frequency and distance traveled by workers, mounds visited, and common trails used by adjacent colonies was obtained by using enamel paint as a marker. Initially, several hundred workers were removed from a colony and a spot of white paint placed on the thorax of each. This method proved to be too tedious and time consuming and the number marked was much too small a portion of the total colony population.

The second method and the more successful of the two was affected by spraying the surface of the mound on which the workers were moving



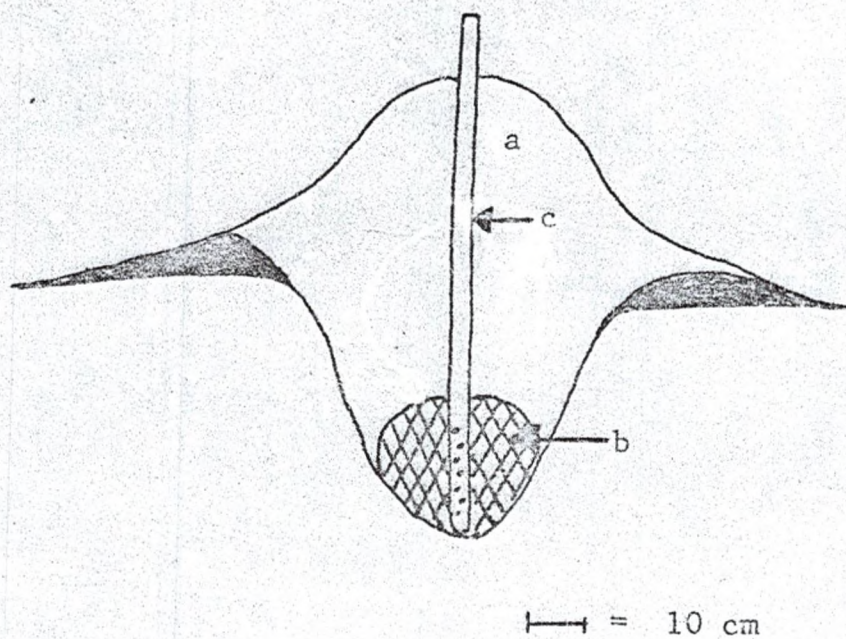


Fig. 1.--Cross section of large F. obscuripes mound showing position of copper tube used in the rapid anesthetization of colony:  
(a) thatch, (b) brood chamber, (c) copper tube.

with Testor compressed air spray paint. The container was held approximately 60 cm away from the surface so that only small specks of paint would adhere to the workers. With this technique, several hundred to about a thousand workers were marked in a few seconds. No apparent adverse effects were observed. A few workers were noted to be specked with paint as long as a month later.

Some habitats, especially those that are composed of dense stands of smooth brome grass (Bromus inermis) or thick grass mats, made the following of marked workers difficult. In such instances dyes taken internally by workers provided excellent results. The dye (gentian violet) was blended with equal parts of peanut butter and honey. A 50-cc vial of this mixture was embedded in the surface of the mound. On successive days samples were taken from adjacent mounds and the workers were squashed between three by five cards. Those workers which had been feeding on the dye produced a violet stain which was easily detected.

Identification of plants common to the study areas was made either in the field or from pressed specimens. The nomenclature followed is that of Stevens (1963). For plants common to specific localities within the study areas additional reference was made to check lists compiled by Facey (1960).

## STUDY AREA

### Geography

#### Location

The area of study is located within and adjacent to the University of North Dakota Forest River Biology Station near Inkster, Grand Forks County, North Dakota. Specific locations include sections 10, 11, and 14 of T154N/R55W (Figure 2). A few references are made to collections from other parts of the state. These areas are: the University of North Dakota Oakville Prairie Field Station in Grand Forks County (Sec. 16, T151N/R52W); The North Unit of Theodore Roosevelt National Memorial Park in McKenzie County, in Sec. 11, T132N/R101W, in Slope County.

#### Climate

Weather data for the Forest River Biology Station near Inkster, North Dakota are lacking. However, information gathered at the Grand Forks weather station (Stommel, 1967), about forty miles to the southeast, is representative of the entire county.

According to Stommel (1967), the temperature range, from summer to winter, is large. The mean temperature for the winter months of December, January and February is  $7.9^{\circ}$  F. Minimum temperatures drop to zero or below on an average of 60 days each year. The average temperature for the summer months, June, July and August, is  $66.7^{\circ}$  F. High temperatures (about  $90^{\circ}$  F) occur only occasionally. The average annual precipitation at Grand Forks is 20.02 inches, of which more than three-fourths falls

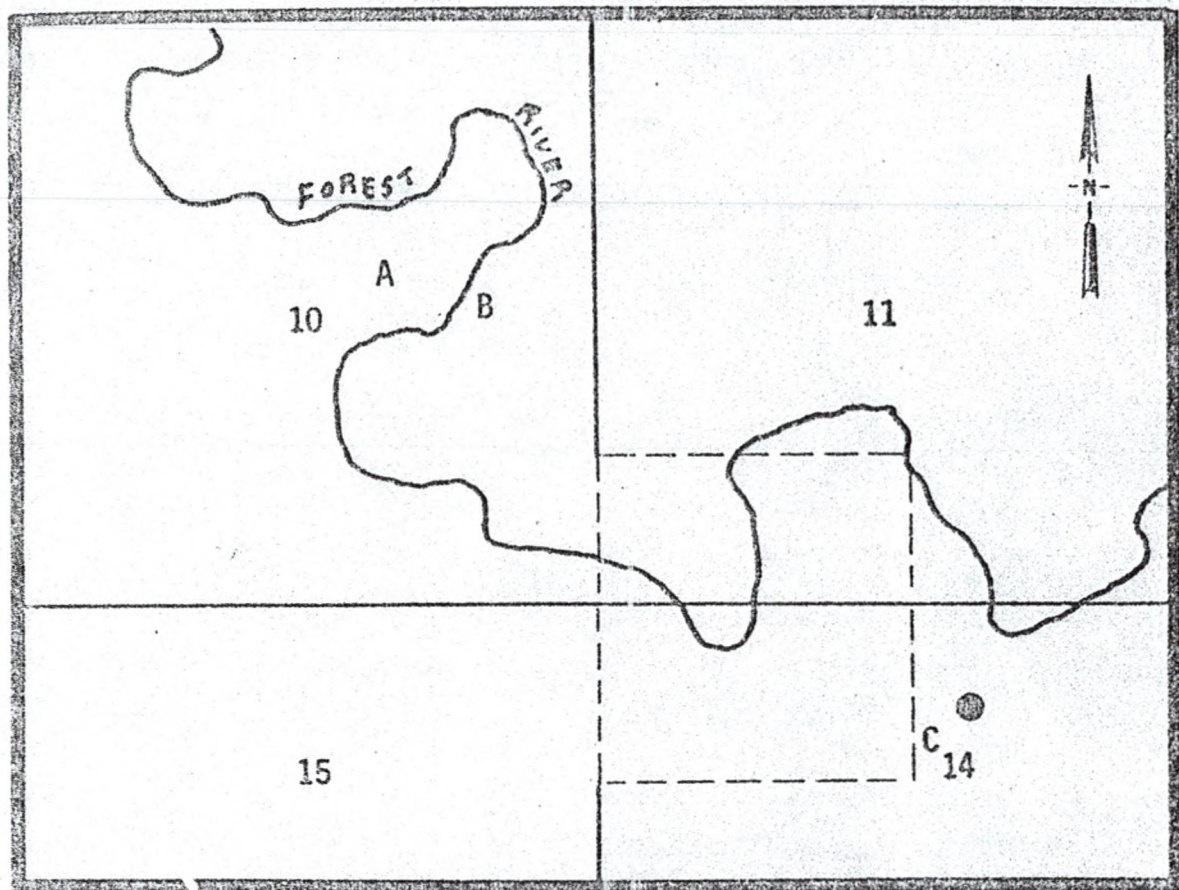


Fig. 2.--Map of the University of North Dakota Forest River Biology Station and vicinity. A, B, and C indicate location of T. obscuripes cluster; F. oreas comptula cluster is indicated by a dot. Boundaries of biology station are shown by dashed lines.

during the growing season, which extends from mid-May to later September. About 35 inches of snowfall can be expected in an average year. Snow has occurred in all months except July and August. The maximum fall occurs in the five-month period, November through March, with each month averaging about six inches. The humidity is relatively low throughout the year. During the summer high humidity seldom occurs with high temperatures.

### Geology

#### Physiography

Study areas 1 and 2 lie within the Western Young Drift Section and the Agassiz Lake Plain District. This district in eastern North Dakota is a flat area which slopes toward the Red River (Fenneman, 1931).

The westernmost boundary of the district in Grand Forks County is along the west edge of an outwash plain. The lake plain slopes from an elevation of 353 meters above sea level in western Grand Forks County to about 276 meters in the northeastern part.

The western edge of the county is characterized by end moraines, outwash and beach ridges (Hansen and Kume, 1970).

#### Surface Geology

Geologic and land form maps of Grand Forks County indicate the presence of three main deposits within the study area and immediate vicinity (Hansen and Kume, 1970):

Alluvium - This is formed of floodplain deposits mostly of dark gray clay and silt along the Forest River.

Shore Deposits - These are composed of clay and silt beach deposits

which make up ridges one to three meters in height.

Soils - The soils are of two types: soils of streams and valleys comprised of loam and silty clay, and the clay soils of the glacial lake plain comprised of silty clay, loams, and silt loams.

The Forest River Biology Station and areas adjacent to it may be characterized by the presence of numerous ravines which have dissected the upland bordering the valley of the Forest River. The average drop in elevation from the rim of the valley to the valley floor below is about 30 meters. The slopes leading down to the floodplain of the Forest River are quite variable with some slopes having a more or less gentle incline and others ranging from steep to cliff-like.

The valley floor is in part a floodplain formed by the meandering of the Forest River. Above the floodplain are bench-like terraces carved into the valley wall. Locally the stream has altered its course, leaving elongate depressions which in early spring or after heavy rains may contain water.

According to Patterson et al. (1968), three soil types are predominant within the area: the Hecla-Ulen, which is mainly a water-laid loamy fine sand reworked by wind and located in the upland North of the Forest River; the Fairdale, which is a medium-textured sediment deposited during periods of stream flooding and occupying most of the floodplain of the Forest River; and the Renshaw, which is a water-laid sandy loam deposited on a surface of sand and gravel. This type is found on the upland south of the Forest River.

## Ecology

The prairie, extensively invaded by low shrubs, is confined to the north and south boundaries of the Forest River Biology Station. Small tapering extensions of the prairie may be found along the divides with occasional openings within the woodland. This native prairie is, in many places, extensively invaded by wolfberry (Symphoricarpus occidentalis) and by Kentucky blue grass (Poa pratensis). Disturbed areas adjacent to cultivated farmland have dense stands of smooth brome grass (Bromus inermis). An ecotone, comprised of herbs, grasses and small shrubs, *i.e.*, wolfberry and juneberry (Amelanchier alnifolia), forms a transitional zone 2 to 4 meters wide between the prairie and forest.

A deciduous hardwood forest occupies much of the valley slopes and floor. On the dry south-facing slopes are found bur oak (Quercus macrocarpa); and American elm (Ulmus americana); the moist north-facing slope may contain stands of aspen (Populus tremuloides), basswood (Tilia americana), and a few scattered paper birch (Betula papyrifera). On the floodplain basswood, boxelder (Acer negundo) and American elm are the common trees.

Study Area 1. This area, from which most samples and data of F. obscuripes were taken, is a more or less open woodland situated on the floodplain and terrace of the Forest River. It is located in pasture land adjacent to the Forest River Biology Station. Unlike most surrounding areas, shading is not heavy with sunlight reaching most of the forest floor during part of the day.

Trees characteristic of the area are bur oak, American elm, basswood, box elder, and green ash (Fraxinus pennsylvanica var. subintegrifolia). Wolfberry is the common shrub whereas a few hawthorn (Crataegus chrysoarpa)

and wild grape (Vitis vulpina) are also present within the immediate sampling area.

Only a few grasses and forbs are found with abundance. Kentucky blue grass is the dominant ground cover, occurring in dense stands in the more open areas. Prairie junegrass (Koeleria cristata), although present, is only sporadic in occurrence. The common herbs are the blue violet (Viola rugulosa), common milkweed (Asclepias syriaca), leafy spurge (Euphorbia esula), and wood stickseed (Hackelia americana).

The ground cover changes considerably during the growing season due to range management. Usually during spring and early summer the area is free of grazing and the grasses and some forbs become quite tall and dense. In late July or August grazing may become quite heavy with a resultant decrease in the amount of ground cover.

Study Area 2. This area is comprised of native prairies bordering the south edge of the valley of the Forest River and the narrow ecotones extending into the woodland. The majority of samples and data relating to F. oreas comptula were taken from this habitat.

Typically, each prairie extension is bordered by bur oak, green ash and occasionally box elder. The ecotone between forest and prairie is composed of the shrubs juneberry, wolfberry, and poison ivy (Rhus radicans). Grasses common to the prairie extension are Kentucky blue grass, little blue stem (Andropogon scoparius), porcupine grass (Stipa spartea) and feather bunchgrass (S. viridula).

Plant species diversity is not great. Those herbs which occur with any frequency are goldenrod (Solidago supp.), bluebell (Campanula rotundifolia), wild vetch (Vicia americana), early meadowrue (Thalictrum venulosum), northern bedstraw (Galium boreale), white sage (Artemisia



ludoviciana), golden aster (Chrysopsis villosa), prairie violet (Viola pedatifida), silver leaf (Psoralea argophylla), indian breadroot (P. esculenta) and spreading dogbane (Apocynum androsaemilfolium).

## DESCRIPTION OF WORKERS

Identification of F. obscuripes and F. oreas comptula workers poses no special problem in collections taken from eastern North Dakota. Key characters used by Creighton (1950) and descriptions by Wheeler and Wheeler (1963) are adequate for separating these species from other members of the rufa group.

The following are key characters of the Subgenus Formica and the rufa group according to Creighton (1950): "Major workers with the antennal scape not longer than the distance from the middle of the clypeal border to the middle of the occipital border or, if longer, the epinotum is distinctly angular and not excessively rounded above;" "large workers with the occipital border at most very slightly concave, usually flat or slightly convex; pronotum in profile evenly convex, not angular;" "bicolored species, the head and thorax ferruginous or yellowish red and notably lighter than the gaster or, if infuscated, the infuscation does not completely mask the ferruginous ground color in the larger workers; frontal area usually shining, frontal lobes strongly divergent behind."

### Major Workers

#### Formica obscuripes Forel

Head dark brown dorsally and strong brown ventrally, thorax dark reddish brown, gaster black; scapes usually without erect hairs, but if erect hairs are present then body hairs are not uniform in length

(Wheeler and Wheeler 1963); median lobe of the clypeus descending to the clypeal fossae through an even curve.

Formica oreas comptula Wheeler

Head clear yellowish red or mostly infuscated with dark reddish brown, thorax dark reddish brown to yellowish red, gaster with each segment very dusky red anteriorly and black posteriorly; scapes with delicate erect or suberect hairs on all surfaces; body hairs of uniform length (Wheeler and Wheeler 1963); median lobe of the clypeus descending to the clypeal fossae through steep-sided faces.

## MOUND MORPHOGENESIS AND COLONY FOUNDING

While reference is made to the typical mound or nest construction of both F. obscuripes and F. oreas comptula, the stages of construction through which they progress are not well defined. In this section of the paper I will attempt to describe each phase in order that variations which exist can be recognized in the field. Descriptions will include general morphology of incipient, mature and old stages, material used as thatch or detritus, and population characteristics.

Colony reproduction will include the study of the establishment of new colonies in virgin territory and the process by which the number of colonies is increased and the relationship between colonies within a given area.

### Formica obscuripes Forel

#### Mound Morphogenesis

Mounds vary considerably in size and external morphology, the end result being an adaptation of the mound to suit a particular habitat.

The typical mound as determined by this study measures approximately 50 cm in total diameter. At the center of the mound is a raised thatched dome of twigs and culms surrounded by a ring of soil excavated from below ground level (Figure 3). This thatched portion of the mound averages approximately 38 cm in diameter and 25 cm in height. The extent to which the thatch material extends below ground level is highly variable; generally, for every centimeter of thatch above ground level,

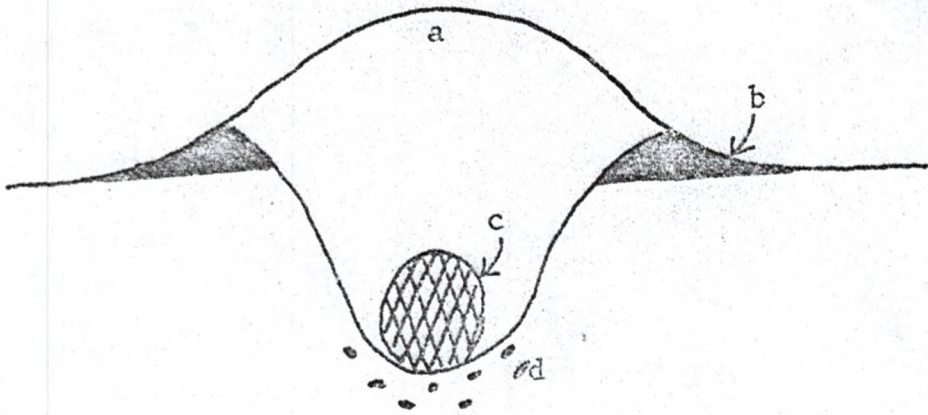


Fig. 3.--Sectional view of typical *F. obscuripes* mound. The basic features as shown are: (a) thatched dome, (b) soil embankment, (c) brood chamber, (d) soil galleries and chambers.

there is 1 cm of thatch below.

Situated within the thatch is a more or less hollowed out area composed of large twigs and culms referred to as the brood chamber. In most instances it is located just above the soil at the point of deepest penetration of thatch (Figure 3). According to Weber (1935) in the late fall this feature is lacking, the spaces having been filled in with small pieces of organic debris.

Mounds of similar size but having a typical form brought about by local environmental conditions are shown in Figures 4 and 5. The extent to which the thatch portion of the mound is raised above ground level is often related to the amount of vegetative growth occurring around the periphery of the mound. The reworked and porous soil of the embankment often provides a habitat more suitable for plant growth than that of the surrounding environment. The resultant vegetative growth may cause the nest to become uninhabitable. This detrimental factor is compensated for by an upward extension of the thatch (Figure 4).

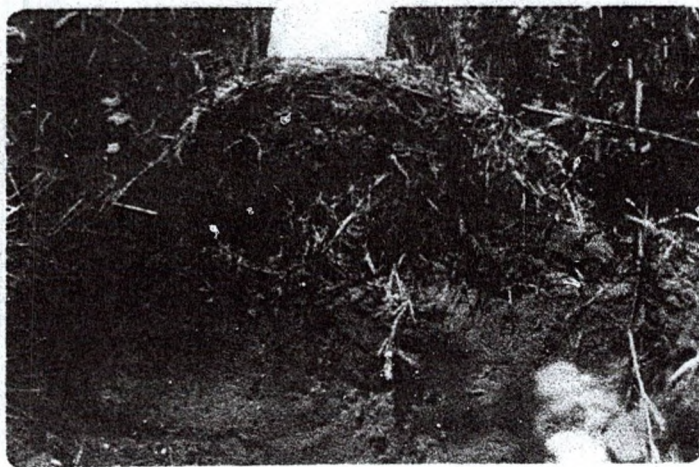
Corresponding changes may also take place with respect to internal nest morphology. In a few mounds little if any of the thatch material is below ground level and the brood chamber may be in the lower half rather than at the apex of the thatch (Plate I).

Examples to the other extreme were observed in well drained overgrazed pasture land. With little or no shading from vegetation the nest is almost entirely below ground level with the total height little more than that of the soil embankment. In such mounds the brood chamber was almost always at the point of deepest penetration of thatch (Figure 5).

SURFACE AND SECTIONAL VIEWS OF FORMICA OBSCURIPES MOUND SHOWING  
ENCROACHMENT OF VEGETATION AND EACH OF EXCAVATION.



1. Surface view showing encroachment of vegetation on the soil embankment and periphery of thatch surface.



2. Cross section showing the raised thatched mound with excavation confined to soil chambers and galleries.

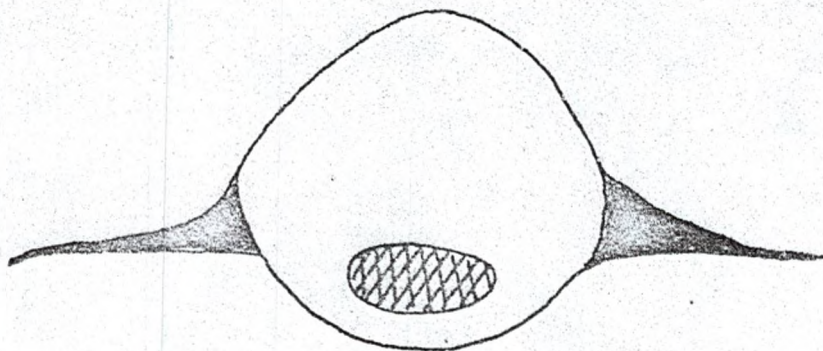


Fig. 4.--Sectional view of F. obscuripes mound typical of habitats having poor drainage and encroachment of vegetation upon the soil embankment.

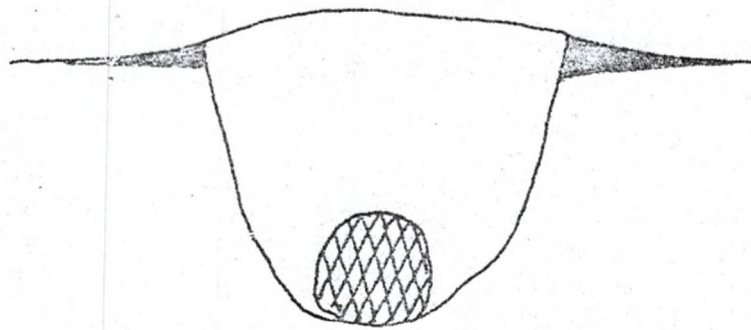


Fig. 5.--Sectional view of F. obscuripes mound typical of habitats with little ground cover and good drainage. Thatch surface usually only a few centimeters above ground level.



Materials Used in Nest Construction

The organic remains of herbs, shrubs and trees used in mound construction represent most of the species found in the immediate vicinity of the nest. While most mounds are constructed of either twigs or grass culms, depending on availability, other material is used as well. For example, a seasonal phenomenon is the deposition of dried seeds and fruiting bodies on the surface of the mound. The attraction of the worker to these new additions to the environment is so great that other materials, at least for a time, are almost completely covered by basswood fruits or the winged fruits of the green ash.

Generally, species diversity of nest material increases with the size of the mound. At least eleven mounds measuring no more than 11 to 16 cm in diameter were found to be constructed of twigs essentially from one species of plant, the American elm. Kentucky blue grass was the common ground cover but was used only sparingly as thatch. Following the initial dome construction the number of plant species used increases. Mounds larger than 50 cm are comparatively diverse in the number of plant species used, usually limited only by the species diversity of the immediate environment and by the size and weight of the material. Exceptions to this were found in nests located in the North Unit of the Theodore Roosevelt National Memorial Park in western North Dakota. Two mounds were constructed entirely of twigs of the badlands cedar (Juniperus scopulorum), although grasses and herbs were abundant in the nest area. Apparently the cedar twigs were attractive building material even though these had to be transported about 15 meters to the nest site.

The selection of material by each worker may be one of imitation.

That is, the selection made by the first worker may be repeated by others that follow. This may explain why fragments of few plant species are used in the early stages of mound construction and why some materials seem to be excluded as a building material in one nest and extensively used in another. It seems probable that odor may play an important role. Materials, such as cedar twigs, basswood fruits, and some seeds may be highly attractive in this respect. Sight is likely also important in the selection of material. Marikovsky (1965) in his study of the red ant, Formica rufa L., indicated that workers display a high degree of interest in new additives to the environment, particularly if these additives are different, i.e., shining or glittering. He also demonstrated that the attention of old ants to new material was more intensive than that shown by the younger ones.

The size of material used varies considerably. Grass culms, which are relatively light, may exceed 10 cm in length, while material which is denser such as twigs of oak and elm may be no longer than 7 or 8 cm. Pieces of organic material less than 1 cm in length are included in the thatch as well as particles of sand and soil pellets less than 2 mm in diameter.

Samples of thatch taken from the mound surface, the mound 10 cm below the surface, and the brood chamber of 20 nests were classified according to the following arbitrary categories: thatch less than 15 mm in length; 15 to 30 mm in length; and greater than 30 mm. The mean length of thatch in the 30 mm and larger categories was found to be 36.7 mm as compared to a mean of 22.1 mm for thatch between 15 and 30 in length. The mean was not determined for thatch less than 15 mm. The percent of sample by weight of each of the three categories is

shown in Figure 6. On the average the percentage of material less than 15 mm in length was found to be more than the combination of the other two categories. This relationship between large and small material was not expected. The general appearance of the thatch surface and the dissected mound suggests that the bulk of the thatch would be made up of culms and twigs in excess of 30 mm in length.

Twelve additional samples of surface thatch were collected from nests and, on the basis of total mound diameter, four mounds in each of three categories were included: 0 - 25 cm; 25 - 50 cm; and 50 - 75 cm. Each sample was then separated into two categories: culms larger than 15 mm in length, and those smaller than 15 mm in length. The results of these measurements are expressed as a percent of the total sample as to both volume and weight in Table 1. The volume was determined by placing the thatch into a graduated beaker and gently shaking until no further settling of the material occurred. The tabled data was then analyzed statistically using the chi-square method in order to determine whether any significant differences are to be found in the type of thatch used when comparing small and large mounds. Field examination of nests seemed to indicate that small mounds have little material that cannot be classified as thatch and also that twigs and culms seem larger and more extensively used than in larger mounds. As the data have shown, there is no significant difference between the three size categories. Even more surprising was the fact that the material, both with respect to percent of weight and volume, was so nearly uniform.

I suggest that the erroneous conclusions reached by a cursory field analysis were due to two conditions. First of all, the apparent shift in size between small and large mounds may have been illusory, twigs

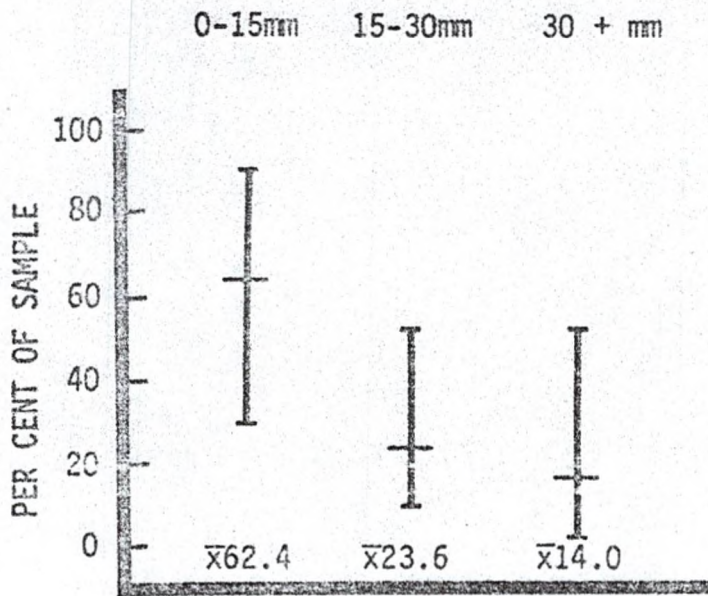


Fig. 6--Percent of sample by weight of each of three categories of thatch.

TABLE 1

## PERCENTAGE OF VOLUME AND WEIGHT OF CULMS AND DETRITUS

AS RELATED TO SIZE OF F. OBSCURIPES MOUND

Mound Size 0 - 25 cm					Mound Size 25 - 50 cm					Mound Size 50 - 75 cm				
Percentage Culms		Percentage Detritus			Percentage Culms		Percentage Detritus			Percentage Culms		Percentage Detritus		
Mound #	ml	g	ml	g	Mound #	ml	g	ml	g	Mound #	ml	g	ml	g
1	46	21	53	78	5	63	43	37	57	9	45	30	55	70
2	28	27	71	73	6	40	29	60	71	10	50	41	50	59
3	66	30	34	70	7	88	35	12	65	11	45	28	55	72
4	54	40	46	60	8	63	46	37	54	12	42	30	58	70
Mean	48	29	51	70		63	38	36	61		45	32	54	67

and culms simply appearing small on a large thatch surface; and secondly, on older mounds the thatch is compact with more of the detritus being retained on or near the surface.

#### Stage I. Incipient Colonies

Site Selection - In prior studies at other localities the most frequently mentioned nest sites are those associated with sagebrush in Idaho (Cole 1932) and wolfberry, Symphoricarpos occidentalis, in north central North Dakota (Weber 1935). Wheeler (1910) describes nests of woodland forms associated with stumps and logs or the roots of plants.

The site selected either by the queen or by workers, as the case may be, is probably a random choice dependent on local ecology. Any vegetation, living or dead, or inorganic material which affords easy access to shelter at or below ground level may be utilized. At the Forest River Biology Station wolfberry or tufts of grass are the most frequent loci about which mounds may be constructed in the prairie habitat, while within the woodland habitat construction is usually associated with decomposing logs, stumps or branches (Plate II).

Excavation frequently revealed some characteristics of initial mound construction (Plate III). In extreme cases, small logs 10 to 15 cm in diameter and 60 to 90 cm in length were completely buried; in others the intact root systems were found in the area of the brood chamber or just below it. In young mounds the stems were frequently found attached to the trunk.

Preparation of Site - Although evidence is circumstantial, the control of mold and the suppression of the growth of higher forms of

## PLATE II

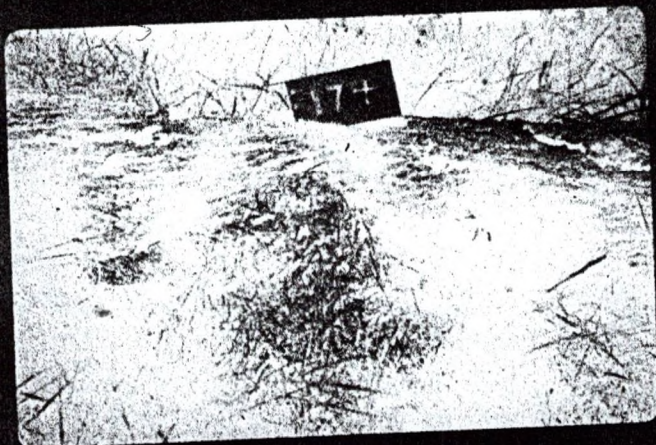
SURFACE VIEWS OF OBSCURIPES MOUNDS

1. Surface of mound showing protruding stems of dead and decaying wolfberry.
2. Mound associated with a large partially decomposed log. Thatch banked along one side with chambers and galleries extending into log.
3. Mound formed around the end of a small log about 10 cm in diameter.

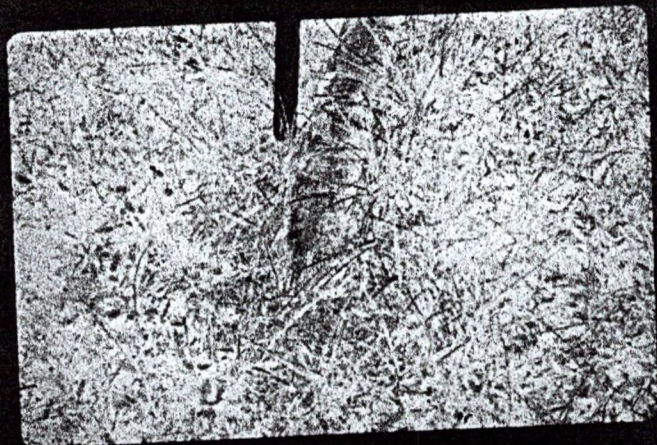
PLATE II



1.



2.





## PLATE III

DISSECTED OBSCURIPES MOUNDS

1. Dissected mound showing the buried root system and stem of wolfberry.
2. Dissected mound showing a partially decomposed stump about which the mound was constructed.
3. Mound with a small rock as a nucleus about which the incipient nest may have been constructed.

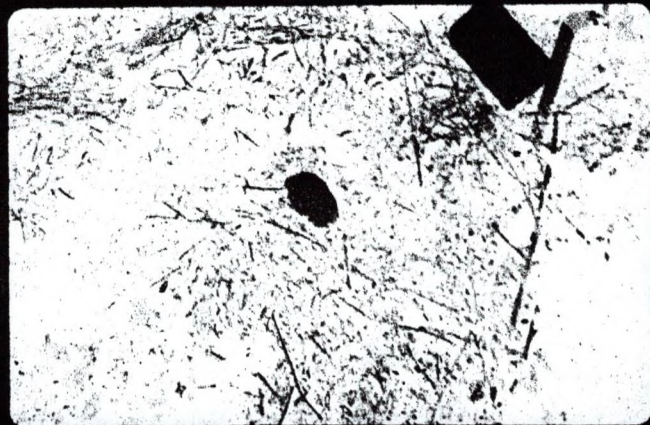
PLATE III



1.



2.



3.

plants seem to be of utmost importance in the early stages of mound construction and in maintaining the mound in later stages.

Cole (1932) noted that F. obscuripes workers sprayed formic acid on the cambium of young plants which were growing up through the mound. The dead stems and leaves were later removed and incorporated into the existing thatch. I have observed this phenomenon also in mounds associated with dense stands of smooth brome grass. In each case, the grasses were first killed, and when dry, the culms were cut at thatch level. These pieces, 30 to 40 cm in length, were cut again and the smaller lengths placed on the thatch surface.

Of its European equivalent, Formica rufa, Marikovsky (1965) stated that in the process of building their nest the workers do not carry building materials through the nest entrances except for some small sticks which may contain resin. This is not used as building material but rather the resin appears to be a source of disinfectant which prevents molding.

Since the thatch at the deepest point of penetration, except in very old mounds, is usually found in a remarkable state of preservation, one must assume the obscuripes workers also have a means of keeping mold at a low level. Circumstantial evidence would seem to indicate that the formic acid may be sprayed directly on the thatch and in this way suppress the growth of mold. On several occasions, when it was necessary to excavate a mound without first anesthetizing the workers, the thatch was removed from its pocket in the soil and laid to one side, within 2 days much of the scattered thatch had been reworked into a new mound about  $\frac{1}{2}$  the size of the old. Such mounds have a strong formic acid odor both within the thatch and in the grass mat below it. About

a week later this mound was found to be vacated, the colony probably having dispersed due to the loss of its queen. The thatch was removed at this time and the grass mat exposed. The root systems as well as stems and leaves appeared to be dead, and no further growth was observed for a period of at least one month following abandonment of the nest.

Description - Typically, mounds in the initial growth stage are 10 to 15 cm in diameter with a height of 5 to 8 cm; a soil embankment and defined brood chamber are lacking.

The thatch surface may contain several openings leading to small tunnels and chambers located within the leaf mold or soil (Plate IV). The amount of tunneling is slight, the majority not exceeding 30 cm in length nor more than 8 cm in depth. Five percent of observed mounds fall within this category.

#### Stage II. Mature Colonies

Stage II mounds range in size from 15 to 75 cm in thatch diameter with a total diameter of 40 to 150 cm. The height varies considerably. The lowest measured were no more than 3 to 5 cm above ground level and the highest slightly less than 1 meter.

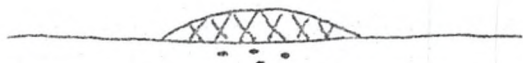
The mound may be characterized by the presence of a soil embankment, thatch which in part is below ground level, and a brood chamber (Plate V). Approximately ninety five percent of the mounds studied fell within this category.

Of particular interest is the manner of dome construction and soil removal. Mounds established in a habitat consisting of a single dominant plant species, such as smooth brome grass, provided a means by which this process was followed.

## PLATE IV

STAGE I MOUND OF F. OBSCURIPES

1. Stage I mound with small thatch surface about 15 cm in diameter. Thatch composed entirely of smooth brome grass culms.



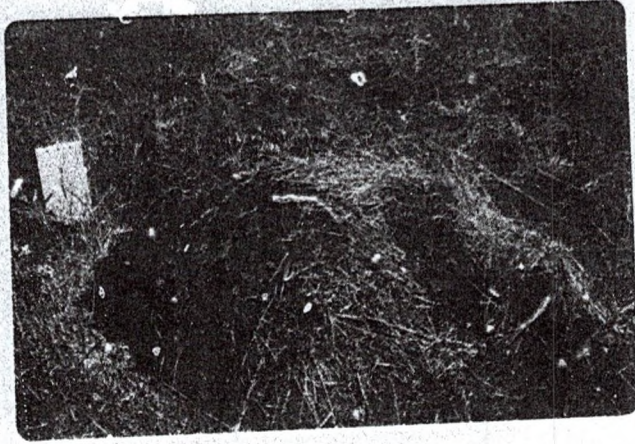
—|—| = 10 cm

2. Section of the same mound redrawn from field notes. Lack of excavation is typical of mounds within this category.

## PLATE V

STAGE II MOUND OF F. OBSCURIPES

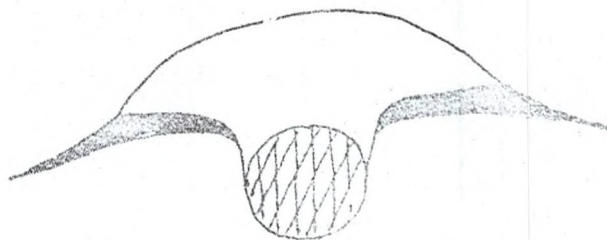
1. Surface view of typical Stage II mound.
- 2-3. Cross sectional view of this mound showing soil embankment, excavated pocket containing thatch and brood chamber.



1.



2.



3.

Soil removed from below the thatch and deposited at its periphery is an excellent site for invasion by pioneer plants, such as quack grass (Agropyron repens). Two such mounds were dissected and samples of thatch removed from three areas (Figure 7): 1) the surface, 2) the approximate center of the mound above the brood chamber, and 3) at the thatch periphery about 15 cm below the surface. Culms were randomly selected from each sample and identification made on the basis of epidermal characteristics. As previously noted, grasses growing on the periphery of a mound are often killed and then cut into sections. These are easily distinguished from other material by their peculiar appearance and degree of preservation. Most material utilized in construction was selected from available debris and shows a certain degree of deterioration while freshly killed and cut material does not. This type of material was noted in other mounds. In this manner the absence of the invading plant species could be determined.

Analysis of samples one and two showed the presence of two species in samples one and two (smooth brome grass and quack grass) and one species (smooth brome grass) in sample two. This pattern suggests that as the soil is added beneath the thatch the dome continues to grow by the addition of material at the surface; however, there is no mixing of the material. Apparently the thatch at the base of the mound is the original thatch and is not replaced during the lifetime of the nest. The grasses are distributed on the surface and along the side of the mound by a horizontal growth not only by compression and collapse but also by new material falling into spaces created by the thatch (Figure 8). Chauvin (1968), in his study of the European



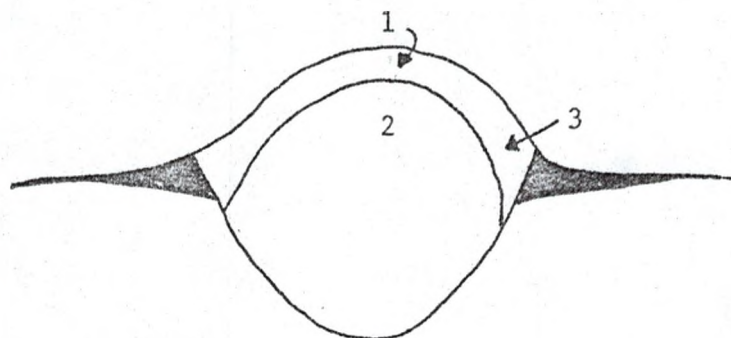


Fig. 7.--Sectional view of *F. obscuripes* mound showing locations from which samples were taken.

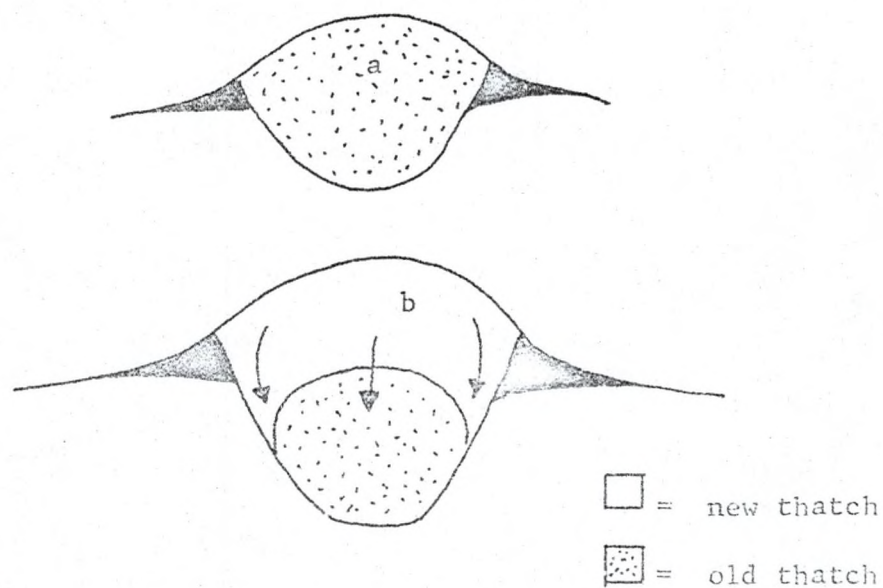


Fig. 8.--Sectional views of *F. obscuripes* mounds showing probable movement of thatch material as the mound grows in size.

red forest ant, Formica rufa, found that the surface thatch was constantly being redistributed, possibly for the suppression of the growth of mold. However, there was no indication that the process was repeated with material below the immediate surface.

Shading and the direction of greatest solar intensity have been shown by Scherba (1958) to be significant factors in nest orientation and construction in Formica ulkei. He concluded that alternation of direction of greatest solar intensity is accompanied by corresponding alterations in the orientation of the long slope of nests. While no consistent slope values have been noted for F. obscuripes, it became apparent that a certain number of Stage II mounds had an east-west axis 2 to 5 cm longer than north to south. Some of these value differences were attributed to excessive mound erosion, but most seemed to be related to the amount and direction of sunlight received. Since the majority of the asymmetrical mounds were in areas of little or no shade, it was assumed that the workers were reacting negatively to light.

The activities of workers of ten mounds, five shaded and five without shade, were observed on warm (70-80° F) summer days from early morning until near sunset. On cloudless days surface activity on exposed mounds was essentially limited to the west slope during morning hours, north slope during midday, and east slope in late afternoon. No differences in activities were observed for those mounds receiving shade from clouds or vegetation. Construction, i.e., the placing of culms and twigs on the mound surface, was therefore limited to surfaces which afforded some degree of protection from the sun. In this manner the east-west axis received greater attention on the part of workers. Correspondingly, the lack of activity on the south face of the mound

caused the north-south axis to be shorter.

### Stage III. Senescent Colonies

Mounds within this category were not numerous, only eight in various stages of activity and decay were observed during the six year study period.

The most striking characteristic is the crater-like appearance when viewed in section (Plates VI, VII). This is the result of collapse and compression of the thatch material in the lower two-thirds of the mound.

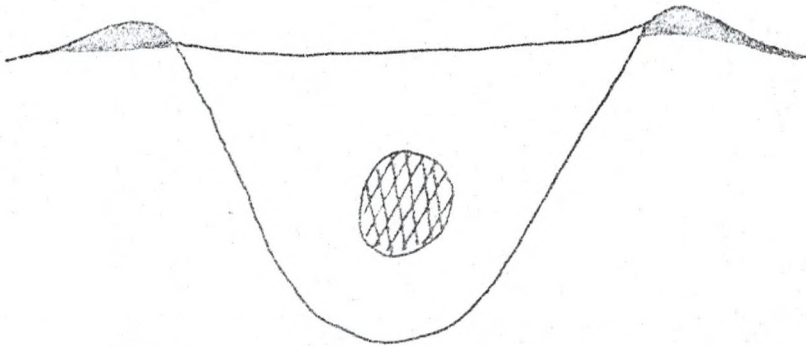
Most evident, on first opening the nest, is the musty odor of decomposing organic material. Dissection of mounds transitional between Stages II and III indicated that this process was quite rapid (3 to 5 years) and increases with decline in population. Low counts of the worker population suggested that the colony was no longer able to suppress the growth of mold and as a result the thatch began to decompose and undergo compaction. This factor, along with the lack of surface construction, caused the formation of the crater.

Deterioration of the nest begins with the decomposition of thatch at its apex (Plate VIII). With further reduction in colony size this deterioration extends upward along the wall of the excavation and then inward toward the center of the mound as viewed from the surface. In the largest and probably the oldest mounds the characteristic thatched appearance, when viewed in section, was almost obliterated. Few passageways and chambers existed in the lower two-thirds of the nest. The brood chamber, when present, was reduced to a fraction of its original size and decomposition had altered much of the thatched material until it had the appearance of rich, coarse, brown humus (Plate VII).

## PLATE VI

STAGE III MOUND OF F. OBSCURIPES

1.

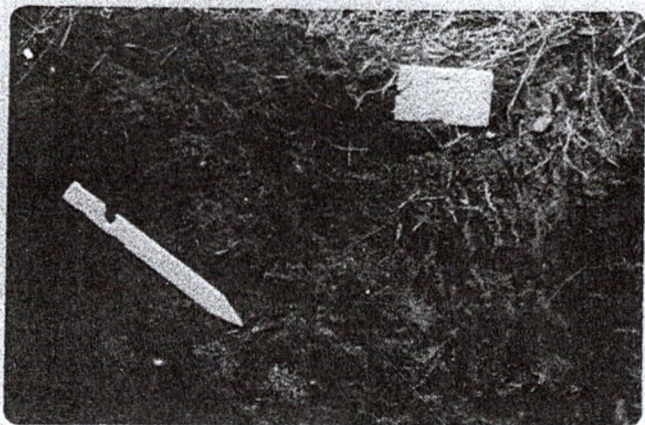


2.

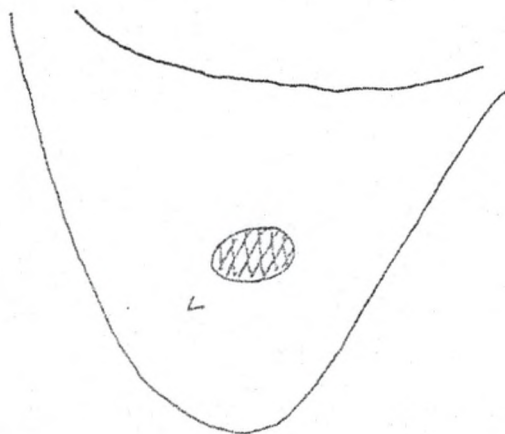
1-2. Surface and cross sectional views of a Stage III mound showing the initial collapse of the thatched dome resulting in a small crater.

## PLATE VII

## CROSS-SECTIONAL VIEWS OF STAGE III

OF F. OBSCURIPES

1.

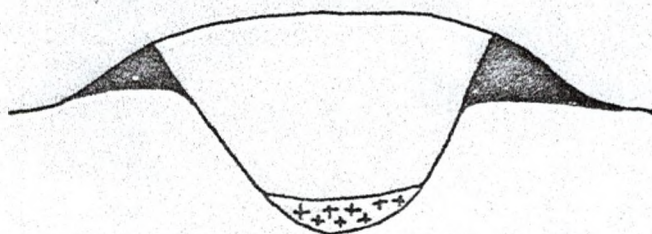


2.

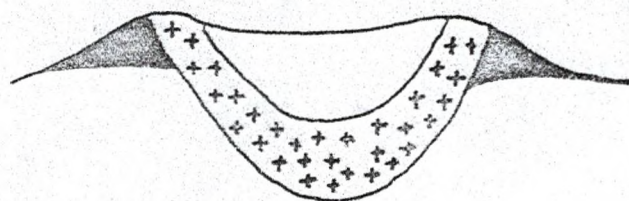
1-2. Stage III mound showing typical crater formation. Pointer indicates tip of marker stake placed on surface about five years prior to dissection of mound.

## PLATE VIII

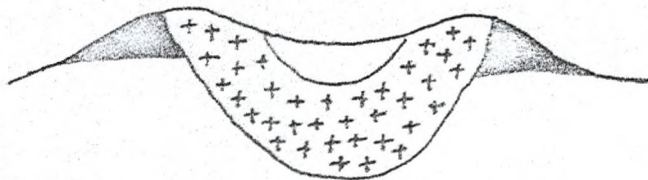
DIAGRAMMATIC REPRESENTATION OF SENESCENCE OF

F. OBSCURIPES MOUND

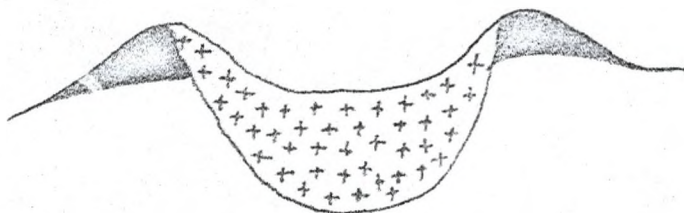
1. Late Stage II.



2. Early Stage III.



3. Mid-Stage III.

4. Complete extinction and  
crater formation.

Craters vary in size with the largest about 85 cm in width and 28 cm deep. These apparently persist for a number of years following nest extinction. A few were partially obliterated by the effect of water erosion and were often further obscured by the growth of grasses and herbs. However, the organic material in the center of these structures is undoubtedly the fine remains of thatch, thereby attesting to their origin. Complete sequence of mound development shown in Plate IX.

#### Growth Curve

It has been shown that the mound growth rates of some species of ants follow a predictable pattern. Andrews (1925) measured the growth in size of a single mound of Formica exsectoides over a 19 year period. His observations indicated a period of slow growth followed by an acceleration, a leveling off, and finally a decrease in size as the mound becomes inactive. King and Sallee (1953) reported similar growth patterns for the first year's growth of F. obscuripes.

To determine whether or not the mound growth rate for F. obscuripes has a predictable pattern beyond the first year, measurements were made of fifty active mounds. Selection was made to include equal numbers in each stage category. In all cases two measurements were made, one of total diameter (= thatch plus soil embankment), and the other of thatch diameter only. For purposes of establishing a growth curve only, the latter was used because the soil embankment was found to be too variable. In some mounds, it was quite extensive and in others apparently of the same size it was totally lacking. The amount of thatch also proved to be more useful in determining whether or not a colony was flourishing or declining.

Of the fifty mounds selected for this study only sixteen persisted

## PLATE IX

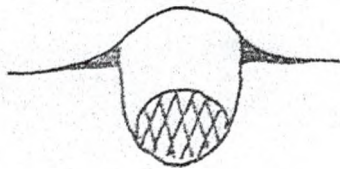
NEST SERIES SHOWING PROBABLE SEQUENCE THROUGH WHICH  
MOST F. OBSCURIPES MOUNDS PROGRESS.



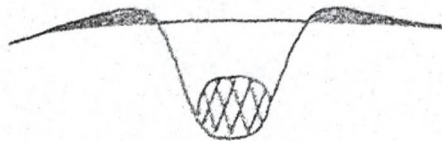
1. Stage I mounds.



2. Stage II mounds.



3. Stage II mounds.



4. Stage III mounds.



long enough to provide useful data. The relationship with respect to growth rates between mound diameter and age is shown in Figure 9.

Two mounds were observed throughout the initial period of construction beginning in the latter part of June and continuing until the end of August. Total growth for the two mounds during this period of time averaged 30 cm. Both were destroyed the following winter. Three small mounds, apparently in their first season of growth when discovered, were studied. Their mean thatch diameter was 18 cm. At the end of two and one half seasons of growth mean thatch diameter was 43 cm. Five mounds which had a mean thatch diameter of 28 cm when first measured averaged 58 cm at the end of six growing seasons. Six additional mounds were measured during the second year of the study period. The mean diameter of the first measurement was 60 cm and the mean of the final measurement six years later was 67 cm. Mounds which have reached their zenith, that is, maximum size has been attained (75 to 90 cm thatch diameter), may remain stable for a number of years. Annual measurements of eight mounds within this category have shown no further change. Beyond this point, probably between 10 and 15 years (maximum queen longevity is believed to be about 15 years), the growth rate becomes negative. Much of the original thatch surface falls into disrepair. That which is maintained by workers, such as removal of new plant growth and number of openings into the mound, may decrease by as much as 50 percent. Since only four of these mounds were available for measurement and then only during the seventh year of the study period, I have no data on the rate at which this negative growth occurs. That these colonies are young is a possibility. In several instances it seems quite likely that a new colony was established in the old

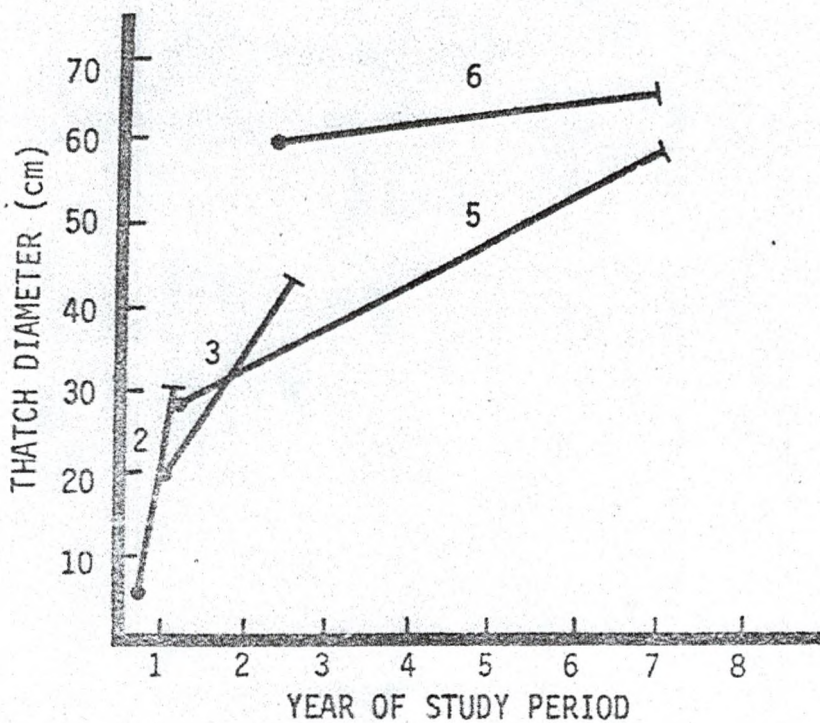


Fig. 9.--Mean growth rate of 16 F. obscuripes mounds measured annually during all or part of a seven-year period. Number of mounds measured and averaged within each size range is indicated above line.

mound following its extinction. Such mounds are typically asymmetrical, that is, the thatch material and brood chamber are not centrally located but are to one side. However, the four mounds referred to earlier did not have these features and were in all likelihood first generation mounds.

Of the 28 mounds in cluster A, study area 1, measured during the summer of 1970, ten were relocated and remeasured in July of 1971. The results which are similar to those described above, are presented in Table 2.

TABLE 2

ANNUAL GROWTH RATE OF TEN F. OBSCURIPES MOUNDS MEASURED  
DURING THE SUMMERS OF 1970 AND 1971.

	Diameter 1970	(cm) 1971	Total growth
Stage I	28	38	10
	28	46	18
Mean			14
Stage II	41	51	10
	46	56	10
	46	48	2
	46	56	10
	58	69	11
	66	61*	-5
	71	66*	-5
Mean			4.7
Stage III	76	76	0

\*Negative growth rate

Mounds either within the Stage I category or transitional between Stages I and II showed the greatest amount of growth with a sharp decline in the larger Stage II nests. Two mounds showed negative growth rates. Both of these were large, averaging 68.5 cm when first measured; however, measurement of mounds of this size is subject to error because the point of contact between the thatch and the soil embankment is not always well defined. On the basis of form and population only one mound of the original 28 could be considered as being within the Stage III category.

The overall growth curve is shown in Figure 10. That part of the curve extending beyond the seven years of the study is based upon extrapolation of data. Growth during the initial stage is rapid, the thatch diameter doubling in the latter half of the first growing season. Growth continues at a slower rate for the next two years while growth beyond three years is uniform and arithmetic. The declining phase may be of short duration since only a few in this growth form have been observed in an active state. These were subsequently dissected and thus not available for annual measurements.

#### Population Characteristics During

##### Mound Growth

##### Major-Minor Ratios

As earlier results have shown, there is a positive correlation between mound size and population. To what degree these changes in population size are reflected in major-minor ratios is of special interest since such ratios may throw some light on events which lead to mound extinction.

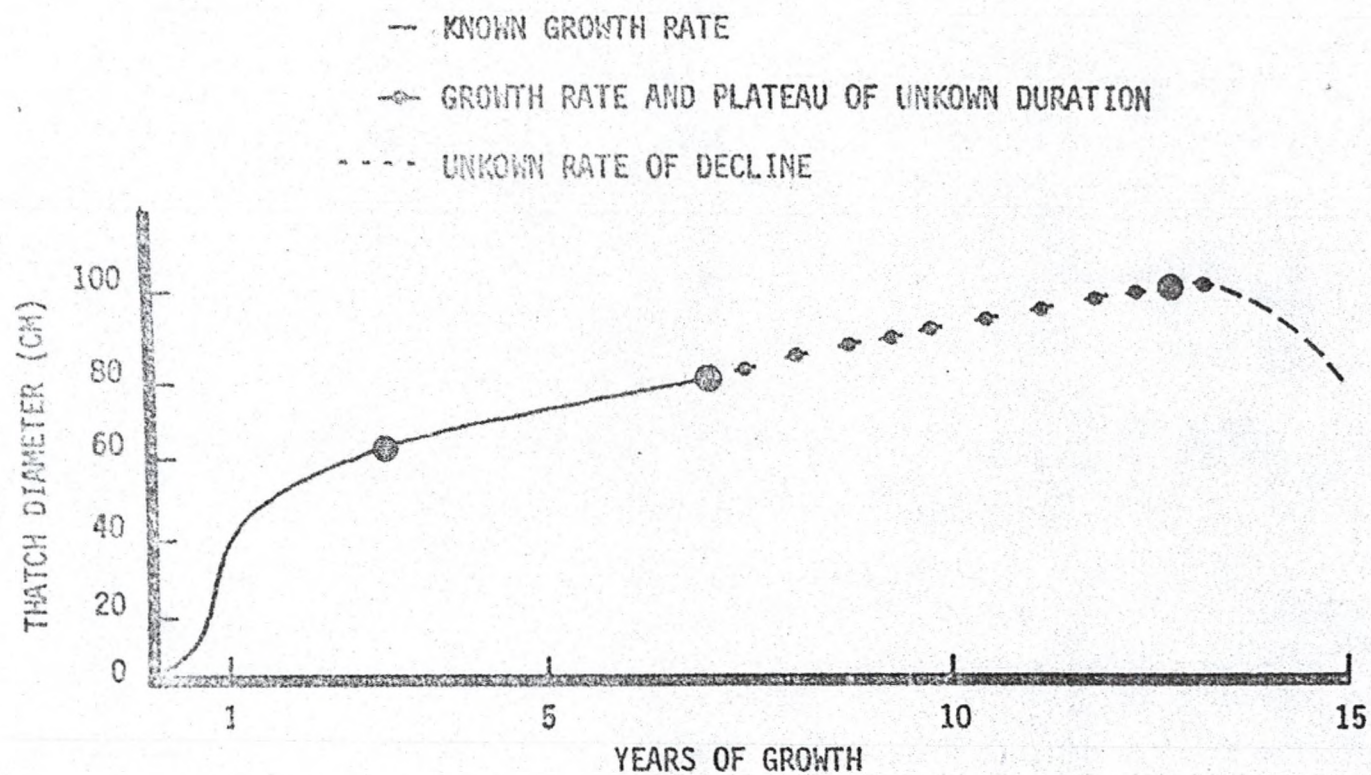


Fig. 10.--Growth curve of F. obscuripes mounds based on an extrapolation of data covering a seven-year period. Dashed line is based upon Stage III mounds which gradually die out.

Nine random samples were taken from mounds ranging in size from 38 to 193 cm in total diameter. No mounds in early Stage I were selected because of the possibility of worker cooperation and/or communication between nests. The thorax of workers from each sample was measured, anterior to posterior on the lateral surface, and on this basis the worker population was separated into three arbitrary categories: majors, larger than 2.75 mm; medias, smaller than 2.75 and larger than 2.50; minors, smaller than 2.50. These measurements corresponded generally with head color, i.e., red of majors, dark red of media, and black of minors. Total mound width, sample size, number and percentage of workers in each category are shown in Table 3.

TABLE 3

TOTAL MOUND WIDTH, SAMPLE SIZE, NUMBER AND PERCENTAGE OF WORKERS AS RELATED TO MOUND WIDTH IN F. OBSCURIPES.

Sample No.	Total Mound Width	Sample Size	Majors		Medias		Minors	
			#	%	#	%	#	%
1	38cm	254	58	23	83	32	114	45
2	46	156	31	20	54	35	70	45
3	64	72	15	21	24	34	32	45
4	124	123	11	9	38	31	73	60
5	140	210	31	15	44	21	135	64
6	152	288	63	22	49	18	173	60
7	173	328	42	13	114	35	170	52
8	183	89	9	10	13	15	65	75
9	193	192	38	20	29	15	123	65

In sample 1, a relatively small mound, the combined percentage of majors and medias is slightly greater than the percentage of minors; whereas, in a large stable mound, i.e. in sample 5, the combined percentage of majors and medias is much less than the percentage of minors.

The largest minor percentage is found in sample 8. This collection was taken from a large mound inhabited by a relatively small colony population, which correlated with the degree of deterioration of the thatch surface. In addition, very few workers were observed on the surface or within the mound; however, those present were actively engaged in maintaining the nest. In all probability, the colony was near extinction.

The mean value of percentages for each category within the range of mound sizes is plotted in Figure 11. The majors show the least amount of variation, as expressed as a percentage of the random sample from each of the nine mounds sampled, having a mean value of 17 percent with a high of 23 and a low of 9. The mean value for medias is 26 percent with a high of 35 and a low of 15. The greatest variation is found within the minors, the mean being 56 percent, with a high of 74 and a low of 45.

The percent of sample in each worker category in relation to mound diameter is graphically represented in Figure 12. As indicated by the relationship between mound size and percentage, the majors and medias, taken as a group, show the least amount of variation. Both categories display a tendency toward decreasing frequency with increased age of colony, while the minors show a definite increase in frequency in samples taken from large Stage II mounds. The meaning of these correlations is not clear; however, some inferences can be drawn based on studies of polymorphism and caste origin.

Ford (1966), Sheppard (1966) and Wigglesworth (1966) suggested that polymorphism is probably due to the interplay between the genetic constitution of the individual and its reaction to complicated environmental factors during development. Michener (1966) pointed out that nutrition plays an important role in the production of castes, colonies

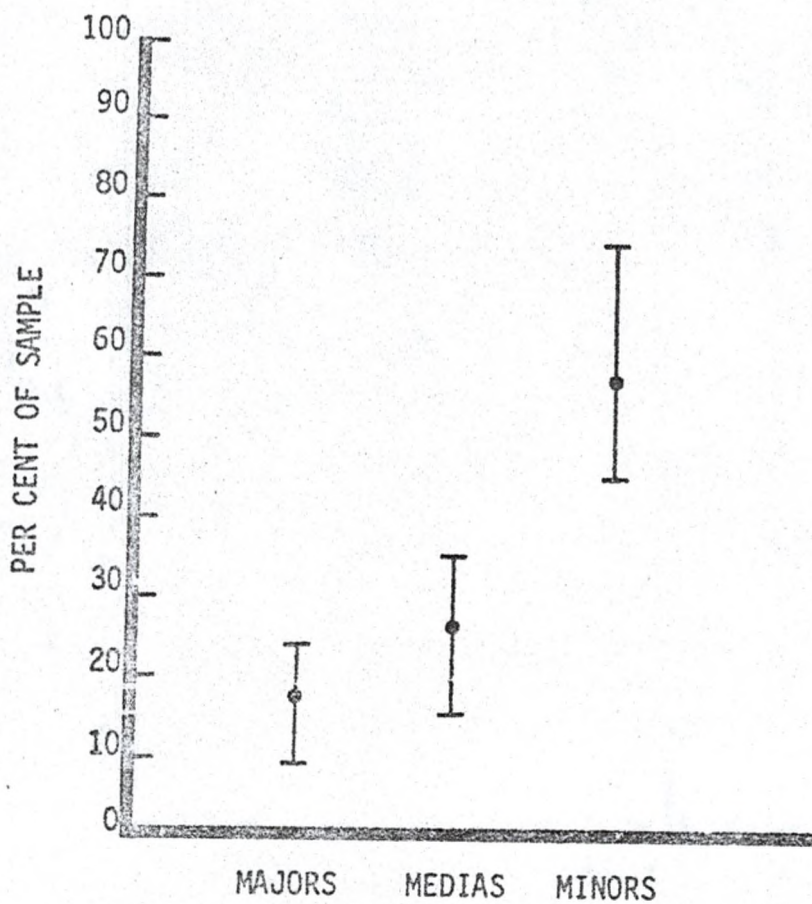


Fig. 11.--Populations of majors, medias and minors from random samples of 9 F. obscuripes mounds. The means are indicated by solid dots and the ranges by vertical lines.



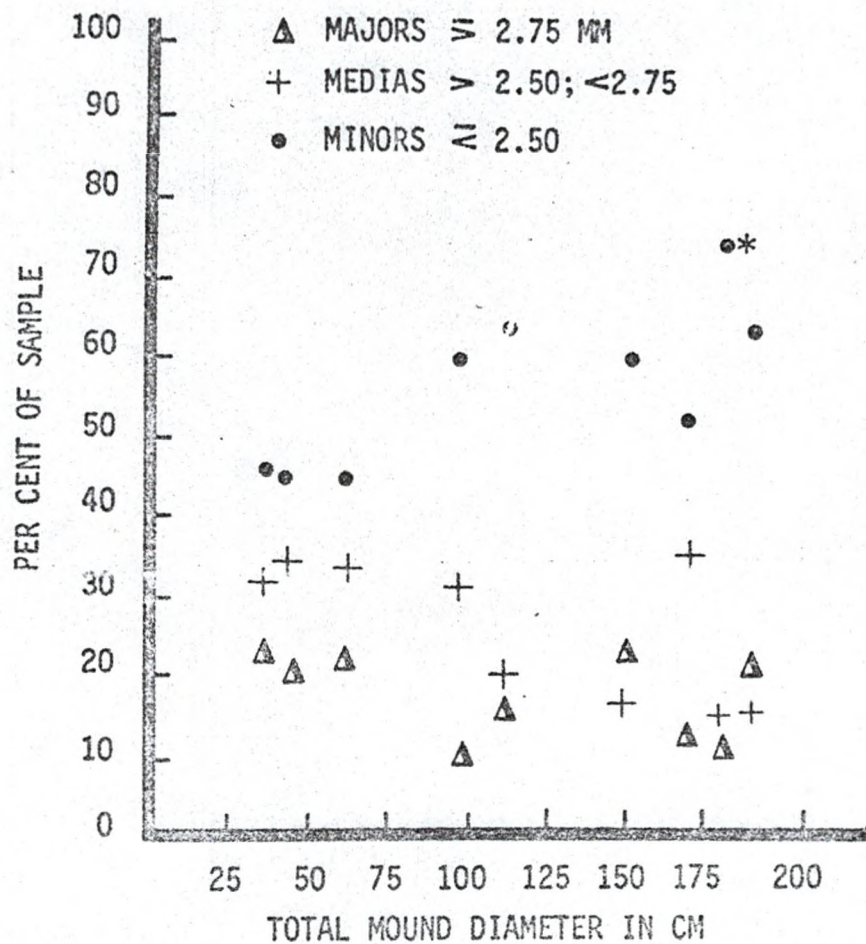


Fig. 12.--Number of *F. obscuripes* medias and minors plotted as a percentage of each random sample. Asterisk marks declining Stage III mound.

with normal diets producing both soldiers and workers, while those with abnormal diets produce all workers. In Pheidole pallidula Nylander the first workers produced by the starved queens were unusually small. A similar report by Flanders (1952) stated that the production of worker castes is influenced by the environment of the queen or the state of the colony.

If F. obscuripes colonies follow a predictable life cycle as shown by nest form and population counts, such factors as queen senescence and population size may indeed have an effect on worker ratios, although data to substantiate this hypothesis are lacking.

The five smallest workers from each nest were measured for scape length and head width. The results, plotted in Figure 13, show a separation of workers from small and large mounds, the smaller workers in general being from the larger mounds. It remains to be seen whether the production of smaller-sized workers is due to colony senescence or to the state of the colony, as suggested by Bodenheimer (1937) and Flanders (1952).

The major-minor ratios in this study represent collections taken at a single point in time, and only from the nest surface. It is not known whether these ratios at the surface may change during the day, but it is certainly a possibility. King and Walters (1950) found a distinct division of labor among F. obscuripes workers with minors attending aphids and the majors on trails seemingly carrying honey-dew collected from the minors. If such activities are altered during the day, it seems possible that the daily routine of workers may be reflected in the major-minor ratios.

Ratios may also reflect seasonal changes. Markin and Dillier

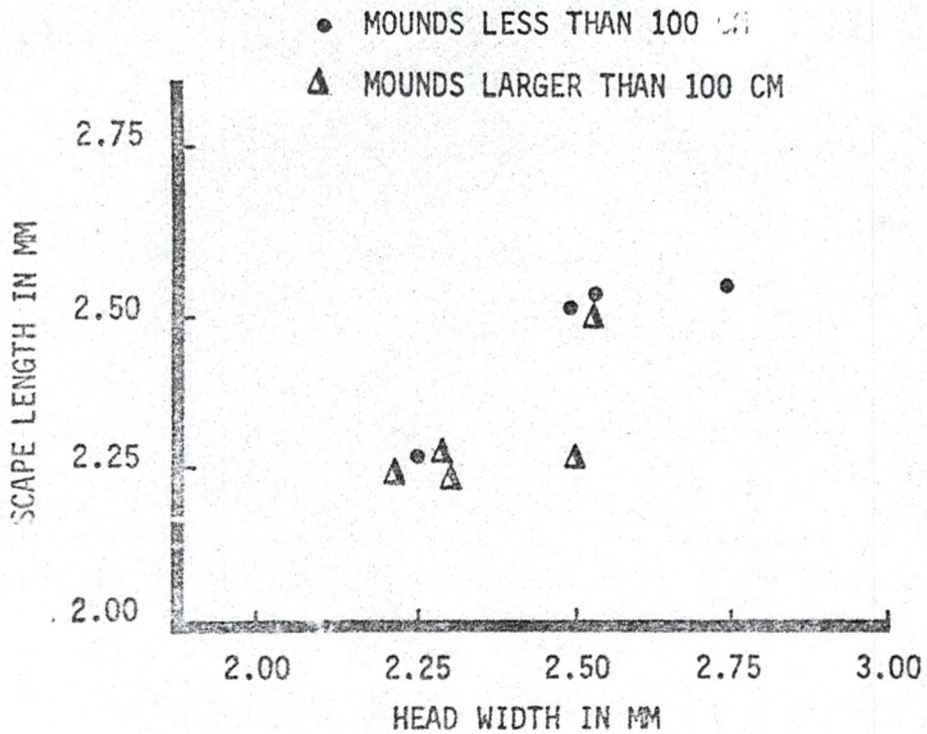


Fig. 13.--Relationship of smallest *F. obscuripes* workers to mound diameter. Each point represents the average of the smallest five workers from each sample

(1971) in their study of the imported fire ant, Solenopsis saevissima richteri Forel, in the southeastern United States found a seasonal change in major-minor ratios with the highest percentage of major workers occurring in April and May and the lowest in October and November. They attributed this shift to the fact that majors could survive the winters better than minors.

Hsu (1970), in his biometrical studies of interspecific differences between species, found that different ant hills may show a more or less strong variation in size indicating a lack of uniformity of the species.

Sanders (1964) determined the frequency distribution of head widths of workers from three colonies of Camponotus herculeanus (L.). All three showed a tendency toward a bimodal curve. Minors were found to be more frequent than majors, especially in the smallest colony. As mentioned previously, this finding is in accord with Michener's (1966) contention that starved queens produce small workers.

A high frequency of minors in small colonies was not found in any samples taken from Stage I mounds used in this study. As shown earlier, distribution patterns tend to indicate that most of these colonies resulted from budding. Queens are apparently adopted into the nest following establishment of the bud colony. This kind of colony development likely provides the queen with adequate nourishment so that the proportion of minors is relatively low. As a result colonies in Stage I may not fit the pattern of development suggested by Michener (1966)

#### Population Growth Curve

Most investigators have concluded that on the basis of actual worker count there is little correlation between mound size and population. Yung (1900) emphasized the wide differences found in mounds

of Formica rufa, one having a population more than five times another with no correlation between mound size and number of inhabitants. Dreyer (1942) estimated colony size of Formica ulkei by excavating the entire mound. He concluded that much variation exists within size categories but that generally larger populations occupy larger mounds. According to Weber (1935) F. obscuripes may be exceptional in this respect, the type of material used in construction dictates that mounds of large size cannot be maintained by a small population without undergoing extensive deterioration.

The correlation of mound size to population can be arrived at in a number of ways. Weber (1935), Cory and Haviland (1938), and King and Walters (1950) in studies of species of Formica excavated the entire nest and counted the worker population. Bitancourt (1941) used openings into the mound to determine colony size, making the assumption that an increase of openings into the nest was an indication of an increase in the worker population. Golley and Gentry (1964), Brian, Hibble and Stradling (1965) and Stradling (1970) used the mark - recapture method with phosphorus - 32 as a marker.

I excavated several entire nests of F. obscuripes, two mounds in Stage I, one in Stage II and two in Stage III. Additional Stage II counts have been made by Weber (1935) and King and Walters (1950). However, none of these counts is complete since no attempt was made to collect workers which were foraging or engaged in other activities away from the nest site. This method also has the disadvantage of resulting in the destruction of the nest.

Population counts of colonies inhabiting nests in the Stage I category have revealed no definite growth pattern. The smallest nest

(about 10.2 cm in thatch diameter) was found to contain only 24 workers and no brood. This colony may not have been solitary; therefore, the count may reflect workers migrating between parent and bud nests. The second Stage I count was of a colony taken from a nest 24 cm in diameter. The population consisted of 530 workers and 274 pupae and larvae. This count is probably quite conservative since it includes only those workers which were either engaged in nest construction or care of brood. The brood count in turn reflects only those immature forms which were collected along with the thatch material and does not include those which may have been located within soil chambers and galleries. A higher and more accurate count would have been achieved by taking the nest during cool evening hours after the majority of foraging workers had returned.

As shown in Table 4, population counts of colonies from Stage II mounds show a significant increase over those of Stage I.

The largest count (25,000 workers) was taken by King and Walters (1950) from a nest 83 cm in diameter. A total estimate made on the basis of this count was 50,000. Although from a larger mound (135 cm in diameter), Weber's count is less, with 16,481 workers and an estimate of several thousand brood. My third count was from a small Stage II mound (65 cm total diameter). Following anesthetization the workers were collected along with thatch and a count was made from  $\frac{1}{2}$  of the material. An estimate of 9,000 was made for the entire colony.

The vast amount of material incorporated into large Stage III mounds makes any attempt at worker count very difficult. For this reason only two mounds which seemed to be near extinction were examined. Both mounds were characterized by a deterioration of the thatch surface (only a fraction of the total area was maintained) and a collapsed dome creating

a pronounced crater. The first (170 cm in total diameter) was anesthetized and the maintained portion of the nest removed. The population was only 74 workers and five pupae. The remainder of the nest was then removed, but the degree of decomposition of thatch and the lack of chambers and galleries indicated that the peripheral area was no longer inhabited. The second Stage III mound was examined in a similar manner. A total of 11 Workers were found in the maintained portion of the nest. No brood were found and the brood chamber was lacking. Whether this nest represented the final stage of a declining mound or one being visited by stray workers was not determined; however, the lack of brood and the state of the thatch suggested that the nest had probably been vacated for some time.

TABLE 4  
WORKER POPULATION OF F. OBSCURIPES COLONIES AS  
RELATED TO MOUND DIAMETER.

Stage I		Stage II		Stage III	
Diameter	No. Workers	Diameter	No. Workers	Diameter	No. Workers
10 cm	24	65 cm	9,000	165 cm	11
24 cm	530	*83 cm	25,000	170 cm	74
		**135 cm	16,481		

\* King and Walters (1950)

\*\* Weber (1935)

As shown in Figure 14, there is a positive correlation between mound size and population of Stage II and Stage III mounds if a comparison is made, not on the basis of total mound diameter, but on the basis of that portion of the thatch surface which is kept in repair.

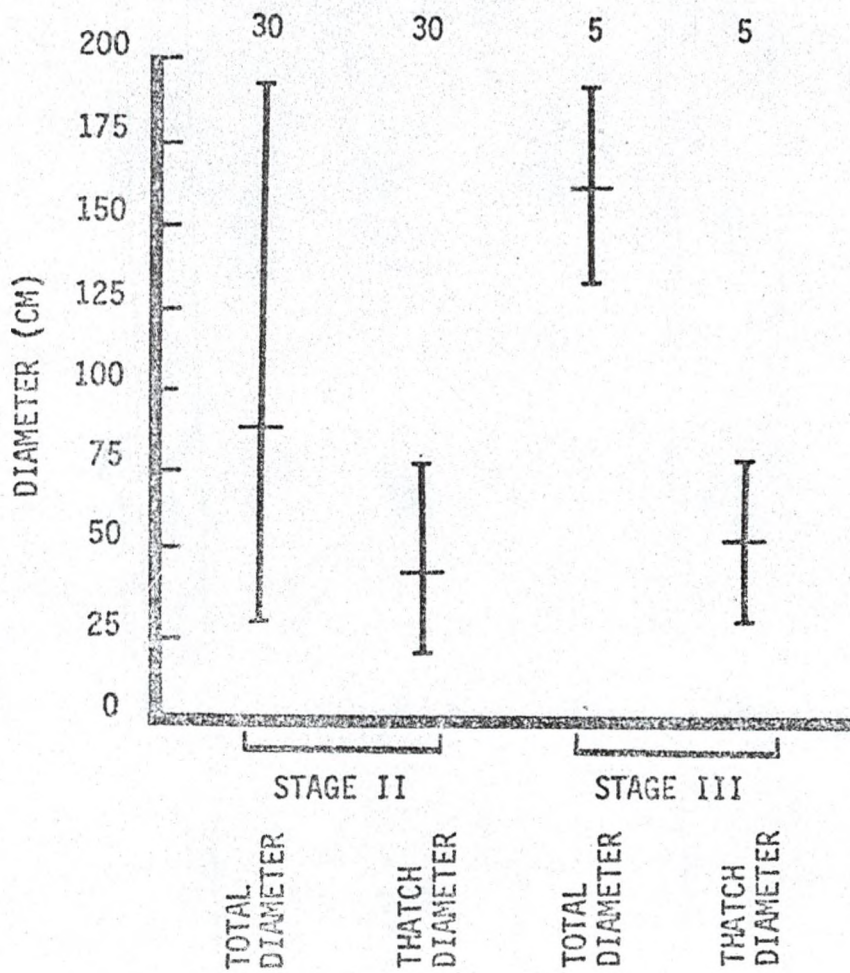


Fig. 14.--Comparison between total and thatch diameters of Stage II and Stage III F. obscuripes mounds. Vertical line represents the range of values and the horizontal line the mean. Number of samples is indicated above each line.



This relationship may be expressed as a ratio between total mound diameter and thatch diameter.

The mean of Stage II mounds with respect to total diameter was found to be 87 cm while that of thatch diameter 42.5 cm. The ratio of total diameter to thatch diameter was approximately 2:1. The five Stage III mounds are those which on the basis of thatch deterioration and the crater-like effect appear to be in a declining phase. The mean diameter was 160 cm and for that of thatch 55 cm. The ratio between total and thatch diameters was approximately 3:1.

### Colony Reproduction

The terms applied to colony reproduction are somewhat inconsistently used and need clarification. For example, the term "swarming" generally relates to the flight activity of alates (Kannowski, 1963), but has also been used with respect to the movement of entire colonies of ants from one site to another as reported by Muckerman (1902), Andrews (1932) and King and Sallee (1953). Golley and Gentry (1964) also describe a similar process, but in general terms. The term "budding" has also been used in a broad sense, usually referring to the establishment of a new colony by a queen and/or workers of the parent colony. King and Sallee (1953), Scherba (1958) and Talbot (1961) used the term, but without defining the final relationship between the parent and daughter colony or colonies.

For this reason the following terms and their restricted definitions are proposed: a) "swarming" is restricted to the aerial aggregations of alate ants and to the nomadic phase movements of army ant workers; b) "colony division" is used to cover cases of colonies splitting into two parts, each with one or more queens, each colony developing independently; c) "colony budding" refers to those cases where parts of a colony leave the mound and establish secondary mounds which remain connected at least temporarily to the main mound by trails; and d) "colony translocation" describes the case where an entire colony vacated an old nest and moves to a new one.

### Colony Translocation

Translocation in F. obscuripes was first reported by Muckerman (1902) and a detailed account was given by King and Sallee (1953). Apparently this phenomenon is rare. During my field studies from 1963 to 1970 I witnessed this event only twice, once in a prairie in Cavalier County.

North Dakota and again in the woodland habitat near the Forest River Biology Station.

The translocation process consists of the moving of workers, queens, pupae and larvae to the new nest either previously constructed or in the process of being constructed by the major workers. Few minor workers seemed to be engaged in this type of activity. Numerous pupae and larvae were observed being carried to the new nest and at times a major worker was observed carrying a minor or media worker. The apparently reluctant workers were picked up bodily and carried to the thatch surface of the nest. Once deposited they either disappeared inside or attempted a return. Of interest was the complete submission of the workers being transported; the entire body took on a relaxed attitude and remained so until released.

The time required for complete relocation is unknown. King and Sallee (1953) observed this process over a period of two days and noted only a small net movement toward the new site. Wheeler (1910) in his studies of the ant Pogonomyrmex molefaciens (Buckley) (now known as P. barbatus (F. Smith)) observed that it required almost three weeks for the old nest to be vacated.

There is no conclusive evidence as to the causes of colony translocation. Of the two colonies I have observed, neither seemed to be affected by adverse environmental conditions. Indirect evidence based on a number of recently abandoned sites indicated that most were no longer habitable, either because of excessive shading by trees or by plant growth surrounding the mound. At the University of North Dakota Oakville Prairie Field Station near Emerado, North Dakota I have observed several vacated nests near active mounds. The distance between

old and new mounds was no more than about 3 meters. These vacant mounds were characterized by dense stands of grasses and herbs growing on the soil embankment and thatch.

A negative reaction to shading has also been found in other species. Scherba (1958) found that most movements of Formica opaciventris colonies were from heavily shaded to less shaded environments. A similar account was given by Andrews (1932) for F. exsectoides.

#### Colony Division

The establishment of new colonies by this process is quite common among the exsecta group and detailed accounts are given by Scherba (1958) and Talbot (1961). Within the rufa group I have found this form of territorial expansion common to both F. obscuripes and F. oreas comptula. However, the process as it relates to these taxa has not been well studied. The only prior studies have been two concerning F. obscuripes (Weber, 1935 and King and Sallee, (1953).

During the summer of 1964, four areas containing concentrations of F. obscuripes mounds were located near the Forest River Biology Station. In each case the pattern of dispersion, i.e., a large mound associated with two or three smaller mounds, was highly suggestive of the possibility that each of these small clusters was the result of budding from a single mound. In order to determine if there is a relationship between the process of colony division and aggregate patterns within a cluster, three such areas were mapped: Area 1, cluster A (Figure 15) in 1964; and Area 1, cluster B (Figure 16) in 1969; and Area 2, cluster C (Figure 17) in 1965.

Mapping consisted of dividing the area of study into quadrats 5 meters square. The size and position of each mound was then plotted

Fig. 15.--Map of area 1 cluster 4 showing distribution of mounds and trails used by workers during nest construction and foraging.

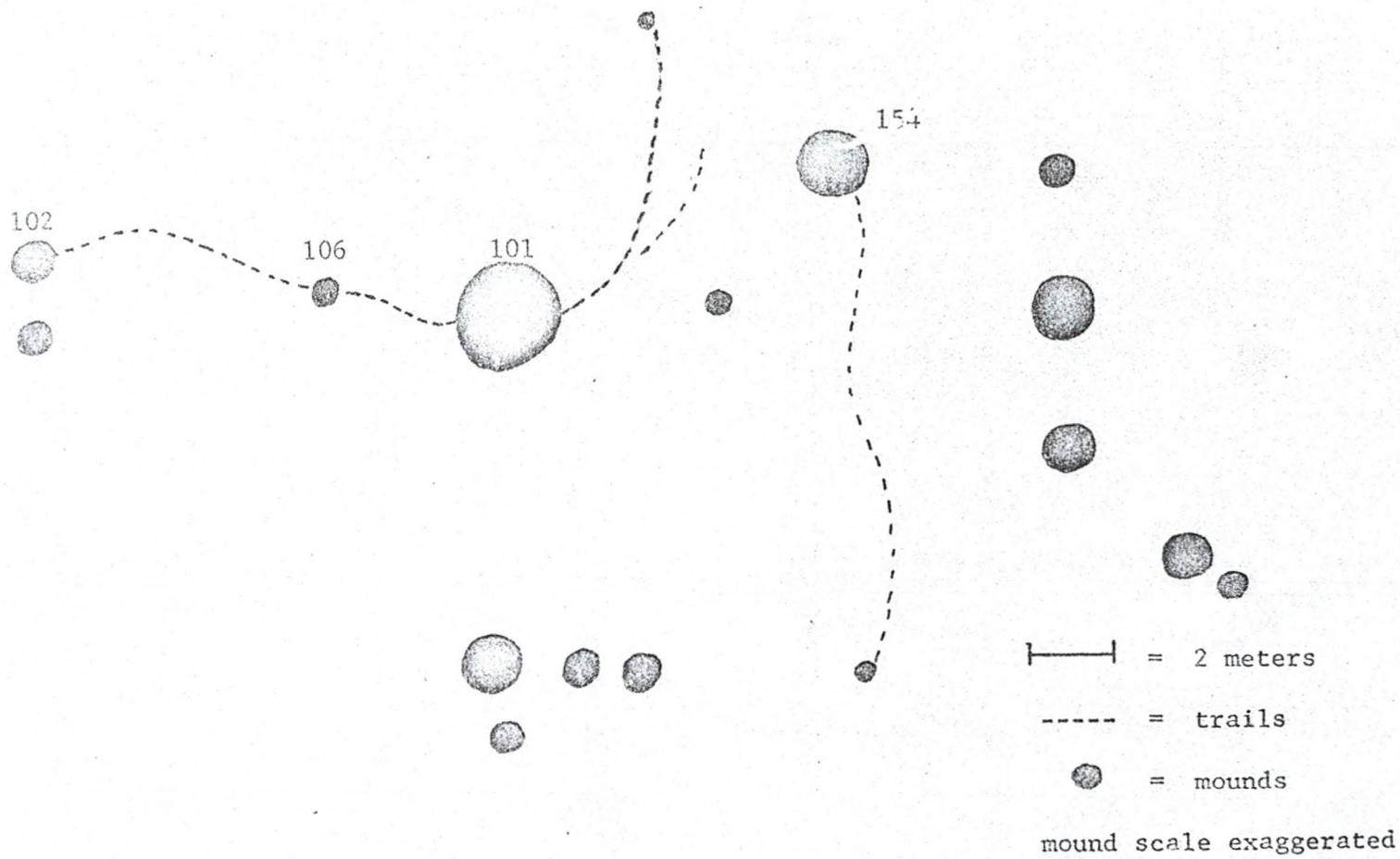


Fig. 15

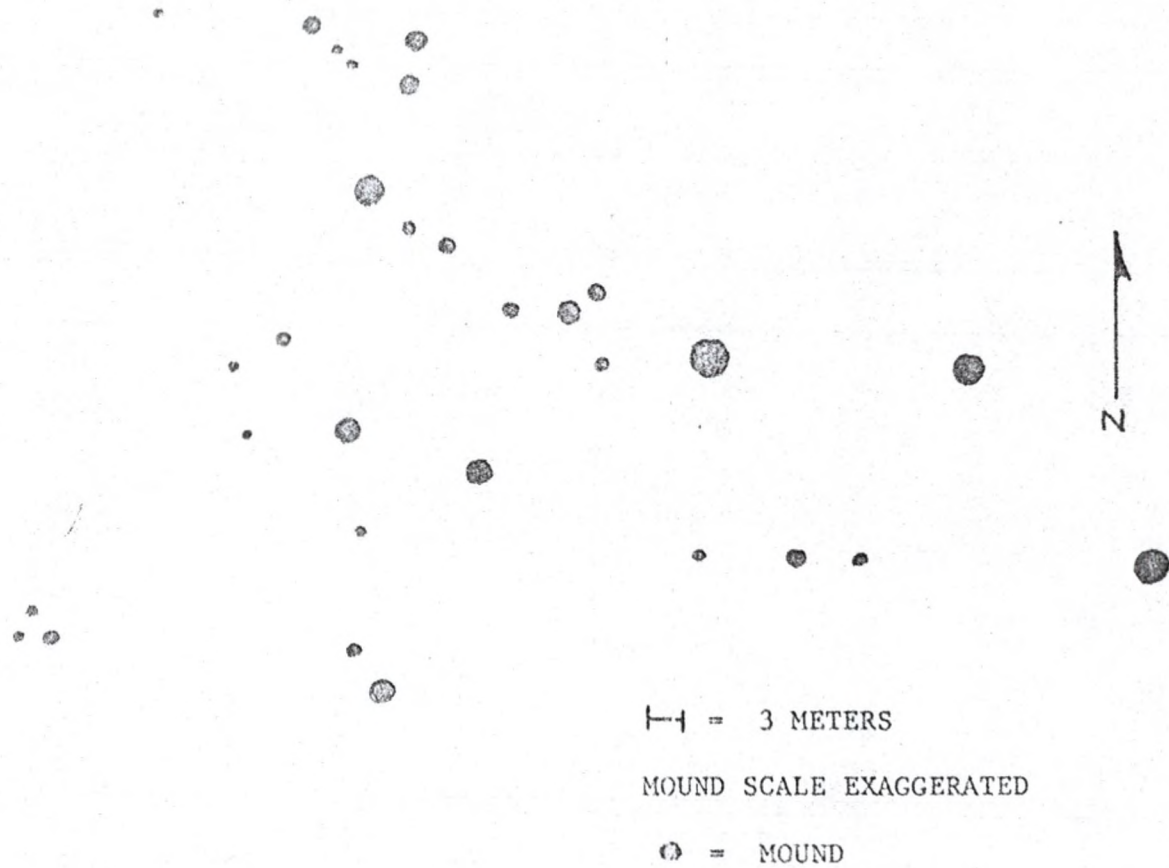


Fig. 16.--Map of Area 1 cluster B showing clumped distribution pattern and size relationship of mounds.

and the data used in determining the spatial relationship of colonies within clusters. Since isolated colonies are randomly dispersed the degree of aggregation of colonies within a cluster would indicate that most if not all of these colonies were the result of the process of colony division.

The type of distribution for clusters A and B was determined by the variance/mean method (Cox, 1967). This method is well suited to the use of quadrats when aggregates are closely grouped and widely spaced (Pielou, 1969). The ratios obtained by this method have values ranging from 1.0 for randomly dispersed populations, less than 1.0 for populations having uniform distribution patterns and greater than 1.0 for populations tending toward clumping. The results showed a high degree of clumping with a ratio of 1.7 for cluster A and 1.9 for cluster B. Cluster C was represented by few mounds, therefore, no analysis was made of the distribution pattern.

Within cluster A, on the basis of size and position mound 101 is clearly the focal point about which other mounds are scattered. Foraging trails originated from at least five different points on this mound. Three were followed for about 9 meters with no definite terminus; the fourth terminated at the base of a bur oak and the fifth, by far the longest (about 58 meters), led to the edge of the Forest River and to what appeared to be an incipient *F. obscuripes* colony. This mound (102) could not have been more than two months old since flood waters had inundated the area in early spring. The trail was well marked with workers moving rapidly in both directions, at times forming a column almost 5 cm wide. I estimated the column to be comprised of more than 5,000 workers.



The distance between mounds made it too difficult to follow individual workers from one mound to the other. Nevertheless, it was assumed at the time that a cooperative effort was taking place. The rapid rate at which the mound was built (28 cm thatch diameter when first measured) suggested that workers from 101 were actively taking part in its construction.

In August, a second mound (106) was found on this same trail about midway between 101 and 102. Its relationship to 102, if any, was not determined since the trail leading to the Forest River was no longer used. However, the trail continued to be well traveled between 106 and 101. Mound 102 was revisited in 1965 in order to determine whether or not communication with neighboring mounds had been reestablished but all indications were that the mound had attained completely independent status. Such evidence, while indicative, is not conclusive, in as much as what appears to be communication or cooperation between mounds may only be overlapping foraging trails. As I found later, this, in part, may indeed have been the case.

On July 1 of the following year, an estimated 500 to 1000 workers of mound 101 were marked with small specks of white enamel and their activities noted on the following day. Numerous marked workers were observed on the trail between mound 101 and 106, with a high count of eleven at any one time. While marked workers often approached within four or five feet of 106, none was observed on the mound itself. If cooperation or communication existed between these mounds the previous year, the relationship had subsequently been altered. Workers of 106, which were followed from the time they left their nest, and marked workers of 101 were observed to make frequent contacts, but the nature

of the contacts suggested that each recognized the other as an alien. Apparently this trail was of common usage to both colonies as a point of egress to foraging areas.

On July 14, a second trail was found. It originated at mound 154 and terminated under a small branch about 28 cm in length and 5 cm in diameter. The total length of this trail was about 9 meters.

The workers of 154 were marked with paint on July 15 and their movements traced. For a period of two weeks workers were observed moving in both directions along this trail with no unusual activity noted except that an increased number of workers were seen passing through a single opening concealed in part by a branch. Soil chambers and galleries may have been enlarged during this time, but no deposits suggesting excavation were found to support this view.

At the beginning of the third week, July 30, a small amount of thatch (bur oak twigs and grass culms) was noted to have been placed above the opening, the total collection of material making up a nest no larger than 8 to 10 cm in diameter and about 3 cm high. A final measurement made two weeks later showed an additional growth of 5 cm in diameter. Here, for the first time, was evidence supporting the view that *F. obscuripes* expands its territory through the process of budding.

The relationship among mounds within a cluster is an interesting one, since the degree of communication between the parent and bud colonies may indicate whether or not individual colonies, once established remain interconnected or if the individual mounds may ultimately become independent. This communication may take the form of an exchange of workers, pupae, and larvae (Talbot, 1961) or may simply be visiting back and forth of worker, as stated by Wheeler (1910).

The events discussed thus far suggest that while communication between the parent and bud colonies may take place during the nest construction phase, this communication may be broken off or at least reduced as the new nest becomes established and self sustaining.

Two methods were used to determine the degree of visitation between mounds within a cluster. The first involved the marking of workers with white spray enamel and the second consisted feeding a colony a mixture of gentian violet and honey.

Cluster C in Area 2 (Figure 17) was selected to test both methods in order that a comparison of results could be made. The area is characterized by a dense stand of smooth brome and Kentucky blue grass. Foraging trails, if they existed, were not visible.

The largest mound (90) was selected for the marking experiments.

On June 15, 1965 an estimated 200 to 300 workers were marked with paint. On June 15, 1965 an estimated 200 to 300 workers were marked with paint and the results noted on the following seven days.

The six surrounding mounds which form a part of the cluster were checked daily. Mounds were gently tapped to bring additional workers to the surface. The results were negative. Not until the sixth day were marked workers observed anywhere except at the site of marking, at which time two marked workers were found. One of these was found at mound 92 where it seemed to wander aimlessly over the thatch surface and be quickly recognized as an alien although no animosity was shown by other workers. The usual behavior exhibited involved the touching of antennae two or three times until no further interest was shown. This routine was repeated with each worker encountered. After several minutes the marked worker disappeared into the nest and did not reappear. The second marked worker was found in a sample collected

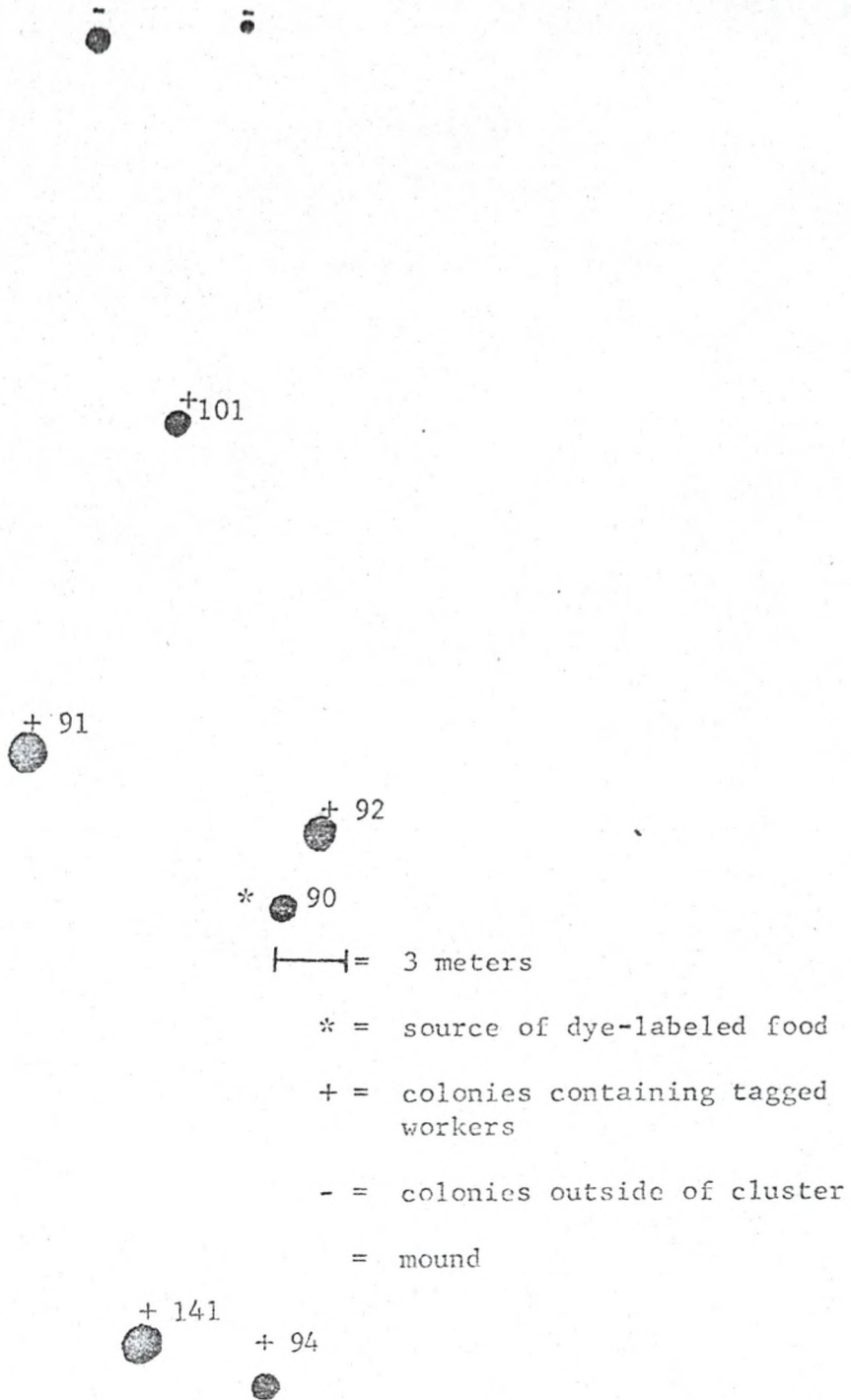


Fig. 17.--Map of area 2 cluster C showing distribution of mounds and location of tagged workers.

from mound 91. At the end of one week marked workers were still observed on mound 90, although in smaller numbers.

Considering the fact that 200 to 300 workers were marked, the number which took part in visiting was insignificant and somewhat surprising. There is, however, some indication of a degree of acceptance, possibly based on similarities of colony odors among workers of colonies within a specific cluster.

Having established the fact that visiting does take place, but on a very limited basis, I attempted to determine the extent to which visiting could be induced.

On July 16, a vial of gentian violet and honey mixture was embedded in the thatch of mound 90. The following day a sample of workers was taken from the mound and each squashed between index cards. Each worker left a discernible spot of stain. Samples taken the same day from neighboring mounds within the cluster gave negative results.

Positive results were not obtained until July 28 when about 85 percent of the samples of mound 91 and 92 contained marked workers. Additional marked workers appeared August 1 in about 55 percent of the samples taken from 94 and 141. The total area from which workers were attracted measured 15 by 42 meters. Samples taken from clusters outside of this area contained no marked workers.

Results obtained by Scherba (1964) indicated that visiting decreases with distance; however, increased distance may also be indicative of decreasing parent-bud relationships within the cluster.

Hangartner et al, (1970) concluded that orientation to nest material by Pogonomyrmex badius may be related to the odor of specific soils and debris used in nest construction and that these odors are incor-

orated into the epicuticle of the worker. This may account for the acceptance of workers in colonies other than their own, if such colonies are of the same environment, and for the rejection of workers from dissimilar environments.

The function of visiting is not clear and, as shown by behavioral reactions, may be nothing more than the occasional wandering movements of workers while carrying out daily activities. Certainly if importance is to be attached to this phenomenon, the degree of visitation should have been greater than observed. However, even such small frequencies of visitation may play a role in the rapid transfer of information between colonies within a cluster when conditions warrant it. Such may have been the case of the induced communication between colonies when a new food source was made available.

The role of the queen in establishing bud colonies has as yet not been defined. Excavation of fifteen mounds within clusters showed a considerable variation in number of dealates present. In the early Stage 1 phase (0 - 13 cm) no queens were found, although all thatch, soil galleries and chambers were carefully followed to their limits. In the late Stage 1 phase (13 - 25 cm) multiple queens were common. One colony had a single queen, two colonies had two, one had three and one thirteen. Four mounds in Stage II had each a single queen, and one in Stage III had none. This does not, however, preclude the possibility that other queens could have been present since Stage II and III mounds require the sifting of vast quantities of material and examination of numerous soil chambers. A queen could easily have been overlooked.

Formica oreas comptulaMound Morphogenesis  
Mound MorphogenesisHabitat Selection

Nest site preference is to some extent determined by the nature of the habitat. Generally, in areas composed of dense stands of grass (predominantly Kentucky blue grass), most mounds are associated with lodged stands of grass from the previous year's growth and grass mats several centimeters thick. When the ground cover is thin, (that is, the humus is exposed over a major portion of the habitat), site selection is associated more frequently with rotting logs, stumps, flat rocks or upright, partially decomposed trees.

Shade seems to be an important factor in site selection. All nests whether in open woodland or ecotone receive some shade during the day. Local conditions permitting, shading of nests occurs more often during the morning than afternoon hours. Of 22 nests in three prairie extensions along narrow north-south ridges only four mounds were found on the west side of the clearing. This factor also may have been important within the open woodland, but if so it was not noted with any frequency.

Preference is also given to areas which are well drained. Only a few mounds were found on the flat floodplain of the Forest River. All others were on slopes or terraces leading to the floodplain.

Typical Mound Description

Few nests of F. oreas have been described. Creighton (1950) described the nest of F. oreas oreas as a mound of detritus which under favorable conditions rivals in size those of F. obscuripes. Cole

(1932) stated that in Utah F. oreas oreas colonies are founded in open sunny areas and beneath stones which the workers banked with detritus. Wheeler and Wheeler (1963) reported that most North Dakota nests of F. oreas comptula were associated with detritus of fine plant debris.

In the Forest River study area a representative mound will average about 25 cm in height and usually be dome-shaped, but occasionally one has the appearance of an inverted cone (Plate X). Detritus used as a building material is uniform in size and content throughout the mound. The internal compartmentalization is not predictable. The location and size of chambers change constantly with some parts of the nest being completely abandoned and others with newly created open areas.

The surface material shows some degree of cohesiveness and compaction probably resulting from frequent rains. This layer, 8 to 20 mm in thickness provides a certain amount of protection from the external environment. Few openings are located on the nest surface, those present being used only during the cooler morning hours or when there is adequate shade. During foraging activities and the transfer of brood, openings which are located at the periphery of the mound are used. In areas of dense grass these are not exposed, but are entered from trails concealed within the grass mat.

Nests associated with logs or stumps are highly variable in size and shape. Generally, the detritus is placed along one or both sides of the log, but much of the chambering and gallery formation is located within the decomposing wood. By far the largest nest of this type occupied a fallen tree about 30 cm in diameter and four meters in length.

No specific orientation with respect to shading or drainage was

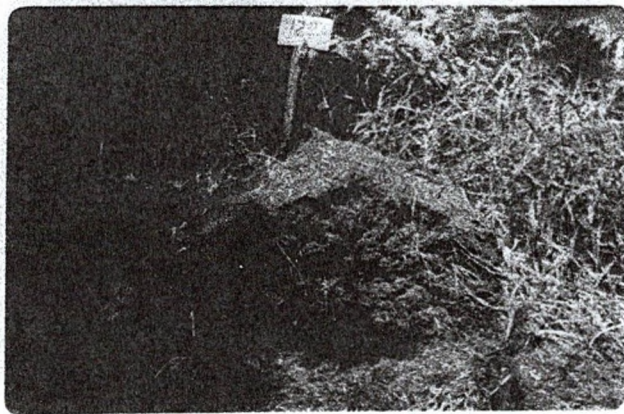


## PLATE X

SURFACE AND SECTIONAL VIEWS OF

F. OREAS COMPTULA MOUND

1. Surface view of isolated mound with a height of 76 cm and base diameter of 115 cm.



2. Partial dissection of mound showing compact surface and internal chambering.

noted. However, one large aggregation of nests declined rapidly in numbers over a period of several years as a result of overgrazing. The lack of vegetation caused excessive erosion of ground cover and as a result nest development shifted to an area having more protection from small shrubs and trees.

#### Stage I. Incipient Colonies

Site Selection -- The selection of a suitable site for nest construction seems to be related to the availability of lodged stands of vegetation. Dense mats of Kentucky blue grass seem to be the preferred in the study area. Eight of ten areas which contained clusters of nests were associated with material of this type. In moderate to heavily grazed pastureland, the preferred sites were stumps, logs, and, less frequently, large rocks or boulders. In a few instances, when ground cover was almost completely lacking, *i.e.*, on steep slopes, the nests were confined to decaying upright trees.

Description -- The term incipient as used in describing Stage I nests refers only to the establishment of new colonies through budding. The nature of incipient nests as founded by solitary queens is not known.

Even in early stages F. oreas comptula nests have no typical shape or form. A mound may be round, oval, flat, or asymmetrical depending on its origin. Each nest begins with the removal from within the grass mat of plant debris which is deposited about the stems of grasses and herbs or laid on the lodged surface of the past year's growth. The interior of the nest is a very open structure having poorly defined chambers. Spaces may be three or four cm in width, others as large as seven or eight cm. No defined galleries were observed. Chambering

and trail formation within the grass mat may be quite extensive before any mound construction becomes apparent. Earlier events such as the construction of chambers and tunnels below the grass were not observed.

Many of the small nests, 8 to 10 cm in length, may be temporary structures utilized only during periods of peak brood population. Pupae have been observed being carried both in and out of these structures. Such structures may be termed succursal.

### Stage II. Mature Colonies

Description -- The morphology of F. oreas comptula nests as described here refers only to the typical mound composed essentially of detritus. As shown in Figure 18, the nest is comprised of a number of similarly constructed units which are connected by trails hidden within the grass mat. The major features are the dome-like asymmetrical mounds averaging approximately 30 to 40 cm in diameter. Excavation of soil beneath the mound is limited. Small chambers 4 or 5 cm long and 1 or 2 cm high have been found within the grass mat, with interconnecting galleries. Few defined chambers have been found in the soil, but small galleries or tunnels have been found leading to lower levels. These were followed for a few centimeters and then lost. The depth of penetration and length of the tunnel were not determined. Peripheral areas of the grass mat, especially where trails radiate away from the nest, are almost completely hollowed out. The expanded entrance to the trail is continuous with the internal compartments of the thatched portion of the dome. A few of these trail entrances were found to be nearly 30 cm wide and 4 cm high with a smooth surface.

Nests are frequently established within the hollow core of decomposing stumps or upright trees. One nest occupied the interior of

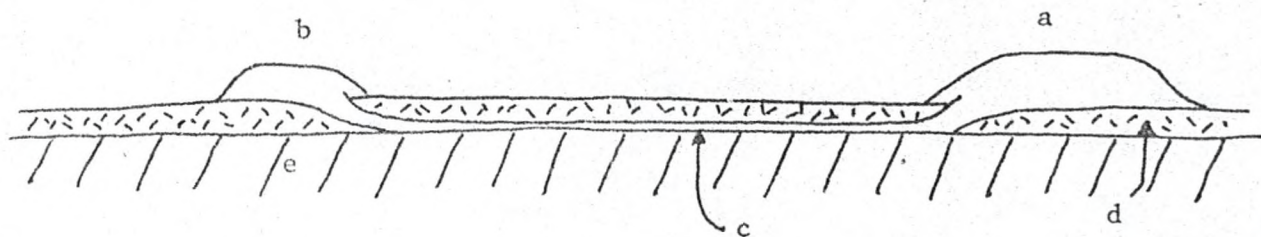


Fig. 18.--Diagrammatic sectional view of *F. oreas comptula* Stage II mound complex: (a) parent mound, (b) bud mound, (c) interconnecting trail, (d) grass mat, (e) soil.

a paper birch tree from its base to a point just under two meters above ground level. In such cases, detritus is banked against the foot of the tree and carried into the larger hollowed out pockets beneath the bark. Hollow stumps are usually filled to the point of overflowing, resulting in detritus spilling over onto the ground. If the stump is small, i.e., no more than 30 cm in height, it may become completely buried. The location of brood within the nest is not predictable, any area meeting specific environmental requirements, i.e., temperature and humidity, probably being used. Pupae have been found in soil chambers, within the grass mat, in chambers within decomposed wood, and in all areas of detritus.

Most nests were found to grow in size by the addition of new material to the surface either in the form of detritus collected from the immediate vicinity, usually not more than one or two meters away, or of material removed from within the nest.

Nest building activities were confined either to cool days or to times when there was no direct sunlight. On cool mornings when the nests were shaded, workers were frequently observed carrying pieces of leaves and small grass culms, but more often blades of grass which appeared to be, on the basis of weathering and decomposition, several seasons old. In the early stages of mound construction, building material is apparently randomly selected from available material, but during the advanced stages of construction when bud nests and temporary brood shelters are constructed, the construction material is removed from large areas within the grass mat. These areas eventually include the system of trails connecting the various components of the mound complex.

The size of the mound does not necessarily indicate the number of its inhabitants. Depending on conditions, such as the amount of rainfall during a short period of time or the amount of shading, parts of a mound or mound complex may be abandoned in favor of another. This shift in population brings about differential growth rates causing the mound to become highly asymmetrical. The net affect is to produce on the surface of the mound a number of blister-like protuberances (Figure 19).

During the winter when the above-ground level portion of the nest becomes vacant, snow may compress the detritus by as much as two-thirds of its original height. In the spring when the colony again becomes active, the internal galleries and chambers within the detritus are lacking. In such cases (and this process has also been observed following heavy rains) the nest rechambered by workers transporting material out through the major openings and depositing it on the outside surface. This process is continued until compartments within the nest are reestablished and the mound has regained its original size.

Not all pieces of leaves and stems are removed. The surface cap, as it is buried, remains intact, the workers selecting material which is more easily detached. Older mounds of unusual size, two-thirds to one meter high, may show three or four compression levels (Plate XI). Such levels may be related to the age of the mound, but this has not been established. Since the upper compression levels are more distinct than the lower, it seems quite probable that some levels are eradicated with time.

During early summer when brood populations are high there develops

## PLATE XI

SURFACE AND SECTIONAL VIEWS OF F. OREAS COMPTULA

## MOUNDS SHOWING COMPRESSION LEVELS

1. Surface view.
2. Sectional view of same mound.
3. Diagrammatic representation of the compression levels of this mound.

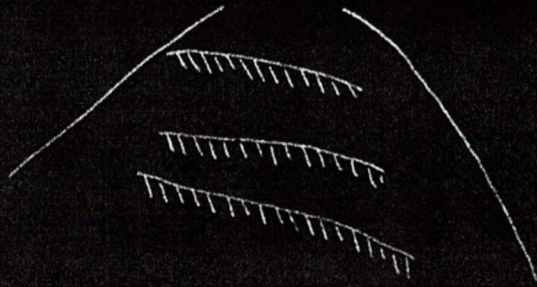
PLATE XI



1.

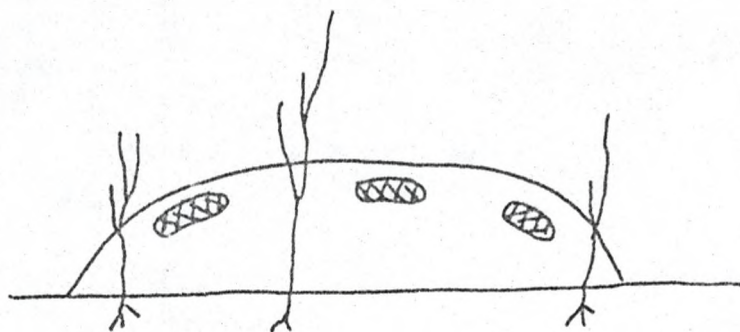


2.

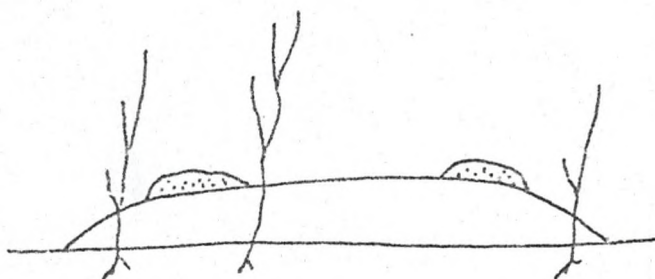


3.





A.



B.

Fig. 19.--Diagrammatic representations of F. oreas comptula mound showing location of brood chambers.

- A. Usual appearance: (a) brood chambers, (b) dense thatch, uninhabited.
- B. Same mound showing new blister-like brood chambers added to surface following saturation and compression of mound during heavy rainfall.

a rash of nest building in which the parent and bud nests are connected by underground trails (Figure 18). Usually the bud nest was found to be associated with a previous trail, but occasionally a new trail was formed with a bud nest constructed at its terminus. I did not observe any isolated nest which later became attached to the parent nest by a trail. Nest complexes were observed to be composed of from only two mounds to as many as five major and twelve minor mounds. This physical relationship is the rule and not the exception. During the seven year study period only two mounds could be classified with any certainty as isolated.

### Stage III. Senescent Colonies

Description -- Aging patterns were not observed. Nests were often completely abandoned only to be found as flourishing colonies a month later. A few mounds, after a season of inactivity, were found to be reactivated. Only one colony was followed through more than two seasons, and over the course of five years it had shifted at least 60 cm from its original position. However, the rate of decay is so rapid, that it is possible a new mound could have been constructed while the other was declining. The aging process is further obscured by the polydomous nature of the colonies whereby a single colony may be represented by as many as twenty nest units making up an integrated and unified complex. Mounds which are permanently abandoned or which show evidence of decline, deteriorate rapidly. On compaction, the growth of mold and the resultant decay progress so rapidly that by the end of a single season a nest is difficult to recognize as such. This problem will be considered further in the section dealing with the process of colony reproduction.

Colony Reproduction

The expansion of territory, other than the founding of isolated colonies, takes place through a single process, colony budding.

The first example of this process was observed during the summer of 1965. Five mounds, the largest no more than 17 cm in diameter, were situated in a dense stand of Kentucky blue grass. Examination of the grass mat indicated the presence of covered trails interconnecting the five nests. Three of these nests each contained one queen.

A second cluster, situated in the ecotone of a north-south peninsular opening in the forest (Area 2), was mapped on July 1, 1965. The arrangement and size of mounds and interconnecting trails are shown in Figure 20.

Typically, most clusters grow in a linear fashion, following either lodged stands of grass or shade provided by trees and shrubs. The relationship is similar to that found in F. obscuripes in that a large mound forms the nucleus about which other smaller mounds are clustered. Dissection of mounds to reveal compression levels indicated that the younger mounds were peripheral and that generally the older mounds were larger and centrally located.

The spacing of mounds within a cluster shows a certain amount of aggregation. The variance/mean ratio was 1.25, which is statistically not significant at the 95% level. A larger area containing more nests is needed to determine whether or not the distribution pattern tends to be random or clumped.

With some exceptions all permanent structures within the cluster were found to be connected by trails. These were exposed in order to

Fig. 20.--Map of F. oreas comptula cluster showing distribution of mounds and connecting trails in the summer of 1965. Labeled arrows show movement of tagged workers. W= workers from mound #145 marked with white paint. G= workers from mound #146 marked with green paint.

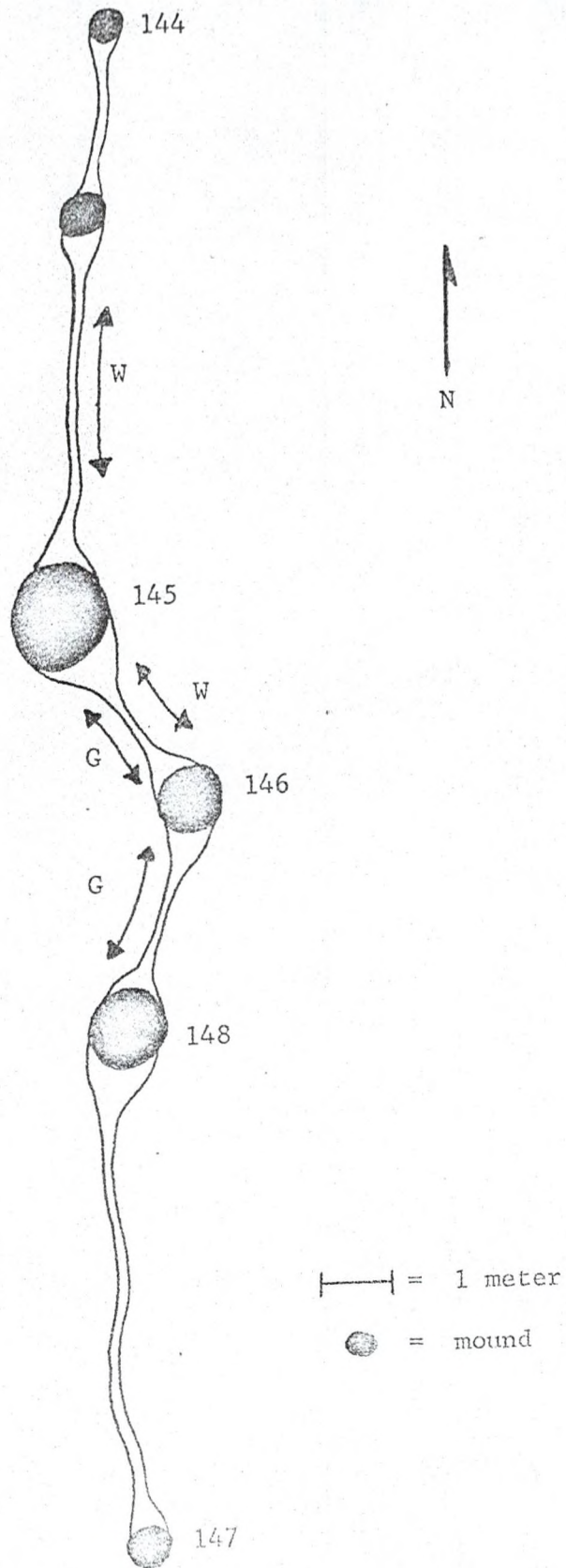


Fig. 20.

determine the spatial relationship of mounds within the cluster. Each trail was then recovered except for short segments which were used as observation points. Almost all trails were found to be utilized as a means of communication between mounds but not to the same degree. Near the nucleus of the cluster, trails were actively used with columns of workers moving in either direction. On one occasion at least eight workers were observed to be carrying pupae away from the main nest (145) and transporting them to small pockets or chambers adjacent to the trail.

Trails in the remote areas of the cluster were used to a lesser degree. For example, the trail between 148 and 147 was used only intermittently. During some observation periods lasting from 10 to 15 minutes only two or three workers would be found moving past a given point and at other times no workers were observed at all.

The relationship between mounds as indicated by worker movement was determined by marking workers with spray paint. On July 12, 1965 the workers of 145 were marked with specks of white paint and their movements traced over a period of several days. On the following day marked workers were observed in mound 146 and moving on the trail between 145 and 144. No marked workers were found in 148 or 147. On July 15, workers of 146 were sprayed with specks of green enamel. The following day marked workers were found in 146, 145 and 148. None was observed on trails between 148 and 147 or 145 and 144.

This same cluster was remapped July 21, 1970, (Figure 21). Of significance is the expansion of this cluster and relocation of mounds. Since no measurements were made during the interim period, it is not certain which, if any, of the dominant mounds corresponds to those of

Fig. 21. --Map of *F. oreas comptula* cluster showing distribution pattern and trails in the summer of 1970. Relative amount of worker movement between mounds is indicated by the width of the arrow.

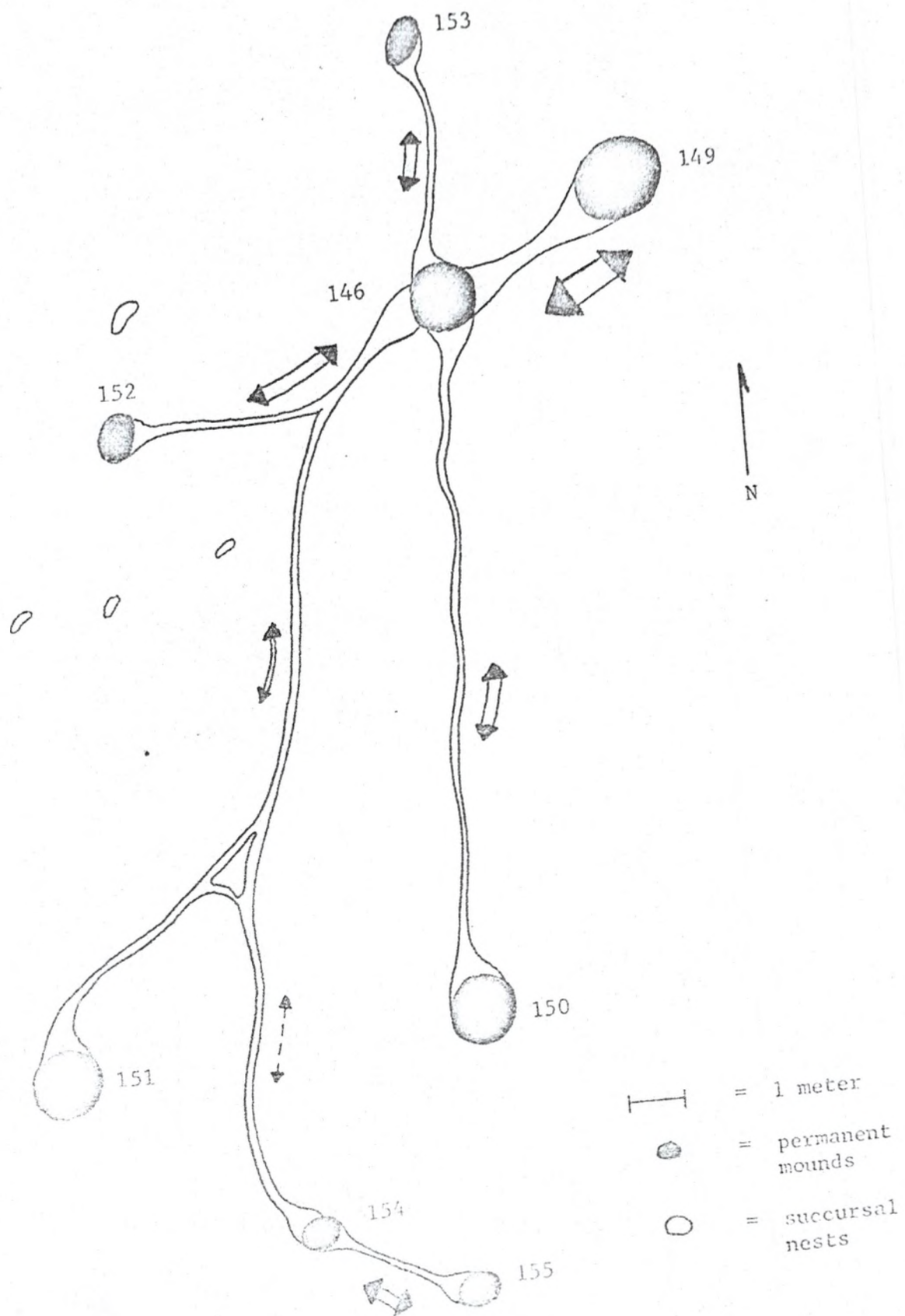


Fig. 21.



the 1965 mapping. Only one (146) is in or near its original position.

As before, all trails were traced to their limits with segments left exposed to facilitate a count of worker movement. A relative determination of worker cooperation (or visitation) between mounds was arrived at by counting the number of workers moving past a specific point within a 5 minute interval. Unlike the information obtained from the previous cluster (Figure 20) it is not known what percentage of workers were in transit between adjacent mounds or to peripheral regions, such as succursal nests and foraging areas. However, observations of workers on two trails left completely exposed indicated that the majority traveled the entire distance between mounds. Only a few were seen making side excursions to succursal nests or into the dense grass mat where they could no longer be followed. As expected, the trail between the dominant mounds (149 and 146) was used with greater frequency than any other. The trail between 146 and 152 was second in frequency of utilization. Frequency of travel seemed to decrease with increasing distance from the cluster. Although well established the trail between 146 and 151 was little used. During a 15 minute interval only two workers were observed. Two smaller mounds (154 and 155) had in previous years been attached to the cluster, but trails connecting them to other peripheral mounds had fallen into disrepair. No trails were evident between 150 and 155.

Small succursal nests, numbering as many as 15 or 20, were found associated with peripheral mounds or well established trails. Such nests were intermittent, most appearing during June and July when the cluster reaches the height of productivity. Unlike permanent structures, succursal nests are comprised of fine detritus placed about lodged

leaves and stems of grass. Soil chambers are usually lacking.

The behavior of workers while in transit did not in anyway suggest different degrees of relationship between mounds. Whether on short or long trails workers showed no observable differences in behavior towards each other. Tagged workers, unlike those of F. obscuripes, were not recognized as being alien when observed in mounds other than those in which they were marked.

The number of queens per nest varies. Generally the large nests have multiple queens. One isolated mound approximately 1 meter in diameter contained four queens each located in a peripheral chamber between the grass mat and humus. Two mounds measuring between 65 and 70 cm each contained three queens. Five nests less than 25 cm in diameter each contained a single queen. Temporary or succursal structures, that is, those which lack soil chambers and connecting trails, had no queens.

#### Materials Used in Nest

##### Construction

The material used by F. oreas comptula workers in nest construction is dependent upon the type of vegetation found within 1 or 2 meters of the nest site. Generally, small pieces of decomposed grass blades (Kentucky blue grass) are selected over any other material, and when found in abundance, make up approximately 70% of the nest by weight. Nests in undisturbed areas of the ecotone were usually of this composition. In grazed pastureland, where ground cover was light, the building material was more commonly composed of leaves and particles of soil. In either habitat culms and twigs were infrequently used and made up

only a small fraction of the material in any nest sampled. Those that were utilized in construction showed signs of 2 or 3 seasons of decomposition. There seemed to be no attempt on the part of workers to keep the nest from being overgrown with vegetation. Grasses growing up through the detritus of the nest showed no signs of being attacked by workers. None of the nests was found to contain freshly cut culms.

In order of decreasing frequency the thatch and detritus used in F. oreas comptula nests were found to be composed of the following species of plants: Kentucky blue grass, blades and culms; wolfberry leaves; seeds of ash and elm; Juneberry leaves, decomposed or freshly cut; dried fruits of Juneberry; bur oak leaves and occasionally twigs; and smooth brome grass leaves and stems. Of all the material used, freshly cut Juneberry leaves, which were found scattered over the surface of nests, are of most interest. The cut edge was the same in each case, serrate in appearance and crescent shaped. I never observed any workers actually cutting pieces from attached leaves. Possibly, the leaf cuttings were produced by other insects and then gathered by the F. oreas comptula workers. If not, the positive reaction of workers to Juneberry leaves remains a mystery. The leaves, as far as I was able to determine, were used only as thatch.

The size of material used is quite uniform both with respect to diverse habitats and nests of varying sizes. A few samples contained culms and leaves measuring 8 and 6 mm in length, but the average size of the largest material used was 4.1 cm.

As shown in Table 5 the building material may be separated into two categories: thatch, which was more than 4 mm in length and greater than 2 mm in diameter, and detritus, less than 4 mm in length and less than

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TABLE 5

PERCENT OF SAMPLE BY WEIGHT OF THATCH AND DETRITUS FROM SIX

F. OREAS COMPTULA NESTS LOCATED IN THE ECOTONE.

Nest Diameter > 37 cm			Nest Diameter < 37 cm		
Mound #	Thatch	Detritus	Mound #	Thatch	Detritus
1	36%	64%	4	38%	62%
2	34	66	5	30	70
3	31	69	6	36	64
Mean	33.7	66.3		34.6	65.3

In samples taken from the ecotone, the detritus by weight made up about 66 percent of the material used in nest construction. There was no significant difference between nests of different sizes.

A similar analysis was made of building material taken from nests situated in grazed pastureland (Table 6).

TABLE 6

PERCENT OF SAMPLE BY WEIGHT OF THATCH AND DETRITUS FROM SIX

F. OREAS COMPTULA NESTS LOCATED IN GRAZED PASTURELAND.

Nest Diameter > 37 cm			Nest Diameter < 37 cm		
Mound #	Thatch	Detritus	Mound #	Thatch	Detritus
1	49%	51%	4	48%	52%
2	42	58	5	49	51
3	46	54	6	37	63
Mean	45.7	54.3		44.6	55.3

This cluster was located on a terrace just above the floodplain. As in the ecotone, detritus makes up the greatest amount of material, having a mean percentage of 54.3. Again there was no difference between the two categories of nests. The increase in the percentage of thatch over detritus when comparing the ecotone and pastureland material can be attributed to the increase in the amount of soil particles used in the nest of the latter. An average of about 7 or 8% of the thatch material by weight was composed of angular particles of soil about 2 or 3 mm in diameter.

### Population Characteristics

#### During Mound Growth

#### Major-Minor Ratios

As described in the sections on mound morphogenesis and colony reproduction, the nests were found to be interconnected by underground trails. Only two nests sampled during the seven year study period were solitary and these were questionable cases. For this reason the data obtained from samples of clustered mounds may not be valid if one attempts to relate the obtained major-minor ratios to stages of mound growth.

In order to determine whether or not any relationship exists between the major-minor ratios of F. oreas comptula and mound growth, a preliminary study was made by obtaining samples of thatch and detritus along with attached workers from 8 mounds of various sizes. It was assumed that the workers collected in this fashion would be a representative sample of the nest population. No collections were taken from nests associated with stumps or logs. All nests were from a single cluster. The thatch was collected from the surface of each mound to a depth of

about 3 or 4 cm. The workers were then separated from the thatch and measured from anterior to posterior on the lateral surface of the thorax. A distinct separation between majors and minors was found to be between 2 and 2.5 mm. On that basis, the majors were arbitrarily classified as being larger than 2.5 mm and the minors smaller than 2.5 mm.

The results of these measurements are shown in Table 7. The percentage of majors and minors was not found to be predictable. In sample number 5, a mound of average size, the majors were found to be 79 per cent and the minors 21, while the largest mound (sample number 1) had 71 per cent majors and 29 per cent minors. Lesser percentages of majors were found in both small and large mounds. The mean percentage of major workers for all samples was 57.4 and for minors 42.6.

TABLE 7

PERCENTAGE OF MAJORS AND MINORS OF F. OREAS COMPTULA  
AS RELATED TO MOUND DIAMETER.

Sample No.	Mound Diameter	Sample Size	% of Total Sample Majors	% of Total Sample Minors
1	80 cm	41	71	29
2	73 cm	128	42	58
3	70 cm	123	49	51
4	64 cm	114	56	44
5	56 cm	72	79	21
6	51 cm	96	73	27
7	33 cm	86	37	63
8	30 cm	78	52	48
Mean			57.4	42.6

## DISCUSSION

The distribution of Formica obscuripes colony clusters within the Forest River Biology Station and adjacent areas has shown the species to be quite adaptable to varying habitats. Formica obscuripes colonies were common both in the open pastureland adjacent to the areas of study and to the woodland habitat. Those colonies associated with the latter were more successful both as to population size and density. No specific associations with vegetation types were noted. Successful colonization seemed to be directly related to the ability of the colony to suppress the growth of vegetation encroaching upon the mound. Habitats in which the dominant ground cover was smooth brome grass were usually lacking this species.

Although unsubstantiated by any direct analysis, grazing seems to be an important factor in the establishment and maintenance of flourishing F. obscuripes colonies in this woodland habitat. In 1965 numerous colonies were found in heavily grazed pastureland of section 11, a habitat very similar to that of Study Area 1. This same area revisited in 1970 was found to contain only a single colony. The only apparent cause of this mass extinction was the lack of grazing during the summers of 1968 and 1969. Of obvious note was the increase in growth shown by the dominant ground cover, Kentucky blue grass. Apparently, such dense stands encroach upon the F. obscuripes mound thereby causing the demise or migration of the colony.



The type of vegetation within the immediate vicinity of the nest plays an important role in mound morphogenesis, especially as it relates to the structure of Stage II nests. Since the internal environment of the nest is important to the care and growth of the brood, the nest takes a form which is best suited to the conditions of the habitat. In habitats containing rank vegetation or in some cases, a high water table, the dome of the nest was projected upward; conversely, in habitats having good drainage and grazed vegetation, the dome was scarcely above ground level.

Distribution of F. obscuripes colonies does not seem to be related to soil types with the exception that no mounds were excavated into soil developed directly over a substratum of sand or gravel. Soil deposits or the underlying sediments did not affect the growth of the nest nor its structure except in those cases in which the nest was excavated into a clay deposit. The thatched dome of such nests seemed to be more compact and the thatch material at least partially cemented together by the adhering clay particles.

Mounds were found established on the sides of the Forest River Valley having slope values in excess of 30 degrees, but not on slopes having values over 40-45 degrees. Under these conditions, Stage II mounds were noticeably altered in form, having elongated thatch surfaces of about 8 to 10 cm in the direction of slope. Soil embankments were usually lacking (apparently washed away during heavy rainfall).

The distribution patterns of F. obscuripes mounds fall within three categories: the random distribution pattern of isolated mounds, the uniform pattern associated with mounds of the prairie and the

clusters found within the woodland habitat.

Within the woodland habitat the importance of colony division as a means of expanding territory is obvious; however, the characteristic pattern produced by colony division, i.e., mound aggregates, was not observed within the prairie habitat. In Slope County, North Dakota, a pasture of about 60 acres was found to contain 18 F. obscuripes mounds. An analysis of the spacing of the mounds showed a definite tendency toward uniform distribution suggesting that each mound was totally independent, as to origin, from all other mounds. The distances between mounds was found to be in most cases greater than the measured distances between known parent and bud mounds of the woodland habitat. On this basis one may conclude that each mound was probably founded by a single queen following the marriage flight.

Isolated and randomly dispersed Stage II and Stage III mounds of the woodland habitat were usually situated within habitats that would not allow for expansion of territory. Such mounds were located in the narrow ecotone between the forest and cultivated fields and in small open areas within the woodland. As far as could be determined, isolated mounds were beyond the limits of foraging trails and known limits of territorial expansion through colony division and in all likelihood were not the result of this type of colonization.

The third type of distribution was characterized by the presence of numerous colonies having a clustered pattern. This type was common only to the woodland habitat. Within this pattern Stage I and small Stage II mounds were frequently grouped about a large Stage II mound and less commonly associated with Stage III mounds having the appearance of being near extinction.

The observed differences between the prairie and woodland patterns may be related to the plant communities in which they are found and the relationship of these communities to the prevailing climate and the seasonal short term variations which may occur. Bodenheimer (1958) stated that "fat and meager" years with respect to insect population were related to cyclic weather changes. However, as related to distribution patterns, the density-independent factors such as climate and weather play only an indirect role and it is the density-independent factors which determine the equilibrium of a population. Accordingly, these factors may cause pressures within a colony which would lead to variations in distribution patterns. For example, during peak periods of growth, both with respect to vegetation and food sources, individual colonies may show a more rapid growth in population than can be adequately maintained. Brian (1965) indicated that temperature buildup within the nest, the inability to diffuse metabolic wastes of solids or liquids and the limitations of nest size are density-dependent factors which tend to limit populations. Such factors may play a minor role in the prairie habitat since the availability of food may limit the size of colonies, but in the woodland habitat seasonal fluctuations in the weather may produce optimal conditions during which time food may become abundant. It is during this period of time when maximum growth in population probably occurs and the manifestation of this growth may be expressed in the initiation of the colony division process. This would account for the fact that colony division is a sporadic and unpredictable event having been observed only during two out of the seven summers of the study period.

The effect that colony division has on the parent colony is not at all clear since the bud colony in its initial state has few workers. It would seem that this factor alone would do little to increase the internal efficiency of the parent colony. In pleometrotic colonies the periodic release of queens along with workers would reduce the growth of the colony, but in those mounds examined flourishing F. obscuripes colonies have not been found to contain more than a single queen.

The growth of F. obscuripes colonies was indirectly obtained through the extrapolation of data on mound growth over a seven year period with the assumption (based on a number of actual counts) that there was a positive correlation between population and mound size. Because I found that the diameter of the thatched surface kept in repair was proportional to population size, this factor was utilized in determining the growth curve.

The growth of F. obscuripes colonies was found to be typical of that ascribed to all social insects by Bodenheimer (1937): "(1) the initial period of colony foundation, (2) the period of expansion and vigor, (3) the period of senescence and death."

Within incipient colonies, the growth rate observed during the first season may be attributed to the few workers associated with the bud nest, although even during this period of time nest construction proceeded at a rate greater than expected. When first observed, few workers were in transit or engaged in the construction of the nest. Following a period of approximately 2 to 3 weeks the number of workers in transit between the parent and bud mound increased dramatically and was accompanied by a corresponding increase

in the rate of mound growth. Since the rapid growth was the result of a cooperative effort between the parent and bud mound, the growth rate in this first phase was probably much greater than that of mounds established by colonies produced by isolated queens.

Late Stage I colonies were occasionally found to be polygynous or more commonly without queens. In the early Stage I phase of development colonies were always found to be monogynous. Therefore, it seems doubtful if queens played any role in the rapid growth of the nest as experienced by young colonies.

The rapid increase in colony size which takes place in the second and third year can probably be attributed to the wintering over of a certain proportion of the worker population and the acceptance of a fertile queen into the colony. The number of brood found in late Stage I mounds was always quite large in comparison to older mounds. In one actual Stage I count, the ratio between workers and brood was approximately 2:1, whereas a Stage II count by Weber (1935) produced a ratio of approximately 8:1.

In the third and fourth years the rate of growth slows to an arithmetic rate of increase and continues until a plateau is reached at about 10 years. It is probably during this period that the colony experiences optimal conditions both within the nest and the external environment. However, the relationship between the queen, brood and workers is one of fluctuation since it is the Stage II colony that emit sexuals and responds to internal conditions leading to colony division.

The final phase of growth leading to the decline of the colony may be related to an interacting relationship between an aging queen,

brood and workers. Such factors as egg viability, care and feeding of the larval stages and general nest activities may be related to the observed rapid decline of both brood and worker population in Stage III colonies. The decrease in population was also found to be accompanied by a change in the ratio between major and minor workers with the latter showing a significant increase. Marikovsky (1962) stated that transitions in worker size may be related to different phases of colonial organization designed to meet the complex relationships which exist within the colony and the external environment; however, ratios which may be of benefit to a vigorous Stage II colony, may bring about an eventual collapse of social organization (i.e., repair of nest, decrease in foraging activities and care of brood) in the final Stage III phase of colony growth and development.

Evidence concerning the relationship between mounds within a cluster has indicated that the expansion of territory was through the process of colony division. The degree of movement between mounds, inducement of communication within a cluster and number of queens observed in individual nests suggest that the maturation of units within a cluster follows a predictable course of events. Based on the findings of this study I propose the following sequence as related to the founding of new colonies:

- (1) Following the marriage flight, a new colony is established in virgin territory by a solitary queen.
- (2) Workers from the parent mound initiate construction of a bud nest.
- (3) Once established, communication between parent and bud colonies decreases to the point of occasional visiting.

- (4) Following the marriage flights one or several newly-fertilized queens are adopted into the bud colony.
- (5) One or possibly two queens remain within the colony during its lifetime. There is no evidence to suggest secondary pleometrosis.

The distribution of F. oreas comptula colonies within the Forest River Biology Station and vicinity was found to be more limited than that of F. obscuripes. The nests of the former were not found in the more shaded areas of the flood plain of the Forest River. None was found in the heavily grazed areas of the ecotone or open pasture land.

Without exception, all F. oreas comptula colonies, both within the ecotone and woodland, were found to be associated with Kentucky Blue grass and were usually within foraging distance of thickets or areas of the ecotone in which Juneberry, a shrub, was common.

When not constructed in logs, decomposing stumps or upright trees, nests varied except as to size and to a lesser extent, the material used. Nests situated in the undisturbed ecotone were composed essentially of small bits of grass, leaves, and less commonly of partially decomposed leaves of herbs and shrubs. In habitats lacking dense grass mats, increased amounts of soil particles were used in the construction of the nest.

Permanent changes in nest form to compensate for undesirable environmental conditions were not observed. Unlike F. obscuripes, F. oreas comptula workers did not react to the growth of grasses surrounding the nest or growing up through the detritus even though such growth, when excessive, caused shading which apparently was beyond the limit of tolerance. Under such circumstances, nest con-

struction would shift in the direction of more favorable conditions or the nest would be permanently or temporarily abandoned.

There is little evidence concerning the origin of isolated F. oreas comptula colonies. Only one polydomous unit composed of three incipient nests was found. However, even in this early stage multiple queens were present. That F. oreas comptula queens may establish new colonies by temporary social parasitism is a possibility, but apparently there is no record of the occurrence of mixed populations.

With the few exceptions cited earlier all F. oreas comptula nests were part of a more or less integrated cluster. As was shown by the movements of tagged workers, maintaining communication between mounds within a cluster apparently becomes more difficult with increasing distance. Within the F. oreas comptula cluster communication drops off significantly if the distance is in excess of 35 meters from the dominant or centrally located mound and may stop altogether for distances beyond 40 meters. Within these limits, communication in the form of visiting, transfer of pupae, and possibly cooperation in nest construction attests to the fact that the F. oreas comptula clusters are composed of nests which are not discrete but polydomous, and that a single colony is represented not by one nest but by all nests which maintain communication within the cluster. A similar relationship was found by Torossian (1960) in his studies of the ant Dolichoderus quadripunctatus in which the polycalic colony was composed of a number of "calies" each of which could develop with time independent status but with a certain amount of brood and population exchange.

Such a relationship among the nests within a cluster may be the



result of selective advantage. Scherba (1964) suggested that the evolution of colony structure has produced polydomous colonies from ancestral single nest colonies. It is not known what selective pressures may have brought this about but an advantage (as opposed to the discrete colony of F. obscuripes) may be found in the ability of the cluster to perpetuate itself. Over the past seven years F. oreas comptula clusters were found to be highly stable as a complex, but the individual units within the complex were not found to be so.

Most F. oreas comptula nests within a polydomous cluster were polygynous, the largest colony having as many as 4 or 5 queens. Small colonies of recent origin were found to be monogynous. As nests continue to grow in size, additional queens are probably accepted into the colony, possibly from one having a surplus or as a result of the acceptance of fertilized queens following the marriage flight. In this sense, F. oreas comptula colonies are immortal as opposed to the discrete and limited life span of the F. obscuripes colony.

The following sequence is suggested as the probable means by which the polydomous colony of F. oreas comptula becomes established:

- (1) Following the marriage flight, a new colony is probably established in virgin territory by a solitary queen.

Evidence that queens may form new colonies by temporary social parasitism is lacking.

- (2) Succursal nests are constructed near foraging trails.

These may eventually become permanent structures upon the adoption of a fertile queen.

- (3) As nests grow in size, both with respect to structure and population, additional queens are accepted into the colony.

- (4) Colonies which have become overextended as to territory occupied begin to fragment into subunits which may eventually become isolated forming separate polydomous colonies.
- (5) Provided that environmental conditions are not drastically altered, mound clusters may be more or less self-perpetuating in the sense that new construction and the adoption of additional queens constitute a continuous process.

Formica obscuripes and F. oreas comptula appear to have allopatric territories, although both species were found in what seem to be similar habitats. Even where clusters of the two species were within foraging distances of each other, I was not able to locate any overlapping trail systems nor any foraging trails that were even in close proximity to each other. While foraging areas are not usually defended, the territory occupied by the polydomous units of F. oreas comptula were found to be interconnected by underground trails and therefore may be considered extensions of the nest. In such cases the defense of colonies may extend beyond the nests to the borders of occupied territory.

Of the narrow prairie extensions located on the south edge of the Forest River Valley, only one contained thriving F. obscuripes colonies, whereas three contained mound clusters of F. oreas comptula. The three prairie extensions in which F. oreas comptula colonies were located were characterized by dense stands of Kentucky blue grass, intermixed with a few forbs and shrubs. The prairie extensions in which F. obscuripes colonies were located were similar in some respects but noticeably lacking in lodged and partially decomposed mats

of grass culms and leaves. Wolfberry was more common to areas of established F. obscuripes colonies than to those of F. oreas comptula. It is questionable whether or not these minor variations in habitat are significant enough to limit the distribution of either species. It would seem more probable that whichever species was established first in a habitat suitable to both, the other would be excluded.

On the terraces and floodplains, both species occupied very similar habitats. Flourishing F. oreas comptula colonies were quite abundant on the upper and descending levels of the terrace where ground cover was greater and diminished in number of colonies as the floor of the floodplain was reached. Formica obscuripes colonies were found in small numbers on the terrace and increased in abundance on the floodplain. Apparently there was a narrow zone for which both species would compete.

While gradients in vegetation are probably the deciding factors in the separation of the two species, additional data on this aspect are needed before any definite conclusions can be reached.

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