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RAID SITE LOCATION, RECRUITMENT AND AGE POLYETHISM IN THE SLAVE-MAKING ANT POLYERGUS LUCIDUS MAYR (HYMENOPTERA, FORMICIDAE)

City University of New York PH.D. 1982

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RAID SITE LOCATION, RECRUITMENT AND AGE POLYETHISM IN THE SLAVE-MAKING ANT *POLYERGUS LUCIDUS* MAYR (HYMENOPTERA, FORMICIDAE)

by

ELLEN COOL-KWAIT

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1982

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The raiding behavior of the slave-making ant *Polyergus* has intrigued biologists for more than 150 years. Although extensive field observations characterised the early studies of the mating, nesting and raiding of the European form (*P. rufescens rufescens* Latreille: Huber 1810; Forel 1874; Wasmann 1891), the early references to the North American forms (*P. rufescens* ssp., *P. lucidus* ssp.) are few and comprised principally of chance observations (Burill 1908; Wheeler 1910). In 1910, W.M. Wheeler summarised what was known about these species, but it was not until the mid 1900's that an American form was systematically observed throughout an active season, and hence in the full range of behavioral contexts. Some of these more recent studies have obtained data concerning the ecological parameters affecting mating, nesting and raiding (Talbot 1967, 1968; Harman 1968; Marlin 1971) while others have focused on the behavior of *P. lucidus* in the midwest (Talbot 1967; Marlin 1968,1969). In the work concerning *Polyergus*, however, manipulation and controls have rarely been utilized, and the occasional experimentation has had very limited goals. For these reasons the analytical scope of previous investigations has been restricted; major gaps in our understanding of the behavioral processes organizing scouting and raiding still exist.

There have been many hypotheses concerning the way in which raid targets are located by *Polyergus*. One early conceptualization was that most *Polyergus* workers scouted as individuals exploring the environment in search of a *Formica* host colony. With this individually acquired information it was thought that the scouts could direct themselves and other workers in unison to an appropriate target (Emery, Forel and Wheeler in Wheeler 1910). Some later authors suggested that these ants raid along a well frequented path and attack any nest of a slave species which is discovered on the way (Dobrzanska and Dobrzanski 1960; Dobrzanski 1961). It has now been demonstrated, however, that potential raid sites are located by individual ants, who then return to the mixed *Polyergus*/*Formica* colony; one of these scouted sites may then be raided later in the day (Talbot 1967; Marlin 1969). Because it has been shown that same-day scouting sometimes precedes raids, the inference has been that such a sequence always occurs. In order to test the validity of this assumption, I have monitored the behavior of all scouts outside the nest.

Suspicion that same-day scouting may not always occur arises from the description by Wheeler (1910) of a raid perpetrated on the former nest site of a colony which had recently emigrated. Talbot (1967) has reported similar cases. Such observations indicate either that scouting had taken place on a day prior to the raid (and emigration), or that same-day scouts responded to the odors of *Formica* nest sites after their residents had emigrated. Superficial nest entrance exploration of potential targets characterises the scout behavior in other slave making species (*Harpagoxenus americanus*, *Leptothorax duloticus*; Alloway 1979) although these species do not raid empty target nests. Unproductive raids are common for *Polyergus* (Talbot 1967) suggesting that scouting only locates a nest but does not determine the amount of brood present. I have therefore also explored the hypothesis that scouts only superficially assess the suitability of the raid targets they locate.

Prior to a raid, some *Polyergus* circulate excitedly on their nest surface. Although these ants have been named 'activators' (Dobrzanska and Dobrzanski 1960), a title which implies that they can be distinguished as a group by their participation in raid initiation, in actuality nothing is known about any unifying role played by these individuals. Some of these circling ants leave to scout while others simply circle continuously (Marlin 1969). Dobrzanska and Dobrzanski (1960) stated that the removal of the 'activator' group eliminated raiding, but they did not indicate how membership in this group was determined, nor how scouts and 'activators' were distinguished. Scouts are not irrelevant to the raiding process as those investigators assumed (Marlin 1969) and both groups are also active at the same time of day, at least in *P. lucidus*, and so the distinction between scouts and circlers is crucial. Without this distinction 'activator' removal could often be scout removal. According to Dobrzanska and Dobrzanski (1960) the direction in which the 'activators' aggregate on the nest surface predicts and may determine the choice of paths taken by the raiding column. Since some of the circling 'activators' leave to scout and subsequently return and circle, these aggregations may reflect scout behavior. Particular behaviors characterize scouts; the marking of individuals allows them to be readily distinguished at any time following the execution of such identifying behavior. Through marking and monitoring, the distinction between who is a scout and who is only a circler may be made and the respective contributions of these groups to raiding can be noted. That procedure underlies my investigation of the identity and behavior of individual *Polyergus* outside the nest before raids.

Several raids often occur simultaneously or closely following one another, but subsequent raids may not take the same path. This is noteworthy because the odor of the first trail has been strengthened by the passage of the first group of raiders, and yet a different trail is taken. Many *Polyergus* act as scouts on a given day, and since it is probable that more than one return with information regarding potential targets, a choice must often be made between alternatives. What criteria are available to the raiding *Polyergus* for making the choice? To answer this question I have explored the relationship of the behavior of each scout and the scouts as a group to the subsequent specific target choice in the laboratory.

The raiding column of *Polyergus* is believed to follow a chemical trail without leadership (Wheeler 1910; Talbot 1967; Marlin 1969). The absence of leadership has been presumed because individuals at the head of the column continually changed places. The production of a normal raiding column, however, apparently requires more than the chemical trail, since artificially laid trails induced raids poorly organized in terms of group coordination (Talbot 1967). Without marked individuals, the behavior of individual ants in a large dynamic group is obscured. For this reason, and since leadership of raids has been demonstrated in other slavemakers (Alloway 1979), I have questioned the assumption that no leadership is shown in the raiding *Polyergus*. In the artificial trail experiments (Talbot 1967) the role of scout was circumvented, and so I have investigated the source of group coordination through a more complete description and analysis of the behavior of the individuals comprising the scouting group.

Polyergus do not forage or perform nest maintenance, but they do assume various behavioral roles as raiders, circlers and scouts. Where certain individuals in a colony consistently perform a set of tasks not performed by some other group the division of labor is termed polyethism. These differences in behavior may be between individuals of the same age or between individuals differing in age (Otto 1958; Wilson 1971; Topoff 1971; Topoff and Mirenda 1978). In other ant species where the division of labor is by age, young individuals usually work within the nest and later in life they forage and perform extra-nidal tasks. This study investigates whether the several behavioral roles of *Polyergus* were consistently performed by particular groups, and whether these groups were defined by relative age.

Although raiding is not usually a source of heavy mortality in *Polyergus*, a steady decline in the number of individuals participating in raids is seen as the season progresses (Talbot 1967). The eclosion of worker brood is occurring in the latter portion of the season; the ability of callows to assume adult roles in raiding and emigration might be relevant to the ability of the colony to accomplish these tasks efficiently at that time. This study is the first investigation of the development of behavior in *P. lucidus*.

The onset of the raiding season is variable in timing; colonies in a given area may begin their raids at times more than a week apart (Harman 1968). My preliminary observations indicated that early raiding was correlated with good nest insolation. Well insolated nests of other ant species are known to achieve more rapid brood development than shaded ones (Brian and Brian 1951). Early raiding by better insolated nests might then reflect either the abiotic conditions, or an effect of those conditions on brood maturity.

The slave species is active earlier in the year than *Polyergus* both in freeliving and mixed nests, and brood appears correspondingly earlier in the *Formica* nests. Suitable conditions for raiding include a specific range of temperatures and light conditions (Talbot 1967; Harman 1968), and these may occur irrespective of the weather of the preceding spring. While abiotic conditions do not predict the presence of raidable brood in the habitat, brood developmental stage in the nest does since it reflects the approximately equivalent weather history of the season for mixed and target colonies alike. The presence of *Polyergus* larvae in the mixed nest could thus provide a proximal cue to the workers that raidable brood is present in the freeliving *Formica* colonies. Since the presence of larvae in the nest excites the workers of many ant species to more intensive activity and in some cases produces a qualitative change in their behavior (Schneirla 1938; Haskins and Haskins 1950; Brian 1973), the most interesting result would be scouting and raiding immediately after the appearance of the larval brood. In the documented cases in other ants the excitement produced by the larvae is associated with changes in foraging for food. Similar correlation in this dulotic species would imply a possible correspondence of stimuli once associated with intensive food getting and now associated with raiding. Much of the slave species' brood taken by *Polyergus* is probably eaten, since a far smaller number of individuals eclose than are taken as brood on raids (Dobrzanski 1961; Talbot 1967). *Formica sanguinea* eats a large proportion of the brood obtained in raids (Wasmann 1891; Wheeler 1910), and they also retrieve insect parts from raid sites (Dobrzanski 1961). *Polyergus* is thought to be phylogenetically derived from formicine ancestors; for this reason similarities with the behavior of the facultatively dulotic *Formica sanguinea* group may provide insight into the origins of the more advanced obligatory dulotic behavior of *Polyergus*. My laboratory observations allow the description of the uses of brood retrieved by *Polyergus*.

It is known that newly dealate *Polyergus lucidus* queens locate nests appropriate for adoption by following raids (Creighton 1950; Talbot 1968); it has merely been assumed that adoption sometimes actually ensues. This assumption has been challenged for American forms because experiments with P. *lucidus* queens from P. *lucidus*/F. *incerta* and P. *lucidus*/F.*p. nitidiventris* mixed nests have not produced supporting evidence (Wheeler 1910; Marlin 1968) although the phenomenon has been reliably demonstrated in artificial nests of the European P. *rufescens* (Viehmeyer 1908; Emery 1909). In addition, Marlin (1968) observed many instances of colony founding by budding, which may be the principal method of colony founding by midwestern *lucidus*. I have investigated nest founding of the eastern form of P. *lucidus* in mixed nests with F. *schaufussi*. In conjunction with the nest founding, I was interested in determining whether the *Polyergus* queens following raids were allocolonial or syncolonial, and whether matings ever occurred between males and alate queens of the same nest.

Although spring nest changes have been described for *Polyergus* mixed colonies, my observations report the emigrations of these colonies to the overwintering nests in the fall.

MATERIALS AND METHODS

TAXONOMY

All species of *Polyergus*, represented in North America, Europe, Central Asia, China and Japan, are obligatory slave-makers. D.R. Smith (1979) recognises three North American species: *P. lucidus lucidus* Mayr, *P. lucidus longicornis* Smith, and *P. breviceps* Emery. Since Mayr first described *P. lucidus lucidus* in 1870, it has been the most studied of all the American forms. This species enslaves *Formica* belonging to the *pallidefulva* group of the sub-genus *Neoformica*, a complex which has stimulated considerable taxonomic controversy. Three *pallidefulva* subspecies, *nitidiventris*, *fuscata*, *schaufussi* and a variety of *schaufussi* called *incerta* were recognised by Emery in 1893 in a revision of Mayr's 1886 classification of all these forms as part of the *schaufussi* species. W.M. Wheeler accepted Emery's arrangement when he monographed *Formica* in 1913, but he recognised that there was great morphological variability in each of these forms, especially the variety *incerta*. Workers from several colonies and even sometimes from a single *incerta* colony may exhibit intergrading forms whose key characteristics range between those of *schaufussi* and *nitidiventris*. Since their key characters did not reliably separate the forms, Creighton (1950) felt that these three forms (*schaufussi*, *incerta* and *nitidiventris*) could not be legitimately distinguished. Using morphological and biogeographic evidence, he derived only two forms, *Formica pallidefulva nitidiventris* and *Formica schaufussi*.

My field observations of the *Neoformica* of Long Island indicate that while there is variability between nests, there seem to be consistent differences in the modal characteristics of four types of *Neoformica* colonies with respect to color in life, size, and overall proportions. Although the morphology of the slaves in a mixed nest is even more variable than in a single freeliving *Formica* nest because it represents samples from a series of nests of the slave form, there still exists an apparent modal type with regard to the features described as can be distinguished by eye in the field. This becomes especially apparent when *Polyergus* colonies are compared and four kinds of mixed colonies can usually be distinguished by modal slave type. The differences between these mixed nests necessarily derive from differences in the nests raided. Two of the slave types are easily distinguished by size (*fuscata* and *schaufussi*) and these are distinct from a third form (*nitidiventris*) on the basis of color in living specimens, its more spindly form and intermediate size. The fourth form (*incerta*) is not easily distinguished from *schaufussi* and *nitidiventris;* its characteristics are the most intergrading, as Emery, Wheeler, and Creighton have indicated.

Some biological differences in life cycle and ecology are evident among the *Formica* forms. Although the *schaufussi, incerta,* and *nitidiventris* forms may all be found in the same general habitat, that of a pine barren with sandy or loosely packed topsoil, each seems to inhabit sections with differing amounts of shade. The *schaufussi* form will be found in open or lightly shaded sections, *incerta* in relatively more shaded places, and *nitidiventris* in the most shaded parts. The nests of all three appear very similar, but *nitidiventris* is the only form which periodically builds a small mound. The fourth form, *fuscata*, is found most often in densely shaded areas with heavier soil. Whereas the worker pupae of *schaufussi* and *incerta* are predominantly cocooned, those of *fuscata* are naked and those of *nitidiventris* are sometimes in cocoons. These differences also obtain for *Formica* pupae in the mixed nests of the respective slave types.

The presence of biological distinguishing features separating all four *Formica* types seems clear on the basis of the following observations: If four colonies of *Polyergus*, each using a different slave type, are dug and transplanted into portable nests, and if each of these nests is placed sequentially on different days in the same position in an area containing many freeliving colonies of the four types of *Formica*, each *Polyergus* colony raids different nests. In every case the raid targets of a particular colony will be nests of what can be prejudged to be the slave type which that colony has been using (with a small margin of error occurring between F. *schaufussi* and F. *incerta* nests). The result of specificity of target type is that a different set of nests is attacked by each of the mixed colony types. If one portable nest is replaced by another using the same slave type, the second colony will raid the same apparent *Formica* type as the first, and the same target nests. I have repeatedly observed this specificity of target choice in exactly the manner described: the substrate for these observations was made available to me through the extensive efforts of Mr. Raymond Sanwald of Medford, Long Island (pers. comm.). Mr. Sanwald monitors the position of each of hundreds of *Neoformica* colonies on an acre of partially cleared pine barrens. Annually he excavates four mixed colonies of *Polyergus*, each using a different representative of the four forms of *Neoformica* as slaves, maintains these in portable nests, and allows them to raid throughout his acre of *Formica* nests. His records show which freeliving *Formica* nests are raided by which mixed colony type. There is year-to-year consistency with virtually no overlap in the *Formica* type nests used by the corresponding mixed colony type, although each year different particular mixed colonies of each type are used. If some of the *Formica* slaves of the mixed colony are removed and placed in another mixed colony using the same slave type, in a very short time and with few injuries to any individuals, the replacement slaves are accepted in the new colony and function there normally. If, on the other hand, *F. schaufussi* slaves are removed from a *P. lucidus* colony and placed in a mixed colony having another form of *Formica* as slaves, the residents and the newcomers fight and many individuals are killed. I repeatedly observed this phenomenon in experimental introductions Mr. Sanwald made to his various types of mixed colonies to illustrate this point. Although at least three *Formica* types nested within raiding range of my study colonies, only *schaufussi* was raided by a *Polyergus* colony using *schaufussi* slaves.

As is clearly established through these observations, the varieties of *Neoformica* recognized by *Polyergus* correspond to those distinguished by Emery and Wheeler. For this reason it is their classification that I will utilize. Although Emery's key can only be used with difficulty, the classification separates varieties along lines which are biologically meaningful. Key characteristics now need to be found which can more reliably separate these forms. Dr. A. Francoeur of the University of Quebec (Chicoutimi) has many samples of *Neoformica* from freeliving and mixed nests with ecological data and he will be attempting a revision of the *Neoformica*.

DISTRIBUTION

Polyergus lucidus lucidus Mayr, the only representative of this genus in the northeastern U.S., ranges from Massachusetts to North Carolina and west to southwest to Colorado and New Mexico. *P. lucidus longicornis* Smith is known only from type specimens from North Carolina and Georgia. The third species, *P. breviceps* Emery is found from Ontario and British Columbia south to California, Arizona and New Mexico.

FIELD LOCATION

My study site was in the westernmost portion of the natural pine barrens in Suffolk County on Long Island, New York. The area containing regularly observed mixed colonies was a strip of land 1 km. long and 60 m. wide. The colony chosen for continuous observation was the most vigorous of any found naturally occurring in the western part of Suffolk County in terms of *Formica* and *Polyergus* activity outside the nest. The area utilized by this main study colony was a circle with a radius described by the length of the longest raid, or 48 m. Most of this area was cleared with a power mower immediately prior to the onset of the raiding season. Although the nest itself was located in a relatively clear area in the midst of a grassy habitat, most vegetation within 1 m. of the nest entries was trimmed to the sand surface or burned with an acetylene torch to provide open ground to facilitate observations.

The topsoil in the study area was fairly light and well aerated with a sandy texture. Grass and brushy ground cover ranged between 10 and 60 cm. in height, but frequently interspersed throughout were open patches of sandy soil. The predominant trees in the habitat were white oak, scrub oak, pitch pine and choke cherry, none of which were over 4 m. high. The habitat was bordered on both sides by a row of white oak and hickory trees over 6 m. high and 6 m. deep.

PERIOD OF STUDY

Polyergus colony M2 was observed in the field two days per week from mid-July through mid-September 1976 and from mid-June through mid-July 1977. From mid-July through the first of October 1977 field observations were made seven days per week. The activity of the colony was monitored continuously at all hours when *Polyergus* were active outside the nest. Field observations of nest M2 totaled 60 hours in 1976 and 375 hours in 1977.

Laboratory observations were made five days per week between 10 AM and 6 PM. Different *Polyergus* colonies were studied: The first (L1) from June 24 through September 28, 1976 and the second (L2) from June 18 through July 22, 1977. Laboratory observations totaled 450 hours in 1976 and 190 hours in 1977. Colony L1 was replaced in the field May 20, 1977 and the activity of its marked *Polyergus* workers was monitored periodically during the raiding season of 1977.

METHODS OF STUDY : LABORATORY

Complete queenright mixed colonies of *Polyergus lucidus* Mayr and *Formica schaufussi* Mayr were removed from their naturally occurring nests in the pine barrens of South Centereach, Long Island in both 1976 and 1977. Removal of these two colonies was accomplished by excavating the entire nest, placing dirt and ants in large glass containers, and aspirating stray individuals. Separation of dirt and ants was later implemented by inducing the colony to emigrate from a box containing the contents of the collecting jars into modular laboratory nests. Freeliving queenright colonies of *Formica schaufussi* were similarly dug and transferred into modular nests whenever they were needed as raid targets in the laboratory; often only a portion of worker force was retained for laboratory use.

The permanent laboratory nest for the mixed colonies consisted of four round plastic boxes (18 cm. diameter) with dental stone substrates. These boxes were interconnected with vinyl and lucite tubing (1.25 cm. diameter) in such a way as to allow movement among modules to the exterior of the nest directly. Two of the four modules were provided with pairs of 1.25 cm. I.D. tubes which connected the exterior of the module to the undersurface of the dental stone substrate. One of each of these pairs was shaped to receive water and allow it to slowly diffuse into the dental stone; the other of each pair allowed the evaporation of the moisture from the stone into the air outside the nest. This differential moistening of the components of the nest produced a gradient of humidity ranging from approximately 20 to 90% as measured by pH Hydron paper.

Formica colonies were kept in module pairs, one of which was moistened as described above, and the other of which was kept dry and heated when room temperature fell during the use of the air conditioner. Ambient air temperature varied with outdoor temperatures from 10 AM until 4:30 PM, at which time the room was gradually cooled so as to reach night time temperatures 3° to 6° C below those in New York City to correspond with the lower temperatures in the Long Island habitat.

The mixed nest was kept in a separate chamber with opaque walls and connected by a single 1.25 cm. tube to the remainder of the complex. The nest was observed both by eye and with the use of a Nikon swivel binocular microscope which adjusted to view all parts of the nest. In 1976 this chamber was illuminated by red lights; however, since the mixed colony behaved similarly when maintained in diffuse white or red light, the observation chamber was illuminated by ground glass diffused white light in 1977. *Formica* colonies were kept in individual wood frame boxes whose filtering sides allowed only red light penetration. A semi-opaque covering for these nests was necessary because these colonies were located in the main part of the laboratory and the continuous activity would otherwise have been disturbing to them. All nests were cushioned by foam rubber pads to minimize the vibration caused by laboratory activity.

The mixed nest connected to a lucite walled foraging area with a white (gypsum) sand substrate. This area was illuminated both by diffuse fluorescent room light and by four pairs of 75 watt flood lights angled over it from east to west above the sand. Each pair of lights was timed individually to produce an east to west sequence of changes in direction and intensity during the course of the day.

The main foraging area interconnected with four similar foraging areas (Figure 1), each of which had three 1.25 cm. openings leading to a single *Formica* nest. The interconnections between foraging areas were 3.8 cm. drawn lucite tubing with sand floors of 1.25 cm. max. depth. Each nest had 24 hour access to its adjacent foraging area, but the interconnecting tubes were open only during observation hours.

Insects collected live from the ants' natural habitat were frozen and provided freshly-thawed daily to the mixed colony. Both the mixed and slave species colonies also received freshly killed Tenebrionid larvae and pupae (raised in the laboratory) and a 50% honey/distilled water solution. These foods and water were supplied ad libitum.

In both the 1976 and 1977 mixed colonies each *Polyergus* worker was marked with three dots of enamel 'flo-paque' paint, one each on the thorax, petiole, and gaster. The use of seven different paint colors allowed the generation of a unique color coded sequence for each individual. Particular colors used in specific positions indicated the birth season of individuals whose times of eclosion were known. To mark the ants, single individuals were isolated in petri dishes, immobilized by exposure to -2°C for 3-5 minutes, held with reverse forceps under a dissecting microscope and painted. Each was then warmed, and when fully mobile, placed with other newly painted *Polyergus*. Syncolonial *Formica* were added in a ratio of one *Formica* for every three *Polygus*. This group was then isolated with food and water in a screen-covered lucite module to allow odors to dissipate for 36 hours. Although grooming and paint removal occurred, most markings remained and those removed were replaced.

Continuous observations were made on the behavior of all *Polyergus* in the complex from the time of tube opening until raiding activity ended for the day, or until 6 PM on days of no raids. Records were kept concerning the behavior, labor role, and individual identity of each *Polyergus* active outside the nest. Outgoing and returning paths of travel and positions attained were described with respect to time. Through marking and monitoring, the behavior of each individual *Polyergus* could be described throughout the course of the day, and their particular preraid activities related to their behavior during raiding. Raid records indicate the behavior of the raiding group, participating individuals, timing, target site, and booty retrieved from the raid. Double counts made daily before tube opening provided estimates of the population size in each of the developmental categories.

METHODS OF STUDY : FIELD

On observation days the behavior of all *Polyergus* outside the nest was monitored continuously. Observations of activity prior to raiding were made from a raised seat 1 m. from the nest entrances. The behavior patterns characterizing the daily activity sequence were closely monitored, and the specific roles of marked individuals were noted.

Identification of individuals was accomplished in the same manner as in the laboratory, except that only scouts were marked, and isolation was for 24 hours at 5°C above ambient air temperature. In the laboratory scouts were defined as those individuals who moved more than 70 cm. away from the home foraging area; in the field they were those active beyond a marked 1 m. perimeter. They were so defined because in pilot studies, I found that individuals active at these distances from the nest predictably continued outbound exploration.

In 1977 a plaster ring 8 cm. wide was poured into an excavated shallow ditch around the perimeter of the nest at a 1 m. radius. This ring was marked with compass bearings; small aquarium stones of various colors embedded at the edge of the ring indicated 10° intervals. Different colors were used to readily distinguish the various principal intervals. In this way the movements of individual ants with respect to compass direction could be determined instantaneously.

The observer followed all raids except when more than one occurred simultaneously, in which case the largest group was traced and the others loosely monitored for path direction and target site. The paths of raids were marked with aquarium stones while they were in progress. After raiding was completed for the day, the stones were gathered and replaced by fast drying enamel spray paint. The raid sites were sampled by mouth aspiration of fleeing workers at the time of the raid; the nest entrances were overlaid with a flat paint-marked rock whose undersurface was often subsequently used by the colony for brood warming. The paths of the raids were subsequently mapped using a Silva compass and a Rolatape measuring wheel.

RESULTS

DAILY ACTIVITY SEQUENCE DURING THE RAIDING SEASON

In the field no *Polyergus* appeared at the nest surface until the afternoon. The morning nest activity was characterised by *Formica* foraging and nest maintenance. Occasionally single *Polyergus* appeared outside the nest in the morning but no directed activity occurred. This observation contrasts *P. lucidus* with other representatives of the genus, who reportedly scout during morning hours (Dobrzanska and Dobrzanski 1960). *Formica* activity typically decreased during the warmest hours of the day, and as their numbers increased again in the afternoon, *Polyergus* also began to leave the nest for scouting activity. Typically the scouts left the nest area one by one during the period just following the hottest soil temperatures of the day, or more rarely, closely preceding the hottest temperature time (Table 1). When raids occurred they usually followed the initial scout appearance by an hour or more (Table 1). According to both laboratory and field observations, soon after the appearance of the first *Polyergus*, many accumulated at the nest entrance. Some traveled in circular and zigzag patterns on the nest surface, reentering and exiting the nest periodically, their numbers increasing generally throughout the afternoon and dramatically just prior to raiding. Typically the number of scouts reached a peak within an hour or so after the first scout departure, although some individuals departed throughout the afternoon, even after raiding began.

The days on which scouting and raiding occurred were characterized by a soil surface temperature range shown in Table 1 with clear or slightly clouded skies. The weather conditions typical of the Long Island raiding season in general are shown in Table 2.

SCOUTING

The movements of each *Polyergus* within the laboratory raiding complex were monitored throughout the day, and the records thus show which nests were scouted on any given day and by which particular scout(s). One important result from both laboratory and field studies is that same-day scouting of the raided nest is the rule. Of 27 days on which raids occurred in the laboratory, 25 initial raids were on nests which had been scouted on the day of the raid while only two raids in this 3.5 month period were on nests not scouted on the same day, although the paths to the nests had been partially retraced prior to the raid. In both of these anomalous cases, the same nest site had been raided on the previous raid day; in one case this meant the previous day and in the second case, two days earlier. Even when the same nest is raided several days in succession, however, it is much more usually rescouted on each day raided. In the seven other instances where the same laboratory nest was raided on two sequential raid days, the reraided nest was scouted again on the day of the second raid.

Removal of all scouts on each of three days in the field and on seven days in the laboratory resulted in the absence of raids on those days, and the removal of outgoing and incoming scouts from a particular 180° sector of the 360° perimeter of the field nest resulted in the absence of raids in that sector on three of four days, and in no raids on the fourth removal day. In one instance in the field, when a *Formica* nest was reraided on the subsequent day, the raid followed a completely different, less direct path to the same target, indicating that it had certainly been rescouted on the second day. All of these results clearly indicate that for *Polyergus lucidus*, raiding rarely occurs in the absence of same-day scouting of the raided nest.

In the laboratory no nests were raided unless a *Polyergus* scout had gotten at least as far as the interior of the nest entrance; often this was as far as the scout did penetrate, and yet a raid later ensued. This evidence would indicate that a fairly superficial assessment of the contents of a nest is enough to qualify it as a potential target. In both the laboratory and field, raids were often perpetrated on apparently inappropriate nest sites, occasionally those containing no brood, or no queen and no brood, and twice on the previously occupied nest of a recently emigrated *Formica* colony (Table 3). Detailed assessments of the condition of the colony were thus not always made.

Polyergus scouts fully entering target nests in the laboratory were frequently captured by groups of *Formica* workers. While the scout sometimes freed itself, even multiple times, once its legs were all pinned by 5-6 *Formica*, capture usually meant death. Since the artificial nests were perhaps more difficult to escape from than a natural nest, no data were taken on the frequency of scout death. Scout capture was observed frequently enough in the field, however, to indicate that the risk involved when more than a surface assessment is made is probably quite high.

SCOUT LEADERS

The departure of the raid column is partially organized and directed by the individual scout that located the target nest. Although raids can occur when a chemical trail (whole body extract) is artificially laid from the mixed nest to a *Formica* nest, these raids are poorly organized in terms of group coordination (Talbot 1967). My observations have shown that the scout who located the target nest runs at the head of the column intermittently; periodically she moves back in the column, weaving in and out between the raiders, and then running again in a forward direction parallel to or zig-zagging in and out of the column, soon reaching a leading position again. In all instances when the identity of the successful scout who had located the target nest was known, this individual was the scout leader of the raid. The behavior of the scout leaders was observed on 13 days in the laboratory and on three days in the field. The scout leader does not lead the returning column. Even when a raid was conducted on an abandoned or broodless nest, the scout who had located that nest site became the leader of the raid. Thus even when raids are failures, the target sites have been located by a scout, and so failure raids, seen often in the field, may represent the shortcomings of the scouting procedure and not unscouted nests or differently organized raids. In both laboratory and field, the role of the scout leader is apparently especially important at certain junctures in the trail. A column will often stop and mill in a particular place, continuing the raid only when the scout leader returns to the head of the column. The scout leader is sometimes also the first individual to enter the target nest; in four of the five cases in the laboratory where the scout leader and the first entering raider were known, they were one and the same; in the other instance, the scout leader was second into the target. The role of the scout leader at the moment of the raiding column's entry into the target could only be observed in the laboratory. Since some raids continue without any milling along the way, and often the target entrance is found immediately by many raiders, the role of the scout leader in indicating the route and the entrance to the *Formica* nest may not always be important. The scout leader is not infallible at relocating the trail and target nest; often the raiding column will mill at a juncture and never relocate the trail, or will come within a foot of the target and not find the nest entrance, eventually returning unladen to the mixed nest. Failure raid trails are often rescouted and the targets located and subsequently successfully raided.

Since there were typically several possible targets located by several scouts, it was not possible to predict which target would be the subject of a raid and hence who the scout leader would be until after the direction of the raid was established. Thus the recruitment method of the scout leader could not be determined. On the basis of the accumulated data, the nest to be raided can now frequently be predicted by the relative numbers of scout trips toward the alternative nests (Table 4).

SECONDARY SCOUTS

My laboratory observations show that a *Formica* nest may be entered by a single scout once or many times, or more than one scout may enter it on a given afternoon. Although *Formica* nests are often raided after only one scout entry, more than one scout frequently goes at least partway toward the potential target nest, often multiple times, after it has been located by the first scout (Tables 4,5). The activities of scouting *Polyergus* are varied; while they sometimes fully enter target nest cavities (N), they may only explore the interior of the nest entrance (NE), or return to the mixed nest after traveling on 2/3 of the distance in the direction of a potential raid site (FA). This suggests that some of these trips may be supplementary to the original nest-entering trip, perhaps differentially reinforcing the trails or the recruitment behavior of the preceding nest-entering scouts, and potentially influencing subsequent raid direction choice. Excited return by a nest-entering scout is probably accompanied by the deposition of a chemical trail (Talbot 1967). Alternate trails so formed might be differentiated by subsequent scouts traveling over all or part of the trail and adding their own chemical deposits. In assessing the influence of the number of full and partial trips made by scouts on the subsequent raid site choice, the predictive value of the number of nest-entering scout trips for the target site raided was checked. Similarly the target predicted by combined complete and partial trips (N+NE+FA) was compared with the actual sites later chosen (Table 6B). The latter (combined) measure has a predictive consistency of 57%, with 24% ties and 19% chance of an incorrect prediction. This result is in agreement with the hypothesis of differential reenforcement of trails; the number of incorrect predictions which remain with this combination is still large enough, however, to indicate that other unmeasured factors differentiating the scouts or the trails may also be playing a role in direction choice.

All scouts were marked so that the number of unique individuals which performed each scouting task could be monitored. The predictive value of the number of different scouts going to each potential target was then checked (Table 6B). If individual behavior in recruitment with respect to a given direction was more important for raid direction choice than the overall number of trips on the trail, then more correct and fewer incorrect predictions would occur by this measure as compared to total trips. The data indicates that this is not the case: 28% of the individuals going 2/3 or more of the distance towards a potential target nest made more than one trip per day, while in all, 34% of all scouting trips are multiple trips. Although the measured 'trips' and 'individuals' are highly related, the trips factor is at least as reliable a predictor of direction choice, making far fewer clearly incorrect predictions than the number of different individuals traveling toward the target (Table 6B). No separate group of 'activators' as described by Dobrzanska and Dobrzanski (1960) could be distinguished, but from what I have found concerning the activity patterns of the *Polyergus* before raids, it seems that many different scouts may influence raid direction choice; the 'activational' role is very likely implemented by the scout who successfully attains a target site and those who subsequently reenforce her trail or respond to her recruitment behavior with secondary recruitment behavior directed towards other *Polyergus*.

Since 50% of the time the successful scout leader made more than one trip to the target nest (Table 6A), successful scouts clearly number among the 34% of all scouts who are making more than one trip per day. Since the 'trips' factor appears important in the raid direction choice and since the contribution of the successful scouts to the 'trips' factor is significant, successful scouts may be particularly influencing the direction choice of the raid by their added contribution to the trail emphasis, influencing the direction choice in a manner additional to the physical directional leadership of the column as scout leader.

Once a scout has located a *Formica* nest and returned home, there may be anywhere from a 2-60 minute lag to raid time (Table 5).

SCOUTS AND CIRCLERS

The group of ants active on the nest surface and circling within a 1 m. radius before the raid has a dynamic composition. *Polyergus* scouts typically return to the nest and are active on its surface as circlers for varying periods of time, entering the nest or going off again to scout intermittently prior to the raid. Thus, unless scouts are marked and their activity earlier in the day is known, they are indistinguishable from the other ants which circle at the nest surface and never leave a 1 m. radius prior to the raid. Although circling behavior is distinctly different from scouting behavior, circlers are not a separate group.

All scouts circle on the nest surface and go on raids, but many *Polyergus* circle and raid without prior scouting. Most raiders neither circle nor scout on any given day. An average of only 8.3% of all raiding *Polyergus* were scouts on that day; only 5-15% of the raiding *Polyergus* were active before the raid as either scouts or circlers. These percentages represent changing groups of individuals from one day to the next. This implies that individual *Polyergus* exhibit different behavior from one day to the next. In order to determine the sequence of behavior transitions in individuals, data was taken concerning the behavior of 49 different *Polyergus* for consecutive periods of 5-14 days in the laboratory. The behavior changes of interest were the transitions between raider and circler and scout, and so the ants chosen for comparison were known to scout at one time or another. The most frequent transition was from circling on one day to scouting on the subsequent day. The next most common change was from scouting to circling (Table 7). Once an individual appears as either a scout or a circler, it is probable that alternation of these preraid exterior roles will continue for a series of consecutive or nearly consecutive days. This period is of variable length, and scouts and circlers often also become only raiders or remain in the nest on certain days and then return after 1-5 days to scouting or circling. If more than about five days elapse since their last preraid activity however, they then predictably only raid or remain inactive in the nest subsequently. It seems that scouting is not the consistent role of certain individuals, but an alternative role for some *Polyergus* for a period of time in their life.

ONTOGENY OF BEHAVIOR AND AGE POLYETHISM

Since scouting and preraid circling are behaviors different from those being expressed by 85-95% of the *Polyergus* in the nest on a given day, some form of polyethism is apparently occurring. Although each age group is represented by some scouts as of the second week of the raiding season (the new brood of *Polyergus* has not yet eclosed), only a small percentage of the *Polyergus* of each age group act as scouts on any given day (Table 8). Thus the polyethism seen is based partly on differences in behavior between individuals of the same age. Table 8 also shows that a smaller percentage of the youngest age group act as scouts than is the case for the older age groups. This indicates that scouting becomes more common with age and so the polyethism seen is also based partly on differences in behavior between individuals of different ages.

By marking age groups differentially in the laboratory, I found that the first scouts of the season are among the oldest individuals in the colony; workers from the intermediate age groups are represented in the scouting force soon afterward. In the field it is usually extremely dark *Polyergus* who appear first in the season as scouts; such deep pigmentation usually indicates greater age of individuals. The *Polyergus* eclosed at the end of the previous season are the last to be represented as scouts; their participation increases as time goes on. The two older groups continue to be represented throughout the season.

No callows acted as scouts in the season of their eclosion (two brood seasons per year). Some of the callows appearing in the nest during the latter part of the current raiding season participate in emigration and emigration raids when they are as young as three days post eclosion. While some also participated in slave raids and retrieved booty at this age, most of these callows did not appear in raids until the season after their eclosion. Thus it is not likely that early participation in raiding is of substantial consequence to raiding efficacy when callows are part of a large, mature colony.

ONSET OF THE RAIDING SEASON

By checking the undersurfaces of stones placed over the nest entries of known *F. schaufussi* and mixed colonies in the field (1976, 1977) I found that *Formica* brood is available in freeliving colonies, predictably one to four weeks ahead of the *Polyergus* brood in mixed colonies. A similar brood timing lag also holds for the *P. lucidus* and their slave species in Illinois (Harman 1968). In my 1977 laboratory colony, the appearance of larvae in the mixed nest was followed on the next day by the first scouting activity of the year, and four days later the first raid occurred. For the 10 days preceding larval appearance the same environmental conditions had been maintained as those of the days on which raids later occurred. The timing of the onset of raiding in the field colony in 1977 is known within four days, as is the timing of the emergence of the callows. Since I have determined the transition time from the appearance of a larva to its eclosion (Table 9), by counting back from the time of callow emergence, I have determined that the first larval appearance occurred within that four-day range of days wherein raiding began for the season in this mixed colony. The stage of development of the brood in the mixed colony reflects the weather history of the season for the mixed and freeliving colonies alike in a particular habitat. Since the *Formica* broods are present earlier in any given season, the presence of *Polyergus* brood in the mixed colony predicts the presence of raidable brood in the habitat.

CHARACTERISTICS OF THE RAIDING SEASON

In the field nine raids successfully retrieving brood in 1976 and 50 in 1977 were observed, all emanating from the same study colony. In the laboratory, raids were monitored on 22 days (29 raids) in 1976 and on seven days (13 raids) in 1977. From my 1977 field data I have estimated the number of raids per season, the total quantity of brood retrieved, the proportion of raids which find their targets and the number of raids which either fail to find their target or to retrieve brood (Table 3). In both laboratory and field there was often more than one raid per raid-day (Table 3). Multiple raids on different nests at simultaneous or overlapping times were common, as were reraids on the same nest. The distances typically traveled to target nests can be seen in Figure 2. The utilization of the freeliving *Formica* colonies within this range by the *Polyergus* colony can be described by the distribution of the raided colonies in the habitat and by the pattern of reraiding of particular colonies. Since the maximum distance attained by a raid was 48 m. the theoretical range within the habitat which can potentially be exploited by a *Polyergus* colony of this size is a circle with this radius; in practice, however, the area utilized emphasized certain sectors (Figure 2). Temperature requirements of these ants for raiding are described by the maximum and minimum temperatures at which raiding occurred. The empirical values from the field were: 47.5° C max., 23° C min.

RAID RETRIEVED BROOD

When the raiders return to their home nest with their booty, they drop it at the entrance to the nest or carry it into the nest and either drop it or relinquish it to a *Formica* nestmate. It is then placed by *Formica* either in areas of the nest where other brood is kept or it may be immediately eaten or, in the case of pupae, immediately decocooned and eaten soon afterward.

A large proportion of all raid retrieved brood in the 1976 and 1977 laboratory mixed colonies was eaten. Furthermore, many of the pupae were immediately decocooned by F. *schaufussi* slaves, which precluded the eclosion of all except for those ready to eclose at that particular time. Many eggs and larvae brought in from raids were eaten by *Polyergus*, *Formica* and larval brood; it is unknown whether any of these younger stages survived to eclosion. At the end of the 1977 active season the field colony retained 6067 *Formica* adults (Table 11). These ants live at least two years, so if at least half (or 3034) survived from the previous year, since 11,753 brood were taken on raids during that season, only 3034 of these raided brood would be represented as adults working in the colony; 8719, therefore, having presumably been eaten. This represents 75% of the total larval and pupal brood taken on raids. If the number of *Formica* surviving from the previous year was smaller, which it would be by the time of fall excavation because of summer mortality, the proportion of raid retrieved brood assumed eaten would be smaller, but even if the entire population of *Formica* was replaced during the raiding season, 48% of the raid retrieved brood would still have to be presumed eaten.

MATING AND NEST FOUNDING

When *Polyergus* males and alate queens from the same mixed colony were confined together, within 12 hours most of the queens had become dealates, indicating that mating had occurred between brother and sister. Alate *Polyergus* queens did not lose their wings if confined with *Polyergus* males from mixed nests using a different type of *Formica* slave, which suggests that *Polyergus* populations using different slave species may be reproductively isolated.

Alate queens in the known *P. lucidus*/*F. schaufussi* mixed nests in the habitat of the field study were marked differentially to indicate their nest of origin before mating flights began in 1977. During the entire mating season, 25 newly dealated queens from the three marked nests and at least one unknown nest arrived at the study colony and nine followed the slave raids of the mixed colony on five different days of the latter part of the raiding season. Some of these new queens were known to originate from the study colony, having mated and returned. Since not all alates were marked, more syncolonial queens were probably represented than Table 12 indicates. Some new queens were seen following paths of scouts or raids made earlier in the day, both on outbound and mixed nest-bound directions. This indicates that they may be following odor trails to locate mixed nests after their flights, and perhaps sometimes locate potential adoption sites subjected to earlier raiding in the same way. The new queens arrived at the mixed nest as much as two hours before raiding began, continuing to arrive during and after the day's raids. By climbing on stems and hiding in nearby brush, they avoided contact with other *Polyergus* until a raid began. They sometimes waited several days for this event. As many as three different queens followed a particular raid, but some queens missed the raid departure altogether (Table 12). When following raids, queens typically remained alongside the raiding column or behind it; contact with *Polyergus* workers often evoked hostility, and in one case a queen was killed by a raider. One new queen originally from the mixed colony and known to have mated with a brother male was picked up by a *Formica* of her colony and carried into the nest; she did not soon reappear. She was not still there, however, when the nest was dug at the end of the raiding season. Although in two instances a dealate from the alternate study colony was found beneath the rock covering the entry to her nest of origin, only a single nest queen was found in each of the six mixed colonies excavated in fall and spring. In the adoption attempts witnessed, new queens followed raiding columns and entered the target nest with the column or alone after the raid, remaining there after all the other *Polyergus* had departed. It was difficult to determine the results of these adoption attempts since new colonies are formed towards the end of the active season and apparently often relocate before they can be checked for brood production in the spring. Of the four adoption attempts witnessed, only two nests remained in the same place until spring. One of these produced *Polyergus* brood and the other was known to retain the *Polyergus* queen but moved before brood was seen. None of the adoption attempts was known to have failed. This sample, although small, would indicate that queens entering raided nests may have a substantial survival rate, at least until the following year. In two years of observation, no budding was ever witnessed with *Polyergus* workers remaining at the target nest with the queen. Since the excavation of six mixed nests in fall and spring revealed only the nest queen and no overwintering dealates, it is unlikely that spring budding is a usual mechanism for colony reproduction in the eastern form of P. *lucidus* using F. *schaufussi* as slaves.

INTERNAL ACTIVITY IN THE MIXED NEST

Polyergus ergatoid reproductives were found in some of the mixed nests; the 1977 laboratory colony had 10 ergatoids when excavated in May. The largest individual laid eggs later in the year; the nest queen was laying eggs concurrently. Four other ergatoids were present in the nest while egg laying was occurring, but these had no *Formica* attendants, went out of the nest on raids, and were never seen laying eggs.

Formica ate eggs, larvae, pupae, insect parts and honey water. *Polyergus* occasionally drank independently and obtained and ate eggs. Although workers of *Polyergus* usually were fed by regurgitations from *Formica* nestmates, as well as from other *Polyergus*, often eggs or larvae were given to *Polyergus* by *Formica*. *Polyergus* grasped the larvae in their mandibles antennating them and stroking them with forelegs and licking the secretions then exuded; frequently this squeezing was so intense that the larvae were mangled and could not have survived. Larvae themselves were given a solid food, eggs, and were also fed by regurgitation from *Formica*. The nest queen was never seen to eat anything but a single egg and regurgitated matter from *Formica*, and much more rarely from *Polyergus*. Some of the eggs eaten were known to be from the ergatogyne, some were *Formica* eggs from raids and some were from the nest queen.

The queen was typically surrounded by a number of *Formica* workers, usually 12 - 40, but more when the queen was laying. Although a small number of *Polyergus* sometimes entered this group, more often they clustered with one another or remained separate well away from the queen. The queen frequently behaved aggressively towards *Polyergus* workers; the characteristic response of *Polyergus* to the approach of their queen was to flee. When the queen and the ergatoid were both laying in the nest, each had a cluster of *Formica* and some *Polyergus* around her, and these clusters were well separated spatially. It is not clear whether particular individuals were uniquely attentive to one or the other reproductive. The day after the death of the nest queen, the laying ergatogyne was killed by several *Polyergus* workers.

Eggs and small larvae stuck together in clusters carried about or overseen by *Formica*. Larger larvae were separated from the smaller ones, but they too were kept clustered until they neared pupation. These brood stages were found most often in the warm, moist chamber of the nest. Larger larvae were often kept in the same area as the pupae, characteristically in the warm dry chamber. It could not be determined whether *Formica* eggs and larvae from raids were kept separate from similar *Polyergus* brood, but both types of pupae were kept in the same area and intermingled.

Eggs hatched in approximately 12 days to become larvae, remaining larvae for 9-12 days. Larvae required dirt or sand near their mouthparts and covering their surfaces in order to successfully make cocoons. *Formica* covered them with this material at the appropriate time. Cocoon formation took 3½ hours or more, and *Formica* removed the cocoons from under the dirt after completion, placing them with the other pupae in warm, dry areas of the nest. Eclosion occurred after 20-23 days, or 41-44 days following the production of the egg (Table 9). The process of eclosion took place with the assistance of *Formica* workers, and occasionally *Polyergus* workers participated. It occupied varying amounts of time, about 25 minutes being typical. Immediately upon eclosion the callows stood, walked and groomed. *Formica* and *Polyergus* adults also groomed the new ants.

Callow *Polyergus* typically clustered together for the first few days after eclosion, then they moved around the nest increasingly and associated with the mature *Polyergus*. In nests taken from the field, I obtained information on the relative proportions of *Formica* and *Polyergus* adults, and in some cases, the proportion of the *Polyergus* which represented the production of the previous eclosion season (Table 11).

Mixed colonies are not stable in size; at least up to a certain size or age dramatic increases in the *Polyergus* population are possible from one year to the next. In 1976, the field study mixed colony was represented by a maximum of 291 *Polyergus* raiders. In 1977 however, as many as 710 individual *Polyergus* appeared as raiders, an increase of 144% over the previous year. Although not all *Polyergus* go on any given raid, these maxima are comparable, and probably represent the bulk of the *Polyergus* population. In both 1976 and 1977 the largest number of *Polyergus* raiders was seen during the early part of the season. By August of 1977 the maximum number represented on a raid in the study colony had fallen from 710 to 470, a force only 66% of its original size. Only 408 fully pigmented *Polyergus* remained in the colony in the fall when the nest was excavated; we can conclude that the attrition rate for the raiding season was at least 57.5%.

EMIGRATION RAIDS

Raiding behavior has not been previously reported in the genus *Polyergus* in contexts other than the slave raid (however, see Huber 1810), but I have found that raiding is an integral part of the emigration occurring at the end of the slave raiding season. In the morning and early afternoons, the fall emigration was much like that described for those in the spring (Marlin 1971); *Formica* workers carried *Polyergus* and *Formica* adults and brood to the new nest, meanwhile moving unladen from the new nest to the old. As the afternoon progressed, however, *Polyergus* workers, both mature and callow, began to participate in the emigration by returning to the old nest and carrying *Formica* adults and a few pupae to the new nest. During these parts of the day the movements of both species between the nests were low frequency and continuous from their respective times of onset. The number of ants acting as carriers during the emigration may be much smaller than the data indicate since it was not possible to mark individuals and each carrier may have made many trips between the nests. The return of many unladen individuals from the new nest to the old would seem to support an hypothesis of repetitious carrying by certain individuals. Two recognizable *Formica* and one marked *Polyergus* were seen to make many trips between the nests.

The emigration raids began in the late afternoon, at approximately the same time of day as raids occur during the slave raiding season. A column of mature and callow *Polyergus* workers moved rapidly from the new nest site towards the old one, entered the old nest and momentarily each *Polyergus* reappeared carrying a *Formica* adult or, occasionally, a pupa (Table 13). The column then reformed and returned directly to the new nest with its principally adult cargo. On both emigration days the first emigration raid was followed by a return to an activity level and pattern similar to that characteristic of each species earlier in the afternoon, before the raid began. On both days a second emigration raid occurred; following that activity, levels for both species were very reduced, and soon all activity ended for the day (Figure 4). Adult transport, while frequently implemented by *Formica* workers at other times of the year, is never seen in *Polyergus* in any context other than emigration. In rare instances a few callow *Formica* were retrieved during slave raids, but mature adults were never carried. It is also interesting to note that *Polyergus* workers never carried other *Polyergus* during the emigration; they never do so under any circumstances. Callow

Polyergus, some as young as 3-5 days, participated as transporters during emigration raids and traveled singly between the nests during the course of the afternoon.

Polyergus mixed colonies do not always emigrate in the fall, nor do they always move in the spring. The colony observed emigrating in the fall of 1976 did not move the following spring, nor did they change nests in the fall of 1977, although a new nest site was available and many *Formica* and some *Polyergus* carried nestmates to and from that nest site sporadically over a period of weeks. Other *Polyergus* colonies in the same habitat made nest changes in the fall of 1977 however. The queen of one emigrating colony was apparently moved very late in the emigration, while in the 1976 observation colony she moved in the early or middle portion of the emigration.

The activity pattern and timing of slave raids and emigration raids were markedly similar (Figures 4,5). The stereotyped behavior of *Polyergus* was essentially identical in both contexts of raiding.

DISCUSSION

SCOUTING

The results of this study clearly show that in the eastern *Polyergus lucidus* using *Formica schaufussi* as slaves, scouting activity occurs exclusively during afternoon hours, and that the scouts locating *Formica* nests make an assessment of potential target nests which requires an entry by the scout only into the nest opening, but may include a deeper penetration. Superficial assessments apparently often satisfy the criteria necessary for scout return home and subsequent recruitment to the target nest. Scouting is very hazardous; full entry into a nest often means capture and death. Since a large proportion of freeliving *Formica* colonies during the raiding season will have brood available, any nest entrance of the appropriate species found by a scout guarantees a reasonable rate of raid success without the risk of entering nests. Target entrance location without penetration is also the strategy used by lone scouts of the slave-makers *Harpagoxenus americanus* and *Leptothorax duloticus* (Alloway 1979).

This work establishes that raiding is characteristically preceded by same-day scouting of the target nest, resolving the controversy that has surrounded the method of raid site location (Dobrzanska and Dobrzanski 1960, Dobrzanski 1961, Talbot 1967, Marlin 1969). My documentation of the occasional reraiding without rescouting of nests scouted and raided on immediately preceding days explains certain observations of Wheeler (1910) and Talbot (1967) which had cast doubt on the direct relationship of same-day scouting to raid site location. The question of a causal link between the exploration of the environment by scouts and the choice of direction and target by the raiding column is certainly resolved here. This relationship is direct. A single scout is responsible for the initial discovery of a potential target. The trail she returns on is often then checked by secondary scouts which may travel partially or the entire distance to the target along her path. Secondary scouts clearly influence the choice of direction of the raid, however, I have not determined whether this occurs by reenforcing the trail of the initial scout or through individual interactions between secondary scouts and raiders, indicating recruitment at the nest after scout return from the trail checked. It would seem that trail reenforcement has a greater influence, since the number of trips on the trail better predicts the choice of trail by the raiders than the number of different individuals preceding them on the trail. The activity of the *Polyergus* in the entryway and nest of the mixed colony certainly increases upon the return of many of the primary and secondary scouts. The excitement in the nest, expressed by the speed of individual movements and increased tactile contacts was notable whenever scouts returned. Since the number of scout trips to a target nest does not accurately predict raid direction, other factors must play a role: Mechanical and chemical stimulation of raiders by recruiters are both likely candidates influencing raid direction. This hypothesis is probable since the recruitment strategy of many other ants includes such stimuli (Leuthold 1968, Szlep-Fessel 1970, Hölldobler 1971, 1974, Chadab and Rettenmeyer 1975, Topoff and Mirenda 1978). Certainly, directional recruitment occurs at least between the primary scout (scout leader) and the raiding column, both chemically through the trail first laid (and often retraced by her), and further through her direct mechanical or chemical recruitment during the raid.

The role of the preraid circlers is still unclear, although primary and secondary scouts circle at times during the afternoon. It may well be that the circlers are active in the recruitment process before the raid or on the trail during raiding. The level of excitement expressed by their activity is definitely greater than that of other *Polyergus* in the nest, and their proximity to returning scouts places them physically in a position to receive and pass recruitment stimuli; my observations show that they frequently reenter and exit from the nest at times of scout return. When one recruiter must transfer arousal to many recruitees, as is the case for *Polyergus* since all the raiders must be aroused for column raiding, the logistics of recruitment are complex. In group and mass foraging species which have the same logistical recruitment problem, repetitive recruitment behavior involving a chain reaction of secondary responders is common. This phenomenon is called secondary recruitment (Szlep-Fessel 1970, Chadab and Rettenmeyer 1975, Topoff et al 1980). The most frequent day-to-day behavioral transitions in *Polyergus* are from scout to circler and from circler to scout. Since a scout so frequently becomes a circler (and often returns to scouting soon afterward) some of the recruitment behavior which she can express when acting as a scout leader may well be expressed in similar behavior as supportive recruitment when she is a circler.

ONTOGENY OF BEHAVIOR AND AGE POLYETHISM

Division of labor between *Polyergus* workers occurs since only 8.3% are scouts and only 5-15% are active at all before raids on a given day. The division is partly between individuals of the same age, but there are also age related differences in behavior. *Polyergus* assume the various behavioral roles of raiders, circlers and scouts. In other ant species, younger individuals usually work within the nest and later in life forage and perform extranidal tasks. Within the *Formicinae*, this sequence is remarkably constant (Wilson 1971). Although I have found that callow *Polyergus* participate in raids and emigrations, they do not scout until the season after their eclosion; early in that season more individuals that eclosed two years before participate in scouting than do individuals that eclosed the previous year. Developmental schedules are consistent with the differential risks of activities so that ants perform less hazardous tasks during the early portion of their life, the total number of working hours provided to the colony in each lifetime thereby being extended. This kind of an adaptive outcome is likely for *Polyergus* since my observations indicate that scouting has a high mortality rate while relatively few individuals are killed during raids. The capacity for scouting behavior in the season after eclosion is certainly important in light of the need of newly established colonies for an input of slaves.

Some callows participate actively in emigration and raiding as early as three days post eclosion. While in the large, mature study colony the impact of this participation was not great, callow participation could be important for new or small colonies. It is also possible that the per cent callow participation might increase when there is a small raid force since all behavior associated with raiding is clearly present very early.

RAID-RETRIEVED BROOD

My data show that the appearance of larvae in the mixed nest immediately precedes the onset of scouting and raiding for the season. I have also clearly demonstrated that many of the captured brood are used as food within the mixed colony. In many other ant genera the appearance of larvae in the nest is associated with changes in the behavior of workers resulting in foraging for food (Schneirla 1928, Haskins and Haskins 1950, Mirenda and Topoff 1980). The onset of raids providing great quantities of food for the colony suggest a possible correspondence of stimuli once associated with food-getting and now associated with slave-raiding. This has implications for the understanding of the origins of slave making in *Polyergus*. Since they are thought to be phylogenetically derived from Formicine ancestors, similarities in the behavior of the facultatively dulotic *Formica sanguinea* group may provide insights into the origins of the more advanced obligatory dulotic behavior of *Polyergus*. *F. sanguinea* eat a large proportion of the brood obtained in raids (Wasmann 1891, Wheeler 1910), and they retrieve insect parts as well as brood from raid sites when both are available (Dobrzanska 1961). Brood retrieval is highest in years when small insects, used by them for food, are lacking (Marikovski 1963). Since my nest observations and field data concerning the uses of brood show that most are eaten, raiding behavior clearly results in the acquisition of food for the colony, and this could be either an original or a derived function of slave raids. The service of this function in F. *sanguinea* indicates that it may have been an original one.

MATING AND NEST FOUNDING

Adoption of lone dealates into *Formica schaufussi* nests after raids was the only method of colony reproduction observed for queens from mixed P. *lucidus*/F. *schaufussi* nests. While Marlin (1968) indicates that this method of colony reproduction occurs with dealates from P. *lucidus*/F. *nitidiventris* mixed nests in Illinois, he also describes the budding of such *Polyergus* queens with groups of *Polyergus* workers into freeliving *Formica nitidiventris* nests in spring and fall as a typical method of colony formation. Since I never observed such budding in the P. *lucidus* using F. *schaufussi* as slaves, and since excavation of six of their nests in fall and spring revealed no overwintering dealates, the budding method of colony reproduction is either extremely rare or absent in these *Polyergus* on Long Island.

I have observed the dealation of queens fertilized by brother males. These queens and those originating from other P. *lucidus*/F. *schaufussi* colonies both followed the raids of the study colony and attempted adoption of freeliving F. *schaufussi* nests. Although there were mixed colonies of P. *lucidus*/F. *incerta* nearer to the study colony than any of the P. *lucidus*/F. *schaufussi* colonies from which raid-following queens originated, no queens from these unlike colonies came to the study nest after mating. This is what we would expect if the successful adoption of a new queen requires locating a nest of the particular *Formica* species which was enslaved by her parent colony; since the raids of a *P. lucidus/F. schaufussi* colony lead to *F. schaufussi* nests, the following of such raids by a queen from a *P. lucidus/F. incerta* mixed nest would be inappropriate. The non-following of *P. lucidus/F. schaufussi* colony raids combined with the lack of mating in experimental isolation between queens of *P. lucidus/ F. schaufussi* nests and males from *P. lucidus/F. incerta* nests indicates that there may be fundamental biological differences between the *P. lucidus* using the different slave species. The extent to which this mating specificity occurs is now an important line of enquiry since it is possible that reproductive isolation is present between the *P. lucidus* using different slave species, and thus the respective *P. lucidus* slave-makers may be distinct species. The raiding territories of mature *P. lucidus/F. schaufussi* colonies almost never overlap. (*P. lucidus/F. schaufussi* colonies do, however, overlap with the raiding ranges of *P. lucidus* colonies using *F. incerta* or *F. p. nitidiventris* as slaves.) The alternatives for the success of a new colony are thus probably limited to adoption and emigration resulting in nesting in a range unused by a mixed nest with the same slave species or the gradual overtaking of an area previously used by a mixed colony which was destroyed or whose queen is aging and whose raiding capabilities are diminishing. Where the habitat is new and not occupied by mature colonies regularly distributed throughout the usable range, the success rate of new colonies would be expected to be high, allowing a habitat to be quickly populated by the species. The system of nest founding explains the observed distribution of *P. lucidus*/*F. schaufussi* nests; where one is found, and the appropriate habitat exists in adjoining areas, there will predictably be a continuous, range-spaced distribution of mixed colonies throughout until the habitat is broken by other vegetation types or man-made obstacles with widths greater than *Polyergus*' flight range. I found that mixed colonies are not necessarily located in many apparently suitable habitats containing *F. schaufussi* colonies where these habitats occur sporadically and are isolated by geographical barriers.

While territorial interactions between *Polyergus* colonies were not observed in this study (none would have been expected since no *Polyergus* colonies were ever found within raiding range of one another in my thorough habitat explorations during the raiding season), the raiding range-spaced distribution of colonies seen probably reflects the existence of periodic territorial interactions. Although these are between mixed nests they reflect behavior which may have been more general at some previous time. These inferred territorial interactions, together with my hypothesis of brood predation in *Polyergus*' ancestors give strength to Alloway's (1980) model containing these factors as requirements of a species for preadaptation to slave-making. The other factor requirements he delineates are: (1) proximity of the evolving parasite and host and a high density of colonies allowing frequent territorial interactions, and (2) a tendency by the species becoming a host to adopt newly-mated queens of their own species, preadapting them as hosts by facilitating the adoption of queens of the evolving parasite. *Formica schaufussi* Mayr, probably the closest living relative of the ancestral *Polyergus*, are distributed at a high density where they are found; separate colonies are often located very close to one another (Figure 3). Their colonies are frequently polygynous indicating a predisposition to adopt newly fertilised queens. Thus Alloway's model, derived principally from a knowledge of the behavior and biology of two other genera, is reenforced by a further understanding of the biology and behavior of the slave-maker and slave in this third generic group since the factors he models can be projected as probably having been present in the ancestors of these species as well.

EMIGRATION RAIDS

The expression of raiding by *P. lucidus* in emigration represents an entirely new context for this behavior and serves a completely new function for the species. The rapid transportation of nestmates to the overwintering site increases the efficiency of the overall emigration both in terms of the time spent on the ground surface, vulnerable to predation, and in terms of the number of days necessary to complete the transition at a time of year when the weather is becoming increasingly unfavorable. It is interesting to note that emigration behavior and adult transport to the new nest is common to most *Formica* including *F. schaufussi*, and was probably present in *Polyergus*' ancestors long before slave-making developed and raiding behavior appeared. The use of raiding, a relatively new behavior pattern, in a context which utilized other behavior patterns at an earlier time is an interesting evolutionary transition whose adaptive advantages are apparent. At the same time, it is notable that some *Polyergus* still transport *Formica* singly between the nests as part of colony emigrations using behavior much like those of *F. schaufussi* and other freeliving *Formica*.

TABLE 1. Soil Temperature Changes and Scouting and Raiding Onset

Field data for 14 raid days. Temperature at soil surface, °C.

Date	Highest Soil Temperature		First scout out		Raid onset		Minutes elapsed
1977	Time	Temp °C	Time	Temp °C	Time	Temp	1st scout-raid
7/10	2:00	50	2:45	42	4:27	44	102
7/16	3:15	52	3:40	47.5	4:54	39	74
7/17	3:30	53	3:55	51.5	4:53	43	58
7/22	2:47	56	3:10	53	4:50	32	100
7/26	3:20	49.5	3:20	49.5	4:44	40	84
7/27	3:30	53	3:33	52	4:37	46	64
7/28	3:10	49.5	3:10	49.5	4:26	47.5	76
7/29	2:45	43	3:15	40	4:14	31	59
7/31	2:45	45	3:05	44	5:31	28	146
8/2	2:25	45	1:30	39.5	4:29	36.5	179
8/4	1:52	39	2:45	37	4:45	37.5	120
8/9	3:45	46	3:30	43	4:05	45	35
8/15	2:55	45	3:05	38	4:30	37	85
8/21	3:15	42	2:28	35	3:39	41	71
			Min = 35		Min = 28		Min = 35
			Max = 53		Max = 47.5		Max = 179

TABLE 2. Record of Temperature and Precipitation as Obtained by the Brookhaven National Laboratory, Upton, N.Y.*

MEAN TEMPERATURE (°C)

Month	1976	1977	1949-1973
June	20.1	18.1	18.6
July	21.1	22.3	21.6
Aug.	21.2	22.0	20.7
Sept.	16.4	18.4	16.8

MEAN DAILY MAXIMUM TEMPERATURE (°C)

Month	1976	1977	1949-1973
June	25.9	23.8	24.8
July	26.7	28.6	27.4
Aug.	26.9	27.6	26.7
Sept.	22.9	23.2	23.1

TOTAL MONTHLY PRECIPITATION (cm.)

Month	1976	1977	1949-1973
June	8.31	10.95	6.91
July	10.97	3.84	8.87
Aug.	19.23	13.95	11.53
Sept.	5.26	14.55	8.74

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* This laboratory is located in the center of Long Island in a pine barrens approximately 47 km. directly east of the study site. Temperature readings were taken on a Friez hygrothermograph at 15.24 meters elevation. Precipitation was measured with a Friez weighing-type rain guage.

TABLE 3. Raiding Activity, Field: 7/9/77 - 9/22/77

Number of raids observed	50
Total brood taken on observed raids	5,573
Average raids per raid day	3.5
Reraids within 24 hours	8
Number of different nests raided	22
Nest finding failures	11
Failure to find brood at nest	2
Failures as per cent of total raids	26%
Estimated total raids for season (6/25-9/22)	107
Estimated total brood taken (6/25-9/22)	11,753

TABLE 4. Predictive Value of Scouting Activity for Subsequent Raid Sites

Scouting activity is defined as any trip wherein an individual achieves at least 2/3 of the distance from the mixed nest along the path to a particular target. If the closest point to the target is the latter's foraging area, the trip is labeled FA. If the scout continues and the nest entrance is attained, the trip is labeled NE, and if the nest cavity is entered it is labeled N.

(A) predictions of the target chosen are those made by totaling the N and NE trips to each.
(A) + (B) predictions include all FA, N and NE trips summed to find the most scouted target.
COR = correct prediction with this measure
INC = incorrect prediction
TIE = the nest later raided was tied in the number of scout trips with one not raided

		(A) Nest Sites Scouted (N & NE)					(B) Scout Activity Reaching Foraging Areas or Beyond Before & After Nest Scouting (FA)				
Date	Raid Site	I	II	III	IV	Prediction from (A) trips	I	II	III	IV	Prediction (A) + (B) trips
1976											
8/3	I	1	1	0	0	TIE	1	3	0	0	INC
8/4	I	0	1	0	1	INC	7	2	0	0	COR
8/5	II	1	3	0	3	TIE	0	1	0	0	COR
8/9	I	4	4	2	2	TIE	7	2	1	1	COR
8/11	I	0	1	1	5	INC	12	12	4	0	INC
8/17	IV	0	1	2	2	TIE	0	0	4	4	TIE
8/18	II	4	1	2	2	INC	10	2	5	0	INC
8/20	II	1	2	2	2	TIE	0	2	0	1	TIE
8/26	III	2	3	4	2	COR	3	15	10	0	INC
8/27	II	1	1	0	0	TIE	0	5	1	0	COR
9/14	III	2	2	4	1	COR	0	0	9	0	COR
9/15	IV	0	2	0	2	TIE	0	0	0	0	TIE
9/17	II	0	4	3	1	COR	0	5	2	0	COR
1977											
6/27	II	0	1	0	0	COR	1	3	1	0	COR
7/4	I	8	3	3	0	COR	3	0	7	2	COR
7/7	I	1	1	2	0	INC	5	2	0	1	COR
7/8	I	3	2	0	0	COR	6	0	0	0	COR
7/11	I	2	4	2	2	INC	11	9	8	5	TIE
7/12	II	0	2	0	0	COR	0	7	0	0	COR
7/13	I, II	6	3	2	1	COR	9	10	11	2	COR I TIE II

Totals: (A) Trips

40% correct
35% tied
25% incorrect

Totals: (A)+(B) Trips

57% correct
24% tied
19% incorrect

TABLE 5. Activity of Known Identity Scout Leaders: Partial and Complete Trips on Trail to One Nest

Date	Scout	Site	Time of scouting trip		Time of raid(s)	Lag (min.)
			leave	return		
8/3/76	FGY	LAB	5:55	5:59	6:50	51
8/9/76	FGG	LAB	4:32	4:42	5:23	41
8/17/76	WRO	LAB	3:59	4:10	6:00	60
			4:45	5:00		
8/18/76	GOR	LAB	5:30	6:00	6:39	39
8/20/76	COW	LAB	4:20	4:25	4:35	10
9/15/76	WRC	LAB	4:00	5:00	6:00	6
			5:45	5:54		
6/27/77	BBW	LAB	1:10	1:30		
			3:09	3.26		
			3:48	3:50		
			3:58	4:02		
			4:17	4:19	5:08	49
7/4/77	GPC	LAB	3:15	3:20		
			4:10	4:12		
			4:20	4:23	4:35	12
7/7/77	CYF	LAB	5:49	6:00		
			6:22	6:25		
			6:33	6:36	6:41	5
7/8/77	OBR	LAB	7:20	7:27	7:53	2
			7:48	7:51		
7/11/77	BFF	LAB	4:46	4:55	5:00	5
7/12/77	GOC	LAB	5:05	5:25	5:30	5
7/13/77	GOC	LAB	5:15	5:18	5:35	17
7/10/77	YBP	FIELD	3:54	4:00	4:08	8
7/10/77	CWP	FIELD	3:15	?	5:02	1
			4:54	5:01		
8/9/77	CWW	FIELD	2:35	?	4:05	35
			3:00	3:30		

TABLE 6A. Patterns of Scouting Activity

50% of known scout leaders make more than one scouting trip per day

34% of all scouts make more than one scouting trip per day

72% of all scouting trips represent different individuals

TABLE 6B. Scouting Trips and the Predictability of Raid Site Choice

The number of partial (FA) and complete (N + NE) scouting trips (section 1) or individuals going (section 2) in the direction of each of the 4 potential target nests were summed for each day; the actual nest raided was compared with the nest site that would be predicted by the most trips or individuals.

Symbols indicate the most proximal point achieved in relation to one of four target nests: FA=2/3 of the distance to a nest NE=nest entrance N=the interior of the nest

Data based on 20 observation days of laboratory *Polyergus* colonies raiding in 1976 and 1977.

Position Attained	% Predicted Correctly	% Ties	% Predicted Incorrectly
1) # TRIPS:			
N + NE	40	35	25
N + NE + FA	57	24	19
2) # INDIVIDUALS			
N + NE	40	30	30
N + NE + FA	55	5	40

TABLE 7. Scouts, Circlers and Raiders -
Transitions Between Behavioral Roles by *P. lucidus*

Data based on the laboratory observations of 14 different scouts on 5-14 consecutive days.

Transition type	Frequency of transition type	% of all transitions represented
Scout - Circler	25	15
Scout - Raider	13	8
Scout remains in nest	14	9
Scout returns to exterior role	13	8
Circler - Scout	38	23
Circler - Raider	16	10
Circler remains in nest	15	9
Circler returns to exterior role	4	3
Raider - Scout	7	4
Raider - Circler	10	6
Raider remains in nest	5	3
Total Observed Transitions	162	

TABLE 8. The Relationship of Scouting Activity to the Age of Individuals and the Progress of the Raiding Season

O= oldest, third active season; M= mature, second active season; Y= youngest, eclosed previous season

	% of individuals scouting			Individuals scouting as % of total in age class		
Date	O	M	Y	O	M	Y
6/27	100	0	0	5	0	0
6/28	100	0	0	7	0	0
6/29	80	20	0	7	2	0
6/30	45	36	18	8	7	1
7/4	46	31	23	10	7	1
7/5	33	27	40	9	8	3
7/6	53	20	27	7	5	2
7/7	40	20	40	4	2	1
7/8	40	20	40	4	2	1
7/11	23	18	59	9	7	6
7/12	33	28	39	11	9	3
7/13	44	31	31	11	7	2
7/14	19	19	63	5	5	4

TABLE 9. Brood Development Time

Based on laboratory observations: 1976

Egg = 12 days

Larva = 9 days

Worker Pupa = 23 days

Male Pupa = 20 days

Minimum total transit time = 41 - 44 days

TABLE 10. Ontogeny of Raid Related Behavior in *Polyergus*

1.	Immediately post-eclosion:	groomed by many *Formica* and *Polyergus*, cluster with other callows, fairly immobile in nest
2.	Three days post-eclosion :	most still cluster with other callows, some move around individually in nest, some leave nest, participate in raids, and retrieve booty; also participate in emigration raids and carry nestmates; circle at nest surface but do not scout
3.	1st season post-eclosion :	some participate in scouting but not in the beginning of the season; more of this age group scout as the season progresses; full participation in slave raids and emigrations
4.	2nd season post-eclosion :	large per cent survival, appear early in season as scouts, large representation from this age group throughout season as scouts
5.	3rd season post-eclosion :	some survive to this season, often these are first scouts of season, most, if not all, die by end of 3rd season

TABLE 11. Colony Size and Per Cent of *P. lucidus* and *F. schaufussi* in Mixed Nests

Nests excavated in South Centereach, New York

Date Excavated	Total Adult *Polyergus*		Recently Eclosed *Polyergus*	*Formica*	
	#	% of pop.		#	% of pop.
4/76 - lab colony	416	14	unknown	2502	86
5/77 - lab colony	385	20	245	1500	80
10/77 - field colony	1139	16	731	6067	84

TABLE 12. Activity of Dealated Queens Arriving Naturally at the Study Colony

Series of all days on which mating flights occurred in 1977.

M2 = dealates known to be from study colony, mated and returned to follow raids

Date	# Arrived at study colony	# Returning, present previous day	# Follow raid	# Attempt adoption at raided nest
1977				
8/2	1		on return trip	
8/4	1		no raids	
8/5	1		arrives after raid; follows trail 10 m	
8/12	1		no raids	
8/15	8		2	1
8/16	6	2	no raids	
8/18	1(M2)	1	no raids	
8/19	2			
	1(M2)	1	3	
8/20	6	3	no raids	
8/21	2	2	2	
8/22	3	2	2	1
8/23	2	1	no raids	
8/26	2	0	no raids	
TOTALS:	25 individuals		9	2

Total successfully completed adoption attempts = 2/25 = 8%

Total queens flying from study colony = 237

Total males flying from study colony = 395

TABLE 13. Quantitative Description of Emigration Raids

Date		Time(P.M.)	*Polyergus* on raid	*Formica* retrieved	*Pupae* retrieved	Retrieval success (%)
9/19/76	RAID 1	3:25	56	37	3	71
	RAID 2	4:25	45	35	0	78
9/20/76	RAID 1	4:20	69	30	0	54
	RAID 2	5:03	30	15	0	50

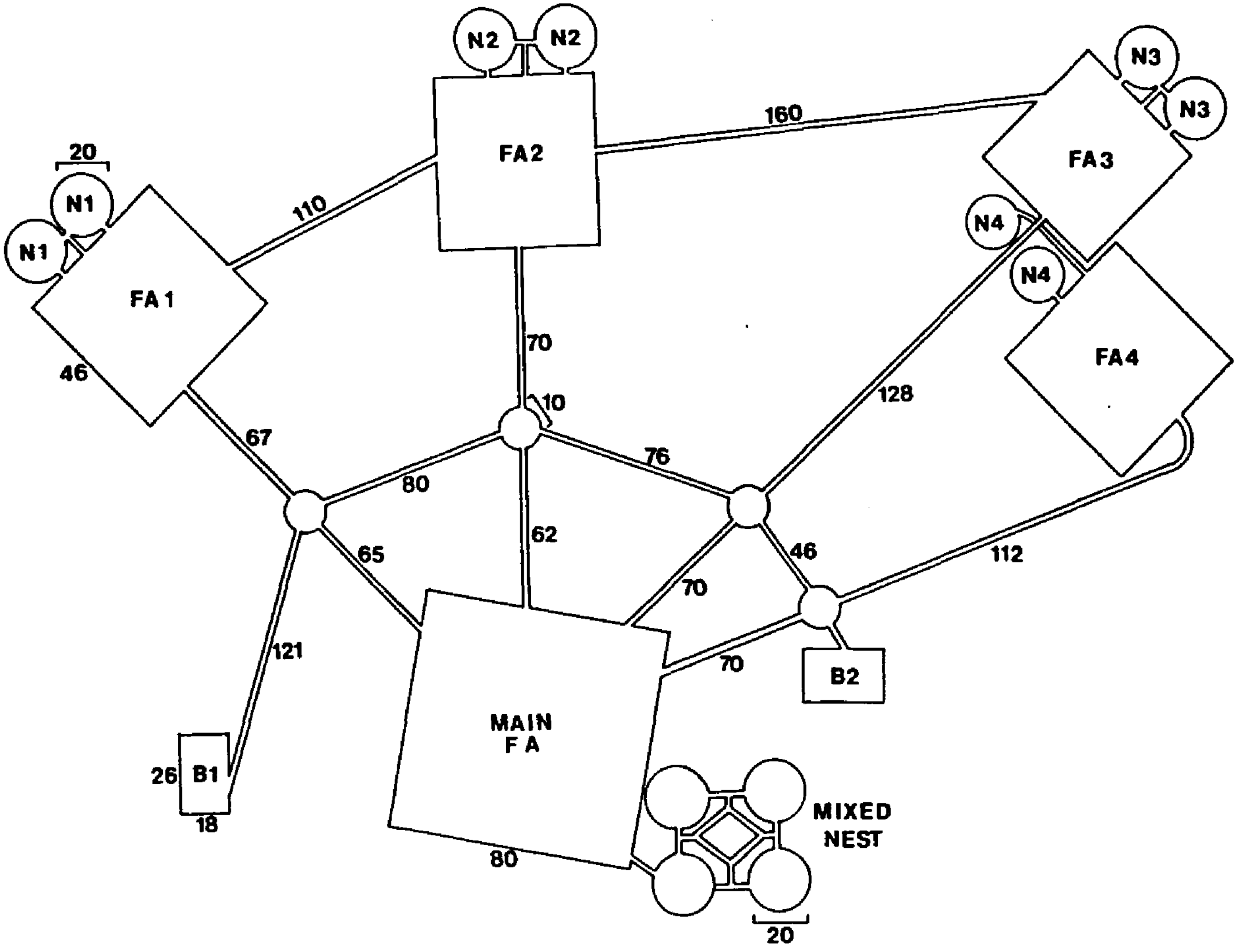

Fig. 1 - Laboratory Complex of Interconnecting Nests and Raid Paths

N = nest FA = foraging area B = blank foraging area (measurements in cm.)

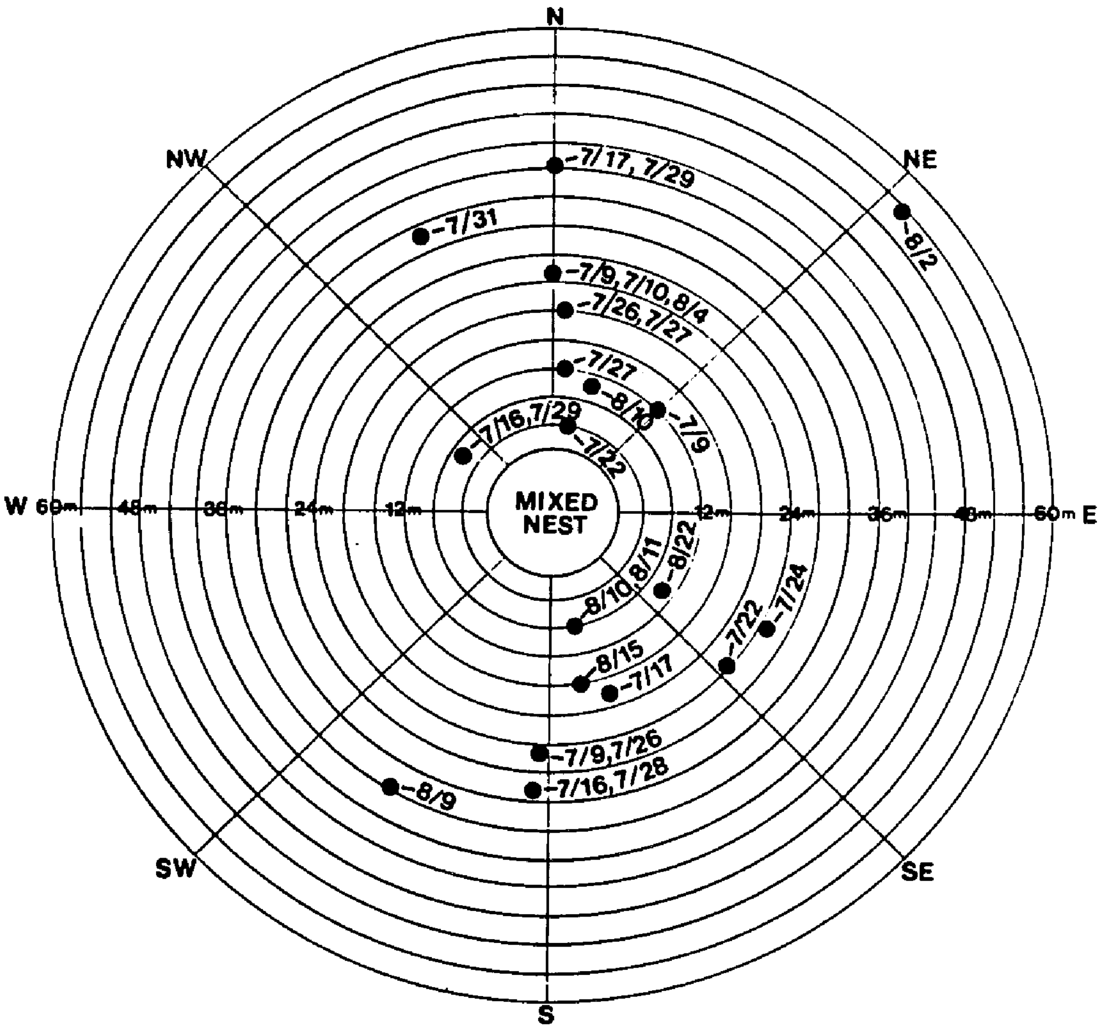

Fig. 2 - Successfully Raided F. *schaufussi* Nests: Field 1977

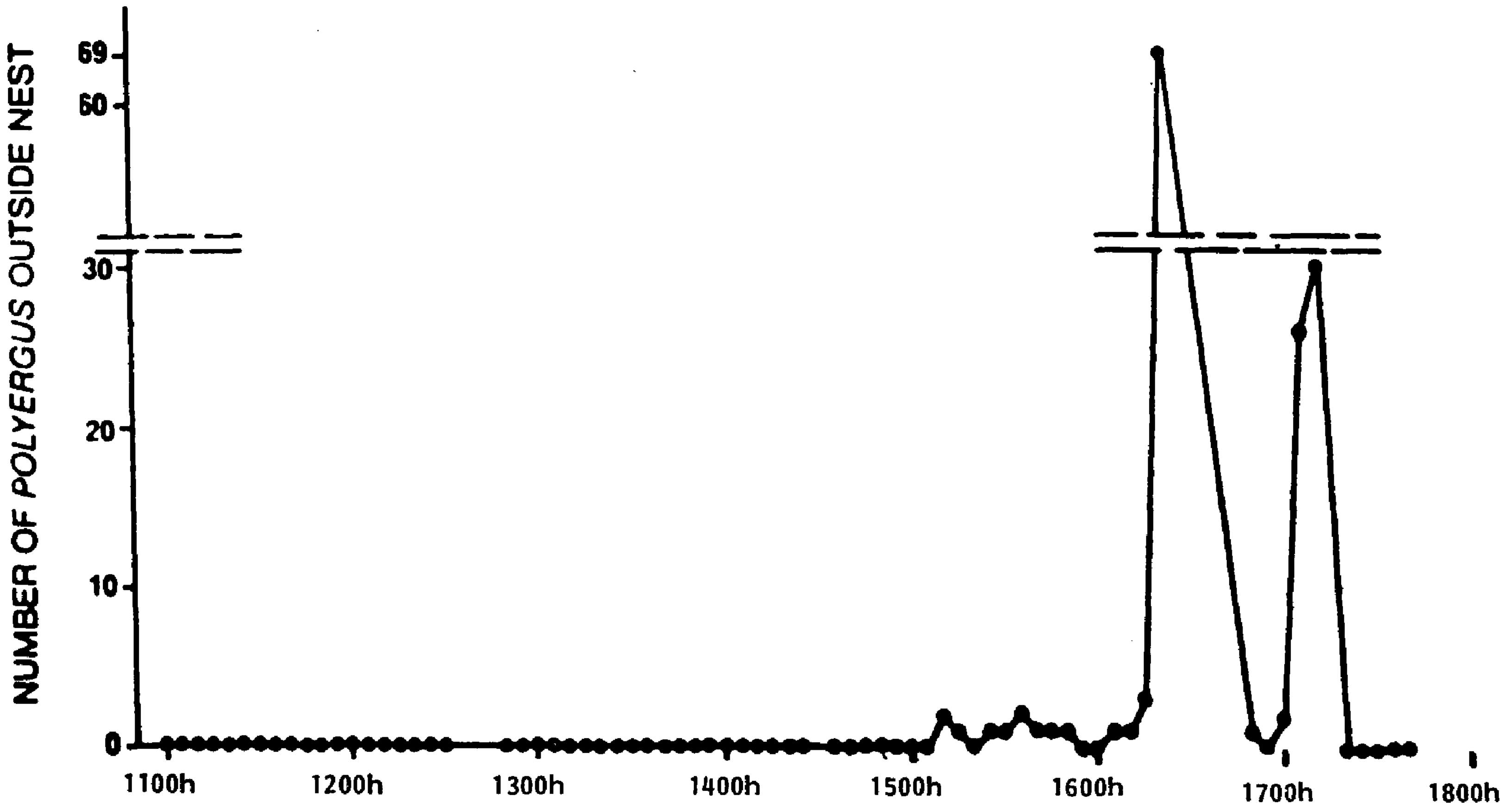

Fig. 3 - Emigration Day 2: *Polyergus* Activity Including Two Emigration Raids

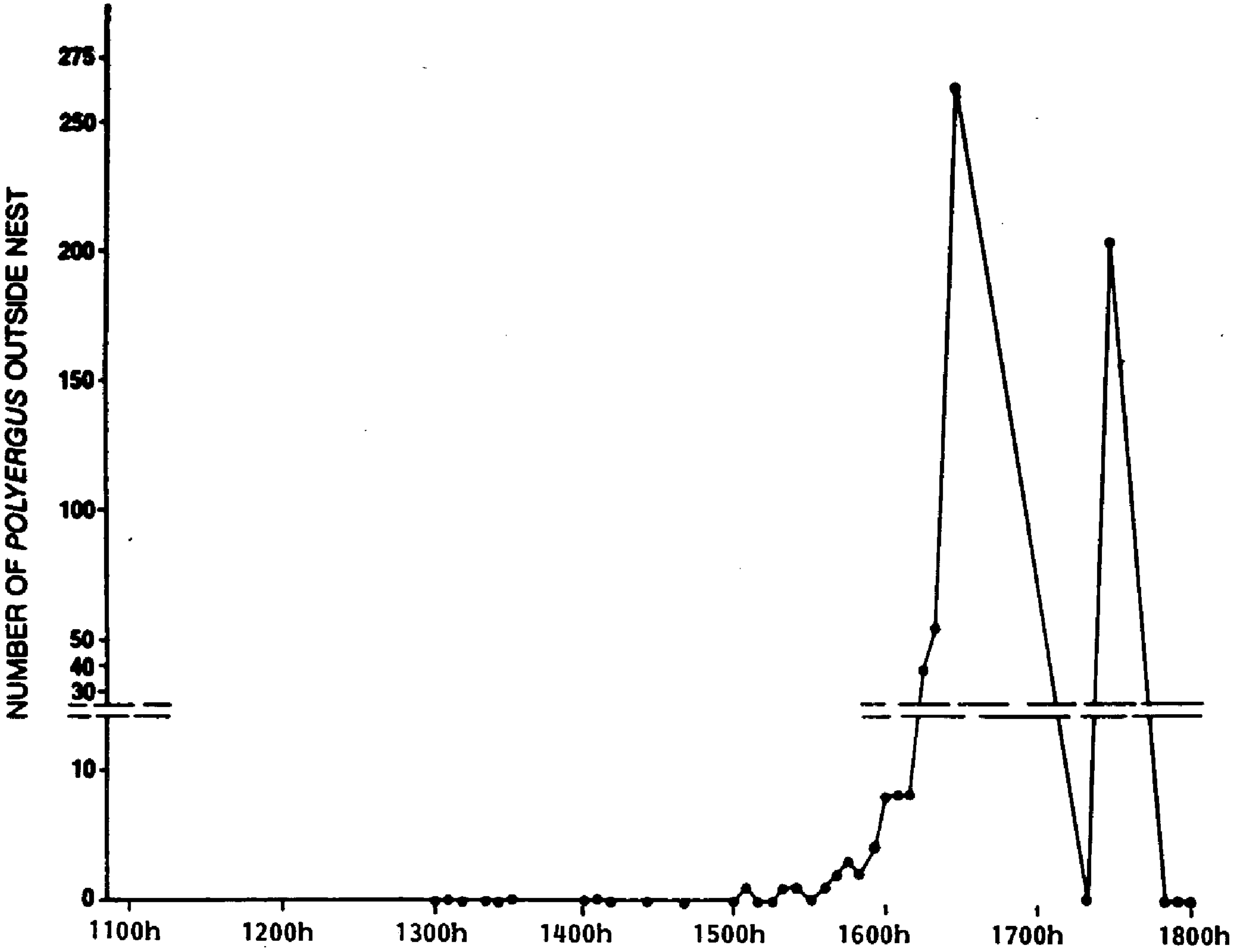

Fig. 4 - Slave Raid Day: *Polyergus* Activity Including Two Slave Raids

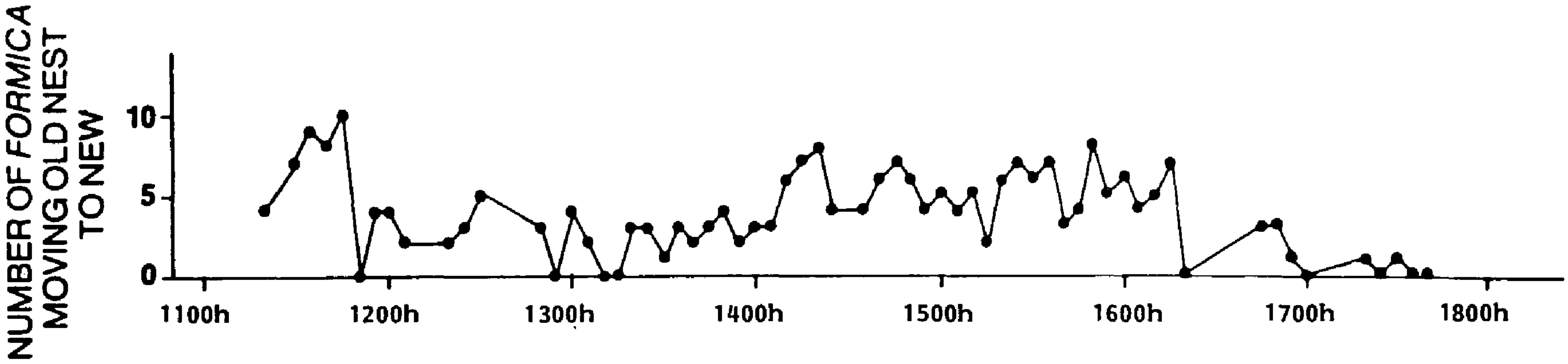

Fig. 5 - Emigration Day 2: *Formica* Activity

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