

RAID ORGANIZATION AND BEHAVIORAL
DEVELOPMENT IN THE SLAVE-MAKING ANT
POLYERGUS LUCIDUS MAYR

E. COOL-KWAIT (1) and H. TOPOFF (2)

(1) Department of Biology, City College of Cuny, New York, N.Y. 10031, U.S.A.

(2) Department of Psychology, Hunter College of Cuny, New York, N.Y. 10021, U.S.A.
and The American Museum of Natural History, New York, N.Y. 10024, U.S.A.

Reçu le 5 septembre 1983.

Accepté le 18 juin 1984.

SUMMARY

Mixed-species colonies of *Polyergus lucidus* and *Formica schaufussi* were studied in New York. Slave raids were conducted in late afternoon, past the peak in diurnal temperature. Multiple raids on different *Formica* colonies were common, as were re-raids on the same colony. In laboratory nests, about 75 % of the raided *Formica* brood was eaten.

Of 27 days on which raids occurred in the laboratory, 25 were on *Formica* nests scouted on the day of the raid. *Polyergus* scouts are among the oldest individuals in the colony, and callows do not participate in scouting during the entire season of their eclosion. The group of *Polyergus* workers that circle on the surface near the nest prior to raiding has a dynamic composition. The most frequent behavioral transition was from circling on one day to scouting on the next. The next most common change was from scouting to circling.

The first scouting of the spring season occurred only one day after the appearance of *Polyergus* larvae. The first slave raid was conducted 4 days later. *Formica* brood was present in freelifing colonies from 1-4 weeks earlier than *Polyergus* brood in mixed nests. Although workers of *Polyergus* were usually fed by regurgitation from *Formica*, they occasionally drank and ate eggs independently. The *Polyergus* queen was surrounded only by *Formica* workers. *Polyergus* eggs hatched into larvae in approximately 12 days, with the larval stage lasting an additional 9-12 days. Eclosion of callows took place within 20-23 days after pupation.

Newly mated *Polyergus* queens follow slave raids and attempt adoption into target nests when the *Formica* are scattered during a slave raid. The process of budding was never observed.

ZUSAMMENFASSUNG

überfallsorganisation und Verhaltensentwicklung in der Sklaven-
machenden Ameise *Polyergus lucidus* Mayr

Im staate New York sind Kolonien gemischter Arten von *Polyergus lucidus* und *Formica schaufussi* untersucht worden. Am späten Nachmittag, nach dem Höhepunkt

der Tagestemperatur, wurden Sklavenraubzüge ausgeführt. Mehrfache Raubzüge auf verschiedene Kolonien von *Formica* gerichtet waren normal. Dazu gehörten auch wiederholte Raubzüge auf dieselbe Kolonie. In den Laboratoriumnestern wurden etwa 75 % des geraubten *Formica* Gebrüts gefressen.

Aus einer Gruppe von 27 Raubzüge die im Laboratorium stattfanden, wurden 25 auf *Formica* Nester ausgeführt die am Tage des Überfalles erkundschaftet worden waren. *Polyergus* Kundschafter gehören zur den ältesten Individuen der Kolonie; frischgeschlüpfte Erwachsene beteiligen sich nicht an Erkundungen während ihrer ganzen Schlüpfungsaison. Die Zusammensetzung der Gruppe von *Polyergus* Arbeitern die unmittelbar vor dem Überfall auf der Oberfläche in der Nähe des Nestes umhergehen, wechselt sich kontinuierlich. Die verhaltensänderung die am häufigsten auftrat war die vom Herumgehen an einem Tag zum Kundschaften am nächsten Tag. Die zweithäufigste Änderung war die vom Kundschaften zum Herumstreifen.

Das erste kundschaften der Frühlingssaison fand nur einen Tag nach Erscheinung der *Polyergus* Larven statt. Der erste Sklavenraubzug wurde dann 4 Tage später ausgeführt. *Formica* Gebrüt war in frielebenden Kolonien bis zu 4 Wochen früher anwesend als *Polyergus* Gebrüt in gemischten Nestern. Obwohl *Polyergus* Arbeiter gewöhnlich durch Erbrechen des Speisebreies von *Formica* gefüttert werden, tranken und frassen sie gelegentlich auch Eier unabhängig von *Formica*. Die *Polyergus* Königinnen war immer nur von *Formica* Arbeiter umgeben. *Polyergus* Eier kriechen in etwa 12 Tagen zu Larven aus, worauf das Larvenstadium noch 9 bis 12 Tagen dauert. Schlüpfung der Erwachsenen fand 20 bis 23 Tage nach dem Puppenstadium statt.

Frischbefruchtete *Polyergus* Königinnen folgen Sklavenraubzüge und versuchen von den überfallen Nesten adoptiert zu werden indem sie die Verwirrung der *Formica* während eines Überfalles benutzen. Abspaltung von Tochterkolonien wurde nie beobachtet.

INTRODUCTION

Social parasitism in ants, whether facultative or obligatory, occurs principally in eight genera belonging to two ant subfamilies (ALLOWAY, 1980). In Europe, detailed studies have been conducted on the behavior and ecology of *P. rufescens* (BÊRGSTROM and LÖFQVIST, 1968; CZECHOWSKI, 1977; DOBRZANSKA, 1978; DOBRZANSKA and DOBRZANSKI, 1960). In North America, the ecology and orientation behavior of the western species *P. breviceps* has been investigated by WHEELER (1916) and by TOPOFF *et al.* (in press, a, b, c). By far the most thoroughly studies species in North America is *P. lucidus*, for which we have extensive data on the ecology of raiding (TALBOT, 1967; HARMAN, 1968; MARLIN, 1969) and on colony reproduction (MARLIN, 1968, 1971; TALBOT, 1968).

In this paper we present the results of field and laboratory studies on the ecology of raiding behavior, nest founding, and behavioral development in *Polyergus lucidus*. The success of the study was facilitated by our ability to individually mark *P. lucidus* workers, and to establish colonies of *Polyergus* and *Formica* in the laboratory so that species-typical slave raids could be observed under controlled conditions.

METHODS AND MATERIALS

Field studies

Mixed species colonies of *P. lucidus* and *F. schaufussi* were studied during the summers of 1976 and 1977, in South Centereach, Long Island, N.Y. In this pine barrens-type habitat, the predominant trees are scrub oak, pitch pine, and choke cherry.

On observation days, *Polyergus* workers were monitored continuously during periods of daytime activity. Identification of individual *Polyergus* was accomplished by the same marking technique used for the laboratory study (see below), except that only individuals performing specific tasks (e.g., scouting) were marked.

During the 1977 season, a plaster ring (8.0 cm wide) was poured into a shallow ditch around the perimeter of the nest at a radius of 1 m. The ring was marked with compass bearings (at 10 degree intervals) to facilitate quantifying the movements of inbound and outbound ants. All slave raids were followed, except when a colony staged simultaneous raids on more than one *Formica* colony. In these instances, the largest raid was traced, while the others were loosely monitored for path direction and target site.

Laboratory studies

Entire queenright colonies of *P. lucidus* and *F. schaufussi* were collected from a pine-barrens habitat in South Centereach, Long Island, and transferred to an inter-connecting complex of laboratory nests and foraging arenas (fig. 1). The permanent laboratory nest for each mixed-species colony consisted of four round lucite containers (18 cm diam.) with a dental stone substrate. These containers were interconnected with vinyl and lucite tubing (1.25 cm diam.) so that ants could move among the nest modules and to the external arena. By differentially moistening the four modules, a relative humidity gradient of 20-90 % (as measured with pH Hydron paper) was maintained within the nest complex. To minimize disturbances from other laboratory activities, the mixed-species nests were cushioned by foam rubber pads and surrounded by an opaque enclosure.

Free-living colonies of *Formica* were kept under similar conditions, except that each nest consisted of only two modules. The *Polyergus-Formica* mixed nest and each *F. schaufussi* nest were connected to a large foraging arena containing a white-sand substrate (see fig. 1 for dimensions). Each nest had 24-hour access to its adjacent foraging arena, but the interconnecting tubes were open only during periods of observation.

Food for the mixed colonies consisted of thawed insects collected from the ants' habitat. Both the mixed and slave species also received mealworm larvae and pupae, and a 50 % honey/distilled water solution.

In the mixed colonies, each *Polyergus* worker was marked with three dots of enamel paint, one each on the thorax, petiole, and gaster. The use of seven colors permitted each individual ant to have a unique color combination. In addition to individual recognition, the color code identified post-eclosion age. Marking was accomplished by isolating and cooling individual ants (at -2°C for 3-5 min.), and then isolating them with *Formica* slaves, food and water for 36 hours.

During the 1976 study season, the mixed nest was illuminated with red light. In 1977, however, observations took place with the ants habituated to low-intensity incandescent light. Behavioral observations were conducted with the aid of a swivel dissecting microscope. Continuous observations were made on the behavior of all *Polyergus* individuals in the complex from the time of tube opening until raiding activity ceased for the day (or until 1800 h on days of no slave raid).

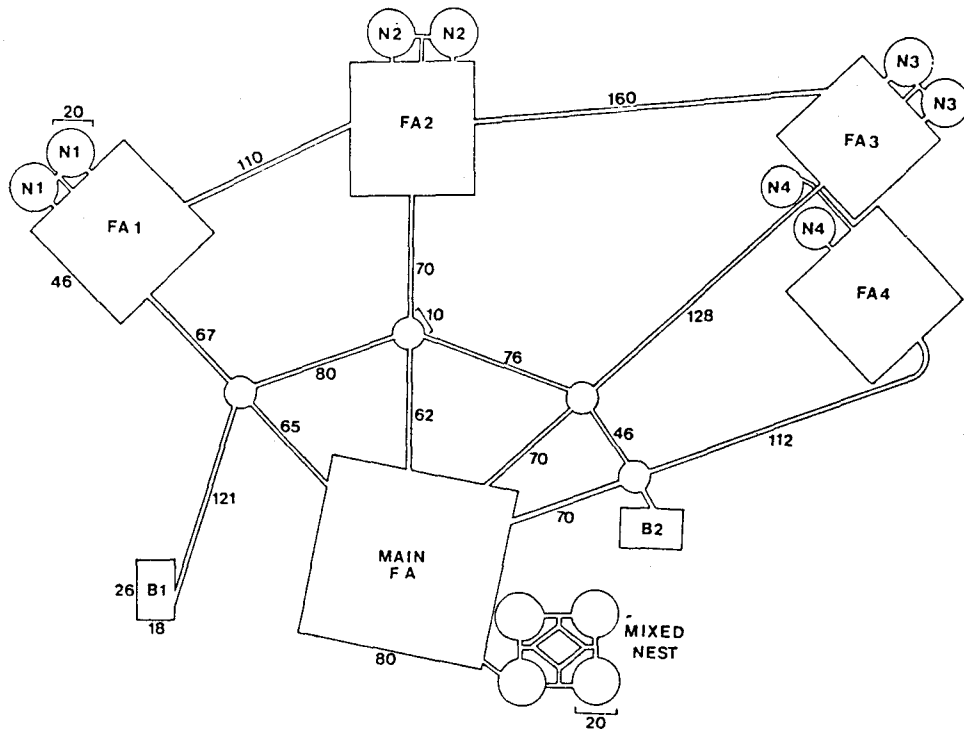


Fig. 1. — Laboratory complex of interconnecting nests (N), foraging arenas (FA), and empty boxes (B). All distances among segments are in cm.

Abb. 1. — Die Anordnung von untereinander verbundenen Nester (N), Futterarena (FA), und leere Gehäuse (B). Alle Abstände zwischen den Segmenten sind in cm angegeben.

RESULTS

Daily activity during raiding season

Three mixed colonies of *P. lucidus* and *F. schaufussi* were completely excavated. The 1976 laboratory colony contained 416 adult *Polyergus* and 2,502 adult *Formica*. The 1977 lab colony was somewhat smaller, containing 385 adult *Polyergus* and 1,500 *Formica* slaves. The 1977 field colony had the largest population, with 1,139 adult *Polyergus*, 731 callow *Polyergus*, and 6,067 *Formica* individuals. Thus despite the large variation in colony size and species composition, the relative numbers of *Formica* slaves were remarkably similar (86 %, 80 %, and 84 % for the three colonies respectively).

In the field, no *P. lucidus* workers appeared outside the nest until early afternoon. Morning activity was dominated by *Formica* foraging and nest

maintenance. *Formica* activity decreased during the warmest hours of the day, and as their numbers increased again in the afternoon, *Polyergus* also emerged for scouting activity. Typically, the *P. lucidus* scouts departed from the nest just after the period of maximum soil temperature. When raids occurred, they usually followed the initial scout's appearance by at least one hour. In both the laboratory and field, the appearance of the first *Polyergus* worker outside the nest was closely followed by the emergence of many individuals that circled around the nest entrance. The number of these circlers increased throughout the afternoon, often reaching a peak just prior to raiding.

Table I. — Raiding activity, field: 7/9/77 - 9/22/77.

Table I. — Jäger, Aktivitätsfeld: 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

In the field, nine successful raids were observed in 1976 and 50 in 1977, all conducted by the same colony of *P. lucidus*. In the laboratory, raids were monitored on 22 days (29 raids) in 1976, and on seven days (13 raids) in 1977. For the 1977 field data, *table I* summarizes the significant parameters of slave raids, including the proportion of successful and unsuccessful raids, and the amount of *Formica* booty retrieved. The directions and distances to target colonies are shown in *figure 2*. Since the maximum distance attained by a raid was 48 m, the potential area that a *Polyergus* colony can cover is a circle with a 48-m radius. As *figure 2* shows, however, certain sectors were raided far more frequently than others. Finally, in both the laboratory and field there was often more than one raid per day. Multiple raids on different nests at simultaneous or overlapping times were common, as were reraids on the same *Formica* nest.

After a successful slave raid, returning *Polyergus* workers either dropped their booty at the nest entrance, or carried it into the nest where it was dropped or relinquished to a *Formica* slave worker. The booty was then either placed with other brood in the nest, immediately eaten, or (in the case of pupae) decocooned and eaten soon afterward.

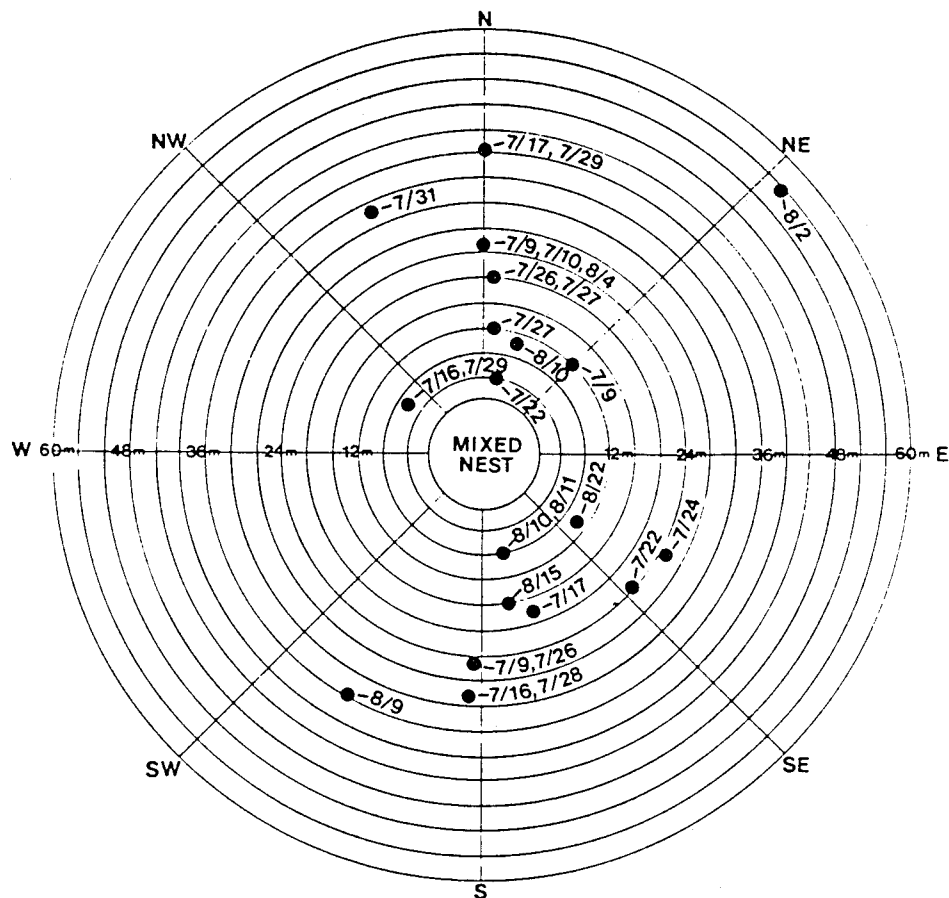


Fig. 2. — Distances and directions of *Formica schaufussi* nests raided during 1977 field season. Dates of raids appear alongside raid site locations.

Abb. 2. — Abstände und Richtungen zu *Formica schaufussi* Nester die während der 1977 Feldsaison überfallen wurden.

In the laboratory colonies, a large proportion of all retrieved brood was consumed. Many eggs and larvae were eaten by *Polyergus* adults and larvae, and by *Formica* adults. At the end of the 1977 raid season the field colony contained 6,067 *Formica* adults, despite the fact that 11,753 *Formica* brood individuals had been captured. These ants live at least two years, so if even half of the population survived from the previous year, only 3,034 of these raided brood individuals would be represented as adults in the 1977 colony (with the remaining 8,719 having presumably been eaten). This represents about 75 % of the total larval and pupal brood taken during raids. Even if

we make the extreme assumption that the entire *Formica* population was replaced during the 1977 season, 48 % of the raided brood would still have to be presumed eaten.

Scouting

In both the laboratory and field, same-day scouting of raided *F. schaufussi* nests was the rule. Of 27 days on which raids occurred in the laboratory, 25 were on *Formica* nests which had been scouted on the day of the raid. In the remaining two cases, the raided nests were attacked on the previous raid day. But in most cases, even when the same *Formica* nest was raided several days in succession, it was typically rescouted on the day of the raid. The duration of the interval between the scout's return from the target colony and the onset of raiding was quite variable, with a range of 1 - 60 minutes.

Removal of all scouts on each of 3 days in the field and on 7 days in the laboratory resulted in the absence of slave raids. Furthermore, the removal of scouts from a particular 180-degree sector on 5 days in the field resulted in the absence of raids in those directions.

Laboratory observations showed that a *Formica* nest may be entered repeatedly by a single scout, or by several scouts during the pre-raid activities of any afternoon. Although *Formica* nests are often raided after only one scout entry, additional scouts frequently go at least partway toward the potential target nest (often several times) after it has been located by the first scout. In many cases, scouts return to the mixed nest after travelling about 2/3 of the distance to the target, and therefore only reach the *Formica* colony's foraging arena. In the laboratory, no nests were raided unless a *P. lucidus* scout reached the interior of the target *Formica* nest entrance. Because most scouts did not get further than the entrance, a fairly superficial assessment of a *Formica* nest clearly qualified it as a potential target. In both the laboratory and field, raids were often conducted on inappropriate targets, including nests containing no brood, or no queen and no brood. Indeed two raids were conducted into unoccupied nests, several days after the *F. schaufussi* had emigrated.

The behavior of marked *Polyergus* scout leaders was observed on 13 days in the laboratory and on 3 days in the field. The scout that initially located the *Formica* nest was typically responsible for arousing and recruiting nestmates to participate in the slave raid. This scout ran intermittently at the head of the *Polyergus* swarm; periodically she moved back in the column, weaving in and out among the raiders, but invariably resumed the leading role. In the laboratory, where the entrance to each *F. schaufussi* nest was known, the scout leader was frequently (but not invariably) the first *Polyergus* raider to enter the target nest. In the field, the scout leader was not always successful at relocating the target colony; indeed on several occasions the scout and slave-raid swarm came within less than 0.5 m of

the *Formica* nest, before stopping, milling around, and eventually returning to their mixed-species nest. On all return trips, regardless of the success of the raid, the scout did not lead the returning ants.

Scouts and circlers

The group of *Polyergus* workers circling within a 1-m radius of the nest entrance prior to raiding has a dynamic composition. Individuals scouting areas away from the main nest typically return and join the circling group for varying periods of time. They may then enter the nest, and later emerge to resume scouting activities. Thus, although circling behavior is distinguishable from scouting, circlers do not comprise a behavioral group of ants that is qualitatively different from scouts.

All scouts circle on the nest surface and participate in slave raids, but many *P. lucidus* workers circle and raid without prior scouting. Finally, 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, which implies comparable changes in individual *Polyergus* behavior. To verify this, the behavioral transitions between raiding, circling, and scouting were monitored in the laboratory for 49 different *Polyergus* workers, during consecutive periods of 5-14 days (table II).

Table II. — 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.

Tabelle II. — Kundschafter, Herumstreifer, Jäger-Rollenwechsel bei *Polyergus lucidus*.

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	

The most frequent transition was from circling on one day to scouting on the subsequent day. The next most common behavioral change was from scouting to circling. Once an individual appeared as either a scout or a circler, alternation between these pre-raid roles continued for several consecutive days. This period was of variable length, and scouts and circlers often also became only raiders or remained in the nest on certain days and then returned after 1-5 days to scouting or circling. If more than about five days elapsed since their last pre-raid activity, they subsequently only raided or remained inactive in the nest.

Since scouting and pre-raid circling were not exhibited by 85-95 % of the *Polyergus* workers, some form of polyethism was clearly in effect. By marking age groups differentially in the laboratory, it was determined that the first scouts of the season were among the oldest individuals in the colony (table III). Workers from intermediate age groups were represented in the scouting force soon afterward. In the field, it was typically deeply-pigmented *Polyergus* individuals that appeared first in the season as scouts. Workers eclosed at the end of the previous raiding season were the last to become scouts. Significantly, no callows acted as scouts during the entire season of their eclosion (even though two distinct broods were produced each

Table III. — 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.

Tabelle III. — Verhältnis der Kundschafteraktivität zum Alter der Einaeltiere und der Verlauf der Beutezugsaison.

Date	% of individuals scouting			Individuals scouting as % of total in age class		
	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

season). Some of the callows eclosing during the latter part of the raiding season did participate in emigrations and emigration raids (KWAIT and TOPOFF, 1983) when they were only three days old. While a few of these callows also participated in slave raids (including booty retrieval), most did not take part in slave raids until the season after their eclosion.

Onset of the raiding season

Checking the undersurfaces of stones placed over nests of *F. schaufussi* and over mixed colonies revealed that *Formica* brood was present in freeliving colonies from one to four weeks earlier than *Polyergus* brood in mixed nests. In the 1977 laboratory colony, the first scouting of the year occurred only one day after the appearance of larvae in the mixed nest, and the first slave raid was conducted four days later. The onset of raiding in the field colony for 1977 was known within four days. Since the developmental duration from larval hatching to callow eclosion had been previously calculated to be 32 days, it was calculated that the hatching of larvae in the field colony also occurred within the four-day range when raiding began for the season. Furthermore, because *Formica* brood is present earlier in any given season, even the first *Polyergus* slave raids typically meet with success.

Activity inside the mixed nest

The 1977 laboratory colony had 10 ergatoid females when excavated in May. The largest individual laid eggs later in the season; the nest queen was laying concurrently. Other ergatoids had no *Formica* attendants, left the nest during slave raids, and were never observed laying eggs.

Formica workers ate eggs, larvae, pupae, insect parts and honey water. *Polyergus* occasionally drank independently and also consumed eggs. Although workers of *Polyergus* were usually fed by regurgitation from *Formica* (as well as from other *Polyergus*), they were often given eggs or larvae by the *Formica* slaves. On these occasions, the *Polyergus* grasped the larvae in their mandibles, antennated and stroked them with their forelegs, and licked the resulting larval secretions. Frequently the squeezing was so intense that larvae were mangled.

The *Polyergus* larvae were given insect parts, eggs, and regurgitated material from *Formica*. The *Polyergus* queen was usually fed by regurgitation from *Formica*, but occasionally also from *Polyergus* workers. The queen was typically surrounded by 12-40 *Formica* workers, and the number increased substantially during periods of egg laying. Although a small number of *Polyergus* workers periodically entered this group, they typically clustered together away from the queen. Indeed, the *Polyergus* queen often behaved aggressively towards her worker offspring.

Polyergus pupae and *Formica* pupae retrieved from slave raids were intermingled in the same area of the nest. It was not possible to determine whether the larvae of both ant genera were similarly mixed. *Polyergus* eggs

hatched into larvae in approximately 12 days, with the larval stage lasting an additional 9-12 days. Eclosion of callows took place within 20-23 days after pupation. The process of eclosion was assisted primarily by *Formica* workers and occasionally by *Polyergus*. Callow *Polyergus* tended to cluster together for the first few days after eclosion, after which they moved freely around the nest.

Mating and nest founding

In the 1977 field study, winged *P. lucidus* queens were marked before mating to indicate their nest of origin. During the entire season, 25 dealate queens from three marked nests and at least one unknown nest arrived at the study colony. Nine of these queens followed the colony's slave raids on five different days. Some of these newly-mated queens originated from the study colony. A few dealate queens were observed following paths of scouts or raids conducted earlier in the day, both on outbound and mixed nest-bound directions. This indicates that queens may follow odor trails to locate *Formica* nests for immediate adoption, or to locate *Polyergus* colonies that will eventually lead them to *Formica* nests.

New queens arrived back at the mixed nest as much as 2 h before raiding began, and continued to arrive during and after the raid. By climbing on stems and hiding in nearby brush, they avoided contact with other *Polyergus* until raid onset. They sometimes waited several days for this to happen. One queen originally from the study colony, and known to have mated with a brother, was picked up by a *F. schaufussi* worker from the same colony and carried into the nest. She was not present in the nest, however, when it was excavated at the end of the raiding season.

When following slave raids, the dealate queens remained alongside or behind the column. Contact with *P. lucidus* workers elicited aggressive behavior, and in one case a queen was killed by a raiding worker. In the four adoption attempts observed, queens entered the target *Formica* colonies with the slave-raid column or alone shortly after the raid. It was difficult to determine the results of these adoption attempts because new colonies form near the end of the active season and frequently emigrate before they can be checked for brood production in the spring. Both of the colonies that remained at the same site through the winter retained the *Polyergus* queen, and the appearance of *P. lucidus* brood was confirmed in one colony during the spring of 1978. In two years of observation, budding (the process in which *Polyergus* raiders remain at the target nest with a new queen) was never observed.

DISCUSSION

The results of this study verify previous reports that *P. lucidus* scouting and raiding take place after the peak in afternoon temperature. Scouts make

a rather superficial assessments of target colonies, because they typically get no further than the interior of the nest entrance. This strategy is successful, however, because most freeliving *F. schaufussi* colonies contain brood during the raiding season. Target entrance location without deep-nest penetration is also typical of lone scouts in the slave-making species *Harpagoxenus americanus* and *Leptothorax duloticus* (ALLOWAY, 1979).

The slave raids of *P. lucidus* are usually preceded by same-day scouting of the target nest, as suggested previously by TALBOT (1967) and MARLIN (1969). This is in marked contrast to the earlier hypothesis that colonies of *Polyergus* simply raid along well-frequented paths and attack any suitable slave nest encountered en route (DOBRZANSKA and DOBRZANSKI, 1960; DOBRZANSKI, 1961). The occasional raids that occur without same-day scouting are invariably directed towards *Formica* colonies that were scouted on the previous raid day. The absence of this information on prior scouting had led WHEELER (1910) and TALBOT (1967) to question the direct relationship of same-day scouting to raid site location.

In a recent study of orientation in the western slave-making ant *Polyergus breviceps*, TOPOFF *et al.* (in press, a) found that scouts use optical orientation (the position of the sun and polarized light) when returning to the mixed nest and when leading the *Polyergus* swarm back to the target colony. During this second outbound trip, however, the scout deposits a recruitment trail for raider orientation, and the raiding workers deposit a chemical trail that they use (together with optical cues) for orienting on the homeward trip after the raid. Although comparable studies on *P. lucidus* have not yet been conducted, it is likely that similar processes of orientation and communication are utilized.

The role of preraid circlers is still unclear, although their proximity to returning scouts places them in a position to receive and pass recruitment stimuli. At the moment of scout return, these circlers increase the frequency and tempo at which they enter and leave the nest. Thus the circlers may be specialized to function in secondary recruitment, a process described for many ant species (SZLEP-FESSEL, 1970; CHADAB and RETTENMEYER, 1975; TOPOFF *et al.*, 1980). This specialization is consistent with the observation that the most frequent behavioral transition in *P. lucidus* is from scout to circler and vice versa.

Division of labor among *Polyergus* workers is evidenced by the fact that only 8.3 % function as scouts and only 5-15 % are active at all before raids on a given day. This distinction is partly among individuals of the same age, although temporal polyethism is also occurring. Thus *P. lucidus* callows do not become scouts until the season after their eclosion. Indeed most will not scout until two seasons post-eclosion. This developmental schedule may be adaptive, in that scouting has a higher mortality rate than raiding. Nevertheless, some callows participate actively in raiding and emigration as early as three days after eclosion. This early emergence from the nest is very similar to the behavior of callow army ants, which also participate in group-

predatory raids by the end of the first week after eclosion (TOPOFF and MIRENDA, 1978 a, b). Thus the early emergence of callows may be a behavioral pattern characteristic of group-predatory ants.

Adoption of single dealate *Polyergus* queens into *F. schaufussi* nests after raids was the only method of colony reproduction observed in this study. Although MARLIN (1968) indicates that this method is typical for *P. lucidus*/*F. nitidiventris* mixed nests in Illinois, he also described budding as a frequent method of colony foundation in spring and fall.

Queens fertilized by brother males, as well as realates from other colonies, followed raids of the study colony and attempted adoption of freeliving *F. schaufussi* nests. Although mixed colonies of *P. lucidus* and *Formica incerta* occurred nearer to the study colony than any *P. lucidus*/*F. schaufussi* from which raid-following queens originated, no queens from these heterospecific *Formica* mixed nests approached the study colony after mating. This is consistent with the hypothesis that the successful adoption of a new queen requires locating a nest of the same *Formica* species which was enslaved by her parent colony. The fact that each colony of *Polyergus* raids only that species of *Formica* which it currently enslaves, combined with the above observation on the taxonomic specificity of raid-following queens, suggests that some form of reproductive isolation may be operative among *Polyergus* colonies enslaving different *Formica* species.

ACKNOWLEDGMENTS. — The research for this manuscript was conducted by the senior author as part of a doctoral dissertation in Biology for the City University of New York. The research was supported in part by NIMH Training Grant 14280. Thanks to Mr. Raymond SANWALD for his assistance in the field.

References

- ALLOWAY T.M., 1979. — Raiding behaviour of two species of slavemaking ants, *Harpagoxenus americanus* (Emery) and *Leptothorax duloticus* Wesson (Hymenoptera: Formicidae). *Anim. Behav.*, 27, 202-210.
- ALLOWAY T.M., 1980. — The origins of slavery in Leptothoracine ants. *Am. Nat.*, 115, 247-261.
- BERGSTROM G., LÖFQVIST J., 1968. — Odour similarities between the slave-keeping ants *Formica sanguinea* and *Polyergus rufescens* and their slaves *Formica fusca* and *Formica rufibarbis*. *J. Insect Physiol.*, 14, 995-1011.
- CHADAB R., RETTENMEYER C., 1975. — Mass recruitment by army ants. *Science*, 188, 1124-1125.
- CZECHOWSKI W., 1977. — Recruitment signals and raids in slave-maker ants. *Ann. Zool. Warsaw*, 34, 1-23.
- DOBZANSKA J., 1978. — Problem of behavioral plasticity in the slave-making amazon ant *Polyergus rufescens* Latr. and in its slave ants *Formica fusca* L. and *Formica cinerea* Mayr. *Acta Neurobiol. Exp.*, 38, 113-132.
- DOBZANSKI J., 1961. — Sur l'éthologie guerrière de *Formica sanguinea* Latreille. *Acta Biol. Exp., Warsaw*, 21, 53-73.
- DOBZANSKA J., DOBZANSKI J., 1960. — Quelques nouvelles remarques sur l'éthologie de *Polyergus rufescens*. *Insect. Soc.*, 7, 1-8.
- HARMAN J.R., 1968. — Some aspects of the ecology of the slave-making ant, *Polyergus lucidus*. *Entomol. News*, 79, 217-223.

- KWAIT E., TOPOFF H., 1983. — Emigration raids by slave-making ants: a rapid-transit system for colony relocation. *Psyche*, 90, 307-312.
- MARLIN J.C., 1968. — Notes on a new method of colony formation employed by *Polyergus lucidus* Mayr. *Illinois State Acad. Sci.*, 61, 207-209.
- MARLIN J.C., 1969. — The raiding behavior of *Polyergus lucidus* in central Illinois (Hymenoptera: Formicidae). *J. Kansas Entomol. Soc.*, 42, 108-115.
- MARLIN J.C., 1971. — The mating, nesting, and ant enemies of *Polyergus lucidus* Mayr. *Am. Mid. Nat.*, 86, 181-189.
- SZLEP-FESSEL R., 1970. — The regulatory mechanism in mass forging and the recruitment of soldiers in *Pheidole*. *Insect. Soc.*, 17, 233-244.
- TALBOT M., 1967. — Slave raids of the ant *Polyergus lucidus*. *Psyche*, 74, 299-313.
- TALBOT M., 1968. — Flights of the ant *Polyergus lucidus* Mayr. *Psyche*, 75, 46-52.
- TOPOFF H., MIRENDA J., 1978 a. — Precocial behavior of callow workers of the army ant *Neivamyrmex nigrescens*: importance of stimulation by adults during mass recruitment. *Anim. Behav.*, 26, 698-706.
- TOPOFF H., MIRENDA J., 1978 b. — In search of the precocial ant. In: G. Burghardt and M. Bekoff, eds.: *The development of behavior: comparative and evolutionary aspects*. Garland, New York, pp. 81-100.
- TOPOFF H., MIRENDA J., DROUAL R., HERRICK S., 1980. — Behavioural ecology of mass recruitment in the army ant *Neivamyrmex nigrescens*. *Anim. Behav.*, 28, 779-789.
- TOPOFF H., LAMON B., GOODLOE L., GOLDSTEIN M., in press, a. — Social and orientation behavior of *Polyergus breviceps* during slave-making raids. *Behav. Ecol. Sociobiol.*
- TOPOFF H., PAGANI M., GOLDSTEIN M., MACK L., in press, b. — Behavioral ecology of the slave-making ant *Polyergus breviceps* in a desert habitat. *S. W. Naturalist*.
- TOPOFF H., PAGANI M., GOLDSTEIN M., MACK L., in press, c. — Orientation behavior of the slave-making ant *Polyergus breviceps* in an oak-woodland habitat. *J. N.Y. Entomol. Soc.*
- WHEELER W.M., 1910. — *Ants, their structure, development and behavior*. New York, Columbia Univ., 663 p.
- WHEELER W.M., 1916. — Notes on some slave raids of the western amazon ant (*Polyergus breviceps*). *J. N.Y. Entomol. Soc.*, 24, 107-118.