SLAVE-RAIDS OF THE ANT *POLYERGUS LUCIDUS* MAYR*

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Since slave-making raids of the genus *Polyergus* are conspicuous and spectacular, they have been studied by a number of myrmecologists. Among these are Wheeler (1910), Forel (1928), Creighton (1950), and Dobrzanska and Dobrzanski (1960). This paper concerns the eastern "shining slave-maker," *Polyergus lucidus* Mayr, on the Edwin S. George Reserve in southeastern Michigan (Livingston County). Twenty-five colonies of this species have been found, scattered quite widely over the fields, on the 2 square miles of the Reserve. Most of the fields tend to be dry, with Canada bluegrass (*Poa compressa* L.) the dominant grass and with forbes such as wild bergamot (*Monarda fistulosa* L.) bush-clover (*Lespedeza virginica* (L.) Britt.), and goldenrod (*Solidago* spp.) common and characteristic. In addition to this main habitat, *Polyergus* colonies may sometimes be found at woods' edge, in low wet fields, and in openings in oak-hickory woods where blueberries (*Vaccinium angustifolium* Ait.), bracken (*Pteridium aquilinium latiusculum* (Desv.) Underw.), sedge (*Carex pennsylvanica* Lam.), and mosses are characteristic. No colony has been found completely within the woods, although the slave ant *Formica pallidefulva nitidiventris* Emery sometimes occurs there.

The slave-raid study was undertaken in the hope of determining the time of day of raids and the environmental factors which influence the time, the days on which no raids occur and the factors which determine this absence, the number of slave colonies used in the support of one *Polyergus* colony, the distances to these colonies and the amount of time it took to reach them, the number of raids in a season, the number of brood taken, the size and characteristics of a raiding force, and the method by which the band of ants could travel over a seemingly unknown path to arrive exactly at a nest to be raided.

Preliminary studies were made on the Lawn Colony, which lived in the cut grass outside the East Gate Laboratory and had been known

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to exist there for 10 years (1956-1965); but the main observations concerned a larger colony, located about a mile away on grid 0-26 and known since 1961. Raids of this colony were recorded during two seasons. In 1964, during 50 days of observation in June, July, August, and early September, 29 raids were seen; and in the summer of 1965, during 54 days of observation, 34 raids took place.

NEST STRUCTURE AND COLONY SIZE

The structure of the compound nests seemed typical of the slave species *F. p. nitidiventris*, which usually dig a shaft into the ground and then excavate chambers from it at various levels. Shafts may be single or multiple and may extend as deep as 3.5 ft. Entrances to the nest (occasionally there are 2 to 5) may be inconspicuous in the grass or may be surrounded by bare excavated soil.

On August 30 and September 1 (it rained all day August 31) of 1965, one *Polyergus lucidus-Formica pallidefulva nitidiventris* mixed colony was dug. This nest lay near the top of a grassy slope in the sandy loam which is common on the Reserve. To judge by a raid seen on July 19, 1965, in which 258 workers took part, it was a medium-sized colony. Thirty-seven chambers were found, extending down to 30 inches and spreading around the central opening for a radius of 8 inches. Because of the lateness of the season, there were no larvae or eggs in the nest; and some of the winged ants had already flown. The *Polyergus lucidus* population consisted of one queen, 291 workers, 299 worker pupae, 115 females, 407 males, and 13 male pupae. The *F. p. nitidiventris* numbered 4,527 workers and 9 worker pupae. Thus the mixed colony contained approximately 5,662 individuals, and the count of 590 *Polyergus* workers (adult and pupae) gave a ratio of 7.7 slaves to each *Polyergus* worker.

TYPICAL RAID ACTIVITIES

The 0-26 colony had an almost bare nest area 18 × 18 inches across, because I had dug into it early in 1964. Generally there was only an occasional ant in sight here during the morning and none during the warm midday period. By early afternoon 2 to 5 *Polyergus* could often be seen circling about or running off into the surrounding grasses. Later, as the sun slanted to the west and the nest came into flickering shade, more ants came out and stayed on the nest area, circling and crossing it in a zigzag running movement. Then, typically, there would be an outpouring of ants until they covered the nest. As they milled about, they explored into the surrounding grasses for several inches. Gradually the group would begin to favor one side, pushing into the grasses a little farther but always running

back and forth. Sometimes they retreated from one place to gather at another. The actual beginning of a foray was not certain until a line of ants extended a foot or more from the nest. Once a trail began, ants drained off from other parts of the nest so gradually that the front line might be as far as 8 feet away before the last got started; but soon the ants condensed to a group 2 to 4 feet long and 6 to 8 inches wide. Once a raiding column was formed, it moved fast — about 3 feet a minute — but always the ants alternated running back and forth and from side to side with the forward movement, so there were never any consistent leaders to the group.

The speed and compactness of the column was usually maintained, but sometimes the column widened to 10 or 12 inches, especially when loose leaves were being investigated. But, while a few ants might search for openings along the way, the main column kept moving steadily forward with no hesitation, following what seemed to be an obvious trail to a definite objective. Usually they arrived precisely at a nest to be raided. Sometimes they missed it by 2 to 10 inches. Once the spot was reached, all of the ants began searching every crevice in a frenzied fashion until the nest entrance was found. If the compact mass of workers did not find the entrance immediately, they began spreading out in widening circles. If the located entrance was open, they poured down it; if it was barricaded with pebbles and soil, they might dig for as much as 3 to 7 minutes before gaining admittance. Most of the *F. p. nitidiventris* colonies in the raided area kept their nests barricaded. Workers usually did not try to defend the nest, nor did they take away brood. Sometimes a worker was carried out and released; sometimes one ran out by itself, but there was seldom any fighting. Once the *Polyergus* gained entrance to a nest, it was only a minute or two until an ant reappeared carrying a pupa or larva. Others followed quickly, carrying out loot and starting for home. They returned by the same general path that they had taken in coming, each ant picking its own way over a 5- to 10-inch width. At home the ants entered the nest with their brood (at the Lawn Nest they sometimes piled it up for the *F. p. nitidiventris* workers to carry down).

When conditions were right, a second raid would take place. Sometimes the second column started before all the first ants had come in; sometimes there was a delay while they milled about the nest. Occasionally the second raid began with ants pouring out of the nest after all had gone below ground. On rare occasions a third raid took place; and once, after a successful raid, 2 columns started out in different directions at exactly the same time.

MEANS OF LOCATING COLONIES TO BE RAIDED

Polyergus raids were definitely not exploratory forays. There was no set pattern of pathways. The ants went directly to the nest to be raided (except that they might follow a contour of the land), and a nest visited twice on different days might be approached by quite different routes. This suggested that individual ants do the scouting and locating of colonies. This was verified, to my satisfaction, during the study. Observations made on July 6, 1965, gave an especially clear picture. During that morning an occasional *Polyergus* worker appeared on the surface; but between 11:15 AM and 2:55 PM none came out, although the temperatures were not especially high (81°-85°F 10 inches above the surface and 91°-95°F on the surface). At 2:55 PM 3 workers emerged, moved huriedly across the bare soil and disappeared into the grasses. For the next 40 minutes there were one or 2 *Polyergus* on the nest area at all times, and at least 10 of these slipped off into the grasses. Gradually more *Polyergus* joined those on the nest until there were 3 to 10 running about, and 2 per minute left the nest until 4 PM. After that time most stayed on the nest and only a few left, but in the whole time from 2:55 PM to 4:15 PM 52 ants were seen to depart. During this time none returned. Then at 4:15 PM a *Polyergus* was seen 3 feet from the nest, coming directly home. It went into the nest entrance, and within a few seconds a whole stream of ants began pouring out. They spread thickly over the nest area and within 5 minutes had started a raid to the west where the scout had come in.

On other days the departure of scouts was less conspicuous, and seldom was one lucky enough to spot a scout coming in. But whenever an ant came in hurriedly from the grass and went directly into the nest, there was an outpouring of ants. It was thus assumed that whenever a sudden emergence occurred it was in response to a messenger arriving with news of a located colony. If this was correct and if the scouting ant, which found a colony, laid down an odor trail on its way home, then the odor must have been quite long lasting, for it sometimes took an ant 30 to 45 minutes to return from a raided nest. It seemed unlikely that a raiding group could be following anything but an odor trail, for it moved rapidly, did not maintain leaders, and usually stopped at exactly the right place.

In contrast to raiding activity, which seemed mechanical and stereotyped, activities of workers while scouting for colonies must require a high degree of individual action and response to the con-

figuration of the surroundings, which results in the ability to come home directly after a nest is found.

Experiments made in 1966 and 1967 seem to verify the odor-trail theory. On August 16, 1966, 10 *Polyergus* workers from nest 0-26 were crushed in dichloromethane to extract pheromones. Next day the colony was visited at 3:30 PM when early preraid activities were beginning, with a dozen *Polyergus* circling about the nest area and surrounding grasses. A pheromone trail, laid down with a small brush, was extended from the nest for 3 feet. Instantly ants began to follow the brush; and by the time the trail was complete, 50 ants were upon it. More came from the nest, and in 5 minutes there were about 75. Each ant ran forward and backward and from side to side, crossing and recrossing the odor trail, just as they did on their own raiding trails. At trail's end they ran forward and to each side, as they did when one of their own trails ended without leading to a nest. Then, finding nothing, they began to return home; and in 25 minutes all but 10 had abandoned the trail. There had been no outpouring of ants from the nest (the odor trail began at nest edge), and ants did not mass in a typical raiding formation. But each ant, going singly on the trail, had acted in characteristic fashion.

The same pheromone solution was then taken to another colony (M-26), which had ants out in preraiding activity at 4:23 PM. A trail 6 feet long was made; and again ants followed the brush immediately, moving back and forth and from side to side along the trail. In this case about 100 ants were attracted. Again they came along the trail singly, explored a little beyond it, and returned when no nest was found.

On August 20, 1966, a trail was attempted under conditions when no ants would normally be out. A dichloromethane solution of 10 crushed ants from M-26 was used. The *Polyergus* colony was visited when it was still in hot, bright sun. No *Polyergus* were in sight until the nest was shaded. Within 10 minutes about 25 *Polygerus* were running about, keeping in the shade. A short trail, stretching 12 inches out onto the hot soil, induced those crossing it to follow; but they came back almost immediately. Subsequent trails were extended out in different directions for 4, 7, and 11 feet. In each case ants followed these trails, although the soil was still hot enough to prevent ordinary raids.

It was found that dabs of solution worked as well as a continuous line, since ants found them readily as they zigzaged back and forth. Putting the brush into the nest entrance caused 25 to 30 ants to come

out, but those which the brush touched were injured by the dichloromethane. Although there was great excitement on the nest, at no time was there any organization into a raiding mass; instead, each ant followed the trail singly. A dichloromethan solution made with *F. p. nitidiventris* workers caused no reaction at all.

On July 6, 1967, a successful raid on *F. pf. nitidiventris* was induced. Several days previously part of a colony had been dug and placed in a transparent plastic shoe box with a door made at one end. Workers excavated cavities in the soil and established their brood there. The box was placed 6 feet from nest M-26, and the *Polyergus* entrance was watched until ants began coming out. When there were 25 to 30 *Polyergus* circling the entrance (4:20 PM), the *F. p. nitidiventris* door was opened and a pheromone trail was laid to it. Ants followed the brush as the trail was put down on the hard pebbly soil; and, as before, there was no organization into raiding formation but simply excited individuals running along the trail. There were perhaps 25 ants on the trail when the first one reached the box, entered, found a pupa, and started home. Almost immediately 3 others entered and found pupae. Their arrival back at the home nest caused a great outpouring of ants, and soon there were about 100 in the box and as many more on the trail. All of the pupae and larvae were hunted out and removed. When many ants returned without booty, the line of outgoing ants began to thin. The whole raid lasted 25 minutes — 4 minutes to the taking of the first pupae, 16 for removing all of the brood, and 5 more of hunting before giving up.

Immediately after the induced raid the ants started out on one of their own. Two hundred and seventy-two ants took part in this raid, so the colony probably had most of its forces involved in the induced one.

The difference between the induced raid and a natural one lay in the fact that the laid pheromone trail caused excitement and raiding action in individuals, while in a regular raid there was mass action, with a large group of ants leaving the nest together and staying in a compact group as they traveled along.

CONDITIONS UNDER WHICH RAIDS OCCURRED

Polyergus raids on the Reserve took place in the late afternoon but varied in time from colony to colony. The 0-26 colony raided early; its mean time for starting a raid was 4:21 PM EST (20 raids), while the Lawn Nest's mean was 5:36 PM (21 raids). Individual raids at 3 other colonies began at 4:50 PM, 5:08 PM and

6:55 PM. Four morning raids were seen at the Lawn Nest in 1959, but this seemed unusual and no others have been observed. Within a colony, raid time also varied widely: from 3:06 PM to 5:16 PM for 0-26 and from 3:50 PM to 6:25 PM for the Lawn Colony. Second raids could start as late as 6:45 PM for 0-26 and 7:30 PM for the Lawn Colony. The latest ended at 8:14 PM.

Colonies in fully exposed places where the sun was bright and the temperature high for longer time started their raids late. The 0-26 raids were early because nearby trees began shading the nest while the sun was still high in the sky, thus reducing the temperature to that tolerated by the ants. Single individuals could run rapidly into the shade of nearby dense grass at almost any time of day, but the raiding group could not form until they could circle on the soil surrounding the nest entrance. The upper limit of tolerance for *Polyergus* was about 91°F for air temperature 10 inches above the surface and 98°F on the surface. (*F. p. nitidiventris* workers could forage normally at these temperatures.)

Frequently during the morning or midafternoon an ant or two would stand at the entrance or move off to explore in the grasses. Then, in late afternoon, as the sun slanted low, or the nest was shaded so that both light and temperature dropped, ants began to come out one or 2 at a time. Sometimes the number increased gradually to full quota, but usually there would be a sudden outpouring which seemed to be in response to an incoming scout. Thus, the starting time of a raid was influenced by time and temperature and perhaps reduced light but seemed more directly dependent on the return of an ant which had laid an odor trail. This seemed quite clear for the late raid which began at 5:16 PM. The ants had begun coming out at 4:10 PM when temperature was reduced to 91°F.* From then on 20 to 50 kept exploring the edges of the nest but seemingly could find no direction to start out. Then suddenly at 5:08 PM more ants poured out, covered the nest, and explored into the grasses until they had organized a raiding party which left at 5:16 PM. It had seemed that weather conditions had been right, and the ants had been ready to start for about an hour before an odor trail was found.

Even at favorable temperatures the ants did not raid until midafternoon. The earliest raid seen began at 3:06 PM at 81°F (83°F on the ground). At 2:30 PM, when the watch began, there were

*Temperatures are those 10 inches above the nest soil unless otherwise stated.

3 to 5 ants out; and the number increased to about 25 by 2:55 PM. At 3:04 PM many pushed out and started off 2 minutes later.

Polyergus raids did not take place at low temperatures. First raids of colony 0-26 never started at temperatures lower than 74°F and ended at 68°F or above. One second raid began at 71°F and ended at 69°F. The record for low temperature raiding was reached by a colony on another part of the Reserve, which started a second raid at 67°F and ended it at 65°F.

Ordinarily the ants raided under a great variety of light intensities ranging from 6,300 to 1,400 foot-candles over the nest at the beginning of a raid to from 2,600 to 700 foot-candles at the end. (In early afternoon, light readings might record as high as 10,000 ft-c.) One late third raid started at 400 foot-candles. Another colony began a record raid one cloudy evening when the light meter recorded only 216 ft-c, and the last ants returned in the semi-darkness of 46 ft-c.

Once a sudden drop in light preceding a storm seemed to prevent a raid. Approximately 50 ants were milling about on the nest at 4:10 PM when a solid black cloud reduced light from 1,500 to 800 foot-candles in 9 minutes, causing the retreat of all but 5 ants. (Temperature stayed high, dropping from 81°F to 79°F.) It continued dark, and rain began at 5 PM.

An approaching rain did not always discourage raiding. One group was caught in a downpour when about one-third was still on its way home.

In 1965, on 19 of the 31 days when no raids occurred, it rained in the afternoon or the ground was wet from a morning rain. On 11 days raids seemed to be prevented by low temperatures, and on one by drop in light. On one day in 1965, when weather conditions seemed ideal, the ants never came out in full force and made no attempt to form a raiding column. Once in 1964, again under seemingly ideal conditions, the ants ran about in full force for 30 minutes and a column moved out for 2 feet before all retreated. It seemed as if there were no trail to follow.

LENGTH OF THE RAIDING SEASON

Observations in 1964 did not begin until June 23, after raiding had started; therefore, in order to determine the beginning of the raiding season in 1965, the 0-26 nest was watched each afternoon, beginning on June 9. This day, as well as the 10th, 11th, and the 12th, was an adequate raiding day as far as weather was concerned; but only occasionally did a *Polyergus* worker come to the surface,

loiter for a few seconds and then retreat. June 13 through June 17 were cool enough so that raiding would not have taken place in any season. On June 18 the *Polyergus* showed their first preliminary activity. They kept coming to the surface, one to 5 at a time. Some retreated quickly, while others moved away from the entrance to circle about on the bare nest area. At least 3 ants moved away into the grasses, exploring back and forth. This was interpreted as the first tentative scouting of the season. Next day, June 19, the first raid occurred. On that day workers began coming out of the nest at 3:55 PM, when the first flickering shade reduced the temperature from 90°F to 84°F. As a few circled about, some went off individually in different directions, moving rapidly out into the grass. At 4:45 PM an ant came in from the northwest and went directly into the nest entrance. Within 2 or 3 seconds *Polyergus* workers began pouring out, covering the nest area with a moving crowd which, 5 minutes later, began traveling off to the northwest on the initial raid of the year.

The raiding season probably started late in 1965, since June had been cold. The earliest raid ever seen was on June 11, 1959. Raiding seems to begin at the time when *F. p. nitidiventris* are accumulating their first pupae. A few newly formed pupae have been collected as early as June 5, in 1963 but were not found in 1965 until June 14.

Polyergus lucidus matures its brood more slowly. A colony dug into on June 15, 1965, had larvae but no pupae; and the earliest record of pupae was June 22, 1964. It would seem that raiding begins when *F. p. nitidiventris* pupae are just becoming available and while most *Polyergus* larvae are still small to medium size. Once raids have begun, they continue on almost very afternoon that the weather permits. The urge to raid seems especially strong during the early part of the season, reaching a peak in early July when there are the most double raids, when ants travel the greatest distance to outlying nests, when more brood is brought in, and when more *Polyergus* workers participate in the raids. By mid-August there is a dwindling of the number of ants which go on a raid. By this time perhaps all of the *F. p. nitidiventris* in the neighborhood have been raided once, twice, or more times; and the number of available pupae and larvae is dwindling. By early September the raiding season is about over. *F. p. nitidiventris* do not overwinter as larvae, and by the last of August no more are present. Pupae have been found in their colonies as late as September 19, but only a few were left at this time; and in colonies raided by *Polyergus* they had probably all

emerged or been captured earlier. In 1964, the last 3 raids seen (August 27, 29, and September 3) yielded only 60, 47, and 37 pupae (no larvae); and there were only 82, 62, and 47 ants participating. It looked as if the raiding season would end soon after observations stopped on September 4. In 1965, on the last raid seen (September 3), 63 ants brought back only one pupa. Observations ceased on September 7.

NUMBER OF RAIDS MADE IN A SEASON

If, as we suppose, the raiding season begins about the middle of June, when pupae are accumulating, and lasts through the first or second week of September, by which time larvae will be gone and pupae are becoming scarce, then the raiding season consists of about 85 days. During 1964, the colony was observed on 50 days, during which time there were 29 raids on 24 days. Twenty-three of the raids were successful, while on 6 no brood was found. On this basis there may have been approximately 49 raids during the season — 39 of them successful and 10 unsuccessful. In 1965, during 54 days of observation, there were 34 raids on 22 days. Twenty-nine were fruitful and 5 were not. In an 85-day season the ants may have made 54 raids — 46 successful and 8 unsuccessful.

In the 2 seasons there were multiple raids on 30% of the raid days observed — 11 days of double raids and 3 of triple ones.

LOCATION OF COLONIES RAIDED

The *Polyergus* colony at 0-26 nested in a little hollow in a field which sloped down to a marsh at the southeast and up to woods on the north and west. There were *F. p. nitidiventris* colonies in all directions, but they were not randomly distributed. *F. p. nitidiventris* avoided nesting in woods or marsh, in heavy grass cover, in low spots on the field, and in a barren spot where gravel had been dug. Favorable places were on the grassy upland slope among sparsely scattered oaks (8 colonies), along a jeep road which made an open strip between marsh and woods (7 colonies), and in the lower field wherever vegetation was not too dense (4 colonies). The *Polyergus* raiding territory had a very irregular boundary which extended for 286 feet to the north and 114 feet to the northwest across fields, 218 feet to the west along the jeep road, 58 feet south toward the marsh, and 65 feet east to the gravel dig.

Measurements were taken of the distance travelel on 54 raids. The mean distance was 75 feet. On their longest raid the ants traveled over a little hill, across a valley, and up another hill to arrive exactly

at a colony 286 feet away. The nearest colony nested only 15 feet from the *Polyergus* nest. During June the ants tended to raid nearby colonies; 20 raids averaged 56 feet per raid with a range of from 15 to 128 feet. By July they had to go farther afield to find new colonies. Eighteen raids averaged 103 feet and ranged from 18 to 286 feet. In August some raids were to distant colonies, and some were reraids of those nearby. Fourteen raids averaged 72 feet, ranging from 17 to 213 feet. The 2 September raids were short — 27 and 43 feet.

NUMBER OF COLONIES RAIDED

During both 1964 and 1965 a numbered stake was placed at each raided colony. In 1964, 17 different colonies were raided in the 23 successful raids seen. In 1965, in the 29 successful raids observed, 20 different colonies were visited. In 1965, the ants found only 2 colonies where they had been the year before; but they located 5 others 3 to 9 feet from a 1964 stake. This would seem to indicate an unusual amount of moving on the part of *F. p. nitidiventris* colonies, a behavior pattern which was probably instigated by the raids. This moving perhaps accounts for the fact that some unsuccessful raids were to what seemed to be obvious nest sites which had been recently deserted.

Reraiding of colonies was common practice. One colony only 24 feet away was known to have been raided on July 22, August 26, and September 3 of 1964 and again on June 20 (2 raids) and June 25 of 1965. During 1964, one colony was known to have been raided 4 times, one 3 times, and one twice. During 1965, 5 colonies were robbed twice and one 3 times. It would seem that, within a raiding season, most of the colonies would be visited more than once. The total number of colonies available may not have been more than about 25. This multiple raiding probably kept the colonies so depleted that they could not gather numbers enough to produce winged forms. Since *Polyergus* colonies tend to stay in one place for a number of years, they probably do not completely destroy *F. p. nitidiventris* colonies; but they may gradually diminish them to the extent that the *Polergus* colony cannot make a living and must move.

RAIDS WHICH ENDED IN FAILURE

Occasionally a raiding group, typical in all respects, failed to find a colony. This seemed to be the result of misinformation on the part of a scout, because the raiding forces were as large as usual and the spots they stopped at were just as definite. The usual routine was

followed at trail's end: that of a compact mass of ants digging in around pebbles, leaves, and grass. When no nest was found, the group began moving in widening circles, out as much as 3 feet. After 2 to 7 minutes of futile search some ants turned homeward, while others dug for another 10 to 20 minutes before giving up. Some of the wrong spots seemed quite evidently places where ants had been living. One had a pile of excavated soil before a wide open entrance into which the ants plunged. Once a colony which had been raided 3 times previously erected such a good barricade that the *Polyergus* never did get in, although they did not give up for 22 minutes. (Later I dug the nest and found the colony still there.) During the 2 years 11 failures occurred in 63 observed raids. Thus, 17.6% of the raids ended in failures which seemed to be due to misinformation. One ended in disaster because the terrain was too severe. The ants started up an almost perpendicular bare bank, but many lost their footing and could not get to the top. The whole group became disorganized, and eventually all returned home without going any farther.

SPEED OF TRAVEL AND TIME REQUIRED FOR A RAID

The time of an entire raid was considered as the interval between the starting out of a raiding column and the return of the last ant. This varied greatly, depending on distance traveled, time required to get into a nest, amount of brood to be brought out, and the length of time that some ants delayed at the nest before starting home. For 51 raids the mean time was approximately an hour (63 minutes). The extremes were 20 minutes for a raid on a colony 15 feet away, to 2 hours and 19 minutes for one on the most distant colony 286 feet away. June raids took a shorter time, averaging 47 minutes in contrast to 73 minutes for both July and August and indicating again that near colonies were raided first.

The preraid organizing, when many ants were moving about on the nest, took from 2 to 25 minutes and averaged 9.6 minutes. The time taken to reach a raided nest averaged 23 minutes and varied from 5 to 65 minutes. The opening of a nest, its penetration, and the emergence of the first ants with loot averaged 4.4 minutes. If the entrance was not obstructed, they could enter immediately; if it was barricaded or guarded, they might require as much as 13 minutes to free it. Once the ants entered, they would have the first brood out within a minute or two. The journey back took a shorter time than the outward one had required. The mean time required for the first ant to reach home was 15.9 minutes with a variation of 3 to 47 min-

utes. The last ant reached home anywhere from 3 to 40 minutes later, the mean being 17 minutes.

The outgoing group of raiding ants moved at a fast pace, in spite of the fact that individuals were constantly running backward and to the side as well as forward. The mean speed of travel to raided nests was 3.1 feet a minute, and the extremes varied from 1.1 foot to 4.9 feet. The ants speeded up when they crossed bare spots at very high temperatures, but the terrain also influenced speed. Travel uphill or through rough areas with large grass clumps slowed speed; and sometimes, in places with leaf cover, the group spread out a bit and explored under leaves as they moved along. It was not surprising that individual ants made better time returning to the home nest, even when burdened with brood. The mean speed was 4.7 feet a minute, with individual records varying from 2 to 6.5 feet.

NUMBER OF ANTS TAKING PART IN A RAID

For 47 raids ants were counted as they returned to the home nest. Not all of the *Polyergus* workers went on each raid, and the number varied considerably from day to day. However, in both years the force reached a peak in early July and dwindled in August. In 1964, the largest number seen on a raid was 370 (on July 10); and in 1965, it was 536 (on July 3). The smallest were 47 (Sept. 3, 1964) and 63 (Sept. 3, 1965). Nineteen raids counted in 1964 gave a mean raiding force of 231, while 28 raids in 1965 averaged 307 workers. It would seem that 0-26 is a vigorous and growing colony, perhaps one of the largest on the Reserve. Counts at other colonies (made for comparison in June and July of several years) gave raiding groups consisting of 272, 258, 194, 112, 54, 31, and 13 ants.

AMOUNT OF BROOD COLLECTED

The success of a raid was unpredictable and until late summer bore no correlation to the number of ants participating in it. One raiding party of 313 ants brought in only 8 pupae and 5 larvae, while another of 310 ants returned with 184 pupae and 32 larvae. The most successful raid took place on July 10, 1965, when 505 ants brought back 446 pupae and 34 larvae. The colony had not been raided before that season.

A raid did not necessarily wipe out the brood in a *F. p. nitidiventris* colony. On June 20 a group of 338 raiding ants secured 235 pupae and 78 larvae. Fifteen minutes after all were back in the home nest they organized another raid, with 284 ants, to the same colony and took 73 pupae and 19 larvae.

Brood collected in 19 raids in 1964 averaged 120 (98 pupae and 22 larvae) a raid. If an estimated 40 successful raids took place during the season, the *Polyergus* captured approximately 4,800 young ants (3,920 pupae and 880 larvae). Since there were probably not more than one-and-a-half times that number of adult *Formica* in the mixed colony, and since many workers live for a number of years, it would seem that a fair proportion of the brood brought in is used for food. The success of the 1965 season was similar. Twenty-eight raids brought in a mean of 116 young ants consisting of a mean of 90 pupae and 26 larvae.

Ants counted as they reached the home nest fell into three categories: those with pupae, those with larvae, and those with nothing. The proportion varied greatly from an extreme of a successful raid in which 438 carried brood and only 18 did not, to an unsuccessful one in which 32 carried brood and 410 returned without. In 1964, 48% of the ants returned wihout brood, while in 1965 the unsuccessful ones constituted 66%. The second season may have been simply a bad year; or perhaps after a *Polyergus* colony reaches a certain size, the number of brood captured depends not on the strength of the raiding force but upon the number of *F. p. nitidiventris* larvae and pupae available.

An unusual method of collecting brood was seen in 1967 when a *Polyergus* colony raided another *Polyergus-Formica p. nitidiventris* colony at least twice. On the raid seen on August 15, the timing was perfect. Ants from nest "a" traveled for 28 minutes to nest "b," reaching it 8 minutes after all of its *Polyergus* had started on a raid. There was no barricade, and no fighting, and the 76 ants from nest "a" made off with 68 pupae and two larvae. The last ant, carrying a pupa, left just as the nest "b" *Polyergus* returned. They had also made a successful raid, in which 98 ants returned with 97 pupae (and many ants started off immediately over the same trail to bring in more pupae).

Nest "a" had been discovered in 1966, and it seems possible that it is the old Lawn Colony which remained in one place from 1956 to 1965. If this is true, it had moved 61 feet late in 1965 or early in 1966.

RELATIONSHIP WITH OTHER ANTS

The 0-26 colony raided only *F. p. nitidiventris*. The Lawn Colony raided *F. p. nitidiventris, F. lasioides* Emery, and *F. neogagates* Emery; but only the first species were seen at the home nest.

Once, by mistake, members of the 0-26 colony entered a nest of *F. fusca* Linne. They were engaged in a fight and succeeded in taking away only 4 pupae.

Ordinarily a column of *Polyergus* did not disturb other ants which they passed by; but when some individuals aroused a *F. subintegra-F. fusca* colony by investigating openings in the nest, they were attacked by both species of the mixed colony and some were killed. Once *F. obscuriventris* Forel workers intercepted *Polyergus* individuals returning home with brood and hijacked a few pupae.

SUMMARY

At the Edwin S. George Reserve, in southern Michigan, slave-making raids of the ant *Polyergus lucidus* Mayr took place in the late afternoon (3:06-7:30 PM), at high to medium temperatures (91°-67°F) and reduced light (6,300-216 foot-candles). The slave ants were *Formica pallidefulva nitidiventris* Emery, but *F. neogagates* Emery and *F. lasioides* Emery were also raided by some colonies.

It was concluded that scouts individually find nests and lay odor trails back to the home colony. Raiding groups go directly to the nests to be plundered. Pheromone trails, which ants would follow, could be made from a solution of *Polyergus* workers crushed in dichloromethane. A raid on a *F. p. nitidiventris* colony, in a box placed 6 feet away, was induced in this manner.

The raiding season began in mid-June and lasted into September. It coincided with the time when the slave species had pupae in the nest. It was estimated that about 50 raids could be made in an 85-day season. On some days double, or even triple, raids occurred.

Distances traveled to a raided colony ranged from 15 to 286 feet. Ants in a raiding group traveled about 3 feet a minute. An entire raid might be finished in 20 minutes or might take as long as 2 hours and 19 minutes. The mean time was one hour.

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