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THE SLAVE-MAKING ANT *FORMICA GYNOCRATES* (HYMENOPTERA: FORMICIDAE)

Mary Talbot¹

ABSTRACT

Formica gynocrates, a recently described species of slave-making ant, was found at the E. S. George Reserve in southern Michigan. It contrasted with the other five *sanguinea* group species found there by living in dry fields and enslaving a field-dwelling ant, *Formica vinculans*. Slave raids were carried on from 16 June to 11 September and flights occurred between 5 July and 14 August. Three other *sanguinea* group species, *F. subintegra*, *F. pergandei*, and *F. rubicunda*, were most common along field-wood ecotones. They enslaved *F. subsericea*, and *F. pergandei* occasionally took *F. pallidefulva nitidiventris*. *F. subnuda* lived in and under logs and usually had no slaves or a limited number of *F. subsericea*. *F. creightoni* was rare, lived in woods, and enslaved *F. neogagates* and *F. lasioides*. Raids of *subintegra*, *pergandei*, and *rubicunda* took place from late June to September, and flights occurred from the first or second week of July until early August.

The two square miles of the Edwin S. George Reserve in Livingston County in southern Michigan harbor all of the six known eastern species of the slavemaking *Formica* of the *sanguinea* group. Of these, *Formica subintegra* Emery, *F. pergandei* Emery, and *F. subnuda* Emery are common at the borders of fields or in open spots in woods; *F. subnuda* is less common and is associated with logs or stumps in open to dense woods; *F. creightoni* Buren is rare and seems to be confined to woods; and *F. gynocrates* Snelling and Buren is the only one found in the middle of dry fields.

Between 1951 and 1973, 23 colonies of *F. gynocrates* were discovered on the George Reserve. Some colonies have been found and later lost in a number of different fields. They were easily lost since colonies move frequently. However four colonies have been known for 10, 5, 4, and 3 years respectively.

Formica gynocrates is restricted to living where there are numerous nests of its host ant *F. vinculans* Wheeler. This latter species will not tolerate fields with grass cover thick enough to obscure the ground, nor is it found in woods or even woods edge if the soil is heavily matted with dead leaves.

Thus, *F. gynocrates* lives in rather sterile, sandy, upland fields where rapid drainage prevents a lush growth of vegetation. Associations of Canada bluegrass (*Poa compressa* L.) and three-awned grass (*Aristida purpurascens* Poir.) are typical. These, together with a few other grasses, form a sparse ground cover. There are usually small patches of bare soil and larger patches of red-tipped lichen (*Cladonia cristatella* var. *vestita* Tuck) or moss (*Polytrichum juniperinum* Hedw. and *P. piliferum* Hedw.). Beds of pussy's toes (*Antennaria neglecta* Green and *A. fallax* Greene) are frequent and other scattered forbs form a slightly higher layer. The most conspicuous of these are bush-clover (*Lespedeza capitata* Michx. and *L. virginica* (L.) Britt.), St. John's-wort (*Hypericum perforatum* L.), blazing-star (*Liatriis aspera* Michx.) and several species of goldenrod (*Solidago* spp.).

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The ants (*Aphaenogaster treatae* Forel and *Lasius neoniger* (Emery) are typical of these fields and in some places *Formica pallidefulva nitidiventris* Emery is present. *Myrmica americana* Weber, *Solenopsis molesta* (Say), *Monomorium minimum* (Buckley), and *Paratrechina parvula* (Mayr) are usually found on the lower parts of field slopes, while *Formica lasioides* Emery sometimes nests in little swales or near trees where the soil is slightly more moist.

NEST STRUCTURE

Colonies of the host ant *F. vinculans* are usually inconspicuous because workers do not pile up soil around nest entrances nor do they make large, semi-bare nest areas. The mixed colonies are sometimes easier to see because *F. gynocrates* workers, which help with the excavation, are more apt to leave a covering of soil near the openings. This may occur after rains and especially during flight periods when a vague circle may reach 30–60 cm d. This does not mark the limits of the nest and alates may emerge from other openings in the grass beyond. It is characteristic of *F. vinculans* that nests extend for some distance just under the surface of the soil.

Formica vinculans has another characteristic which is carried over into the mixed colonies. It builds small piles of debris around bases of plants on or near the nest. The thatch for these small cones varies and may consist of any mixture of sand grains, tiny pebbles, leaf scales, and bits of dried leaves, lichen, and moss. The shelters may be built among the small leaves of *Antennaria* or around the bases of many kinds of plants such as clumps of grass, rosette leaves of hawkweed, or stems of goldenrod, mullein, star thistle, or blazing-star. These small structures are 2.5–7.5 cm across and usually enclose aphids. They also serve as aboveground chambers for incubating pupae and as a loitering place for alates.

DAILY ACTIVITIES

Excavation of chambers and galleries, performed by both species, was especially conspicuous after rains, when a colony had moved, and during the flight period. Foraging was carried out primarily by *F. vinculans* workers. They attended aphids and brought in numerous small bits of food, usually working singly. *F. gynocrates* carried home larger bits of food and often cooperated in dragging in bulky pieces such as caterpillars or tree hoppers.

Both species were high-temperature ants, becoming more active as the day became warmer. Usually both stayed underground at night and began coming out in the morning as the surface warmed. They walked slowly on the nest at 18°C, ground temperature; at 21° they were moving normally and foraging off the nest. *F. gynocrates* raided normally at 35° and on a raid could run across soil which registered 39.5°C. *F. vinculans* has been seen foraging at 40.5°, ground temperature. At high temperatures they ran rapidly and climbed up off the soil as much as possible. Activity did not depend directly upon temperature because sometimes one colony would be raiding or foraging vigorously while another would be inactive. Three times during the summer one colony was disturbed by a bird (probably a flicker) which made 7.5-cm deep holes over the nest. Each time all excavation and most foraging ceased for half a day or more before the usual activity was resumed.

MOVING

Formica gynocrates colonies did a great deal of moving, typical of species in the *sanguinea* group. During these activities some workers of both species excavated a new site while other *F. gynocrates* carried adults, pupae, and larvae. A few *F. vinculans*

Table 1. Earliest and latest records of brood, alates, flights, and raids of the ants of the *sanguinea* group at the Edwin S. George Reserve.^a

Species	Larvae		Worker Pupae		Alate Pupae	
<i>F. gynocrates</i>	4-6-70	29-8-57	4-6-70	21-9-70	4-6-70	17-7-73
<i>F. subintegra</i>	2-6-69	22-8-73	4-6-70	8-9-69	10-6-70	31-7-56
<i>F. rubicunda</i>	3-6-75	29-8-71	14-6-69	25-9-70	14-6-70	4-8-69
<i>F. pergandei</i>	3-6-71	25-8-56	3-6-71	21-9-71	6-6-73	29-7-69
<i>F. subnuda</i>	4-6-70	24-8-56	5-6-69	28-8-56	6-6-63	20-7-56
	Alates		Flights		Raids	
<i>F. gynocrates</i>	21-6-71	16-8-72	5-7-73	14-8-73	16-6-73	11-9-72
<i>F. subintegra</i>	1-7-70	14-8-56	7-7-70	8-8-56	1-7-70	24-8-73
<i>F. rubicunda</i>	3-7-73	6-8-69	12-7-70	4-8-73	17-6-70	1-9-69
<i>F. pergandei</i>	1-7-70	8-8-69	6-7-73	27-7-56	18-6-70	6-8-69
<i>F. subnuda</i>	16-6-58	28-7-60	15-7-60	18-7-62	— ^b	—

^aNo observations were made before the first week in June.^bNo raids of *F. subnuda* were seen.

workers carried some of the smaller (*vinculans*) pupae. As is usual when ants change nest location, a few ants carried brood and adults back to the old nest while others were taking them to the new. Ordinarily moving was completed within 7-12 days.

Colonies commonly stayed in place during the maturing of the alate brood and until after flights were over. This could be by the end of July for some colonies to the middle of August for others. Some became restless as soon as flying ceased but more waited until raids had slowed or stopped. Most changing of nest sites took place in late August and throughout September.

Distances shifted were often very short, 1-3 m, with most colonies changing nest sites only once in a season. One colony, living on a ditch bank, moved to the flat surface 3 m above in August 1972. In late July 1973 it shifted 2.4 m down the bank, and in late August moved up to a spot just below the 1972 nest. This much moving was unusual. Some colonies remained in one place for a number of years.

In contrast to these short moves, some ants traveled long distances. Three such colonies were lost and not found again. One other, observed while moving, settled on a spot 28 m away from the original nest and another moved 29.3 m. This latter colony, in early September 1973, invaded and took over a colony of *F. vinculans* which it had been seen to raid on 13 July, 1973. It was a large vigorous colony which had put up a full-scale defense at the time. Evidently there was also resistance when *F. gynocrates* moved in because inside the nest were many dead *F. vinculans* workers. Probably this capturing of a *F. vinculans* colony is common procedure when *F. gynocrates* move for a long distance.

BROOD DEVELOPMENT

Larvae and a few worker and alate pupae were already present when observations began in early June (Table 1). Larvae are not overwintered and all had developed into pupae by 19 August. A few worker pupae have been found as late as 21 September. Most records of alate pupae were obtained between 4 June and 8 July, a period of just over a month,

Table 2. Data from 15 flights of *Formica gynocrates* in Southern Michigan.

Nest	Date	Alates climbing			Beginning of flight			Height of flight		
		Time	°C ^a	klx	Time	°C ^a	klx	Time	°C ^a	klx
20	8-7-73	0639	22.2	12.9	0656	23.3	12.9	0703	23.9	15.1
20	9-7-73	0638	22.2	15.1	0657	23.3	15.1	0713	24.4	19.4
18	9-7-73	0650	22.8	15.1	0743	24.4	19.4	0747	26.1	28.0
20	14-7-73	—	—	—	0730	23.3	21.5	0812	25.0	36.6
18	14-7-73	0804	21.7	28.0	0812	23.9	36.6	0817	22.2	23.7
3	20-7-73	0710	22.8	11.8	0840	23.9	17.2	0742	25.0	23.7
3	22-7-73	0646	24.4	10.8	0705	25.0	11.8	0712	26.1	11.8
3	24-7-72	0745	24.4	28.0	0800	26.1	36.6	0812	26.7	40.9
21	29-7-73	0810	22.8	43.0	0833	23.3	56.0	0851	23.9	64.6
6	1-8-73	—	—	—	0905	23.9	60.3	0910	25.0	49.5
21	4-8-73	0759	22.2	28.0	0815	23.9	47.3	0835	26.7	51.6
5	5-8-72	0848	22.2	54.9	0910	23.3	60.3	0930	24.4	65.6
6	7-8-73	0745	21.7	19.4	0809	24.4	28.0	0812	24.4	30.1
21	12-8-73	0748	23.3	36.6	0806	23.9	28.7	0812	24.4	38.7
21	13-8-73	0811	22.8	34.4	0832	23.9	51.6	0838	25.0	45.2
Mean		0735	22.8	26.0	0804	23.9	34.2	0811	25.0	36.3

but in 1973 a few were still present on 17 July. These records were kept over a number of years and during some seasons there is a longer development period than in others.

Adult alates were first seen on 21 June and last seen on 16 August, a period of eight weeks. For a week or two after the first emerged there were still more alate pupae than adults in the colony and adults continued to emerge from the pupal stage for another week or two. Flights began within one or two weeks after the emergence of the first winged adults and considerably before all of the alate pupae had become adult.

FLIGHTS

The flight season in 1973 was from 5 July through 14 August (Table 2). One colony had flights during the entire season but others ran out of alates by 25 July–11 August. Thirty-four flights have been seen in other years but none earlier or later than these except in 1972 when one last male flew on 16 August. There were 16 days of flights in 1973 and 22 days when unfavorable weather conditions prevented flights.

Entire flight records could be secured from only one nest at a time (except for a few cases when a helper was available), so different nests were watched on different days. Sometimes, instead of watching one colony, a survey was made of all the six colonies used. It was found that the colonies were principally either male- or female-producing. Two had only males and one had only females throughout the flights, while two produced only males until near the end of the season when a few females were found, and one produced females with only a few males.

During each of 21 watched flights in 1972 and 1973, an attempt was made to check all of the alates which flew. This could be done fairly accurately because all flights were sparse, but still probably undercounted them. The most alates seen to fly in one day from a male colony was 46, while the greatest number from a female colony was 21. Mean

Table 2 (continued).

Nest	Date	Time	End of flight		Length of flight min	Number flying	
			°C ^a	klx		♂	♀
20	8-7-73	0712	24.4	17.2	17	5	—
20	9-7-73	0758	25.0	30.1	62	6	—
18	9-7-73	0800	27.2	28.0	18	—	8
20	14-7-73	0902	25.0	60.3	93	14	—
18	14-7-73	0845	23.3	28.0	34	—	19
3	20-7-73	0755	24.4	17.2	16	—	13
3	22-7-73	0720	26.7	13.7	15	—	20
3	24-7-72	0825	27.8	40.9	25	—	8
21	29-7-73	0917	30.6	79.6	45	46	—
6	1-8-73	0916	26.1	47.3	12	22	—
21	4-8-73	0847	27.2	51.6	33	45	—
5	5-8-72	0953	25.6	73.2	43	—	21
6	7-8-73	0815	24.4	36.6	7	4	—
21	12-8-73	0842	24.4	62.4	37	22	—
21	13-8-73	0845	25.6	53.8	14	7	—
Mean		0830	26.1	42.0	31	19	15

^aAir temperature measured 25 cm above the ground; many ants flew from vegetation at approximately this height.

number of alates flying per day on the 21 days was 16.1 The 14 male flights averaged 17.6 males released and the seven female flights averaged 15.9 females. Flights were especially sparse toward the end of flight season when colonies were running out of alates and also at the beginning of the season when few alates were mature.

All flights took place in early to mid-morning and flying might begin as early as 0656 hr (EST) or as late as 0910. Flights ended from 0712 to 0953. This variation in time took place because the ants were reacting primarily to warming soil and air. On sunny mornings the first alates could be seen when air temperature was about 17–18°C (25 cm above the ground); on hazy mornings they might stay underground until the temperature reached 21–22°. As soon as the air and the alates warmed sufficiently, some began to climb vegetation. Actual flying usually began when the air temperature reached 23–24°. Females sometimes delayed until it was a bit warmer. Ends of flights did not seem so dependent upon a certain temperature and the last alates might leave at temperatures anywhere from 23° to 30.5°. Light also played an important role; dimming or fluctuating light could delay or stop a flight. The best flight days were those after a cool night when the morning sun was bright, the temperature was rising steadily, and there were no clouds and little or no wind.

During the 1973 season there were 22 days without flights. On some days no alates were out; on the other days a few appeared but there was no true flight. On two days conditions seemed satisfactory but for some unknown reason workers kept the alates from flying.

Before flights began workers of both species engaged in vigorous digging-out of chambers just under the surface and in adding openings. These extra chambers and exits were usually in places where patches of grasses or forbs grew on the nest area or at its rim. Workers were not very active in trying to keep alates from flying. On most days no interference was seen but a few *F. vinculans* workers would intervene when conditions were unfavorable, especially at the beginning or end of a flight. A *vinculans* worker might pull back a male by an antenna, leg, or mandible, or induce it to turn around by nipping

or lunging at it. They were less successful with the larger females and rarely disturbed them. Occasionally a *F. gynocrates* worker would nip a female.

Males and females both tended to climb vegetation to fly. Males usually flew from near the place where they had come from the nest, while females generally walked about on the ground for short distances before climbing. Males could fly from grasses but females usually chose more sturdy stems of *Rumex*, *Lespedeza*, *Solidago*, etc. When ready to fly the alates stretched forward, moved antennae, opened wings, and flew. Sometimes they fluttered wings vigorously before flying, especially if conditions were not ideal.

There was no mass climbing of plants and during most flights only a few alates could be seen on the vegetation at any one time. However, more might accumulate if conditions became unsatisfactory. Once, when females began to climb at 23°C, the temperature dropped 1° and light dimmed from 11.8 to 11.4 klx. At this time 24 females were counted on plants, the most ever seen. As soon as the temperature rose to 24° and light to 17.2 klx, they began to fly and most left in the next 3 min. Males reacted in the same way and never were more than 17 counted on vegetation at one time. These had gathered when the temperature was not rising and light remained dim.

Both males and females climbed down stems when conditions became unsatisfactory, as when a slight wind swayed the plants or the temperature lowered slightly. At times they tended to drop, either while standing still or while trying to take off for flight. Dropping was more frequent toward the end of a flight when temperature rose too high, but might also occur at any time when conditions were not right.

Flights of *F. gynocrates* took place under essentially the same conditions as those of *F. vinculans*. Flights of *F. vinculans*, misidentified as *F. neogagates* Emery, have been reported by Talbot (1966).

RAIDS

The main raiding season extended from about 24 June to 25 August and there were numerous raids on *F. vinculans* colonies during that time. Two, observed on 16 and 19 June 1973, were weak exploratory forays; no nests were found. The latest raid seen was on 11 September 1973, when a colony was entered and a few workers were captured, but no brood was brought out of the nest. Two other late raids, 29 August 1957 and 10 September 1972, were unusual in that they were directed against *Lasius neoniger* colonies. Evidently the raiding season begins when alates are emerging from the pupal state, about two weeks before flights begin, and continues until the time when larvae are scarce in the nest.

Many raids were seen over a number of years but the most concentrated study was made between 12 and 25 August, 1972. These observations covered the latter part of the raiding season when raids were less frequent, but nevertheless the colony made successful raids on seven colonies of *F. vinculans* in spite of a number of days of bad weather. One was raided for two days with *F. gynocrates* workers remaining in the nest overnight and once two colonies were raided on one day. Distances to the raided nests were 3, 4.9, 7.3, 12.5, 15.2, 28 and 31.7 m. In addition to the successful raids, some groups failed to find a colony.

During this period the ants maintained five basic, invisible trails, which were followed by the ants leaving the nest. All led toward the open field and not back to scattered trees at woods edge (where *F. subsericea* Say were abundant but unmolested). Ants leaving by such a trail might deviate from it almost immediately or might follow it for a long distance. Once, workers followed a trail to within 1.5 m of a previously raided colony and then branched off to find a new nest. Sometimes the ants moved quickly to a colony as if they had a good odor trail. More often they took a long time along the way as if they were hunting a colony by searching the ground thoroughly. (Regnier and Wilson [1971] found that they could induce raids of *F. subintegra* and *F. rubicunda* by laying down odor trails made with ether extracts of crushed whole workers or of hindgut.)

Raids might start at any time of day from 0645 to 1645. They were most frequent in early to mid-morning and when the day began to cool in the afternoon, but sometimes started at mid-day if temperatures were not too high. The ants seemed not as sensitive to heat as the other *sanguinea* group species on the Reserve, and were not so apt to have a mid-day lull.

The beginning of a raid was not an especially clear-cut activity. Workers would become more numerous on the nest and then a little group would start off on one of the trails. At first they traveled close together but soon would spread out as individuals wandered back and forth and from side to side, exploring the terrain. As workers moved farther apart the line would become indistinct. Usually other groups left the nest at intervals, followed the first, and extended the line. If any workers found what seemed to be a *F. vinculans* nest others would gather, searching very carefully for openings. If they failed to find a colony quickly some continued to hunt at that place while others would either increase the area of search, move forward, or start back home. Colonies were sometimes easy to find because entrances were obvious; others were so thoroughly concealed and blocked that considerable searching and digging was necessary.

F. vinculans had a characteristic habit when attacked. Some workers rushed out carrying brood up nearby plant stems so that sometimes they were a conspicuous sight, a whole area of grass covered with dozens of workers, each holding a pupa or, more rarely, a larva. Usually the attacking ants did not pursue them but waited until they came down and then took their brood.

Some *F. vinculans* colonies staged a good defense of the nest, either above-ground or down in the nest. Sometimes no defense was attempted; perhaps these colonies had been raided before, possibly several times.

On the morning of 13 July 1973, one *F. gynocrates* colony raided three nests. The first two did not resist but the third did. The first raid began at 0744. By this time many workers were on the home nest and were starting to wander off along a trail. Out in denser grasses the line became sparse and wide, then dwindled to individual workers and was lost. Other groups went out and by 0815 some had found a nest 22 m away. Then the line became well populated. There was no fighting at the *F. vinculans* colony and only a few workers ran up onto grasses holding brood. Almost immediately the raiding ants began to take pupae from the nest, going back over the same trail and meeting others coming out. Very few pupae were found and within 5 min a group began to push uphill, exploring carefully and moving slowly. They found a second colony 3.7 m away in a large clump of dead grass. Here again there was no resistance and brood was carried off for the next 15 min.

A cluster of *F. gynocrates* then found a third nest only 1.2 m above the second. This colony was large and belligerent, staging a good defense. Workers rushed out in great numbers and, while some carried brood up slope from the nest, a great many formed a half circle 25 cm below the three main openings. They fought vigorously all along the line and held the *F. gynocrates* at bay for 40 min. Fighting involved two or three ants of one species holding an ant of the other species by legs and antennae and stretching it until it died. Sometimes this was unsuccessful and, after tumbling about a bit, the group fell apart without any being hurt. Defenders greatly outnumbered aggressors and it looked as if they might win, but a large group of *F. gynocrates* reinforcements arrived, fighting was accelerated, and the tide of battle turned.

At this time it was noted that certain *F. gynocrates* were running forward for short distances among the *F. vinculans* and then retreating swiftly. It could not be seen if they were spraying but it seemed possible that they were releasing an intimidating allomone. (Regnier and Wilson [1971] reported that acetates from Dufour's glands of *F. subintegra* and *F. pergandei* were discharged at defending workers of the slave species *F. subsericea*, causing panic and rapid retreat. They called the chemicals "propaganda substances" because they attract the slave-makers but disperse the defenders.)

Ten minutes later the *F. gynocrates* workers had broken through the *F. vinculans* line and were moving all over the nest site. They did not find many pupae and half an hour later most had returned home. By this time (1030) ground temperature was 49° and workers were running fast and keeping up off the ground as much as possible.

Some colonies carried on their defense within the nest instead of on the surface. One such colony had nested in a bed of moss and its entrances were thoroughly concealed. At 1345, 13 July 1973, *F. gynocrates* workers were digging into the moss at one place and others were exploring for 0.3–1.2 m in all directions. Evidently the hole they opened led to a nest, for soon a *F. vinculans* worker was dragged out and stretched by two *F. gynocrates*. Then several more were extracted. A half hour later the raiding workers were still trying to penetrate farther into this entrance and had made another hole 10 cm away from which they pulled an occasional worker. After another 40 min they began pouring out with brood. Evidently the defense had broken down. At this time there were about 50 *F. gynocrates* at the nest, more were traveling to it, and brood was being carried off at a rate of 6.6/min. By 1555 230 pupae and 89 larvae had been captured. As the stream of pupae dwindled some ants spread out seeking dead *vinculans* workers, which they carried home, and four discarded *F. gynocrates* workers were found.

Not all of the raids were successful. Sometimes exploratory groups started out on a trail, branched from it, and spread out searching, but failed to find a colony. In these cases workers gradually returned home along the trail.

COMPARISON WITH OTHER *SANGUINEA* GROUP SPECIES

Five species of the *sanguinea* groups were well known at the Reserve. The sixth, *F. creightoni*, was collected only four times; no flights and only two raids were seen. Similarities among the species were great. They developed brood at approximately the same rate, had flights at about the same time, and raided over roughly the same period (Table 1). Differences seemed primarily associated with degree of tolerance to heat and to variations in the slave species captured.

Locations of nests were perhaps mainly determined by exposure to heat. *F. gynocrates* was distinct in that it could occupy open fields with no shade. Some colonies of *F. pergandei* were far enough away from trees that they were shaded for only a short time each day. A little over half of the *F. pergandei*, *F. subintegra*, and *F. rubicunda* colonies occupied overlapping habitat. A colony at the edge of a field near a woods, fence row, or clump of trees might be any one of the three species. All three were also found in open woods or openings in woods. A few *F. subintegra* penetrated into dense woods, and a few *F. pergandei* lived in low fields bordering swamp or marsh. *F. subnuda* seemed limited to the shade of woods and perhaps *F. creightoni* was also.

Flight activities were similar for all species but here again *F. gynocrates* showed a preference for high temperatures. Its males and females were never seen to fly at less than 23°C (25 cm above ground) and they flew best at 24–26°. *F. pergandei* could begin flights at temperatures as low as 19° and flew well at 21–23°. *F. subintegra* and *F. rubicunda* followed this same pattern. *F. subnuda* could fly in the shade at temperatures as low as 17° and had no difficulty in flying at 18° if it was warmer in nearby sunny areas.

It was common in all of the species for a colony to produce only males or females, or a predominance of one; consequently many flights were all male or all female. *F. gynocrates* seemed to produce fewer alates than did the other species. The greatest number seen to fly on one day was 46, in contrast with the several hundred alates which might be released in a good flight of the other species.

Tolerance of high temperatures allowed *F. gynocrates* to raid and forage in heat intense enough to cause the characteristic mid-day lull for *F. subintegra*, *rubicunda*, and *F. pergandei*.

Slaves captured by *F. gynocrates* were the field-dwelling *F. vinculans*. A few *F. lasioides* workers also have been found with *F. gynocrates*. These could have been living in a small swale in a field. The *F. creightoni* found were enslaving *F. neogagates* and *F. lasioides*, which differ from *F. vinculans* in forming smaller colonies in more sheltered

places. Usually *F. subnuda* colonies contained a few *F. subsericea* but several nests had no slaves. *F. rubicunda*, *F. pergandei*, and *F. subintegra* typically had an abundance of captured *F. subsericea*. A few *F. pergandei* colonies, living in drier places, had both *F. subsericea* and *F. pallidefulva nitidiventris* Emery or only the latter.

In rare instances brood of other species was brought in, presumably used for food. *F. gynocrates* has raided *Lasius neoniger* Emery and *F. rubicunda* has captured brood of *Myrmica*. *F. pergandei* has plundered colonies of *Aphaenogaster treatae* Forel, *A. rudis* Emery, and *Lasius pallitarsis* Provancher.

Type of nest structure was at least partly determined by the slave species although members of the *sanguinea* group always helped in construction. *F. gynocrates* nested in soil and did not make mounds. The *F. creightoni* colonies found were in piles of leaves or in and under logs. *F. subintegra*, *F. rubicunda*, and *F. pergandei* usually nested in soil and most often formed a "nest area" at the surface (a circle or oblong of openings where excavated soil has slightly or mostly restricted the growth of plants) but they sometimes constructed low mounds. *F. subintegra* and *F. rubicunda* occasionally occupied a log and leaves to its side but *F. pergandei* was never found in this type of nest. *F. subnuda* used logs or stumps almost exclusively and these might be near swamp or in rather open woods. They used thatch to fill in gaps between logs and the matted leaves beside them, and might cover the side of a log with it, forming added chambers outside the logs. *F. subsericea* is quite versatile in its type of nest building which allows latitude in the nesting habits of species enslaving it.

F. gynocrates seemed more willing to fight and did so more fiercely than the others, but this may be due to the pugnacity of the *F. vinculans*. *F. subsericea* rarely offered resistance. However, a vigorous colony might carry on a rather spectacular battle. One such occurred on 15 and 16 July 1970. On the first morning a large colony of *F. pergandei* had a raid line extending 40 m to a fire lane which they were unable to cross because *F. subsericea* workers were defending it. Fighting consisted of individual combats in which one, two, or three ants of one species pulled and mauled an ant of the other species until it died or escaped. Five to seven such groups were fighting at any one time and many ants were moving about until 1200 hr when most of the *F. pergandei* returned to their nest. In late afternoon they returned in great number and formed a mass of ants along 2 m of the fire lane and extending 2.4 m back from it. Fighting increased but none could get across the fire lane. Next morning there were fighting groups all across the lane and some *F. pergandei* had reached the other side, but it was not until 1800 hr that they were crossing in large numbers and were exploring on the other side. They found the *F. subsericea* nest, entered it without resistance, and by 1845 were taking home larvae and pupae. Next day they were in full control of the captured nest and in the afternoon used it as a base for bringing in plundered *F. pallidefulva nitidiventris* brood. The afternoon was very warm and they were storing the larvae and pupae until the evening cool when they carried them to their nest. At the same time they were also bringing in brood from an *Aphaenogaster treatae* colony which they had found nearby.

Like *F. gynocrates*, some colonies of the other species remained in one spot for a number of years, but many moved frequently. Usually moves were late or very early in the season but colonies could move at other times. One *F. pergandei* colony moved during the flight period. The workers had captured, with some fighting, a *F. subsericea* colony on 17, 18, and 19 July 1956, and began moving into the captured nest on 20 July. The moving was accomplished in 11 days during which some females walked to the new nest over the workers' trail. Workers tried to carry some females but had difficulty because when one grasped a female by her mandibles, pulled her back, and then moved forward, the female did not curl up as carried workers do. A worker, then, might try to drag a female or just abandon her. During this time there were four flights with females flying from the old and new nests and the path between.

No complete colonies were counted but from observations of raids, it seems probable that *F. gynocrates* forms smaller colonies than are characteristic of other *sanguinea* group species on the Edwin S. George Reserve.

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