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CASTE AND DIVISION OF LABOR IN *EREBOMYRMA*, A GENUS OF DIMORPHIC ANTS (HYMENOPTERA : FORMICIDAE : MYRMICINAE) E.O. WILSON

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SUMMARY

Erebomyrma, a Neotropical genus of pheidologetine ants with caste dimorphism convergent to that of *Pheidole*, also resembles *Pheidole* in its pattern of division of labor. The major workers of *E. nevermanni*, the species examined during this study, assist in subduing larger prey, defend the nest, and serve as semi-repletes in liquid food storage. Their repertory is limited and specialized when minor workers are present but expands to include foraging and brood care when the minor workers are removed. The expansion is accompanied by a 10X or more increase in general activity rate.

Other details of the natural history and social behavior of *E. nevermanni* are given. The most distinctive properties include the occurrence of defensive retinues around the queen which intensify when the colony is exposed, the use of trunk trails during foraging, predation on arthropod eggs, and the absence of adult transport during colony emigration.

ZUSAMMENFASSUNG

Kasten und Arbeitsteilung bei *Erebomyrma*, eine Ameisengattung mit dimorphen Arbeiterkaste (Hymenoptera : Formicidae : Myrmicinae)

Erebomyrma, eine neotropische Gattung des Tribus Pheidologetini, hat nicht nur einen mit *Pheidole* konvergenten Kastendimorphismus, sondern gleicht *Pheidole* auch in der Form der Arbeitsteilung. Die Soldaten (major Kaste) von *E. nevermanni*, helfen bei der Ueberwältigung von Beute, verteidigen das Nest, und dienen als Speichertier für flüssige Nahrung. Bei Anwesenheit der minor Arbeiterinnen haben sie ein begrenztes und spezialisiertes Verhaltensrepertoire, das jedoch erweitert wird (einschliesslich Nahrungssammeln und Brutpflege), wenn die minor Arbeiterinnen entfernt werden. Gleichlaufend mit dieser Bereicherung des Verhaltensrepertoires erfolgt eine etwa zehnfache Zunahme der allgemeinen Aktivität.

Weitere Einzelheiten zur Biologie und zum Sozialverhalten von *E. nevermanni* werden berichtet. Am bemerkenswertesten ist das »Verteidigungs-Gefolge« um die

Königin, das verstärkt wird, wenn die Kolonie offen gelegt wird; die Nutzung von Sammelstrassen; das Erbeuten von Arthropoden-Eiern; und das Fehlen von sozialem Trageverhalten unter adulten Ameisen bei Kolonieemigration.

INTRODUCTION

Complete dimorphism, in which the minor and major worker castes are unconnected by intermediates, is relatively scarce among the ants. Of 263 living ant genera listed by BROWN (1973), only 10 possess it (OSTER and WILSON, 1978). Within this small group, *Erebomyrma* and its sister genus *Oligomyrmex* display an exceptionally large size difference between the two castes (fig. 1).



Fig. 1. — Portion of a colony of *Erebomyrma neyeri* from La Selva, Costa Rica, including the nest queen, major and minor workers, and various stages of brood. Some of the minor workers are seen riding on the queens as part of the retinue that increased in size when the colony was exposed. (Photograph by Bert Hölldobler).

Abb. 1. — Teil einer Kolonie von *Erebomyrma neyeri* von La Selva, Costa Rica, einschliesslich der Königin, major und minor Arbeiterinnen und verschiedener Brutstadien. Einige der minor Arbeiterinnen reiten auf der Königin; sie sind Teil des Königin-Gefolges, das verstärkt wird, wenn die Kolonie offen gelegt wird. (Foto: Bert Hölldobler).

I have provisionally resurrected *Erebomyrma* from synonymy under *Oligomyrmex*, where it was placed by ETTERSHANK in 1966 without explanation. Although the two genera are indeed very close, all of the New World species I have examined (*eidmanni*, *longi*, *nevermanni*, *panamensis*, *urichi*, and 4 additional undetermined species) possess 4 mandibular teeth with from 2 to 4 or more stiff bristles projecting perpendicularly from the lower mandibular surface; whereas all 18 Old World species examined possess 5 mandibular teeth and lack the bristles. Moreover, all but 2 of the New World species have 11-segmented antennae (*panamensis* has 9 and an undetermined Ecuadoran species has 10), while the Old World forms vary between 9 (usually) and 11 (rarely) segments. These differences, which include a strong biogeographic distinction, make it convenient to separate *Erebomyrma* and *Oligomyrmex*. However, this conclusion is freely granted to be tentative; studies of more species and character states may eventually require their return to a single genus.

While *Erebomyrma* and *Oligomyrmex* taken together occur in most tropical and warm temperate regions of the world and are occasionally locally abundant, neither has hitherto been carefully studied in life, and the pattern of division of labor in particular has remained almost wholly unknown. This gap in knowledge is the more important because of the superficial anatomical convergence of *Erebomyrma* to *Pheidole*, the most widespread and abundant of all dimorphic ant genera. The two differ in important features, such as the suturation of the major worker mesothorax and the segmentation of the antennal club. In fact they are justifiably placed in separate tribes, the Pheidologetini and Pheidolini respectively. Furthermore, both are relatively ancient: *Erebomyrma* has been recorded from the Oligocene Baltic amber (WHEELER, 1914) and Miocene Dominican amber (WILSON, 1985a), while *Pheidole* is known from the Oligocene shales of Florissant, Colorado (CARPENTER, 1930), and the Dominican amber (WILSON, 1985a). In addition, *Eocenidris crassa*, a newly discovered myrmicine of the Eocene Arkansas amber, possesses traits that might place it close to the *Erebomyrma/Oligomyrmex* line (WILSON, 1985b). Division of labor in *Erebomyrma* and *Oligomyrmex* consequently appears to have evolved independently from that of *Pheidole* (see, for example, studies by WILSON, 1976, 1984).

Some general aspects of natural history were described in *Erebomyrma eidmanni* by EIDMANN (1936) and *E. urichi* by WILSON (1962), but very little has hitherto been learned about behavior in the genus. Recently I collected a queenright colony of *E. nevermanni* in Costa Rica and was able to conduct a series of behavioral studies, with special reference to caste.

MATERIALS AND METHODS

The *E. nevermanni* colony was excavated on 23 March 1985, from two separated pieces of a rotting log, about 20 cm thick, lying on the floor of premontane wet forest. The site is at the La Selva Biological Station, which is located in the Province of Heredia, near the confluence of the Rio Puerto Viejo and Rio Sarapiquí (84°02'W, 10°26'N). The colony was placed with a small amount of natural nest material in a plastic chamber 20 × 10 cm and 7 cm deep, the sides of which were lined with Fluon (Northern Products, Inc., Woonsocket, Rhode Island) to prevent ants from crawling on the vertical surfaces. A square piece of clear plastic sheet 8 cm on the side was placed on the bottom of the chamber, providing the ants with a retreat in which they could rebuild their nest.

The behavioral repertoires were analyzed by fitting the frequencies of the behavioral categories to a lognormal Poisson distribution, following the method of FAGEN and GOLDMAN (1977).

RESULTS

Colony composition

When discovered the La Selva colony was bunched into two tight groups in separate logs and comprised a dealate queen, 7 majors, 172 minor workers, and a large quantity of brood in all stages. It was considerably smaller than two colonies of *E. urichi* I censused earlier: at Oropouche Cave, Trinidad, 10 dealate queens, 1 major, 547 minors, and 10 males; and at Bernhardsdorp, Suriname, 1 dealate queen, 4 majors, and 500-1000 minors (WILSON, 1962).

General repertoires

In *table 1* are summed data from 7 hours of observation over the first 5 days following capture of the La Selva colony. In general, the pattern of division of labor resembled that in *Pheidole*, with major workers assuming far fewer tasks than minors. The repertory size of majors may be even smaller under wholly natural conditions. Some of the brood care was recorded within a day after the colony had been installed, when the colony was still in a somewhat disturbed state. As will be shown in a later section, majors of *Erebomyrma nevermanni* (like those of *Pheidole*) have a large latent repertory that becomes fully expressed only under conditions of stress.

Feeding

The *Erebomyrma* minor workers readily fed on freshly crushed larvae and pupae of the yellow mealworm *Tenebrio molitor*, as well as a variety of adult moths that I previously killed and cut apart. They recruited nest-mates to these objects by means of odor trails. They removed eggs from gravid moths and kept them with the brood for two or more days. Earlier I

Table I. — Repertories of different castes in a colony of the ant *Erebomyrma nevermanni*. The numbers given are fractions of the total number of behavioral acts observed for each caste in turn.

Tabelle I. — Verhaltensrepertoire verschiedener Kasten einer Kolonie der Ameise *Erebomyrma nevermanni*. Die Zahlen geben den proportionalen Anteil der Verhaltensakte an, die für jede Kaste beobachtet wurden.

Behavioral category	Minor worker	Major worker
Self-grooming	0.133	0.288
Allogrooming of :		
Minor	0.010	0
Major	0.023	0.008
Queen	0.013	0
Queen retinue (on body of queen)	0.098	0.178
Lick eggs	0.010	0
Manipulate eggs	0.006	0.025
Carry eggs	0.038	0.059
Lick larvae	0.062	0.008
Manipulate larvae	0.023	0.017
Carry larvae	0.087	0.034
Lick pupae	0.016	0
Manipulate pupae	0.019	0.008
Carry pupae	0.039	0
Assist removal of meconium	0.002	0
Assist eclosion	0.002	0
Forage	0.101	0
Prey capture	0.040	0.068
Feed outside nest	0.042	0
Feed inside nest	0.011	0
Retrieve food to nest	0.009	0
Transport food within nest	0.010	0
Regurgitate with :		
Larva	0.016	0
Minor worker	0.022	0.085
Major worker	0.010	0
Queen	0.003	0
Feed solid food to larva	0.003	0
Colony defense	0.040	0.195
Lay odor trail	0.006	0
Follow odor trail	0.062	0.025
Transport nest material	0.043	0
Carry dead nestmate	0.002	0
No. of acts observed	931	118
No. of behavioral categories observed	32	13
Estimated maximum no. of behavioral categories (mean \pm standard deviation)	32 \pm 1	16 \pm 3

had found what appeared to be arthropod eggs among the brood of *E. urichi* in Trinidad. Also, the Suriname colony collected *Armitermes* eggs in the laboratory (WILSON, 1962). Round eggs, apparently also arthropod in identity, were found in the nests of *E. eidmanni* by EIDMANN (1936).

The minor workers of *Erebomyrma nevermanni* are very small. In the laboratory they were also slow and clumsy compared to workers of most ant species, including *Pheidole*. Consequently, the ants did not appear to be very effective as individual predators. In two "cafeteria" experiments, I offered the following potential prey objects collected in the vicinity of the original nest site, by placing them alive and simultaneously in the foraging area of the laboratory nest: isopods, spiderlings (several families), phalangid, millipedes, geophilomorph centipede, japygid diplurans, small elateriform beetle larva, fly larvae, an adult midge, termites (including nymphs), and a homopteran nymph. Nearly all of these organisms were ignored or at most elicited mild, short-lived mandible gaping. The only exception was the beetle larva. When this insect ventured close to the brood area, 10-15 minor workers swarmed out to surround it, attempting to grip it with their legs and mandibles while it thrashed around in a typical larval defensive maneuver. Within 30 secs two majors also rushed out and repeatedly tried to seize the larva with their mandibles. One finally succeeded in gripping it at midsection and crushed it several times in succession, partially disabling it. Soon afterward the majors returned to the brood area. The minor workers continued attacking the larva and eventually dragged it to the brood pile where it was partly eaten. Approximately the same result was obtained later with a second beetle larva and a moth larva.

These results suggest that *E. nevermanni* is a predator and scavenger with only a limited amount of specificity. It is likely that the ants are most successful with small prey. If so the pattern would be similar to that determined earlier for *E. urichi*: workers in the Oropouche Cave were observed returning to their nest with a mite, an entomobryid collembolan, and two arthropod eggs. Later, in captivity, they fed readily on moths and flies that had been freshly killed for them.

Both workers and larvae of *E. nevermanni* were seen feeding directly on fragments of the insect prey. Minor workers regurgitated to each other, as well as to the major workers, queen, and larvae. Minor workers also accepted sugar water and recruited nestmates to it with newly laid odor trails. The initial feeding was followed by unusually intense bouts of regurgitation among the workers.

Foraging for new food sources was conducted exclusively by the minor workers. Many of them moved out along short trunk trails that extended from the nest into the surrounding foraging arena. The workers then fanned out to conduct individual searches. On several occasions majors were

observed to follow odor trails for 2-3 cm away from the nest, but they did engage in separate foraging trips.

Colony defense

Both minors and majors attacked insects intruding into the nest. The defending force contained a higher proportion of majors than occurred in the population as a whole. More precisely, while the major: minor ratio in the nest was 7:172 or 0.04:1.0, the major: minor ratio of adults attacking alien ants placed at the nest entrance during 10 replications was 13:88 or 0.15:1.0. The difference is significant at the 1 percent level (G-test of independence in a 2×2 contingency table). The majors were generally more effective as individuals in disabling the intruders. I also tested for specificity in response by presenting the colony with live workers of the following species of ants that could be expected to be of different degrees of threat to *Erebomyrma nevermanni* in nature: *Atta cephalotes* (little or no threat), *Pheidole* sp. (threat), *Solenopsis geminata* (threat), *Labidus praedator* (threat), *Eciton hamatum* (threat). No difference was observed in the response to the *Atta* as opposed to the other, presumably more dangerous species.

Queen retinue and defense

A distinctive feature of the *Erebomyrma nevermanni* colony was the tendency of minor workers to crowd around the queen and stand in groups on top of her body (see fig. 1). The behavior was most marked when the colony was exposed to the air or otherwise seriously disturbed. At such times some (but not all) of the major workers also drew close to the queen. In contrast, when the colony was fully covered and secure, these attendants mostly dispersed. To test my impression of this general pattern, I conducted 3 replicates of the following experiment on separate days: the numbers of minors on the body of the queen and majors within 5 mm of the queen's body were recorded at 4 intervals 5-30 mins apart; then the cover was taken off the nest, exposing the colony to the open air, and 1-2 counts were made 5 mins later; finally the cover was returned and 2 further counts made starting 5 mins afterward. In a total of 18 counts taken over the 3 days the number of minors on the queen's body when covered (with s.e.) was 1.11 ± 0.21 ; the number when exposed (4 counts) was 5.55 ± 0.50 . This difference is significant at the 1 percent level. In 18 counts the average number of majors within 5 mm was 1.80 ± 0.36 ; the number when exposed (4 counts) was 3.00 ± 0.41 . The difference is significant at the 5 percent level. (Both comparisons were evaluated by the *t*-test for differences between means).

Hence it appears that the intensification of the retinue does occur and serves at least in part to protect the queen when the colony is threatened. In order to test the latter hypothesis, I repeatedly touched the queen with

the tips of a pair of forceps while she was exposed. In each case minor workers swarmed over the forceps tips but did not persist for long. However, a majority of the majors present (as many as 4 all at once!) rushed at the forceps with their mandibles open and seized the tips with such a tight grip that they were difficult to dislodge.

Emigration

Two full-scale emigrations of the *E. nevermanni* colony were observed in the laboratory, one when the brood area was invaded by *Tapinoma melanocephalum* workers and the other following disturbances caused by my experiments. The emigrations consumed 70 and 30 mins respectively. Minor workers, some laying odor trails, began to run back and forth between the two sites. At the height of the transfer, as many as 20 percent of the minors carried pieces of brood; on a single occasion a major was seen carrying a larva. The queen did not move until more than 80-90 percent of the adult workers and brood had departed. She then traveled under her own power, accompanied by a retinue of minors, 8-10 of whom rode on her back at any given time, and a "praetorian guard" of 1-2 majors. No adult transport of any kind was observed, in accord with earlier observations on *E. urichi* in Trinidad (WILSON, 1962). The closest approach occurred when a minor worker ineffectually pulled the queen by a hair on her head, and later, when a second minor tried to grip her head.

Temporal division of labor

As shown in table II, there is a marked division of labor among minor workers according to age. Each of the differences between callows and pigmented, hence older workers is significant at the 5 percent level or better

Table II. — Temporal division of labor among *E. nevermanni* minor workers, expressed as the mean (\pm s.e.) number of workers in 5 snapshot counts for each category. The "foraging" count of the far right column is the first 10 workers seen in the foraging arena, classified as callow (very young) or more fully pigmented (older).

Tabelle II. — Altersabhängige Arbeitsteilung unter *E. nevermanni* minor Arbeiterinnen, ausgedrückt durch den Mittelwert der Anzahl von Arbeiterinnen für jede Kategorie (5 "Schnappschuss"-Zählungen). Für "Furagieren" wurden die ersten zehn Arbeiterinnen, die in der Futterarena gesehen wurden, gezählt. Callow = sehr junge, noch nicht auspigmentierte Arbeiterinnen; voll pigmentiert = ältere Arbeiterinnen.

Classification	On top of brood	Within 1 cm of brood but not on top	On top of queen	Foraging
Callows	8.40 \pm 1.91	1.80 \pm 0.37	0	0
Fully pigmented	3.60 \pm 0.75	16.60 \pm 1.17	7.20 \pm 0.49	10 \pm 0

(*t*-test for difference between means). The pattern is of the kind most commonly found in ants, with the younger workers gravitating toward the brood and the older workers more often foraging. Of special interest is the complete prevalence of older workers in the queen's retinue, a result consistent with the defensive function described earlier.

Elasticity of major worker retinue

In earlier studies I found that the major workers of *Pheidole* expand their behavioral repertoires by a factor of several times and perform as many as 40X more acts of social behavior per unit time when the major: minor ratio is raised to 1:1 or more, in other words when most of the minor worker force is removed (WILSON, 1984). As a consequence, the majors serve as an emergency stand-by caste, able to take over most of the functions of the minors when required. Furthermore, they are able to raise the brood to maturity and replenish the supply of minor workers.

Do *Erebomyrma* majors show a similar elasticity? In an experiment like those performed on *Pheidole*, I recorded the repertoire of majors in the original colony, then again after all the minor workers had been removed, and finally after the minor workers had been restored. The results, given in table III, closely approach those obtained in *Pheidole*. The repertoire size increased 3-5X and the rate of activity rose 10X or more. A substantial new attention paid the brood suggests that majors alone might be able to rear the immature stages to maturity, hence hold the colony together until a new crop of minor workers appears. It is also notable that the rate of self-grooming, a non-social behavior, was elevated many times, as in *Pheidole*. Of equal importance, the enhancement of behavior appeared and disappeared in less than two hours after the minors had been shifted.

Majors as a food-storage caste

As illustrated in figure 1, the abdomens of the majors are somewhat larger relative to their alitrunks than is the case for the minors. That trait taken by itself appears inconsistent in a purely fighting caste. After the La Selva colony was fed abundantly and ad libitum, the abdomens of all the majors (but not those of most of the minors) swelled conspicuously to a semi-replete condition. This state was maintained thereafter, indicating that the majors can function as living food reservoirs, although the direction of food flow was not ascertained during this study. A similar differential in abdomen size and propensity to become semi-repletes occurs in some species of *Oligomyrma* and *Pheidole*.

Table III. — The repertory of *E. nevermanni* major workers in the presence of the full complement of minor workers (A), starting 90 mins after the complete removal of all the minor workers (B), and starting 90 mins after the restoration of the minor workers (C). The numbers are the number of acts observed during a one-hour period.

Tabelle III. — Das Verhaltensrepertoire der *E. nevermanni* major Arbeiterinnen, in Anwesenheit der vollen Anzahl der minor Arbeiterinnen (A), 90 Minuten nach Entfernen aller minor Arbeiterinnen (B), 90 Minuten nach der Wiederherstellung der vollständigen Kolonie (C). Anzahl der Verhaltensakte die während 1 Stunde beobachtet wurden.

Behavioral category	A	B	C
Self-grooming	10	70	12
Allogrooming of majors	0	2	0
Queen retinue	0	3	0
Lick eggs	0	1	2
Manipulate eggs	0	2	0
Carry eggs	0	2	0
Lick larvae	0	55	0
Manipulate larvae	0	21	0
Carry larvae	0	11	0
Lick pupae	1	4	2
Manipulate pupae	0	8	2
Carry pupae	0	4	0
Regurgitate with minors	2	0	2
Forage	0	3	0
Defend nest	0	4	0
No. of behavioral categories	3	14	5
No. of behavioral acts	13	190	20

DISCUSSION

The division of labor of *Erebomyrma nevermanni* proves to be closely similar to that of *Pheidole*. The majors have a limited repertory that nevertheless contributes to a triple role within the colony: subduing difficult prey, colony defense, and food storage. The pattern of elasticity, by which majors expand their repertory and take over from the minors when the latter are reduced in numbers or eliminated, is the same. The similarities are all the more remarkable since they are probably due to evolutionary convergence. Because the Pheidologetini and Pheidolini separated during early Tertiary times, evidently prior to the origin of the major caste, the caste-specific traits of their majors can be assumed to have evolved independently.

This study has revealed at least four notable features in the behavior of *Erebomyrma nevermanni* not directly related to caste, namely defensive queen retinues, the use of trunk trails during foraging, the collection of arthropod eggs, and the absence of adult transport during colony emigration.

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