

AN UNUSUALLY BROAD BEHAVIORAL REPERTORY FOR
A MAJOR WORKER IN A DIMORPHIC ANT SPECIES:
PHEIDOLE MORRISI (HYMENOPTERA, FORMICIDAE)*

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INTRODUCTION

The vast majority of species in the extremely diverse ant genus *Pheidole* exhibit complete dimorphism in the worker caste. That is, the workers are divided into two clearly distinguishable morphological classes: the small but numerous “minor” or “minor caste”, and the larger, less numerous “majors” or “major caste”. This trait makes species of *Pheidole* especially attractive for the comparative study of caste polyethism, the division of labor between morphological castes in social insect colonies.

Wilson (1984) documented variation in the behavioral repertoires of minors and majors across ten species of *Pheidole* collected from different localities in North America, South America, Africa, and Asia. The repertory of the minor caste varied little between species, containing an average of about thirty types of acts (Range = 25 – 35, Mean = 30.4, SD = 3.27). In all species studied, minors took care of the day to day tasks of the colony, including brood care, foraging, and nest maintenance. In contrast, the repertory size of *Pheidole* majors showed great variation between species (Range = 4 – 19, Mean = 10.4, SD = 5.25). Arranged along an “ethocline”, the majors of the ten different species showed a trend towards specialization on one of the following roles: seed milling, guarding food and dismembering prey, or guarding the nest entrance while also serving as repletes for food storage. These findings were consistent with the view of minors as “generalists” and majors as “specialists” in traditional ergonomic theory (Oster and Wilson, 1978).

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This study reports the richest major repertory thus far discovered in the ant genus *Pheidole*. *Pheidole morrisi* Forel, the species in which it occurs, is native to the eastern and central United States, where it occurs along the southern coastal plain from New York to Texas, and north to Ohio and Illinois. Throughout its broad geographic range, it is found exclusively in sandy soils and open habitats, particularly in pine barrens and other open pine woodlands. Nests are marked by irregular craters or low mounds, and mature colonies can contain up to ten thousand individuals.

MATERIALS AND METHODS

A colony of *Pheidole morrisi*, collected near Gainesville, Florida by James Trager in June 1988, was transferred to an artificial nest consisting of a petri dish (14 cm diameter, 1.5 cm height) with a thick layer of plaster of Paris on the floor to hold moisture, and a hole in one side to serve as a nest entrance. This dish was set in a large plastic tub (L = 75 cm, W = 15 cm, H = 13.5 cm), which was coated with Fluon (Northeast Chemical Co., Inc., Woonsocket, RI) on the sides to prevent the ants from escaping. The colony was fed an artificial ant diet (Bhatkar and Whitcomb, 1970), freshly killed cockroaches (*Nauphoeta cinerea*) and mealworms (*Tenebrio spp.*) every two days. A supply of water was always present in the arena in the form of moistened cotton.

Behavioral observations were made with a Wild swing arm microscope (6× - 30×) and a Zeiss Technoscope (6× - 40×). Over a period of ten days, I conducted fourteen observation sessions, each an hour long. These sessions were spread at irregular intervals between 9 a.m. and two hours past midnight. In each session, the colony was scanned and as many behavioral acts as possible were noted for both castes. From these data, behavioral repertoires were compiled for the two castes, and for each caste, the fraction of acts observed falling into a particular category was computed. Estimated true repertory size was obtained by fitting the data to a lognormal Poisson distribution according to the method of Fagen and Goldman (1977).

At the end of the study, the colony consisted of approximately 400 minors, 170 majors, a queen, and brood in all stages of development, including about 30 very large larvae destined to become males.

RESULTS

The ethogram of *Pheidole morrisi* is presented in Table 1. The size of the minor caste's repertory is similar to that of other *Pheidole* minors studied. In contrast, the major caste's repertory falls well above the bounds of other species so far reported. Of the 29 types of behaviors observed for the minor caste, the major performs 25, including brood care, trophallaxis, foraging, and allogrooming of all other castes. Inspection of Table 1 reveals that two of the four acts not performed by majors, assisting eclosion of pupa to adult and regurgitating with the queen, were only rarely observed in the minor caste, suggesting that more hours of observation might reveal the presence of these behaviors in the major's repertory.

The category "lay odor trail" was also rarely observed for minors, but this was because observations were not taken immediately after feeding (when trail laying is most common), not because the minors were deficient in this behavior. During normal recruitment to food, minors of *Pheidole* species lay pheromone trails from their poison gland by dragging the tip of the gaster on the ground while running between the food source and the nest. The trail pheromone releases trail following behavior in other minors and majors, and provides an orientation cue (Hölldobler and Möglich, 1980). No case of trail laying behavior has been documented in the major caste of this or any other *Pheidole* species, and the contents of majors' poison glands are weak or ineffective in eliciting trail following. *Pheidole morrisi* majors, however, exhibit a unique behavior that closely resembles trail laying. If food is presented to a hungry colony, and only majors are allowed to find it, they sometimes return directly to the nest showing gaster-dragging behavior that appears very similar to that observed in trail-laying minor workers. Curiously, this does not lead to recruitment. This behavior, at present, has not been observed in the majors of any other *Pheidole* species. For example, *P. embolopyx* majors, which have a large behavioral repertory, showed no trail laying behavior when a colony was kept hungry and only majors were allowed to find food (Wilson and Hölldobler, 1985). In fact, as far as is known, *Pheidole* majors do not produce the trail pheromone: a physiological study of *Pheidole pallidula* by Ali *et. al.* (1988) revealed that while minors' poison glands contain compounds which are active in trail recruitment, majors' poison glands contain no detectable amount of trail substance. Hence the

Table 1: Ethogram of the ant *Pheidole morrisi* in an undisturbed laboratory colony. The number given for each behavior is the fraction devoted to the behavior among the total number of acts observed in a given caste.

| <i>Behavior</i> | <i>Minor caste</i> | <i>Major caste</i> |
|--|--------------------|--------------------|
| Self-grooming | 0.0912 | 0.2303 |
| Allogroom adult: | | |
| Minor worker | 0.1175 | 0.0773 |
| Major worker | 0.0456 | 0.0515 |
| Queen | 0.0058 | 0.0030 |
| Brood care: | | |
| Carry or manipulate egg | 0.0294 | 0.0106 |
| Lick egg | 0.0312 | 0.0061 |
| Carry or manipulate larva | 0.0618 | 0.0106 |
| Lick larva | 0.2017 | 0.1561 |
| Feed larva solids | 0.0049 | 0.0030 |
| Assist ecdysis to pupa | 0.0023 | 0.0015 |
| Carry or manipulate pupa | 0.0112 | 0.0136 |
| Lick pupa | 0.0259 | 0.0136 |
| Assist eclosion of adult | 0.0043 | 0 |
| Regurgitate with | | |
| Larva | 0.0398 | 0.0258 |
| Minor | 0.0320 | 0.0485 |
| Major | 0.0217 | 0.0364 |
| Queen | 0.0031 | 0 |
| Forage | 0.0876 | 0.0227 |
| Feed outside nest | 0.0124 | 0.0152 |
| Lay odor trail | 0.0017 | 0 |
| Carry food particles | 0.0061 | 0.0076 |
| Feed inside nest | 0.0805 | 0.1121 |
| Carry dead adult | 0.0103 | 0.0030 |
| Feed on dead adult | 0.0211 | 0.0152 |
| Feed on larva | 0.0211 | 0 |
| Handle nest material | 0.0167 | 0.0106 |
| Antennal tipping | 0.0029 | 0.0106 |
| Dispose of infrabuccal pellet | 0.0006 | 0.0030 |
| Guard nest entrance | 0.0026 | 0.0545 |
| Observed repertory size | 29 | 25 |
| Estimated true repertory size \pm S.E. | 29 ± 4 | 26 ± 2 |
| Number of separate acts observed | 3464 | 660 |

retention of what might be a vestigial trail laying behavior may be further evidence for the unusual behavioral flexibility of the *P. morrisi* major.

Table 1 indicates a very broad overlap in the behaviors of the minors and majors of *P. morrisi*, but this should not mask the fact that significant differences exist in the behavior of the two castes. For example, summing the values of the behaviors under the general category of "Brood care" reveals that minors invest more in this activity than do majors. Well over one third (0.379) of total minor acts observed fall into this category, while only one fifth (0.215) of the major acts recorded were directed towards the brood (it is important to keep the distinction between a behavioral act and a *type* of behavior clear in one's mind. Three instances of a major self grooming plus two instances of a minor licking a larva total to five behavioral acts, but only two types of acts). Another important difference exists in the frequency with which foraging is observed in

Table 2: The number of types of behaviors observed for both worker castes in eleven species of *Pheidole*. Data for *P. morrisi* from this study; for *P. hortensis* from Calabi et. al. (1983); for other species from Wilson (1984 and unpublished data). Abbreviations given are used in figures later in the text. For an example of behavioral categories, see Table 1.

| <i>Pheidole</i> species | Minor caste | Major caste |
|--------------------------------|-------------|-------------|
| <i>morrise</i> (mor) | 29 | 25 |
| <i>embolopyx</i> (emb) | 29 | 19 |
| <i>minutula</i> (min) | 35 | 18 |
| <i>pubiventris</i> (pub) | 35 | 14 |
| <i>sp.indet.</i> (spA) | 32 | 13 |
| <i>mendicula</i> (mend) | 31 | 8 |
| <i>megacephala</i> (meg) | 30 | 8 |
| <i>dentata</i> (dent) | 26 | 8 |
| <i>distorta</i> (dist) | 31 | 6 |
| <i>hortensis</i> (hort) | 25 | 6 |
| <i>guilelmimuelleri</i> (guil) | 30 | 4 |
| Range of repertory size | 25-35 | 4-25 |
| Mean repertory size | 30.3 | 11.7 |
| SD of repertory size | 3.1 | 6.7 |

the two castes. Although the majors *do* forage under laboratory conditions, they do not do so nearly as commonly as the minors do, relative to the frequency of their occurrence in the colony.

In addition, the two castes also differed in their level of activity. In numerous samples at various points in the nest, the ratio of inactive to active individuals was higher for majors than for minors (G-test for independence, $G = 236$, $p < 0.001$).

DISCUSSION

Pheidole morrisi majors mark a new extreme on the "ethocline" of *Pheidole* major caste behavioral repertory sizes compiled by Wilson (1984) (see Table 2). What might account for the remarkable flexibility of the major caste of *P. morrisi*? At present, we have no evidence that the characteristic habitat of *P. morrisi* selects in some way for large major repertories. *P. dentata*, which is often sympatric with *P. morrisi* in parts of the southeastern USA, has a major repertory size of only eight behaviors.

Oster and Wilson (1978) predict that major behavioral repertory size in dimorphic ant species should be correlated with their degree of morphological specialization. A simple way to assess degree of morphological specialization is to compare the ratio of minor body size to major body size. Data comparing this ratio to major repertory size in eleven species of *Pheidole* are summarized in Figure 1. As can be seen, the result of this comparison does not support the proposed hypothesis. In fact, the eleven species pictured are remarkable for the degree of similarity they show in relative size of the two worker castes, despite a great range in major repertory size. Similarly, no significant relation is found between absolute size of the majors and their repertory size.

As first pointed out by Wilson (1984), the repertory size of majors is significantly related to their fractional representation in the colony. *P. morrisi* fits this trend very well (Figure 2). The relation supports a prediction of ergonomic theory that increased behavioral specialization in a caste, indicated by reduction in repertory size, will be accompanied by greater efficiency in the remaining behaviors and thus a smaller representation in the worker force (Oster and Wilson 1978).

There are two reasons to interpret this correlation with caution. First, because different species of *Pheidole* are linked phylogeneti-

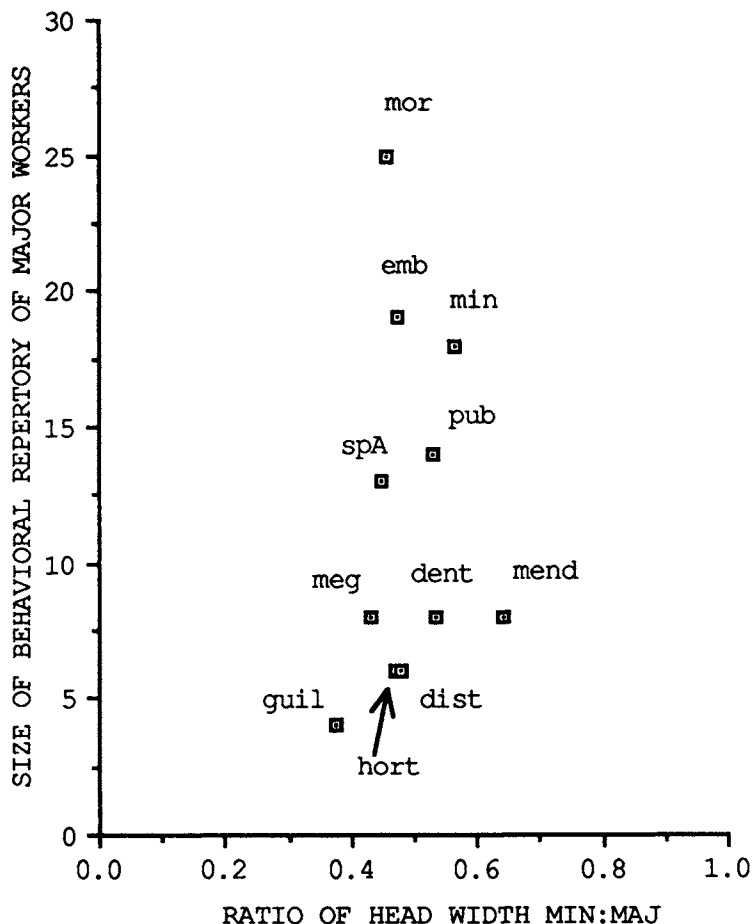


Figure 1. No significant relation is found between the size of the major repertory and the relative size of the minor to the major caste (as measured by head width) in 11 species of *Pheidole*. Points shown are derived from five measurements of each caste in each species. Data for *P. morrisoni* are from this study; data for other species are from Wilson (1984 and unpublished data). For abbreviation conventions, see Table 2.

cally, it is possible that species clustered together on the graph, such as *distorta*, *megacephala*, *mendicula*, *dentata*, and *hortensis*, or *embolopyx*, *minutula*, and *pubiventris*, do not represent truly independent points in a statistical sense, but are simply together because of descent from a recent common ancestor (for a general discussion

of this problem, see Felsenstein 1985). E. O. Wilson (personal communication) believes that phylogenetic "contagion" can be discounted in this case, because the first cluster of five species represents five distinct species groups among them, and the second cluster of these species represents two species groups.

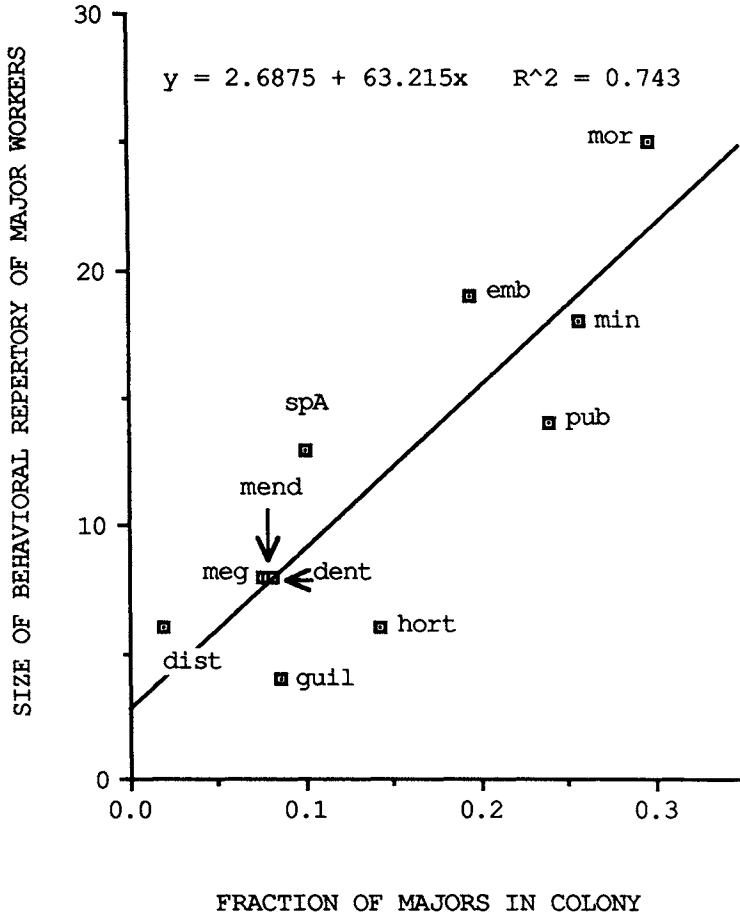


Figure 2. A very significant relation is found between the size of the major behavioral repertory and the fractional representation of majors in a colony in 11 species of *Pheidole*. Data for *P. morrisi* are from this study; data for other species are from Wilson (1984 and unpublished). For abbreviation conventions, see Table 2.

A second reason for caution has to do with variation in caste ratios which occur in nature. It is normal for the fraction of majors to vary between colonies in the wild. Oster and Wilson (1978) reported that in *P. dentata* colonies examined in Florida, the proportion of soldiers could range from 3% to over 50%, though most colonies fell in the range of 3% to 12%. Bhatkar and Whitcomb (undated, unpublished manuscript) report a major to minor ratio of 1 to 16 ($=0.0625$) for *P. morrisi* collected in the Tallahassee Red Hills Region in Florida. If consistent with the correlation shown in Figure 2, the majors of Bhatkar and Whitcomb's colony or colonies should show a repertory size of about 8 behaviors. While finding such a small repertory in *P. morrisi* majors seems intuitively unlikely, in truth we do not yet know how major repertory size varies in response to changing caste ratios during normal colony ontogeny within *Pheidole* species. In experimental situations where caste ratios are changed dramatically by the investigator, *Pheidole* majors *do* show programmed behavioral elasticity in the size of their repertory and in their overall rate of activity (Wilson, 1984). For example, when an artificial subcolony of *P. guilelmimuelleri* was established in which the worker force was entirely comprised of majors, the queen, and brood, the observed repertory size of this caste increased from 4 to 18 behaviors in less than one hour, and the rate of individual activity increased by a factor of 10. This behavioral elasticity allowed the majors to compensate for the missing minors by taking their place in brood care and other activities. Wilson interpreted this result as evidence for the role of majors as an emergency standby caste which could carry a colony through a period of severe minor worker depletion due to starvation, queen infertility, or differential mortality during foraging. It is also possible that the observed phenomenon is an extreme version of the behavioral elasticity that may be demonstrated by majors during normal colony growth, as caste ratios change more gradually. That caste ratio can change significantly during colony ontogeny was recently demonstrated by Gibson (1989), who found that the mean proportion of soldiers in colonies of *Camponotus noveboracensis* increased from 8.9% in incipient colonies (less than 150 workers) to 64% in mature colonies (more than 2,000 workers). A sequential ethogram study of *P. morrisi*, whereby the caste ratio and the behavioral catalogues of the major workers are determined at set intervals

during colony growth, would reveal if caste ratio is in some manner the determinant of major repertory size. To answer the broader question of why majors of different species of *Pheidole* differ in their degree of specialization, comparative ecological field studies are needed.

SUMMARY

This study reports the richest behavioral repertory thus far discovered for major workers in the diverse ant genus *Pheidole*. Previous studies of 10 dimorphic species of *Pheidole* (Wilson, 1984) revealed that minor workers vary little in the size of their behavioral repertory (averaging 30 types of acts), while majors show dramatic differences in repertory size between species (ranging from 4 to 19 types of acts). Majors of *Pheidole morrиси* exhibit 25 types of behaviors, only four fewer than the total number of behaviors observed for the minor caste. This unusually large repertory cannot be linked to an unusually low degree of morphological specialization in the major caste of *P. morrиси*. It is consistent, however, with a trend found by Wilson (1984) which links major repertory size in different species of *Pheidole* to the fraction of majors found in the colony.

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