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Between-caste aversion as a basis for division of labor in the ant *Pheidole pubiventris* (Hymenoptera: Formicidae)

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Summary. When deprived of minor workers under experimental conditions, major workers of the ant *Pheidole pubiventris* dramatically increase their repertory and rate of activity, and the change is due in good part to the greater attention they pay the brood. When minor workers are reinstated in appropriate numbers, the majors reduce their attention to the immature stages to the ordinary, low levels. Their response consists of the active avoidance of minors while in the vicinity of the immature stages. However, majors do not turn from other majors near the brood as much as they do from the minors, and they do not avoid minors at all while in other parts of the nest. In addition, minors do not avoid either minors or majors anywhere in the nest. The result is a striking division of labor with reference to brood care.

Introduction

Major workers of *Pheidole*, which comprise from about 2 to 30% of the adult worker force according to species, display a very limited behavioral repertory and a low rate of activity in comparison with the minor workers. But when the proportion of majors is increased to 50% or more, both the repertory size and rate of activity increase dramatically, almost to the same levels as those of the minors. When the original proportion is restored, the repertory and rate drop to their original levels. Both transitions, that is, from low to high and high to low, occur within an hour or less. Thus the majors serve as an emergency stand-by caste (Wilson 1984).

This striking pattern provides an opportunity to examine the basis of division of labor between the two castes. When the percentage of majors is set between 60 and 80%, both minor and major workers are relatively active, and they are both numerous enough for frequent interactions to occur. During earlier studies of three species (*guilelmimuelleri, megacephala, pubiventris*) I noticed that one of the changes occurring in the majors as minors are restored is the early abandonment of the brood (eggs, larvae, pupae). Moreover, the desertion appeared to be based at least in part on an active avoidance of minors by majors when members of the two castes meet on or close to the brood pile. Accordingly, I extended the study of *P. pubiventris* in a way that allowed me to measure the magnitude of the avoidance in both castes and its dependence on caste ratios and location within the nest.

Methods

A colony of *P. pubiventris* collected near Manaus, Brazil, was cultured until it reached mature size, during which virgin queens were being steadily produced. The techniques of culturing and observation were the same as reported earlier (Wilson 1984). Subcultures consisted of a dealate queen, 40 workers varying in major/minor ratio, and a quantity of brood proportionate to that in the source colony (10 larvae of various sizes, 5 worker and queen pupae, 5 eggs).

Most of the subcultures were set up with either 25 or 75% major workers, in order to allow a comparison of behavior under these two conditions. At the former proportion (25%) the majors remained largely displaced from the brood piles and their behavioral rates were low. At 75% the majors were active on the brood pile and frequently contacted minor workers there.

As the adults approached each other inside the nest chambers, a record was made of the location of the encounter (on the brood or <1 mm from the nearest brood piece versus >1 mm from the brood), the position of the two workers at the moment of antennal contact by one or both, and the response of the ant making the antennal contact. Responses were classified according to one or the other of two categories: "turn away," in which the ant making the contact took at least one turn of 90 degrees or more before travelling more than four body lengths; and "stay" or "proceed," the latter response

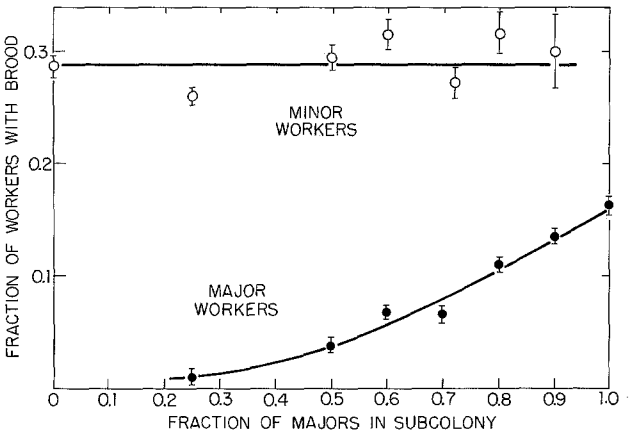

Fig. 1. The fraction of the total *Pheidole pubiventris* minor worker force and the fraction of the total major worker force on or within 1 mm of the brood are given as functions of the percentage of the workers composed of majors. The difference in the slopes of the two curves is due to the avoidance of minors by majors

being a trajectory of four body lengths with turns of less than 90%. The differences in proportions of responses were evaluated by the χ^2-test with two classes.

Table 1. Numbers of major or minor workers, respectively, giving one or the other of two responses (stay or proceed vs turn away) to minor or major workers, either near or apart from the brood. Significant inter-row or inter-column differences are indicated as $*(P<0.05)$ and $**(P<0.01)$

Fraction of majors in colony	Near brood		Apart from brood
	Stay or proceed vs turn away		Stay or proceed vs turn away
A. Majors encountering minors			
0.25	(7 vs 35)	–**–	(52 vs 3)
0.75	(54 vs 67)	–**–	(63 vs 8)
B. Minors encountering majors			
0.25	(25 vs 0)		(39 vs 3)
0.75	(100 vs 8)		(64 vs 7)
C. Majors encountering majors			
0.25	(insufficient data)		(28 vs 4)
0.75	(49 vs 14)	–*–	(141 vs 14)
D. Minors encountering minors			
0.25	(90 vs 3)		(16 vs 0)
0.75	(100 vs 11)		(49 vs 1)

Results

As shown in Fig. 1, the percentage of minor workers (out of the total minor worker force) located on the brood remained constant as the minor/major ratio was varied. The minor worker curve is $y=-0.055\ (\pm 1.182)+2.122(\pm 4.225)x$, with the slope not deviating significantly from zero. In contrast, the percentage of major workers falls off rapidly as minor workers are added: the curve for the range of abscissal values 0.5–1.0 fitted to a straight line is $y=0.381(\pm 0.039)+3.852(\pm 0.371)x$; the probability that the slope is zero is less than 0.001.

The data in Table 1 show that the difference in location between the two castes is due to the aversion of majors to minors on or close to the brood pile. Moreover, the response is specific to that location. The principal results leading to this conclusion are as follows:

(1) Majors turn from minors more at the brood pile than away from it.

(2) Majors also turn more from other majors when on or near the brood, but this aversion is less than that toward minors. (This relative aversion disappears when the adult population consists entirely of majors – as revealed in separate tests not displayed in Table 1, when 147 majors stayed or proceeded, while only 16 turned away.) Also, majors do not avoid other majors when away from the brood.

(3) Minors do not display the above pattern of aversion toward either caste at either location.

Discussion

It is generally assumed that much of the division of labor in social insects is based on caste differences in attraction to stimuli and in thresholds of response to the stimuli, although supporting evidence is surprisingly scarce in the literature (see for example Wilson 1978). The present study shows that division of labor can also be based on caste-specific aversions. The question then arises: is the mechanism of the kind documented in *Pheidole pubiventris* exceptional in occurrence, perhaps linked to the unusual behavioral flexibility of the major caste? The ability of the majors to serve as emergency stand-by auxiliaries depends on some kind of rapid recognition of castes as well as on their location in the nest, and hence the tendency to adjust the entire pattern of response after receipt of the correct stimuli. A simple aversion is one mechanism to achieve this result, and it will be interesting to learn whether it occurs in other categories of division of labor, in other species of social insects, under similar circumstances.

The mechanism of recognition was not established experimentally during this study, but it is almost certainly olfactory rather than tactile in na-

ture. The majors showed the clearest responses after making direct antennal contact with the minors or at least coming within less than a millimeter of them. On the other hand they did not play the antennae over the bodies of the nestmates sufficiently well to obtain clues concerning distinctive shapes of major as opposed to minor workers.

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