Caste Differences in Behavioral Thresholds as a Basis for Polyethism During Food Recruitment in the Ant, *Pheidole pallidula* (Nyl.) (Hymenoptera: Myrmicinae)

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During foraging, societies of the polymorphic ant, Pheidole pallidula, *display several collective patterns which differ in the ratio of recruited majors. The intensity of behavioral stimuli required to induce this majors' recruitment is determined by studying trail-laying and tactile invitations for the following two food recruitments: (1) the slow and weak recruitment of minors, without majors, to a pile of small, individually retrievable fruit flies and (2) the massive recruitment of both minors and majors to large, unretrievable cockroaches. The selective mobilization of majors only to large prey such as cockroaches is due both to their preferential invitation and to their higher behavioral threshold of response to recruiting stimuli. The experimental evidence of caste behavioral thresholds allow us to reconsider behavioral elasticity in the major caste as well as principles of division of labor in ant societies.*

INTRODUCTION

Among social insects, individuals of a given age or size class form castes which fulfill specialized tasks for sustained periods of time. Generally, the numerically dominant physical caste is the one with the largest behavioral repertoire. Indeed,

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medias of *Formica perpilosa* (Brandao, 1978) or minors of *Solenopsis geminata*, *S.invicta* (Wilson, 1978), *Camponotus sericeiventris* (Busher *et al.*, 1985), and *Orectognathus versicolor* (Carlin, 1981) belong to the most numerous caste of these polymorphic species and perform the majority of the tasks in the society. Similarly, in strictly dimorphic species [e.g., *Pheidole* spp. (Wilson, 1976a, 1984; Calabi *et al.*, 1984; Wilson and Hölldobler, 1985), *Erebomyrma nevermanni* (Wilson, 1986), *Oligomyrmex overbecki* (Moffett, 1986), and *Zacryptocerus varians* (Wilson, 1976b)], minors which belong to the numerically dominant caste display the largest behavioral repertoire. Tasks done by minors and majors are slightly overlapping. In *Ph. hortensis*, they do not overlap at all, apart from trophallaxis (Calabi *et al.*, 1984). According to these observations, majors of dimorphic *Pheidole* species appear to be behaviorally and morphologically specialized to perform few tasks during their entire lifetime, ranging from 19 different types of acts for *Ph. embolopyx* (Wilson and Hölldobler, 1985) to 4 for *Ph. guilelmimuelleri* (Wilson, 1984).

However, the behavioral repertoire of majors possesses much more extended potentialities and caste distinctions are blurred when the following two factors are taken into account: (1) the underestimated size of majors' behavioral repertoire due to the sampling method and (2) the behavioral elasticity of majors.

(1) Underestimation of the behavioral potential of majors is due partly to intrinsic biases in the traditional method used. All the behavioral observations were done within an undisturbed nest and in a small foraging arena, in a limited number of contexts. Under such conditions, majors may not have an opportunity to express behaviors such as defensive ones. Moreover, all these repertoire studies are based on sampling the behavior of the two subcastes a number of times proportional to their relative number in the society. Therefore, fewer observations were carried out on majors than on minors. By equalizing the number of observations on minors and majors (50% of the total number of observations made for each caste), the apparent behavioral repertoire of *Ph. pallidula* majors increases from 18 to 33 different acts (Aarab *et al.*, 1988). By taking into account these two biases, the behavioral repertoire of majors from polymorphic species is likely to be larger, with "caste-tasks" associations becoming less distinct.

(2) Majors of *Pheidole* species are known to carry out defensive behavior, food storage, or seed crushing (see, e.g., Buckingham, 1911; Goetsch, 1953). Nevertheless, if the proportion of majors in a *Pheidole* spp. society is artificially increased, they will perform tasks "atypical" of their physical caste. This unexpected behavioral elasticity results in their participation in "typical" minors' tasks such as brood care (Passera, 1974; Wilson, 1984, 1985a). To explain this behavioral elasticity, it is tempting to consider that polyethism may depend on differences between castes in their threshold levels of behavioral response to

stimuli. This hypothesis was suggested by previous experiments on *Pheidole* species, stressing the majors' behavioral elasticity in "abnormal" all-soldier colonies (Wilson, 1984, 1985a).

In the present paper, several experiments on "normal" societies of the dimorphic European ant, *Ph. pallidula*, stress threshold mechanisms accounting for caste polyethism during foraging. We compare recruitment to three different food sources, selected according to their different levels of majors' participation. Intensities of trail laying and invitation behavior are quantified and thresholds of behavioral responses to tactile and chemical invitations are compared for minors and majors.

MATERIALS AND METHODS

Pheidole pallidula is widespread in all Mediterranean countries. Their nests are common in arid areas, on sunny slopes with low vegetation density. They contain up to 6000 individuals, majors representing 2 to 15% of the whole population. Tested societies (1 queen, 2600–3000 minors, 70–100 majors) were collected in the "Pyrénées Orientales" department (Southwest of France) and kept in the laboratory in plaster nests (20 × 20 × 2.5 cm) regularly moistened with distilled water. They were supplied with brown sugar solution (1 *M*), water, and dead cockroaches (*Periplaneta americana*). Artificial lighting was timed on a 12:12-h light:dark regime and temperature was kept constant at 22 ± 1°C.

Each society was connected by a metallic bridge to a large foraging area (80 × 80 cm) covered with fine white sand. The size of the foraging area corresponds with distances followed by *Ph. pallidula* foragers on natural trails in their biotope (Detrain, 1990). Field studies show that *Ph. pallidula* is an omnivorous ant which retrieves prey ranging from very small insects such as Diptera larvae to larger ones such as imagos of Coleoptera (Detrain, 1990). This requires the ant colony to use different foraging strategies: they vary from individual foraging of low-weight prey to intense mobilization of recruited nestmates on trails leading to large items, more scarcely found in nature. In the laboratory, after 3 days of starvation, a food source was put on this area, 60 cm from the metallic bridge. Seven days always elapsed between two successive recruitments. The source consists of a food-covered glass plate (3-cm diameter).

Three food sources were tested:

(1) a pile of dead flies (*Drosophila melanogaster*) offering approximately 100 items, regularly getting in a fresh supply to avoid food depletion during the whole experiment;

   (2) four dead cockroaches (*Periplaneta americana*) transversally cut in
       two pieces; and
   (3) four whole dead cockroaches.

For an equal size of the source, the amount and the characteristics of the avail-
able food are different. Our choice of these three kinds of food sources aimed
at stressing the differences in *Ph. pallidula* recruitment and majors' participa-
tion in relation to (a) prey's amount and retrievability from the foraging area
(comparison of individually retrievable small flies versus unretrievable large
cockroaches) and (b) requirement for prey cutting by a specialized caste of
majors (comparison of whole versus cut dead cockroaches).

Dynamics of Food Recruitment

   Ph. pallidula food recruitment was studied on both colony and individual
levels. In our global level of analysis, we drew dynamic curves of recruitment
and studied the spatial distributions of ants in the foraging area. Kinetics of
recruitment of minors and majors were established by counting workers as they
crossed the metallic bridge linking the nest to the foraging area. To estimate
these flows, ants crossing the bridge were monitored with a video recorder cou-
pled with a time–date generator. Patterns of spatial distributions of minor for-
agers were obtained by taking photographs (Film AGFA Ortho 25 ASA) of the
80 × 80-cm area, every 3 min. Two recruitment events were studied for the
fly food source, three for entire cockroaches, and three for cut cockroaches.

Intensities of Chemical and Tactile Invitations During Exploitation of the Different Food Items

   Trails laid by foragers are responsible for chemical invitation of nestmates
in this mass recruiting ant species (Detrain, 1989). To estimate the intensity of
chemical invitation, ants walking on the bridge either to or from the nest were
observed with a magnifying lens (5×). This allowed us to note when the work-
ers' gaster touched the substrate, assuming that the ants laid chemical marks
each time their abdomen met the surface of the bridge. Data were collected
during the first 15 min of recruitment when the number of ants crossing the
bridge was low enough to allow a precise observation of each of them. They
were classified into trail-laying and non-trail-laying ants. These percentages
were compared for the different food items studied.

   For each kind of food recruitment, we observed ants coming back from
the food source. Their tactile invitation behavior at the nest entrance was
recorded by a high-motion video camera (magnification, 5 times). Tactile con-
tacts between the recruiter and the nestmates were classified into the following
four categories.

(1) Antennations lasting less than 1 s. Ants coming back from the food source quietly antennate every encountered nestmate. These antennations apparently do not differ from interindividual antennal explorations observed independently of any recruitment context.

(2) As in 1 but lasting more than 1 s. These antennations are sometimes followed by trophallaxis from the recruiting ant.

(3) Accelerated antennal beatings given by fast-running recruiters and lasting less than 1 s. These fast-running recruiters were distinguishable on video recordings by their fuzzy image even when they were video taped at 25 frames/s.

(4) As in 3 but lasting more than 1 s.

The respective proportions of these four tactile contacts were quantified during the different recruitments to each exploited food source.

Differential Response of Minors and Majors to Tactile Invitations

Responses to the four types of tactile invitation described above were quantified for both minors and majors present at the nest entrance. After each tactile invitation, we counted the exits of stimulated minors or majors. As the efficiency of tactile invitations decreases with time during recruitment (Szlep-Fessel, 1970), we paid attention on our video recordings only to tactile contacts made during the growth phase of recruitment.

Differential Response of Minors and Majors to Chemical Invitations

The poison gland secretion, which is the source of *Ph. pallidula* trail pheromone (Ali *et al.*, 1988), is able to induce the exit of workers from the nest. Recruiting effects of the trail pheromone were estimated for six increasing concentrations of poison gland secretion scaling from 10^{-3} to 1 poison gland equivalent. These different concentrations were obtained by successive dilutions of a stock extract of 12 poison glands in 300 μl of distilled hexane. At the nest entrance, these extracts were presented to *Ph. pallidula* workers by placing 25 μl of the appropriate dilution on a square of filter paper (0.25 cm^2). These experiments were compared to a control test where only 25 μl of hexane was deposited on the filter paper. Successive experiments were always carried out after an elapsed time of 30 min and following an increasing order of tested concentrations. Behaviors of ants present at the nest entrance were recorded on a video tape. For each concentration, we counted exits of minors and majors. At the beginning of our experiments, the number of minors recorded by video at the nest entrance ranged from 18 to 24, and that of majors from 3 to 4. There was no statistically significant change in these numbers of minors and majors throughout the duration of each test, even at min 5 as well as between the

different tests. Therefore, for a given concentration and for each minute, we were able to pool data obtained during the five experiments.

RESULTS

Dynamics of Food Recruitment

Recruitment dynamics were found to be remarkably constant for a particular food source. Therefore, as a central frame for the discussion of our results, we describe in detail only one typical recruitment curve for each food item studied (Figs. 1a–c). To complete these data, the main parameters obtained for all the observed recruitment curves are presented in Table I.

Before food introduction, the foraging area was explored almost exclusively by the minor caste (Figs. 1a–c). In only one case were two majors recorded on this area, representing 1.1% of the total number of exploring ants. In all the experiments presented in Table I, the mean rates of increase in ants on the foraging area (ANOVA, $F = 43.8$, $P < 0.001$) and the total numbers of recruited ants (ANOVA, $F = 15.3$, $P < 0.001$) were related both the kind of exploited food and the caste of foragers. Interestingly, for a similar exploratory level of about 100–150 explorers, dynamics of recruitment strongly differed when comparing exploitation of small, individually retrievable prey such as fruit flies (Fig. 1a) and large, unretrievable cockroaches (Figs. 1b and c).

When fruit flies were exploited, the increase in foragers on the area was markedly delayed. This latency phase lasted about 40 min (Fig. 1a). The number of minors recruited to the foraging area reached its maximum value (500–600 individuals) only after 2 h of observation (Fig. 1a). This delay was not due to a failure of explorer ants in finding the food source (first discovery of the pile of flies at min 3). Nor was it due to a long time taken by workers to retrieve flies (mean time of retrieval, 625 ± 93 s; $n = 11$). As the first recruiter had already come back to the nest by min 15, the low intensity of tactile and chemical invitations by recruiting ants would seem to be a more likely explanation for this delayed mobilization of foragers (see next paragraph). Concerning the spatial distribution of minors on the foraging area, no trail structure appeared at the beginning of the recruitment to a pile of flies. Progressively, ant density locally increased around the bridge–food source axis but no precise linear trail was observed even at min 90. Minors individually or collectively retrieving flies walked in this spindle-shaped area spreading between the bridge and the food source. Finally, the most important characteristic of the exploitation of flies was certainly the almost complete lack of majors on the foraging area. The first major to be recruited joined the source at min 75 and was followed by only two majors during the whole food recruitment.

The exploitation of cockroaches strongly differed from that of flies.
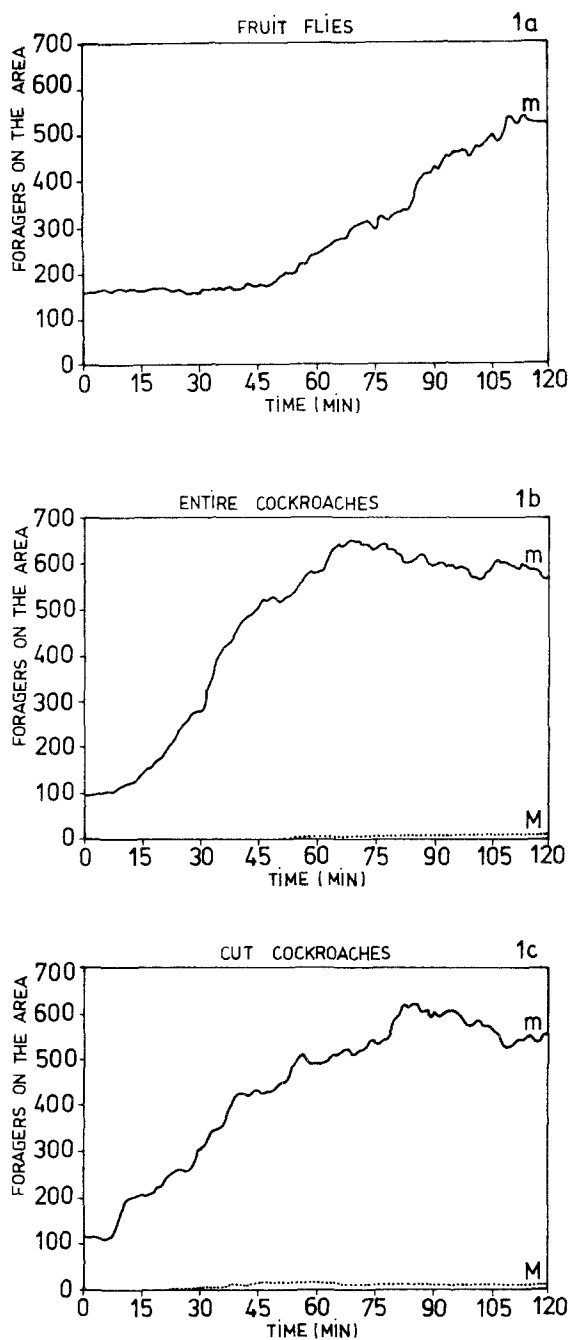
Fig. 1. Dynamics of recruitment to the foraging area of *Pheidole pallidula* minors (m) and majors (M) during the exploitation of fruit flies (a), entire cockroaches (b), or cut cockroaches (c).

Entrances of the first recruiters into the nest immediately induced a massive exit of workers. The mean rates of increase in minors or majors on the foraging area were always significantly higher to cockroaches than to fruit flies (Table I; Newman and Keuls test—for minors, $P < 0.05$; for majors, $P < 0.01$). For instance, during the growth phase of the recruitment, the rate of increase was 27 ± 5 recruited minors/3 min ($X \pm SE$) for whole cockroaches (Fig. 1b) and 19 ± 6 recruited minors/3 min for cut ones (Fig. 1c). These values were higher than the observed rate of delayed recruitment to flies (Fig. 1a; $X \pm SE = 16.5 \pm 5$ recruited minors/3 min). Moreover, a clearly defined trail rapidly took shape 15 min after the introduction of the cockroaches into the foraging area. This trail was followed very accurately by minors. During the first 15 min of experiment, the number of "lost" ants (present on the foraging area but outside of the trail and the food source) markedly decreased to a relative value of 30% of the total forager population.

The condition of dead cockroaches (whole or cut into two) made no difference to the behavior of exploiting ants. The dynamics of food recruitment

Table I. Main Parameters of Recruitment Dynamics to Three Types of Food[a]

	Fruit flies		Whole cockroaches		Cut cockroaches	
	Minors	Majors	Minors	Majors	Minors	Majors
Rate of increase in ants on the area (ants/3 min)						
Expt 1	16.5 ± 5 ($n = 21$)	0.3 ± 0.3 ($n = 8$)	27 ± 5 ($n = 21$)	0.4 ± 0.2 ($n = 26$)	19.5 ± 6 ($n = 26$)	1.0 ± 0.3 ($n = 15$)
Expt 2	19 ± 6 ($n = 20$)	0.1 ± 0.07 ($n = 22$)	46.5 ± 9.5 ($n = 10$)	1.3 ± 0.5 ($n = 16$)	40 ± 12 ($n = 21$)	1.3 ± 0.5 ($n = 22$)
Expt 3			31 ± 6 ($n = 21$)	1.0 ± 0.3 ($n = 21$)		
Total number of foragers on the area						
Expt 1	528 ± 3 ($n = 4$)	3 ($n = 7$)	605 ± 6 ($n = 15$)	10 ($n = 7$)	575 ± 9 ($n = 12$)	14.3 ± 0.3 ($n = 22$)
Expt 2	657 ± 46 ($n = 6$)	3.4 ± 0.2 ($n = 6$)	631 ± 8 ($n = 26$)	22.5 ± 0.3 ($n = 19$)	1370 ± 4 ($n = 5$)	28.2 ± 0.3 ($n = 3$)
Expt 3			849 ± 10 ($n = 10$)	22.1 ± 0.2 ($n = 4$)		

[a] Means and standard errors ($X \pm SE$) were calculated from n values. These values were based on observations performed every 3 min: (a) during the growth phase of the recruitment, for the mean rate of increase of foragers; and (b) from the end of the growth phase till the end of the experiment, for the mean total number of foragers. ANOVA tests were done by using log-transformed data and means were compared by the Newman and Keuls statistical method (significance level, 0.05). For more details, see text.

(Figs. 1b and c) and the rates of increase in minors on the area (Table I; New-man and Keuls test, $P > 0.05$) were similar and seemed to be independent of how prey was given, previously cut or not. Moreover, no preferential recruit-ment of majors was observed when whole cockroaches were offered to the soci-ety (Table I; Newman and Keuls test, $P > 0.05$).

Although the total numbers of recruited minors were unrelated to the type of exploited food items (Table I; Newman and Keuls test, $P > 0.05$), the num-ber of recruited majors was notwithstanding significantly higher to dead cock-roaches (whole or cut) than to fruit flies (Table I; Newman and Keuls test, $P < 0.01$). The mobilization of major workers was thus coupled with the quick and intense recruitment of minors to cockroaches. Indeed, at min 120, for a total number of recruited minors (about 600) similar to that observed for the exploitation of flies, the number of recruited majors was clearly higher, reach-ing up to 14 individuals (Figs. 1b and c).

To summarize, on the one hand, for a similar total number of recruited minors, the mobilization of majors is linked to high rates of increase in foragers during recruitments to large, unretrievable prey such as cockroaches. On the other hand, this mobilization of majors is independent of the condition (whole or cut) of these prey since no preferential recruitment of majors is observed when entire cockroaches are offered. The adaptive significance of such a selec-tive mobilization of majors is discussed in the last section of this paper.
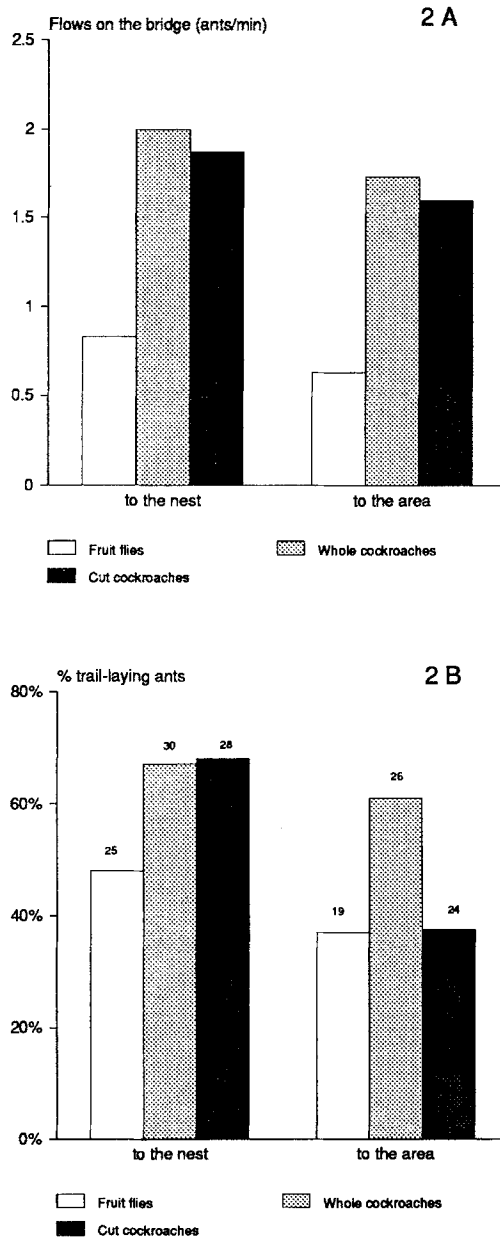
Intensities of Chemical and Tactile Invitations During Recruitments to Different Types of Food

Previous experiments have stressed differences in the foraging responses of minors and majors related to food characteristics. To link dynamics of food recruitment to invitations and to discern the main parameters ruling the parti-cipation of majors, we quantified trail laying and tactile invitation behavior performed by *Ph. pallidula* recruiters for the different kinds of food sources.

Trail Laying

Whatever the exploited food source, trail-laying ants were observed mov-ing in both directions on the bridge (Figs. 2a and b). Ants laying a trail from the nest to the food source were recruiters going back to the foraging area after having invited nestmates or turned back before reaching the nest.

After assessing the pile of flies, scouts weakly reinforced the trail per unit of time, as already suggested by the wide scattering of ants on the foraging area. This weak trail-laying resulted from two combined factors:

Flows on the bridge (ants/min)   2 A

to the nest   to the area

☐ Fruit flies   ▦ Whole cockroaches
■ Cut cockroaches

% trail-laying ants   2 B

to the nest   to the area

☐ Fruit flies   ▦ Whole cockroaches
■ Cut cockroaches

Fig. 2. Intensity of trail-laying behavior for the different food items. Ants' flow (A) is given by the mean number per minute ($n = 30$) of minors crossing the bridge in both directions (either to the nest or to the foraging area). The propensity to lay a trail is given in B by the percentage (%) of trail-laying individuals on the total number (n) of ob-served ants (n: values above each column in B).

(1) the ant flow on the bridge, which significantly differed according to
      the type of exploited food source (Kruskal–Wallis nonparametric test,
      $P < 0.05$), showing flow values to fruit flies two to three times lower
      than to cockroaches (Fig. 2a; Mann–Whitney pairwise test, $P < 0.05$),
      and

(2) the percentage of trail-laying ants in both directions, which was smaller
      when fruit flies were exploited, although this difference was not sig-
      nificant (Fig. 2b; chi-square test, 2×6 contingency table analysis, $P
      > 0.05$). We must emphasize that this smaller observed percentage of
      trail-laying ants could result either from a lower number of trail-layers
      or from discontinuity in their laying behavior.

   As a result, when cockroaches were exploited, both higher intensities of
flow on the bridge and higher percentages of trail-laying ants were partially
responsible for the intense and quick mobilization of nestmates to the foraging
area.

Tactile Invitation Behavior

   During the exploitation of flies, no intense invitation with high recruiting
power such as accelerated antennal beating lasting more than 1 s was observed
(Fig. 3a). Recruiters quietly moving in the nest essentially performed short-
lasting (< 1-s) antennal contacts in front of invited minors, while both short
(< 1-s)- and long (> 1-s)-lasting antennal contacts were equally carried out in
front of invited majors (Fig. 3a). These antennal contacts weakly induce the
exit of ants (8 and 6 % for minors, 0 % for majors). The weak intensity of these
tactile invitations as well as the tendency of invited minors to stay around
retrieved flies inside the nest accounts for their delayed and slow recruitment to
the foraging area (cf. Fig. 1a and Table I).

   When cockroaches were exploited (Figs. 3b and c), their cut or entire con-
dition did not significantly influence the recruiters' behavior (chi-square test—
for invited minors, $P > 0.05$; for invited majors, $P > 0.05$). On the other
hand, the proportions of each kind of antennations (Figs. 3a and b) significantly
differed from that observed during the exploitation of fruit flies (Fig. 3a; chi-
square test—for invited minors, $P < 0.05$; for invited majors, $P < 0.05$). After
discovering cockroaches, highly excited recruiters quickly ran into the nest to
perform intensive tactile invitations. In front of invited minors, the most fre-
quent invitations were always short-lasting accelerated antennal beatings (Figs.
3b and c; 64–75 % over the total number of observed antennations). Occasion-
ally, the most excited recruiters flagellated minor nestmates with their antennae
for more than 1 s (1.5–2.3 % over the total number of observed antennations).
These accelerated antennal beatings were often associated with longitudinal
oscillations of recruiters' bodies and with openings of recruiters' mandibles,
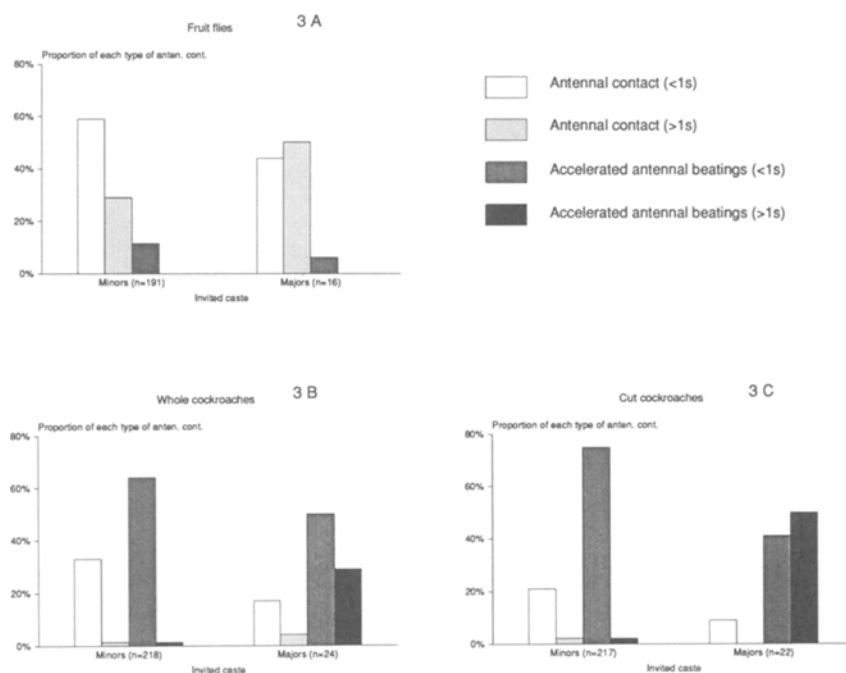
Fruit flies   3 A

Fig. 3. Intensity of tactile invitations of minors and majors during the exploitation of fruit flies
(A), whole cockroaches (B), or cut cockroaches (C). The invitation intensity is given by the
proportions of the four different types of antennal contacts performed by the recruiters to invited
minors or majors. n = total number of observations made on each caste.

probably emitting the alarm pheromone contained in their mandibular glands.
Such accelerated antennal beatings elicited numerous exits (67–75%) among
stimulated minors. These invited minors often enhanced the state of arousal of
the society by quickly running in the nest and thus probably acted as ''secondary
recruiters.''

Interestingly, the proportions of the four different tactile invitations signif-
icantly changed according to the caste of the invited workers (Figs. 3b and c;
chi-square test, $P < 0.001$). Long-lasting accelerated antennal beatings, scarce
for invited minors, were much more frequent when a major individual was
invited (1.5–2.3% of tactile invitation of minors versus 29–50% of tactile invi-
tation of majors). Moreover, the duration of these invitations was nearly twice
longer for majors than for minors ($X \pm$ SE: 1.4 $\pm$ 0.03 s, $n = 18$, for minors
and 2.0 $\pm$ 0.2 s, $n = 18$, for majors). These long-lasting accelerated beatings
induced more majors to exit the nest than other forms of tactile stimulation (43
and 64% of majors' exits occurred after they received this type of invitation).

Recruiters even sometimes grasped mandibles of the invited major and pulled it to the nest exit. This preferential tactile invitation of the major caste during the exploitation of cockroaches resulted in total percentages of exit similar for minors and for majors (20–22% for invited minors and 22–32% for invited majors). The necessity of recruited majors to receive such intensive and long-lasting antennations in order to induce their exit from the nest allowed us to assume a higher inertia of this caste. This last observation is relevant to hypothesized differences in response thresholds for the two sterile castes. To test this hypothesis, behavioral responses to tactile invitations and trail pheromone were compared for minors and majors.

Differential Response of Minors and Majors to Tactile Invitations

During food recruitment to cockroaches, among the four types of observed antennations, the accelerated antennal beatings lasting more than 1 s induced the highest percentage (80%) of exiting minors (Fig. 4). On the opposite, antennal contacts of more than 1 s never induced exit of minors, which simply followed the recruiter in the nest. For all types of tactile invitations, the increased activity level of touched minors strongly differed from that observed when the major caste was invited. The weak tendency of majors to move was systematically showed by their lower percentage of exiting individuals compared to minors receiving the same form of tactile invitation (Fig. 4), although this difference was not significant (chi-square test, $P > 0.05$).

Differential Response of Minors and Majors to Chemical Invitations

Recruiting effects of the trail pheromone were observed by putting, at the nest entrance, a piece of paper impregnated with an extract of the poison gland from minors. Exits out of the nest were then quantified. During the first minute of the experiment, when the recruiting effects were maximum, the number of exits of minors was always significantly different from that in the control (hexane) for all tested concentrations (Fig. 5a). At high concentrations ($> 10^{-1}$ gland equivalent), the number of exiting minors remained significantly higher than in the control experiment even at the end of the experiment. On the other hand, for majors, only concentrations higher than 2.5×10^{-2} gland equivalents elicited a number of exiting majors significantly different from that in the control at min 1 (Fig. 5b). Moreover, the number of majors' exits always rapidly decreased after min 1, even at the high quantity of 1 gland equivalent. Majors quickly relapsed into their usual state of immobility in the society. No fast-running majors were observed even for the highest tested concentration.

% of exiting individuals
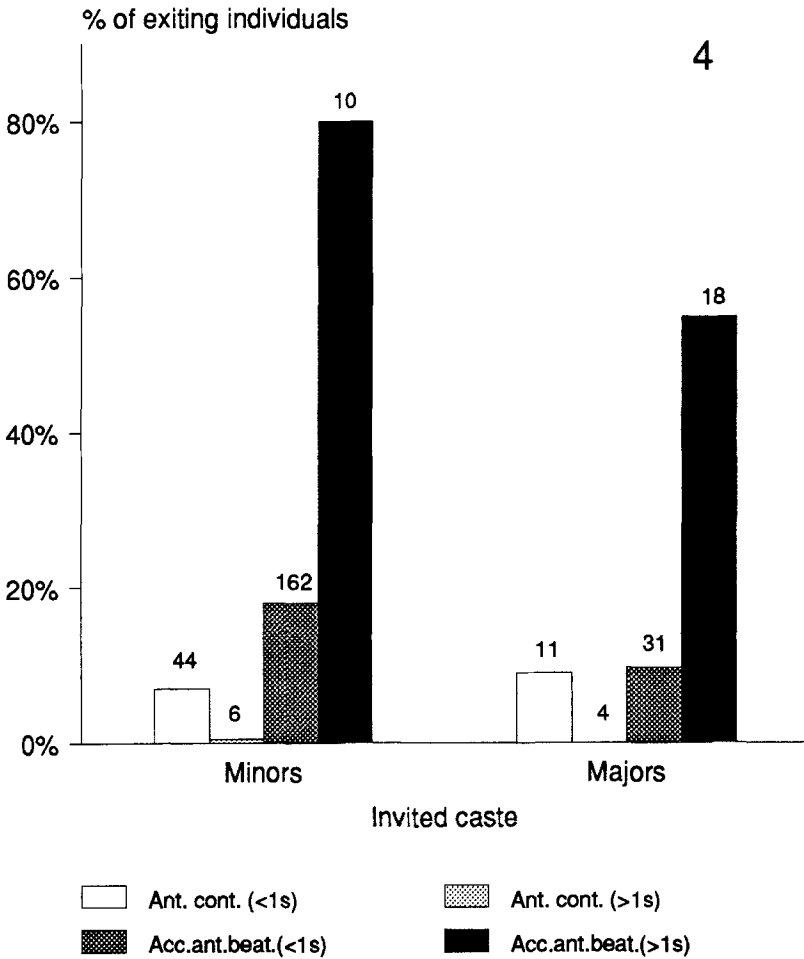
Fig. 4. Exit of minors or majors induced by the four different types of tactile invitations. The caste response to each kind of tactile invitation is given by the percentages (%) of exiting individuals among all the invited minors or majors (the total number of invited ants observed is given above the related column). Note that no exit was induced by the scarcely observed antennal contact (> 1 s).

DISCUSSION

Adaptive Value of Food Recruitment Characteristics

Dynamics of food recruitment and spatial distribution of ants on the foraging area change according to the characteristics of the exploited food items. The weak and slow mobilization of foragers to patches of small prey such as

Number of exiting minors/ min

Time (min)

Number of exiting majors/ min

Time (min)
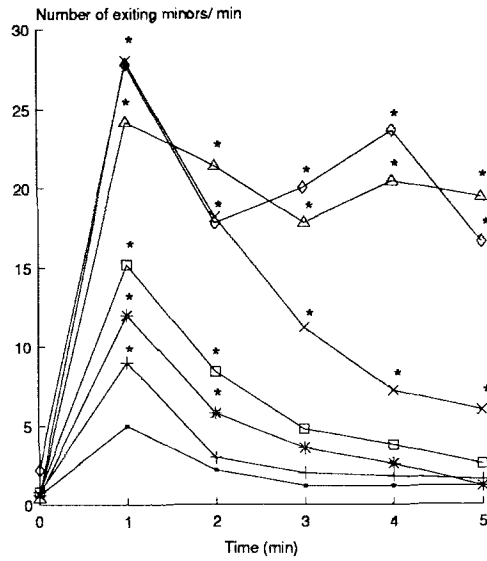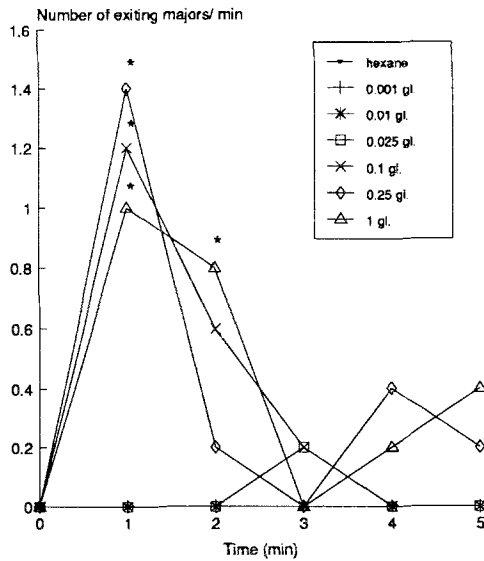
Fig. 5. Exit of minors (a) and majors (b) induced by increasing quantities of minors' poison glands. Each value is the mean number of exits observed during our five experiments. These values are compared to the control (hexane) by a Kolmogorov-Smirnov statistical test. (∗) The difference is statistically significant for the level $\alpha = 0.05$.

flies does not seem surprising since, in nature, it is very unusual for an exploring ant to find another prey beside a small insect. An intense recruitment to a small food source such as a single fly would be disadvantageous for the society. Moreover, especially at the beginning, the dispersed spatial distribution of ants on the foraging area is well suited to the scattered and unpredictable distribution of these small prey in nature. On the other hand, a fast and massive recruitment of foragers as well as an accurate trail following to a large, unretrievable and localized food source such as cockroaches, ensures the monopolization and efficient defense of the prey from competitors. These general characteristics of food recruitment are determined by the trail-laying behavior and the tactile invitations, more intense when large and unretrievable food items are exploited.

Adaptive Value of Caste Polyethism During Food Exploitation

The caste polyethism observed during *Ph. pallidula* foraging is adaptive and highly efficient. As a consequence of the low response threshold of minors to recruiters' invitations, food exploitation is ensured mainly by the minor caste. The minors possess all the qualities required for this task as well as for the exploration of the foraging area.

(1) They are numerous, and relative to their body size, they run faster than other sympatric ant species (Bernard, 1984). This ensures a more intense exploration of their environment as well as a more efficient exploitation of food resources.

(2) Global energetic costs of movement per explorer are supposed to be lower for minor scouts than for heavy majors.

(3) The eventual loss of minors during dangerous tasks such as food search and exploitation affects less severely the society than the loss of majors, which are produced in smaller numbers with higher manufacturing costs [more proteinic requirements and longer duration of majors' larval development (Passera, 1974)].

(4) Only the minor caste is numerous enough to generate and to control precisely mass recruitment and trail genesis. Indeed, such collective behavior resulting from interactions between individuals emerges from nonlinear, autocatalytic mechanisms of self-organization (Pasteels *et al.*, 1987). The snowball effect of recruitment due to trail communication must be generated by the more numerous minor caste, representing about 90% of a society's population. In addition, the inherent stochastic nature of self-organizing processes and the related "loss" of ants outside of the trail can be afforded only by the minors' population.

In every respect, the minor caste seems thus the better adapted and the more advantageous caste to explore the foraging area and to exploit discovered food sources.

The major caste, by its higher threshold of response, is mobilized only after intense chemical (a highly concentrated trail) and tactile recruiting stimuli [e.g., after accelerated antennal beatings, the only antennal contacts taken into account in Szlep-Fessel's (1970) study of *Ph. pallidula* invitation behavior]. Therefore, this caste actively participates only in massive recruitments to large and/or persistent food sources such as cockroaches. Powerful mandibles enable these majors to cut prey and defend food sources against competitive species. The rate of death and the replacement cost of these majors are reduced because of

(1) the selective participation of majors only in recruitment to food sources energetically highly valuable, immediately and massively exploited by foragers, and

(2) the low percentage of majors outside the trail susceptible to becoming lost on the foraging area. This low rate of losing the trail by majors results from their selective mobilization only on well reinforced and highly frequented trails. It could also be due to the accuracy of their trail-following response which is higher than that of minors (Detrain *et al.*, 1988).

Differences in Behavioral Thresholds as the Basis of Polyethism in Polymorphic Ant Species

The specialization of *Ph. pallidula* majors lies neither in reduced competencies nor in a limited behavioral repertoire but in a higher response threshold to task stimuli whose physiological basis is still unknown. We could hypothesize that the juvenile hormone, well known for its morphogenetic role in *Pheidole* spp. (Wheeler and Nijhout, 1981; Passera, 1982), may be involved. Indeed, since age-dependent titer in juvenile hormone of *Apis mellifera* workers influences their response threshold to alarm pheromones (Robinson, 1987), the higher number and volume of cells of the corpora allata of majors (Suzzoni, 1983) could similarly affect their behavioral threshold.

Whatever the physiological basis of these thresholds might be, they can be integrated in an understanding of caste polyethism. The classical theory of the evolutionary optimization of caste implicitly suggested that the number of castes and their ratio in an ant society would be adaptively adjusted to ergonomic and defensive constraints (Oster and Wilson, 1978). However, studies on caste ratios in *Pheidole dentata* (Calabi, 1988) or *Camponotus impressus* (Walker and Stamps, 1986) societies did not show such correlations between caste ratios and ecological characteristics. Moreover, under laboratory conditions, *Pheidole dentata* societies did not modify the production rate of majors according to successive attacks by competitive species (Johnston and Wilson, 1985). In com-

bination with physiological constraints, the behavioral elasticity of majors could explain these failures in correlating caste ratios with the ecological and defensive challenges to be faced by the society.

To understand behavioral elasticity and performances of both "typical" and "atypical" tasks by a given caste, we have previously suggested that observed behavioral repertories resulted from differences among individual ants in their perception and/or response to task stimuli, as recently shown in honeybee colonies (Robinson and Page, 1989; Frumhoff and Baker, 1989). Behavior expressed by an individual ant would be a function of two variables: the exogenous labor needs of the society and the endogenous individual ontogeny (genetic, physiological, and learned components combined). For instance, we could hypothesize that, under normal conditions, majors typically never take care of brood because of their endogenous high threshold of response to larvae stimuli. "Atypical" tasks done by *Pheidole* majors such as brood feeding would be elicited only by exogenous intense requirements of the society for brood care. Such a situation could be encountered when an artificial decrease in the number of minor nurses enhances food begging and contacts of larvae with majors: these stimuli thus cross the response threshold of the major caste. In this paper, our experiments present the first evidence of such a higher behavioral threshold of majors to chemical and tactile invitations. It would be very interesting in the future to extend this line of research to other contexts such as defense, domestic tasks, etc.

Ultimately, according to Calabi (1988), caste polyethism and caste demography in an ant society could result from two sets of selective pressures: for long-term maximization of ergonomic efficiency and for short-term survival of the society. On the one hand, the ratio of physical castes in a society as well as "typical" caste-task associations reflect a long-term adaptive strategy. The caste distribution function of ant societies is the adaptive reflection of the species' life-style resulting from long-term selective pressure. Both the morphology of caste and their frequency are best suited for the main tasks presented, for ages, to the colony by its microhabitat. On the other hand, behavioral elasticity and "atypical" caste-task associations seem to be selected as a short-term strategy. This short-term strategy of behavioral elasticity is very well suited to any modification in food or defensive contingencies of an unpredictable environment. Under the pressure of these proximal factors, it makes possible an immediate response by societies to temporary contingencies without any energetically costly investment in modifying their caste ratio.

The apparent conflict between strict caste-task association of the ergonomic optimization theory and individual task switching fades out since differences between castes in thresholds of behavioral responses could account for both typical and atypical caste behavior.

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