Caste polyethism and collective defense in the ant, *Pheidole pallidula*: the outcome of quantitative differences in recruitment

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Summary. During agonistic encounters, both minors and majors of the European ant *P. pallidula* actively cooperate in defense. Minors seize the legs of the intruder and in some cases induce the recruitment of nestmates whereas majors kill the spreadeagled alien ant. The defensive strategy of *P. pallidula* is very flexible and adapted to both the number of alient ants and to the intruder's superiority in fighting. On the one hand, only a massive invasion of alien minors results in a slow mobilization of resident ants to the combat area, elicited by recruiters performing weak tactile invitations and trail-laying behavior. On the other hand, the presence of 10 majors induces a fast and massive recruitment achieved by intense trail-laying and tactile invitations from the recruiters. Because of their high response threshold to invitations, resident majors are mobilized only during these intense recruitments, their exit being additionally enhanced by their preferential stimulation. The adaptiveness of this defensive strategy is discussed. It is also suggested that simple decision-making rules of recruitment and caste differences in behavioral thresholds could account for the complexity of *P. pallidula* defensive strategies.

Introduction

In the cosmopolitan ant genus *Pheidole*, the sterile worker force is divided into two morphologically distinct castes. In contrast with the wide behavioral repertoire of minors, the large-headed majors (often called soldiers) seem to be mainly involved in the defense of the society (Buckingham 1911; Goetsch 1953; Creighton and Creighton 1959; Creighton 1966; Wilson 1975, 1976; Calabi et al. 1984; Carlin and Johnston 1984; Feener 1986; Fowler 1984; Wilson and Hölldobler 1985; Feener

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1986). Besides, *P. dentata* colonies are characterized by their flexible strategy in dealing with increasing numbers of invading ants (Wilson 1976). This strategy consists of three defensive levels according to the intruder's challenge: (1) destruction of small enemy forces far away from the nest entrance, (2) fighting close to the nest until the elimination of numerous intruders and finally (3) abandonment of the nest when the colony is overrun by too many enemies. This defensive flexibility and the selective participation of the major caste show that colony defense is at least as complex as the most advanced, better known types of social behavior such as food recruitment.

Enemy specification is closely associated with chemical stimuli such as the odor of the body surface of invading ants (Wilson 1975, 1976). An effort was therefore made to reduce the chemical dimension by comparing defensive responses of a *P. pallidula* colony to conspecific enemies from one alien colony. Comparisons were made between defensive responses induced by increasing numbers of *P. pallidula* minor invaders and by invaders of different fighting abilities. In this latter case, we have deliberately compared the defensive responses to conspecific enemy majors and minors in the laboratory, despite the absence of invasion by only majors in nature. In this "artificial" choice, alien minors and majors are standing in for a quantitative range of natural threats. Chemical and tactile invitations were quantified as well as response thresholds of invited castes. We will propose a hypothesis as to how the complexity and the diversity of collective defensive strategies can be generated by elementary behavior of recruiters. Adaptive significance will be suggested for flexibility of defensive responses and for caste polyethism during defense in a *P. pallidula* colony.

Materials and methods

Collection and rearing of P. pallidula colonies

Colonies were collected in southwestern France and consisted of 1000–1600 minors, 70–140 majors, and 1 fertile queen. Ants were

kept in the laboratory in plaster nests (20 × 20 × 2.5 cm) covered with a red glass plate and kept moist by regularly filling water reservoirs at the back of the nest. Each nest was connected by a bridge to an area (50 × 35 × 5 cm) that served both as foraging space and experimental combat area. Colonies were maintained at a constant temperature (22° C ± 1° C). Artificial lighting was timed on a 12:12 h light:dark regime. They were fed with freshly killed cockroaches (*Periplaneta americana*) and brown sugar solution (1 M).

Dynamics of defensive recruitment

Each defensive recruitment was studied for 3 h after the introduction of 10, 40, 60 minor, or 10 major conspecific intruders. Forty-eight hours before the initiation of defensive recruitment, these intruders were marked with a yellow spot painted on their abdomen and reintegrated into their own nest in order to lose any painting odor that could bias future defensive responses of resident ants. Alien ants were introduced into the combat area, 20 cm from the bridge. Video recordings of the flow of workers on the bridge enabled us to know at all times the number of minors and majors present on the combat area. In addition, every 3 min, we counted the number of minors and majors biting the intruders' appendages. The mean duration of bites by resident ants were compared for 40 minor and 10 major enemies. Successive experiments were separated by at least a week in order to limit any bias due to the learning of the presence of an enemy as demonstrated in *P. dentata* (Carlin and Johnston 1984). Tests were carried out on four different societies. Eight replicates were made for each intrusion of 10, 40, or 60 alien minors. Eight recruitments were also induced against 10 intruder majors.

Intensities of the trail recruitment and of the tactile displays

Trail recruitment. Trails laid by minors leaving the combat area are responsible for the chemical recruitment of nestmates. Intensity of trail laying was quantified for defensive recruitments against 40 minor and 10 major intruders. During the first 15 min of these recruitments, ants walking on the bridge either to or from the nest were observed with a magnifying lens (8 ×) and classified into trail laying and non-trail laying individuals. Trail laying ants were recognized by a typical behavior: their gaster touched the substrate, which suggests that the ants laid chemical marks each time their abdomen met the surface of the bridge.

Tactile invitation. We determined at the nest entrance the proportions of the different antennal contacts made by recruiters. These antennations were classified into four categories:
1. and 2. Antennations lasting less or more than 1 s, respectively, performed by recruiters coming back slowly from the combat area to the nest
3. and 4. Accelerated antennal beatings lasting more or less than 1 s, respectively, carried out by fast running recruiters, as previously described during food recruitment by Szlep-Fessel (1970)

The tactile invitations of recruiters and the behavioral responses of invited ants were video recorded at the nest entrance (magnification: 5 ×). They were quantified for each ant we succeeded in following from the combat area to the nest. On these video recordings, fast running ants giving accelerated antennal beatings were distinguishable by their fuzzy image with a video frame advance of 0.04-s steps. After each kind of antennation, the state of arousal of invited ants was estimated by the percentage of moving and exiting individuals. Ants were considered to be moving when they walked inside the nest at least 1 cm. Intensities of tactile invitations and responses of invited ants were compared for defensive recruitment to 40 minor and 10 major enemies.

Results

Dynamics of defensive recruitments

The rate of increase of minors' recruitment (ANOVA, $F = 7.1$, $P < 0.05$), their total number on the area ($F = 7.0$, $P < 0.05$), as well as the total number of recruited majors ($F = 8.55$, $P < 0.05$) are dependent on the number of caste of intruders (Table 1). Dynamics of defensive recruitment from the nest to the combat area strongly differ according to increasing numbers of enemies (averaged curves 1 A–C). Ten intruder minors never induced immediate recruitment of resident ants (Fig. 1 A). Up to 100% of the ants present on the area were directly involved in the fight and were numerous enough by themselves to subdue invading minors. Their progressive return back to the nest merely caused a slight mobilization of nestmates after 2 h. This delayed recruitment had no direct defensive significance since all the intruders had already been killed by this time. However, this indirectly led to the exploration by the colony of its territory and thus to the possible discovery of some enemy not yet subdued. When a higher number of alien minors (40 or 60) were introduced, there was a shift from the absence of recruitment to a mobilization of resident minors resulting in a favorable outcome of the battle (Figs. 1 B, C; Table 1: RI and TN of resident minors significantly higher than against 10 intruding minors, Newman and Keuls test $P < 0.01$). No majors were recruited against 10 intruding minors. Forty or 60 intruders were required to elicit a weak recruitment of this caste (Fig. 1 B, C), resulting in higher total numbers of majors on the area (Table 1, Newman and Keuls $P < 0.01$).

Defensive recruitment against 10 alien majors (Fig. 1 D) deeply differed from those observed against 10 enemy minors (Fig. 1 A). Both the total number of recruited minors and their rate of increase were significantly higher (Table 1, Newman and Keuls $P < 0.01$). In 30 min, the worker force on the combat area doubled with a mean rate of increase reaching up to 19 minors/3 min. During this massive exit, majors were recruited reaching a total number on the area even higher than against 60 alien minors (Newman and Keuls $P < 0.01$). Concurrently, for a mean number of recruited minors similar to that observed against 40 minor intruders, the participation of majors was markedly more important against 10 intruding majors. (Table 1: 3.8 vs 10 recruited majors, respectively, Newman and Keuls $P < 0.01$.)

Combative behavior of resident minors. Although the dynamics of defensive recruitment differed according to increasing numbers of alien minors, the combative behavior of resident workers remained qualitatively similar. When resident foragers encountered a minor intruder, a few fled but most of them immediately bit legs, antennae, or mandibles of the intruder. Both bitten and biting minors displayed vertical abdominal movements that could be associated with stridulation. Less frequently, attacked intruders folded their antennae and legs beneath their body. Each intruder was rapidly sur-

Table 1. Key parameters of defensive recruitments against conspecific intruders (10, 40, 60 minors or 10 majors). Each RI variate (additional ants/3 min) is a mean based on 3-min spaced measures done during the growth phase of recruitment curves. Each TN variate is a mean based on similar numbers of countings on the area done every 3 min from the end of the growth phase till the end of the experiment. The combative behavior (B) is estimated by the minimum and max percentages of individuals biting intruders in the total number of ants on the area; 8 replicates of defensive recruitment were done for each type of attack whose mean values and standard error are shown.

ANOVA tests were done on the response of one caste to different attacks and means compared by the Newman and Keuls method; * $P < 0.05$

Intruders	Rate of Increase on the area (RI)		Total Number of ants on the area (TN)		Min/max percentages of Biting ants (B)	
	Minors	Majors	Minors	Majors	Minors	Majors
10 minors						
Exp. 1	0	0	32	1	50/86%	–
2	0	0	14.5	0	50/100%	–
3	0	0	33.9	1	42/100%	–
4	0	0	18.4	0	–	–
5	0	0	55.3	5	10/45%	–
6	0	0	42.1	2	30/70%	–
7	0	0	68.6	1.4	10/48%	–
8	0	0	58.2	3.7	–	–
Mean ±SE	0	0	40.1 ±7.3	1.7 ±0.7	32/72% ±7/±8.5	–
40 minors						
Exp. 1	0.9	0	33.2	1'	40/100%	–
2	2.0	0	42.0	5	49/100%	0/60%
3	1.9	0	101.6	3	30/90%	–
4	0	0	47.8	4	32/100%	0/75%
5	3.7	0	89.1	1	18/58%	–
6	3.3	0.17	212.8	6	6/67%	0/100%
7	6.1	0.75	101.7	4	17/54%	0/100%
8	4.8	0.33	103.8	5.4	15/52%	0/50%
Mean ±SE	2.8 ±0.8	0.16 ±0.1	91.5 ±21.6	3.8 ±0.7	26/77% ±5/±8	0/77% 0/±9
60 minors						
Exp. 1	3.2	0.40	212.5	10	5/85%	0/100%
2	3.8	0	106.4	4	15/100%	0/100%
3	5.4	0.14	98.1	2.5	34/66%	0/100%
4	1.05	0	85.2	2	24/56%	0/100%
5	4.0	0.31	162.0	9.3	5/78%	0/80%
6	2.9	0.10	157.3	5	16/63%	0/100%
7	6.7	0.36	181.4	12	2/46%	0/100%
8	8.8	0.27	116.7	8.2	4/45%	0/100%
Mean ±SE	4.5 ±0.91	0.20 ±0.06	140.0 ±17.0	6.6 ±1.4	13/67% ±4/±7.3	0/97% 0/±3
10 majors						
Exp. 1	3.4	0.3	65	11.1	9/39%	20/100%
2	3.6	0.27	61.3	13	5/21%	30/100%
3	13	0.25	95	8.8	5/40%	20/90%
4	6.5	0.18	97	11.3	–	–
5	3.3	0.14	84.4	4.6	–	–
6	6.2	0.38	99.9	7.8	2/15%	30/100%
7	19.0	1.27	198.1	13.9	2/48%	30/100%
8	6.8	0.40	137.4	9.7	5/40%	30/89%
Mean ±SE	7.7 ±2.1	0.4 ±0.14	104.7 ±16.8	10.0 ±1.1	4.7/34% ±0.9/±5	25/91% ±2/±5
ANOVA	$F = 7.1$ *	$F = 3.5$ NS	$F = 7.0$ *	$F = 8.55$ *	$F_{min} = 5.6$* $F_{max} = 6.4$*	$F_{min} = 125$* $F_{max} = 3.2$ NS

rounded by 2 or 3 biting resident minors. Similar percentages of recruited ants directly involved in fights were observed when facing 10, 40, or 60 alien minors (Table 1). The first attacker was always the most persistent to bite (duration of the first bite $x \pm SE = 954$ s ± 251, $n = 23$). Once the intruder was immobilized by the first ant, the mean duration of bites by the following ones significantly decreased ($t = 4.08$, $P < 0.01$); bite durations

$x \pm SE = 51$ s ± 23 ($n = 30$); 61 s ± 14 ($n = 90$); 12 s ± 3 ($n = 31$), respectively, for the second, third, and fourth biting ant). This decrease in the aggressivity of resident minors could explain the slight decrease of their mean duration of bites since the start of recruitment, although not significant (Table 2; ANOVA, $F = 0.78$, $P > 0.05$).

Faced by 10 intruding majors, resident ants reacted quite differently than against enemy minors. Intense
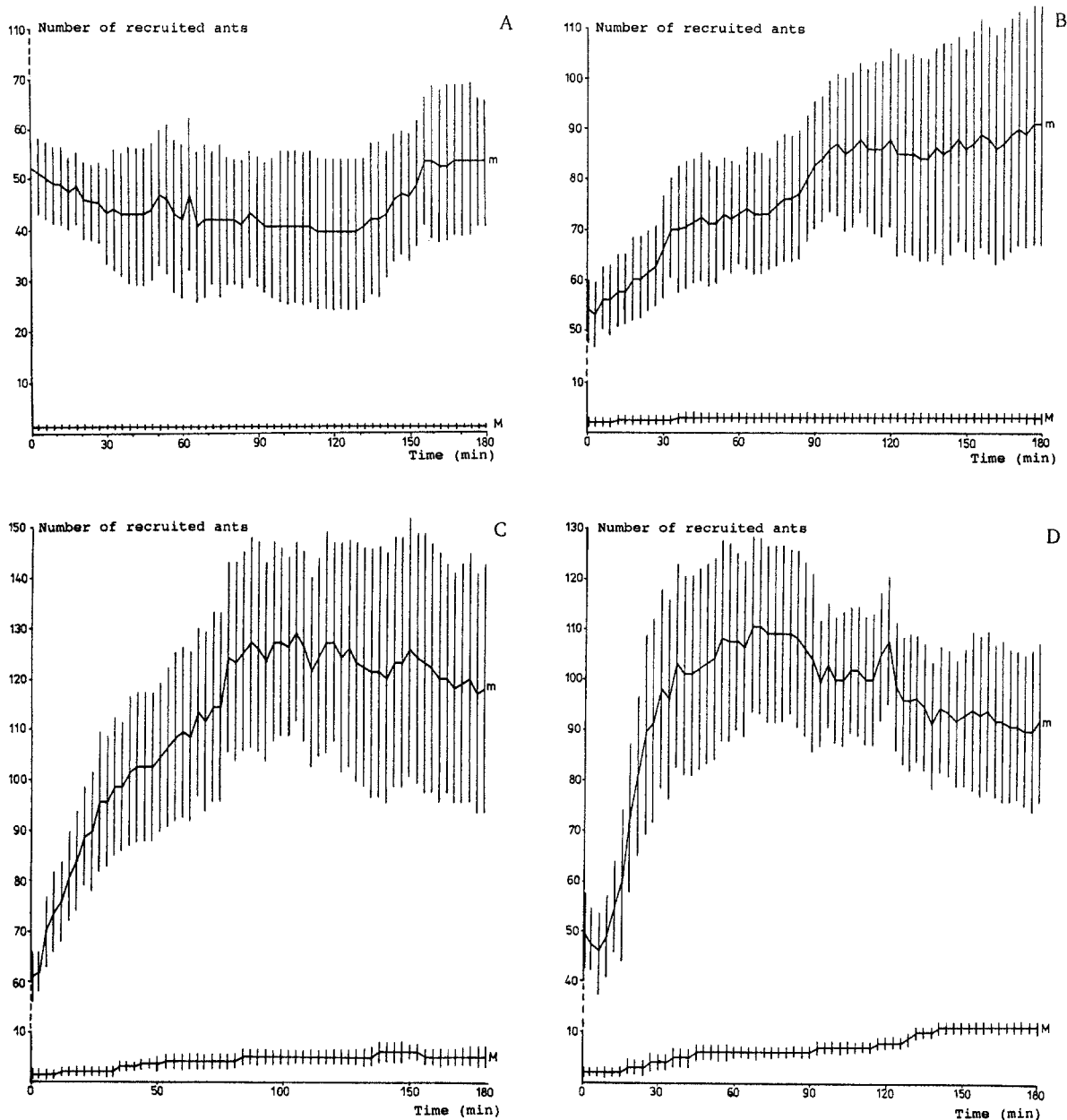
Fig. 1A–D. Averaged curves of defensive recruitment. Total numbers of resident minors (*m*) and majors (*M*) on the area have been measured every 3 min during 180 min. Means and standard error are calculated from 8 replicates with 10 minor (**A**), 40 minor (**B**), 60 minor (**C**), or 10 major (**D**) intruders

alarm behavior was always evoked by these intruders. Highly excited ants snapped each alien major encountered and sometimes even one of their nestmates. Alarm was propagated by their fast runs in irregular loops with wide-open mandibles, probably emitting the alarm pheromone produced by their mandibular glands. The alarm decreased as soon as minors closing their mandibles on the enemy appendages stopped alerting foragers and, perhaps, stopped emitting their alarm pheromone. During the first 30 min, the mean duration of bites by resident ants were significantly shorter than those observed against intruder minors (Table 2, $t = 2.65$, $P < 0.05$). Their difficulty to subdue alien majors and to prevent them from moving as well as their high mortality rate (up to 30%) explain the low percentage of biting

resident minors (Table 1; 4.7% to 34%, minimum and maximum values lower than against intruder minors, Newman and Keuls $P < 0.01$).

Defensive tasks of resident majors. The killing of alien minors always required the intervention of majors that inflicted lethal bites at the petiole or neck. When no major was present on the area, the intruder was taken back alive to the nest where it was immediately surrounded by alarmed resident minors and killed by a nestmate major a few seconds later. No significant change with time was noted in the mean duration of bites by resident majors (Table 2; ANOVA, NS, $P > 0.05$) since this only depends on the resistance of intruder sclerites.

Table 2. Duration $(x + \text{SE})$ of bites by resident minors and majors during defensive recruitments against 40 alien minors or 10 alien majors. n: number of observations. ANOVA tests were done and means compared by the Newman and Keuls methods. See text for more details

|	Duration of bites of 40 intruder minors by		Duration of bites of 10 intruder majors by	
	resident minors	resident majors	resident minors	resident majors
Period of the recruitment				
0–30 min	185 s ± 45 $n = 184$	132.5 s ± 53 $n = 10$	38 s ± 14 $n = 127$	107 s ± 50 $n = 49$
30–60 min	98 s ± 39 $n = 99$	64 s ± 21 $n = 31$	97 s ± 35 $n = 74$	113 s ± 60 $n = 37$
60–90 min	104 s ± 34 $n = 32$	128 s ± 40 $n = 16$	89 s ± 36 $n = 49$	186 s ± 56 $n = 21$
90–120 min	62 s ± 21 $n = 13$	233 s ± 122 $n = 5$	58.5 s ± 11 $n = 30$	655 s ± 290 $n = 21$
120–150 min	33 s ± 11 $n = 18$	150 s ± 88 $n = 4$	31 s ± 5 $n = 34$	687 s ± 270 $n = 23$
150–180 min	44 s ± 28 $n = 7$	190 s ± 156 $n = 7$	32 s ± 5 $n = 37$	509 s ± 215 $n = 12$

Against intruder majors, resident majors behaved differently, participating not only in the killing of the enemy but also in its immobilization and in the alarm propagation. Such alarmed majors ran excitedly or stood with their mandibles held open in a "guarding" position. The others focused their action on the immobilization and the killing of alien ants. Therefore, the minimal percentage of biting resident majors is always significantly higher against intruder majors (25%) than those observed against alien minors (Table 1, Newman and Keuls $P < 0.001$). The mean duration of bites by these resident majors significantly changed with time (Table 2, ANOVA, $F = 38$, $P < 0.01$). Mean values were significantly shorter during the first 90 min of the recruitment when still freely moving intruders were difficult to subdue (Table 2, Newman and Keuls test, $P < 0.05$). After 90 min, the very long lasting mean duration of attacks could be explained by the high resistance of alien majors' sclerites to lethal bites and by the striking persistence of resident majors to handle (up to 50 min) the mandibles of immobilized enemies. This indirectly results in a number of fighting majors similar to that of minors, despite the lower proportion of the major caste (around 10%) in the whole nest population. It is interesting to note that the weight distribution of these attacking majors was significantly shifted towards the low values compared to that of the whole major population (Fig. 2, $\chi^2 = 15.4$, $df = 6$, $P < 0.05$). Only majors with a small abdomen were implied in fights; those with a distended crop remained inside the nest.

Intensities of the trail recruitment and tactile displays

For a similar total number (90–100) of recruited minors, defensive responses to 10 alien majors and 40 alien minors differed (1) by the rate of increase of recruitment curves and (2) by the relative participation of resident majors. Therefore, to understand such differences, we compared chemical recruitment and tactile invitation by recruiters in both cases.

Trail recruitment. Having bitten intruders, some minors ran back to the nest, laying a chemical trail. No major was seen dragging its abdominal tip over the substrate. The intensity of trail deposit by these minors strongly differed according to the caste of intruders (Table 3).
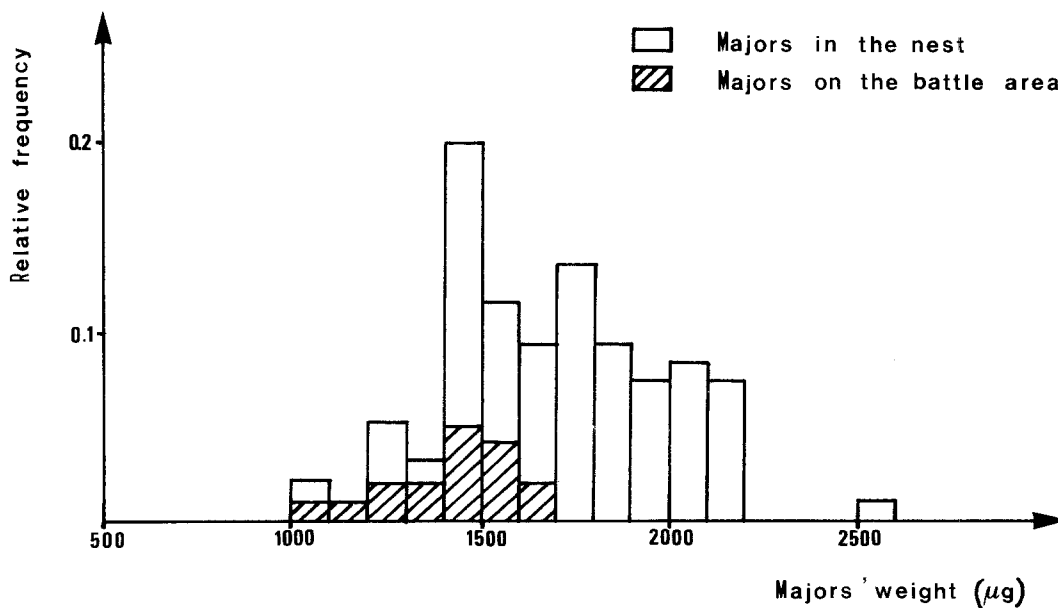
Fig. 2. Relative frequency distribution of body's weights in the major caste. All the majors $(n = 95)$ found inside the nest and on the combat area were individually weighed. The frequency distribution of these weights was drawn with stippled columns representing individuals found on the battle area during defensive recruitments

Table 3. Trail-laying during defensive recruitments. Against 40 minor or 10 major intruders, for the first 10 min, flow intensities are given by the number of minors/min ($x \pm$ SE) walking on the bridge. They are compared by Mann Whitney tests. Percentages of trail laying individuals among the total number of observed ants (n) are compared by χ^2-tests. Values sharing a common superscript symbol are not statistically different ($P > 0.05$)

	40 intruder minors	10 intruder majors
To the nest		
ants/minute	$32. \pm 0.5$•	4.4 ± 1.3•
% trail-laying ants	56%▲	89%△
(n)	(32)	(45)
To the foraging area		
ants/minute	2.2 ± 0.8•	11.9 ± 1.7○
% trail-laying ants	36%▲	33%▲
(n)	(22)	(118)

When faced with 40 intruding minors, only 56% of returning minors dragged their abdominal tip over the ground. In contrast, nearly all the minors (89%) laid a trail after encounters with intruder majors. Moreover, this significant difference ($\chi^2 = 4.8$, $df = 1$, $P < 0.05$) is enhanced by the more intense flow of ants from the nest to the area (Mann-Whitney test $U = 4$, $P < 0.001$) and consequently, the higher absolute number of individuals laying a trail in presence of intruder majors. In this case, the highly concentrated trail could be, at least partially, responsible for the intense recruitment of minors (Fig. 1 d) and could explain why the major caste is mobilized despite its high response threshold to the trail recruiting effect (Detrain and Pasteels 1991).

Tactile invitation. When 40 minors were used as intruders, weakly excited recruiters entered the nest and performed different types of antennations in similar proportions, whatever the caste of the invited ant (Table 4, $\chi^2 = 2.16$, $df = 3$, NS, $P > 0.05$). Accelerated antennal beatings lasting more than 1 s were scarcely observed. The majority of tactile invitations lasted less than 1 s and were performed equally by walking or by fast-running recruiters. These tactile invitations were weakly effective in eliciting movements or exits among contacted minors. They only induced a slow recruitment of minors and had no recruiting effect on the hard-to-move caste of majors.

After encounters with ten intruding majors, workers rapidly rushed back into the nest where their alarmed running was interrupted by frequent self-groomings and snaps from nestmates. Such intracolonial aggressive behavior could be due to the perception, on the recruiter body, of the intruder odor or of the alarm pheromone emitted during the fights. The proportions of the different types of antennations significantly differed from those observed in the presence of 40 enemy minors (Table 4; for invited minors $\chi^2 = 47.4$, $df = 3$, $P < 0.001$; for invited majors $\chi^2 = 39.1$, $df = 3$, $P < 0.001$). After facing 10 intruder majors, the most frequent invitations of resident minors were short-lasting accelerated beatings. Though seldom observed, a few highly alarmed recruiters also carried out accelerated antennal beatings for more than 1 s, which induced very high percentages of moving minors (100%) and exits (56%, Table 4). There was no choice of the invited caste made by the recruiter, minors being invited as frequently as major nestmates. Nevertheless, the types of antennations significantly changed according to the invited caste (Table 4, $\chi^2 = 191$, $df = 3$, $P < 0.001$). Accelerated antennal beatings of more

Table 4. Tactile invitations of resident minors or majors by the recruiters. For each kind of attack (40 minors or 10 alien majors) and for each contacted caste, this table gives the number n (and the proportion) of observed antennal contacts. Their efficiency is estimated by the percentages of moving (m) and exiting (e) individuals on the total number (n) of ants stimulated by a given invitation

Antennal contacts / Intruders Invited caste	Intruding minors		Intruding majors	
	Minor	Major	Minor	Major
Antennations (<1 s) Walking recruiter	$n = 58$ (41%) m: 19% e: 0%	$n = 12$ (48%) m: 0% e: 0%	$n = 65$ (22%) m: 29% e: 9%	$n = 0$ – –
Antennations (>1 s) Walking recruiter	$n = 12$ (8.5%) m: 17% e: 0%	$n = 4$ (16%) m: 0% e: 0%	$n = 0$ – –	$n = 0$ – –
Accelerated antennal beatings (<1 s) Fast running recruiter	$n = 68$ (48%) m: 29% e: 10%	$n = 9$ (36%) m: 11% e: 0%	$n = 210$ (72%) m: 72% e: 27%	$n = 17$ (30%) m: 29% e: 12%
Accelerated antennal beatings (>1 s) Fast running recruiter	$n = 4$ (2.8%) m: 100% e: 50%	$n = 0$ – –	$n = 18$ (6%) m: 100% e: 56%	$n = 39$ (70%) m: 87% e: 59%
All kinds of antennations	$n = 142$ (100%) m: 32% e: 8%	$n = 26$ (100%) m: 7.7% e: 0%	$n = 293$ (100%) m: 64% e: 25%	$n = 56$ (100%) m: 69% e: 44%

than 1 s were more frequent (70%) when inviting majors. Recruiter often rushed at these majors and longitudinally vibrated their body while intensely antennating them. These longer lasting antennations could be due either to a higher inertia of invited majors to move or to a distinct behavior of the recruiter in front of the two invited castes. The latter explanation seems to be more plausible since recruiter antennations were ended when the stimulated ant began to move away. Due to these stronger invitations, the total percentage of exits of invited majors (45%) was even significantly higher than that of minors (25%; $\chi^2 = 8.1$, $df = 1$, $P < 0.01$).

Discussion

P. pallidula has developed a very efficient defensive strategy of cooperative attack: minors immobilize the intruders by seizing their legs, propagate alarm in their surroundings, and initiate the defensive recruitment whereas majors attacks are concentrated against spread-eagled enemies, killing them with their powerful mandibles. Such a polyethism has also been reported in New World *Pheidole* species (Wilson 1975, 1976; Wilson and Hölldobler 1985). By their hypertrophied mandibular muscles and their defensive behavior, majors appear to be specialized in fatal bites to enemies. However, the conventional view regarding *P. pallidula* majors as "soldiers" seems inadequate since 1) minors also participate very actively in the organized and collective defense of the colony and 2) majors' behavioral repertory is underestimated, this caste carrying out non-defensive tasks such as seed crushing (Creighton and Creighton 1959; Creighton 1966), food storage (Calabi et al. 1984), or nursing (Passera 1974; Wilson 1985). An indirect consequence of this underestimation is the lack of correlation between the morphology of *Pheidole* majors (Feener 1986) or their caste ratio in the nest (Ono 1984; Johnston and Wilson 1985; Calabi 1988) and the defensive constraints to be faced by the ant colony, contrary to what is predicted by optimization theory (Oster and Wilson 1978).

Concurrently with research on *P. militicida* and *P. dentata* species (Wilson 1975, 1976; Carlin and Johnston 1984; Feener 1986), our observations on *P. pallidula* colonies have highlighted the strong variability of defensive responses. For increasing numbers of intruding minors, the colony response shifts from a lack of recruitment to a progressive mobilization of workers to the combat area. Moreover, the defensive response differs for intruders of different fighting abilities as shown by recruitments against ten minor and ten major aliens, the latter always eliciting a stronger and faster reaction. These defensive strategies are probably deployed in nature against any enemy species inhabiting the nest vicinity and providing a range of quantitatively different threat intensities. Both caste polyethism and flexibility of the defensive response against invading ants can be considered as a complex and collective defensive behavior generated by simple rules at the individual level. Such simple rules have already been shown to regulate other collective behavior such as foraging activity (Wilson and

Hölldobler 1988; Detrain et al. 1990). In a defensive context, three basic rules were suggested from our observations:

1. Only minors having attacked alien ants or having been bitten by the intruders recruit nestmates to the combat area.
2. The intensities of the trail-laying and of the tactile invitations increase relative to the frequency of the attacks undergone by the recruiter on the combat area.
3. The two neuter castes differ in their behavioral threshold of response both to the trail and to the tactile invitations, majors being less inclined to move (see also Detrain and Pasteels 1991).

These three rules are adequate for generating, at a collective level, very sophisticated, diverse, and adaptive defensive responses. Against 10 intruder minors, the small number of aggressive encounters as well as the long time spent by resident minors biting and bringing the intruders back to the nest are responsible for the small number of weakly aroused recruiters coming back to the nest per time unit and, consequently, for the lack of defensive recruitment. Only higher numbers of intruders (40 or 60 alien minors) and more frequent aggressive encounters increase the number of potential recruiters which in turn induce a slow but noticeable mobilization of nestmates. Specificity of *P. pallidula* defensive response to intruders of different fighting abilities can also be generated by the same rules. Indeed, the number of recruiters and the intensity of their invitation are very high when faced by enemy majors because of the frequent bites undergone by resident minors during these strongly contested battles. This high number of recruiters as well as their very intense invitations are responsible for the fast and intense defensive recruitment against intruder majors. Due to the higher threshold of response to recruiting stimuli, majors are exposed to the dangers of a battle only during these massive recruitments, their exists being additionally triggered by their preferential tactile invitations.

In *P. pallidula* species, but also in other polymorphic ants such as *Orectognathus versicolor* (Carlin 1981), *Erebomyrma nevermanni* (Wilson 1986), *Camponotus spp.* (Buscher et al. 1985), or *Pheidole spp.* (Whitford et al. 1981; Fowler 1984; Wilson and Hölldobler 1985), caste polyethism leads to defensive efficiency at the group level. The location of enemies is ensured by the minors that possess all the qualities required for such a task:

1. They are very efficient in patrolling their territory because they are numerous and quickly moving relative to their body size.
2. Energetic costs for the loss of light-weighted minors during the dangerous first attempts to subdue enemies are less damaging for the colony than those encountered for the loss of energetically more valuable majors.
3. It is the only caste able to announce the presence of intruders by laying a trail: only minors' poison glands produce the trail pheromone (Ali et al. 1988; Detrain and Pasteels 1987).
4. The high number of minors is essential for generating and precisely regulating defensive recruitments. Indeed, the emergence of a collective pattern of defense from

individual recruitment seems to be ruled by self-organizing mechanisms that rely on non-linear, autocatalytic processes (Pasteels et al. 1987). Such a snowball effect can be generated only by the most numerous minor caste. Moreover, this small-sized and abundant caste makes more tolerable the "loss" of individuals outside trails that is inherent to the stochastic nature of self-organizing processes.

Due to their high response threshold, majors only fight at strategic places (around immobilized intruders) in crucial circumstances. This reduces the risks for the colony of losing members of such a valuable caste. Moreover, as in *P. hortensis* (Calabi et al. 1984), only majors with small abdomens actively fight intruders, reducing the costs of mortality inherent to any combat. Indeed, these light-weight majors are nimbler in avoiding opponents' bites while food reserves stored in replete individuals are preserved from hazardous fights. The mobilization of *P. pallidula* majors restricted to massive recruitments has already been found in non-agonistic contexts such as the exploitation of large prey requiring monopolization and defense against competitive species (Detrain and Pasteels 1991).

To summarize, at the colony level, the defensive strategy of *P. pallidula* colonies varies according to the identity and the number of invading enemies in a way that appears to be flexible, economic, and appropriate to defensive contingencies. These strategies as well as caste defensive polyethism can be explained by few decision making rules for recruiters and by quantitative caste behavioral differences without invoking complex behavioral repertoires distinct for the two castes.

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