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The Organization of Colony Defense in the Ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae)*

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Summary. 1. Colonies of *Pheidole dentata* employ a complex strategy of colony defense against invading fire ants. Their responses can be conveniently divided into the following three phases: (1) at low stimulation, the minor workers recruit nestmates over considerable distances, after which the recruited major workers ("soldiers") take over the main role of destroying the intruders; (2) when the fire ants invade in larger numbers, fewer trails are laid, and the Pheidole fight closer to the nest along a shorter perimeter; (3) when the invasion becomes still more intense, the Pheidole abscond with their brood and scatter outward in all directions (Figs. 1, 4).

2. Recruitment is achieved by a trail pheromone emitted from the poison gland of the sting. Majors can distinguish trail-laying minors that have just contacted fire ants, apparently by transfer of the body odor, and they respond by following the trails with more looping, aggressive runs than is the case in recruitment to sugar water. Majors are superior in fighting to the minors and remain on the battleground longer.

3. The first phase of defense, involving alarm-recruitment, is evoked most strongly by fire ants and other members of the genus *Solenopsis*; the presence of a single fire ant worker is often sufficient to produce a massive, prolonged response (Figs. 2, 5, 6). In tests with *Solenopsis geminata*, it was found that the Pheidole react both to the odor of the body surface and to the venom, provided either of these chemical cues are combined with movement. Fire ants, especially *S. geminata*, are among the major natural enemies of the Pheidole, and it is of advantage for the Pheidole colonies to strike hard and decisively when the first fire ant scouts are detected. Other ants of a wide array of species tested were mostly neutral or required a large number of workers to induce the response. The alarm-recruitment response is not used when foragers are disturbed by human hands or inanimate objects. When such intrusion results in a direct mechanical disturbance of the nest, simulating the attack of a vertebrate, both minor and major workers swarm out and attack without intervening recruitment.

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Introduction

The conventional view of defense in ants has been one of relatively complex individual behavior but simple colony organization. The single ant was seen to be sensitive to a wide range of stimuli, including the alarm pheromones of its nestmates, and to respond with generalized forms of aggression or retreat. In cases where the worker caste is divided into minor and major subcastes, the latter was regarded as being the more prone to combat under most or all circumstances. Defense at the colony level was not interpreted to be as well organized as, say, recruitment or caste determination (see review in Wilson, 1971).

All of these generalizations are probably incorrect, at least for some ant species. In the course of studies on the division of labor in the myrmicine *P. dentata* Mayr, I discovered that colony defense is at least as complicated and precisely organized as the most advanced, better known forms of social behavior. This article will show that colonies of *P. dentata* employ a flexible strategy in dealing with invading ants, one that is qualitatively different from defense against vertebrates. The strategy consists of three phases initiated in sequence by an increasing magnitude of the challenge: destruction of scouts and small enemy forces well away from the nest entrances, followed by reduction of the defense perimeter so that fighting occurs closer to the nest until the enemy is eliminated by attrition, and, finally, when the colony is attacked by still larger numbers, the abandonment of the nest premises in a sudden exodus. Most of the defense is orchestrated by the use of the trail pheromone by the minor worker caste. As demonstrated in an earlier, preliminary report (Wilson, 1975), this alarm-recruitment system is evoked only by a narrow range of ant species, the foremost of which are the fire ants and other members of the genus *Solenopsis*. It will be argued that such selectivity, which in effect constitutes enemy specification, is an adaptation to the particular environment in which *P. dentata* lives.

Materials and Culturing Methods

Pheidole is one of the several most abundant, diverse, and geographically widespread ant genera of the world. *P. dentata* is a medium-sized form which is abundant in woodland over most of the southern United States (Creighton, 1950). Like other members of the genus, it is characterized by a sharp division of the worker caste into small-headed minor workers, which forage for food and conduct the other quotidian tasks of the colony, and large-headed major workers, or "soldiers" as they are often called, which function primarily in defense. The majors also have proportionately more distensible crops and hence store larger quantities of liquid food. But the large head, with its massive adductor muscles and clipper-like mandibles, is highly specialized for the fighting role of this caste.

Entire colonies, collected in the field in the Tallahassee region of northern Florida, were placed in plexiglas containers 28 cm × 45 cm and 16 cm deep, the sides of which were coated by Fluon GP-1 (ICI America, Inc., Stamford, Conn.) to prevent escape. The floor of each container served as the foraging space and experimental arena for a single colony. The ants were permitted to move into test tubes 148 mm long with 23 mm inner diameter, kept moist by tight cotton plugs that trap water at the bottom of the tubes. This simple arrangement required a minimum of subsequent care, yet permitted close inspection of the behavior of the entire colony both inside and outside the nests. The colonies flourished when maintained on a mixture of Bhatkar diet (Bhatkar and Whitcomb, 1970) and freshly killed insects, eventually rearing large numbers of winged queens and males.

In the behavioral tests the nest tubes were placed at one end of the container, and the remainder of the floor of the container was kept clear for observations of foraging and colony defense. Alien ants were introduced at a point on the floor approximately 25 cm from the Pheidole tube nests. A positive response was defined as the recruitment of major workers by minor workers to this area. The number recruited was defined as the maximum number seen beyond a line 20 cm from the end of the container (hence, a 20 × 28 cm sector around the invaders) for 30 min following the introduction minus the maximum number of majors seen in the same area during the 15 min immediately preceding the introduction.

Results

1. The Three Phases of Colony Defense

Phase 1 (Distant Alarm-Recruitment). When workers of the native fire ant *S. geminata* are placed within 25 cm of the nest tubes of a laboratory *P. dentata* colony, they soon encounter foraging Pheidole minor workers. Some of the foragers grapple with the intruders, while others flee and travel in irregular loops through the surrounding area. Within seconds, some of the minor workers run swiftly back and forth to the nest, dragging the tips of their abdomens over the ground. The trail pheromone thus deposited attracts both minor and major workers from the nest in the direction of the invaders. The majors have never been seen to lay trails. Their glandular anatomy is very different from that of the minors, and artificial trail bioassays (see Wilson, 1959) employed with them suggest that no part of their body contains a trail pheromone. Thus the communication is unilateral.

Upon arriving at the battle scene the major workers become highly excited, snapping at the fire ants with their powerful mandibles and soon chopping them to pieces (see Figs. 1, 5). The recruited minor workers also join the fighting, but they are less persistent and remain in the area for much shorter periods of time. As a result the majors increase in proportion, and for all but the more transient invasions they eventually outnumber the minors, despite the fact that they constitute only 8–20 percent of the worker population in the great majority of nests. The majors remain in the battle area for an hour or more after the last Solenopsis has been dispatched, restlessly patrolling back and forth (see Fig. 2). Often a single Solenopsis worker is enough to evoke the full response, which brings ten or more Pheidole majors into the field. This is one of the first examples documented of an alarm-recruitment system in ants, a phenomenon previously well known in termites (see review in Wilson, 1971). A second, independently discovered case has recently been reported in *Myrmica rubra* by Cammaerts-Tricot (1974, 1975).

Fig. 1. The first phase of colony defense by the ant *P. dentata*. After contacting fire ant workers near the nest, minor workers of Pheidole run back and forth to the nest, dragging the tips of their abdomens over the ground and laying odor trails (*upper left*). The trail pheromone attracts both minor and major workers to the battle ground. The majors are especially effective in destroying the invaders, which they chop to pieces with their powerful, clipper-shaped mandibles. Some of the Pheidole are themselves crippled or killed by the venom of the fire ants. (Original drawing by Sarah Landry)

Phase 2 (Close Defense). If the initial invading force strongly outnumbers the foraging minors, the colony goes directly into the second phase of defense. If, on the other hand, the invaders increase gradually in number, the colony passes from the first phase into the second. In the second phase few, if any, minor workers lay odor trails to the outer foraging area. Some grapple with the fire ants, but most simply flee from the area back toward the nest. As a result, the fire ants soon advance close to the Pheidole nest. Here they encoun-

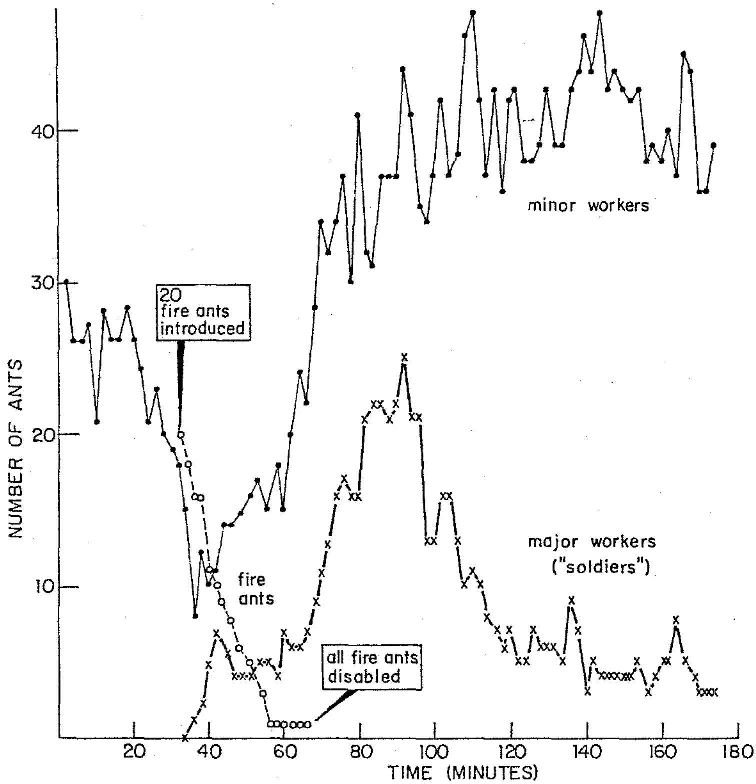


Fig. 2. During the first phase of colony defense, which is initiated by a relatively small force of invading fire ants, the number of minor workers in the 28 × 20 cm area around the invaders decreases, while that of the major workers increases. The majors restlessly patrol the area long after the last fire ant has been destroyed. In the typical experiment reported here, 20 workers of the fire ant *S. geminata* were introduced in a group 25 cm from the Pheidole tube nests

ter and are challenged by majors resting in and around the nest entrances. Some of the Pheidole minors also lay trails at close quarters, bringing still more majors to the conflict. The mass of fighting majors, assisted by a few minors, form a short, tight defense formation around the nest entrances (see Fig. 3).

Phase 3 (Absconding). If fire ants continue to invade the nest area in spite of the efforts of the Pheidole majors, excitement spreads through the workers remaining in the nest. An increasing number of minor workers race back and forth, some picking up and carrying packets of eggs, larvae, and pupae. Others leave the nest and stand or run around in the immediate vicinity of the nest entrances. Then, during a period of only a few minutes, the minors start leaving the nest with pieces of brood in their mandibles. Some remain near the nest entrances, but more and more run rapidly away in various directions, so that the colony as a whole scatters outward. The queen joins the exodus, breaking through the fighting masses of fire ants and Pheidole majors to flee on her own (see Fig. 4). Under laboratory conditions at least, the colony slowly returns

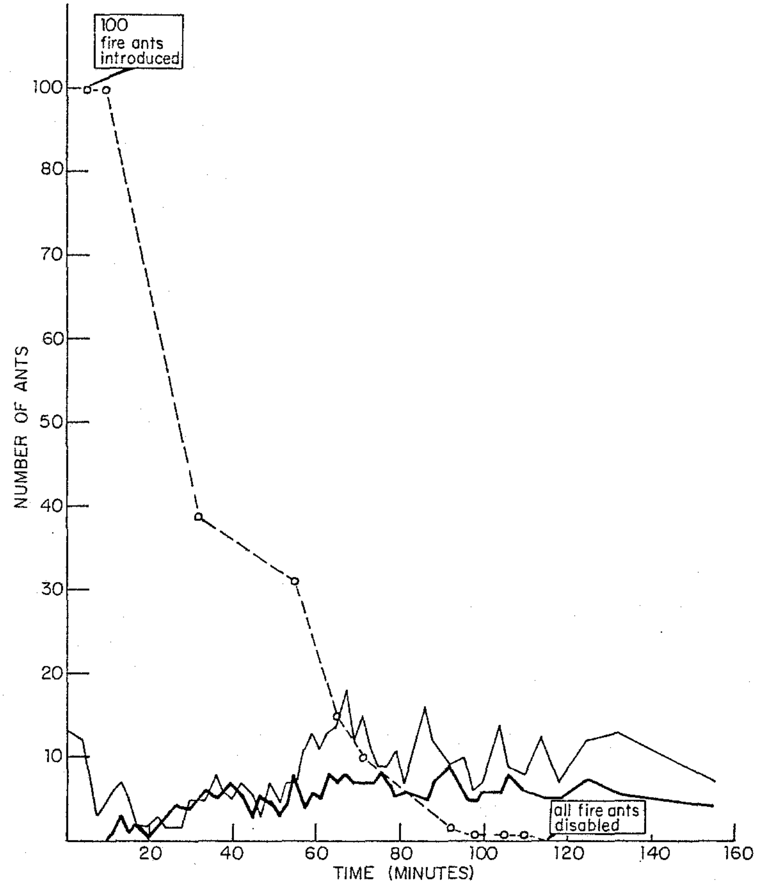


Fig. 3. The second phase of colony defense is initiated when a relatively large number of fire ants are introduced near the nest. In this case 100 *S. geminata* were placed 25 cm from the Pheidole nest tubes (cf. Fig. 1). The number of minor workers (*thin line*) decreases as in the first phase, but now few if any lay odor trails. As a result a smaller number of major workers (*thick line*) are attracted away from the nest. Most of the fighting occurs close to the nest entrances rather than in the 20 × 28 cm outer area from which the above data were obtained

to the nest after the fire ants are destroyed or leave. But when a large fire ant colony is permitted to attack a Pheidole confined to its nest area, it wipes out the defenders and removes and eats their brood.

2. *Analysis of the First Phase of Defense*

The Recruitment Process. Some of the minor workers that have just contacted fire ants run homeward, dragging the tips of their abdomens over the ground. Nestmates that encounter these individuals or cross their paths run excitedly along the paths, usually in a direction away from the nest. It is a reasonable

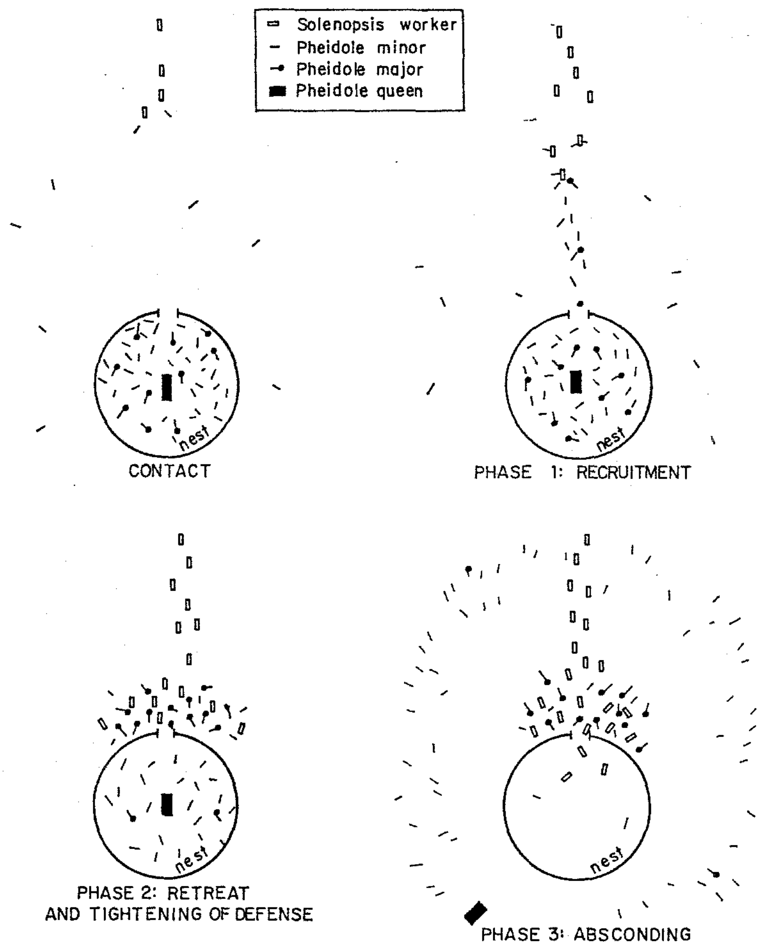


Fig. 4. An abstract representation of the three phases of colony defense

presumption, therefore, that odor trails are being laid from the vicinity of the invaders. In time substantial numbers of minor and major workers can be seen travelling back and forth along the exact paths taken by some of the recruiter ants. No other reasonable explanation of the alarm-recruitment process seems possible except that it is based in large part on the deposition of a trail pheromone.

The source of the trail pheromone was sought by means of the artificial trail bioassay. First, it was established that trails made from ethanol extracts of the whole bodies of minor workers were followed by large numbers of both minor and major workers. Similar whole extracts of major workers failed to cause this response. Next, several of the most likely source organs were dissected one at a time from the abdomens of single workers, washed in insect Ringer's solution, crushed on the tip of a birch applicator stick, and smeared in artificial trails running from one of the nest entrances outward for a distance of 35 cm into the foraging area. The number of workers following the trail for at least half its distance was then recorded. The results, presented in Table 1, appear conclusive. The trail pheromone is concentrated in the poison gland of the minor worker. The paired poison glands proper and the vesicle into which they empty were assayed together. As expected, no trace of the pheromone was detected in the poison gland of the major worker. This structure is proportionately larger than in the minor worker and differently shaped, and it almost certainly serves a different function.

Although the experimenter can easily induce trail-following with the use of the pheromone alone, other elements are present in alarm recruitment that make it qualitatively different from ordinary recruitment. When minor workers of *P. dentata* discover a drop of sugar water, for example, they first feed – often to repletion – and then return to the nest laying a trail. The speed at which they run is no greater than that seen during foraging. When they encounter nestmates they often turn toward them briefly, and a very brief mutual antennation may ensue that appears no different from that exchanged between workers on other occasions. No other forms of tactile communication have been observed. Both minor and major workers follow the trail closely, moving calmly at a rate not greatly exceeding that seen during foraging. The ratio of major to minor workers responding is close to or somewhat below that occurring in the colony population at large (see Table 2); the latter ratio ordinarily falls between 10 and 20 major workers per 100 minor workers.

Alarm recruitment contains differences at every step. After encountering fire ants, Pheidole minor workers lay odor trails while running swiftly. When they encounter other minor workers, their contact consists at most of a fleeting antennation. When major workers are contacted, however, the trail-layers rush at them, strongly vibrating their bodies for a fraction of a second. The major workers respond by rushing outward in short, irregular loops, following the odor trail only loosely and for brief intervals. Their mandibles are held more

Table 1. Response of Pheidole colonies to artificial trails made of various crushed abdominal organs of minor and major workers. A positive response was recorded when a worker ran along the trail for a distance of at least 18 cm. The ranges (and means) of numbers of minors and majors responding are given

Source of artificial trail		Number of replicates	Number following trail	
Caste	Organ		Minor workers	Major workers
Minor worker	Hindgut	6	0	0
	Dufour's gland	7	0	0
	Poison gland + vesicle	7	24–136 (71)	1–22 (8)
Major worker	Hindgut	6	0	0
	Dufour's gland (absent in this caste)	–	–	–
	Poison gland + vesicle	6	0	0

widely open than usual, and the majors rush at any objects they encounter, including their own nestmates. Fire ants are invariably attacked. Minor workers also move in looping movements but are not noticeably more aggressive. As shown in Table 2, the proportion of major workers responding to alarm recruitment is higher than those responding to sucrose recruitment and in the nest population at large. In 27 of the 32 comparisons made, the difference was significant at the 99 percent level or higher. To be sure that the difference was truly qualitative and not simply due to an indifference to sucrose due to overfeeding, I recorded the ratios of majors and minors in colonies that were first freshly fed and then starved for a period of eleven days. The results, given in Table 2, show that the difference in response persists in hungry colonies.

How do the major workers know that they are being recruited to fire ants and not to sucrose water? The vibration of the recruiters could provide a tactile clue. However, it is equally possible that the vibration merely enhances the transmission of an odor cue. The latter hypothesis is supported by the fact that minor workers do not receive the vibrating movement and yet seem to recognize that the object of the recruitment is different. The critical cue may be nothing more than odor accidentally transferred from the fire ants onto the defending Pheidole minor workers during the initial contact. To test this possibility, ten minor workers were seized with flexible forceps as soon

Table 2. The number of minor workers and major workers responding to odor trails laid by minor workers from sucrose solution and ten fire ants, respectively, on successively longer periods after the last feeding. Each count was terminated when 100 minor workers had been recorded

Days since last feeding	Caste responding	Colony No. 1		Colony No. 2		Colony No. 3	
		Sucrose solution	Fire ants	Sucrose solution	Fire ants	Sucrose solution	Fire ants
1	Minor	100	–	100	100	100	100
	Major	6	–	1	23	1	16
2	Minor	100	100	100	100	100	100
	Major	4	30	16	44	6	13
3	Minor	100	100	100	100	100	100
	Major	6	39	25	54	21	23
4	Minor	100	100	100	100	100	100
	Major	13	46	13	40	9	51
7	Minor	100	100	100	100	100	100
	Major	9	18	14	37	20	16
8	Minor	100	100	100	100	100	100
	Major	5	72	21	38	10	17
9	Minor	100	100	100	100	100	100
	Major	5	45	13	39	8	32
11	Minor	100	100	100	100	100	100
	Major	8	37	12	27	9	45

as they contacted fire ants, then dropped into the midst of groups of minor and major workers resting outside the nest entrance. In every case, the first nestmates to encounter the introduced workers rushed toward them in what appeared to be an initially hostile move; in two instances the workers were even grasped by the appendages and dragged about briefly before being released. As controls, ten other minor workers were seized and transported by forceps in a fashion identical in every detail except that they had not contacted a fire ant worker. These individuals were accepted by nestmates with neither a display of hostility nor even an outward show of interest. It is reasonable to conclude at least tentatively that the combined stimuli of pheromone trails and the odor of fire ants are crucial to triggering the distinctive response of the Pheidole alarm-recruitment system. It remains to be learned whether the vibration of the minor worker's body, or other, still unsuspected signals, play auxiliary roles.

Duration on the Battlefield. As the fighting proceeds, the proportion of major workers on the battlefield gradually increases (see Figs. 2, 3). In extreme cases only major workers remain in the end. When the colony absconds, most of the majors stay behind to fight. Furthermore, recruited majors remain in the battle area for much longer periods of time than do recruited minors. In one typical episode 30 majors, chosen at random as they crossed into a 100 cm^2 square around ten fire ants, remained in the square from 4 to 470 secs, averaging 70.5 secs per stay; 14, or 47 percent, remained for more than 50 secs. In contrast, 30 minors chosen at random stayed 2 to 64 secs, averaging 17.2 secs per stay, with only 2 individuals, or 7 percent, remaining over 50 secs.

Fighting Ability. The Pheidole majors are far superior to the minor workers in their ability to disable and to kill fire ant workers. They seize the fire ants by an appendage, the neck, or some portion of the petiole or postpetiole, then cut through the body part with their powerful mandibles. When faced by a phalanx of scurrying, snapping majors, few fire ants remain mobile for more than a minute or two. The Pheidole minor workers attempt the same tactic, but they are less frequently successful. Members of both Pheidole castes are crippled and killed by the bites and venom of the fire ants, but the majors suffer a much lower casualty rate. These differences in performance are exempli-

Table 3. Results of one-on-one combat between each of the two castes of *P. dentata* against minor workers of the fire ant *S. geminata*

	Both separate unhurt	Both crippled or killed	Pheidole crippled or killed, Solenopsis unhurt	Solenopsis crippled or killed, Pheidole unhurt
Pheidole minor worker vs. Solenopsis minor worker	20	5	36	11
Pheidole major worker vs. Solenopsis minor worker	12	7	4	60

fied by the results of 155 randomly chosen one-on-one combats shown in Table 3. The probability that these differences could be due to chance alone is less than one in a million.

3. The Second and Third Phases of Defense

When minor workers encounter large numbers of fire ants, a few grapple with the intruders but most scatter outward in all directions. Only a minority of those fleeing return directly to the nest, and proportionately few odor trails are laid even by these individuals. Consequently the fire ants are able to move quickly to the vicinity of the Pheidole nest. There they encounter stiffening resistance as more minor workers are encountered, a larger number of trails are laid, and a growing force of major workers is assembled. Thus the second phase of defense is only an extension of the first conducted in another location. It may seem paradoxical that when faced with more enemies the colony should recruit majors less efficiently. But this weaker response applies only to the territory farthest from the nest. The result of importance is that the majors are committed to battle close to the nest, where in fact they are now most needed.

If the second phase of defense begins to break down, the colony absconds, which constitutes the final, desperate, yet very effective maneuver. The following events lead to absconding. As the fire ants crowd closer to the nest entrances, an increasing number of Pheidole minor workers lay odor trails all the way back to the brood areas. As a result the excitement of the nest workers increases, and many begin to pick up pieces of brood and carry them back and forth. Meanwhile, the defense perimeter continues to shrink as Pheidole majors are immobilized in combat and more Pheidole minor workers are either immobilized or flee from the nest area after contacting fire ants. Activity within the brood area builds up, sometimes at an apparently exponential rate, and minor workers then begin to run out of the nest, many laden with pieces of brood. At first there is a strong tendency for the refugees to loop back and reenter the nest, but if they continue to encounter fire ants they break away entirely and flee outward. No particular direction is taken by individuals during the exodus, so that the colony ends up scattered over a wide area. The queen also departs under her own power. Later, after settling down, she attracts minor workers who cluster around her. No direct physical transport of one adult by another has been observed. When the fire ants are removed, the Pheidole adults slowly return to their nest and reoccupy it.

In summary, there appear to be two processes contributing to the relative suddenness and *en masse* quality of absconding:

1) As fire ants press in, more and more Pheidole of both castes are killed, while other minor workers simply desert the area. This leads to a steadily decreasing ratio of defenders to invaders and a shrinking of the defense perimeter. A point is reached in which the nest workers are contacting fire ants at a sufficiently high rate to cause them to seize brood pieces and leave. This final, critical level is approached steeply.

Table 4. Effectiveness of thirty ant species in evoking the alarm-recruitment response of *P. dentata*. A positive response was recorded when major workers of *P. dentata* were recruited by the minor workers. Also shown is the change in the number of majors in the battle area. Species indicated by an asterisk (*) occur as native inhabitants in at least part of the range of *P. dentata*

Species	Number of invading workers	Number of repli-cations	Number of positive responses	Change in number of majors in battle area: range (mean)
Subfamily Ponerinae				
Leptogenys manni	1 or 2	5	0	−2 to 0 (−1)
Subfamily Dorylinae				
Neivamyrmex opacithorax	10	16	11	−1 to 16 (7)
**N. opacithorax*	1	5	0	−1 to 1 (0)
Subfamily Pseudomyrmecinae				
Pseudomyrmex elongatus	10	5	0	−1 to 1 (0)
Subfamily Myrmicinae				
**Myrmica* sp.	5	3	0	−1 to 1 (0)
**Stenamma* sp.	10	3	0	−1 to 1 (0)
Pogonomyrmex badius	3	5	0	−1 to 2 (1)
**P. badius*	10	1	1	41
P. occidentalis	2	5	0	−1 to 3 (1)
Aphaenogaster rudis	10	5	1	−2 to 6 (1)
Tetramorium caespitum	10	5	0	0 to 2 (1)
T. caespitum	100	1	1	15
Atta sexdens, minor workers	10	5	0	0 to 1 (0)
Zacryptocerus varians, minors+majors	10	5	0	−2 to 2 (0)
Pheidole dentata	1	18	0	−2 to 5 (0)
**P. dentata*	10	26	4	−3 to 11 (2)
**P. dentata*	100	6	3	−3 to 63 (17)
**P. dentata*	200	4	4	10 to 57 (32)
P. desertorum	10	1	0	2
**P. floridana*	10	3	0	0 to 1 (1)
Xenomyrmex floridanus	10	5	0	−1 to 3 (1)
Crematogaster atkinsoni	10	1	0	0
**C. minutissima*	10	5	0	0
**C. minutissima*	100	1	0	3
Monomorium minimum	10	10	1	−5 to 4 (0)
**M. minimum*	50	2	2	6 to 10 (8)
M. pharaonis	10	4	3	0 to 9 (5)
Solenopsis fugax	1	5	2	−1 to 8 (2)
S. fugax	10	5	5	7 to 12 (11)
**S. geminata*	1	24	19	−1 to 37 (9)
**S. geminata*	10	33	33	3 to 72 (27)
**S. geminata*	100	6	6	4 to 31 (20)
**S. geminata*	200	2	2	3 to 10 (6)
**S. molesta*	10	5	4	1 to 32 (11)
**S. picta*	10	5	2	−1 to 10 (3)
**S. xyloni*	10	5	5	3 to 68 (41)
Subfamily Dolichoderinae				
Tapinoma sessile	10	3	0	0 to 1 (0)

Table 4 (continued)

Species	Number of invading workers	Number of repli-cations	Number of positive responses	Change in number of majors in battle area: range (mean)
Subfamily Formicinae				
**Brachymyrmex depilis*	10	1	0	1
**Lasius alienus*	10	3	0	2 to 4 (3)
Acanthomyops interjectus	5	3	3	5 to 7 (6)
A. interjectus	1	10	3	0 to 10 (3)
**Camponotus fraxinicola*	10	3	0	0 to 2 (1)
C. planatus	5	3	0	−2 to 1 (0)

2) Simultaneously, there is an exponential increase in the rate at which minor workers run back and forth between the vicinity of the nest entrance and the brood chambers. Since many lay odor trails, there appears to be a buildup in the concentration of the pheromone.

It has been possible to induce part of the absconding process by exposing the ants to their own volatile substances. In two replications I first immobilized 50 minor workers of *P. dentata* by freezing, then crushed them simultaneously between two glass slides approximately 5 cm above the nest entrances. The action caused moderate excitement, with both minor and major workers emerging from the nest. The ants were apparently attracted by odor, since many lifted and waved their antennae back and forth in the direction of the slides. They spread over the nest tubes and in the surrounding area; some dispersed outward still farther, trying to climb the walls of the arena. These actions closely resembled the early stages of absconding, although neither brood carrying nor departure of the queen were included. The movement of glass slides in an identical manner but without the crushing of ants did not induce attraction or dispersal.

4. *Enemy Specification*

Perhaps the most surprising discovery made during the entire analysis was the specificity of the alarm-recruitment response by *P. dentata*. In addition to the native fire ant *S. geminata*, five other species of *Solenopsis* tested in the laboratory were found to evoke alarm recruitment when introduced into the foraging arenas in small numbers. These are the red imported fire ant *Solenopsis invicta*, the native fire ant *Solenopsis xyloni*, and the "thief ants" *Solenopsis fugax*, *Solenopsis molesta*, and *Solenopsis picta*. The last three forms are members of the subgenus *Diplorhoptrum*, recognized as taxonomically distinct from the fire ants of the genus *Solenopsis*, and they are among the smallest of all ants. Their effectiveness in producing the response is thus even more impressive. None of the 24 other ant species tested thus far, representing 20 non-solenopsidine genera and six of the eight living subfamilies, proved effective at comparable numbers (see Table 4, and Fig. 5).

The closest approach to an exception is *Pogonomyrmex badius*, which is ineffective when the number of invaders is three, but evokes the response when the number is increased to ten. But compared to the Solenopsis and most of the other ant species tested, *P. badius* is gigantic; a single minor worker

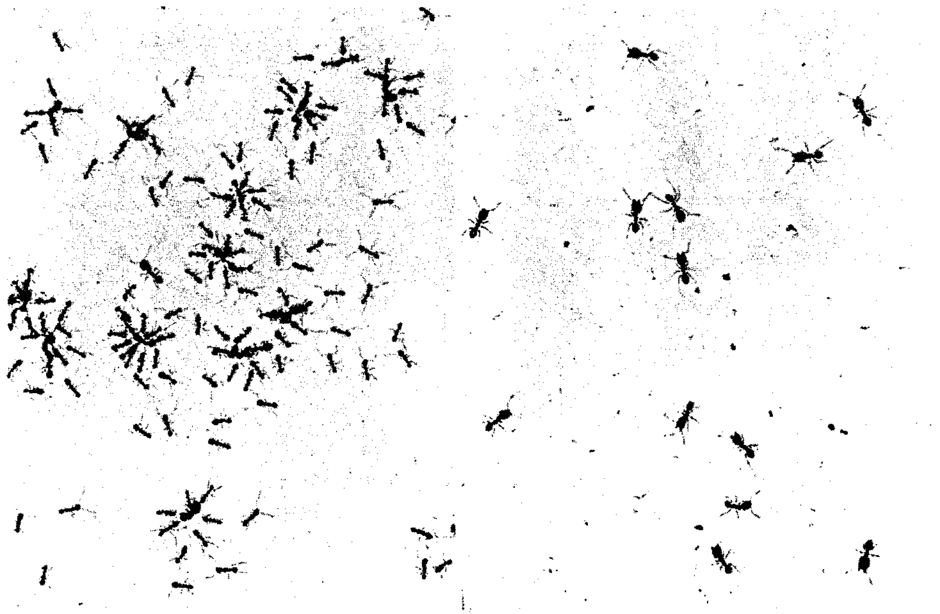
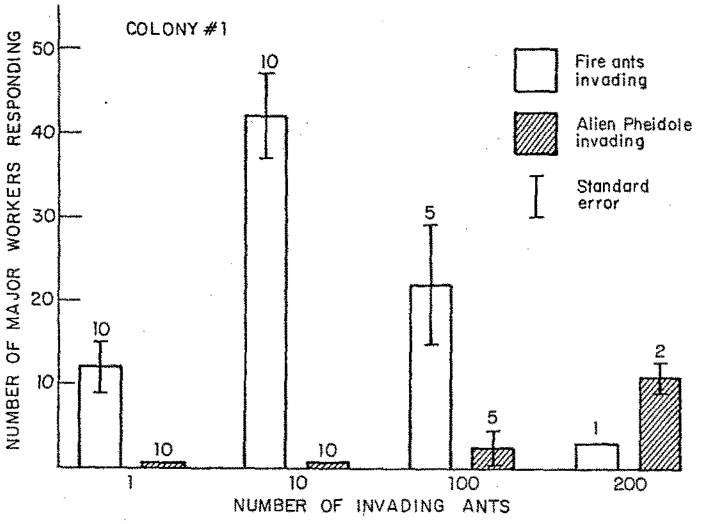


Fig. 5. Different modes of defense by the ant *P. dentata* against two species of invading ants. *Left:* workers of *T. caespitum* are pinioned and disabled mostly by Pheidole minor workers, which have not recruited major workers to their aid. The few majors present were stragglers in the area. *Right:* in response to the same number of workers of the fire ant *S. geminata*, the Pheidole minor workers have already destroyed the invaders and are patrolling the battle area. The scene has been largely abandoned by the minor workers. (From Wilson, 1975)

weighs about 6.88 mg, compared with 0.33 mg in the case of *P. dentata*, 0.38 mg in *S. geminata*, and only 0.06 mg in *S. molesta* (based on the wet weights of ten workers of each species). Relatively mild responses were also obtained by ten workers of the army ant *Neivamyrmex opacithorax*, the myrmicine *Monomorium pharaonis*, and formicine *Acanthomyops interjectus*, but they were well below those produced by fire ants. There may be a level at which any ant species can cause the alarm-recruitment response. One hundred minor workers from alien colonies of *P. dentata* were sufficient to cause it, as were 100 *Tetramorium caespitum*. However, 100 workers of *Crematogaster minutissima* still failed to evoke the response. In general, the numbers of non-solenopsidine ants comparable in size to *P. dentata* and *S. geminata* required to evoke the response is more than ten times that for *S. geminata*.

A more detailed comparison of the effects of two species is presented in Fig. 6. It can be seen that a single fire ant worker causes recruitment, and ten workers substantial recruitment, but 100 of these invaders reduces the magnitude of the response. The decline under more intense pressure has been explained previously; the colony is entering Phase 2 of its defense as more of the minor workers pull back, and fighting is increasingly restricted to the immediate nest vicinity. The data illustrate another phenomenon for which the author has no explanation: a marked variation among *P. dentata* colonies in the pattern of response to fire ants. Considerable differences exist in the intensity of response



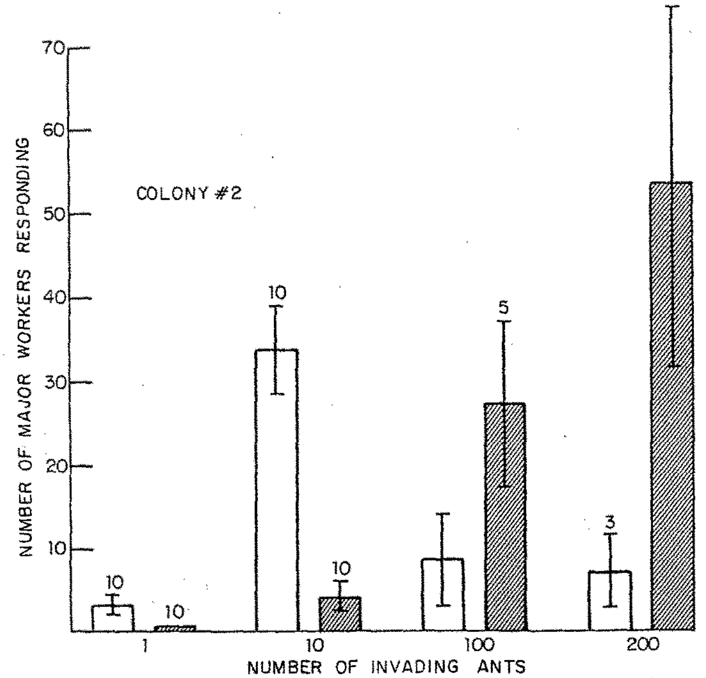


Fig. 6. The responses of two *P. dentata* colonies to increasing numbers of fire ants (*S. geminata*) and minor workers of *P. dentata* from alien colonies. The number of replications are given at the tops of the bars. A second trial in colony no. 1 utilizing 200 fire ant workers, not indicated here, resulted in most of the Pheidole colony absconding. These two colonies were selected because they represent different patterns of response to increasing numbers of invaders. (Fig. based on colony no. 1 from Wilson, 1975)

to particular numbers of invaders. Some variation of this kind has also been displayed by single colonies tested repeatedly over a period of weeks, but it does not equal the variation among many colonies noted in the laboratory on a single day.

In order to determine whether the response specificity is a widespread phenomenon, 15 colonies collected at four localities in Leon and Wakulla Counties, northern Florida, were challenged at successive intervals with ten minor workers of *S. geminata* and ten minor workers from alien colonies of *P. dentata*. All of the colonies responded positively to the Solenopsis, while only two were activated by the alien Pheidole. Moreover, the latter two colonies recruited many more major workers to the Solenopsis than to the Pheidole.

An effort was made to localize the cues by which *P. dentata* recognize Solenopsis.

The procedure followed was closely similar to that employed in the testing of various species of ants. The tests were conducted on *P. dentata* minor workers in the same zone of the foraging arena. Corpses of *S. geminata* tested without movement were simply placed on the floor of the arena shortly after being killed by freezing and rewarmed to room temperature. Movement was achieved in other tests by holding the object to be tested in the tips of fine forceps (which forceps were previously washed in ethanol and water and dried) and rapidly vibrating the object back and forth through a 1-cm arc by hand movement. During the vibration the object was directed at one minor worker after another, striking it lightly and allowing it to attack and depart at will. Bare forceps were also used to seize the legs of the minor workers and to pull them back and forth during the 1-cm movement. In order to test the effectiveness of *S. geminata* venom, the forceps tips were smeared with venom "milked" from three Solenopsis minor workers. Milking was accomplished by breaking off the abdomens of the Solenopsis workers and smearing the droplets of venom directly onto the forceps as the droplets exuded from the tips of the extended stings.

The results of these experiments, which are presented in Table 5, can be summarized as follows. It was found that freshly killed *S. geminata* were ineffective, even in large numbers, and whether intact or crushed. Also, steel forceps and wooden dummies do not cause the response, even when violently agitated among the Pheidole foragers—even to the extent of crippling and killing some of them. But single, freshly killed *S. geminata* workers are effective when held in forceps and agitated. The abdomen alone is more effective than the head or mesosoma alone. Wooden dummies treated with *S. geminata* venom and agitated cause the response, but so do live *S. geminata* workers with abdomens (and hence venom) removed. Thus either contact with venom or the odor of the body surface is sufficient, providing the chemical stimulus is associated with movement. The differences on which these conclusions are drawn are significant to at least the 95% level, and in most instances to the 99% level.

The specificity of response to the body odor of *Solenopsis* is further indicated by the following result. As shown in Table 4, *P. dentata* responds with relatively modest vigor to the presence of ten *M. pharaonis*. The venom of this species has been shown to have an especially repellent effect against other ants (Hölldobler, 1973). When the abdomens of ten workers were removed, and hence the venom, the workers failed to evoke alarm-recruitment in two replications. Hence, unlike the stimuli provided by *S. geminata*, the body odor of *M. pharaonis* was not sufficient by itself to trigger the response.

Table 5. The response of *P. dentata* colonies to various objects laid motionless on the arena floor or held in forceps and agitated. The object of the tests was the localization of the cues by which *P. dentata* recognize fire ants (*S. geminata*) and initiate alarm recruitment

Objects tested	Procedure	Number of replications	Number of positive responses	Number of Pheidole major workers responding
Controls:				
Wooden square 3 mm wide	Agitated 4 min	10	0	0 to 1 (0)
Forceps	Tips agitated and used to seize Pheidole during 4-min periods	9	1	0 to 2 (1)
Tetramorium caespitum (1 worker)	Fresh corpse held in forceps and agitated 4 min	6	0	−1 to 1 (0)
Experimentals:				
Solenopsis geminata (10 entire workers)	Fresh corpses placed on arena floor	10	0	−1 to 1 (0)
S. geminata (10 workers with abdomens removed)	Live workers with abdomens removed placed on arena floor	10	10	7 to 28 (15)
S. geminata (1 entire worker)	Fresh corpse held in forceps and agitated 4 min	10	7	0 to 10 (6)
S. geminata (1 head)	Head of corpse held in forceps and agitated 4 min	10	4	−1 to 5 (1)
S. geminata (1 mesosoma)	Mesosoma of corpse held in forceps and agitated 4 min	10	2	−2 to 2 (0)
S. geminata (1 abdomen, incl. pedicel)	Abdomen (incl. pedicel) held in forceps and agitated 4 min	10	7	3 to 18 (8)
Forceps with *S. geminata* venom	Tips smeared with venom and agitated 4 min	10	10	5 to 23 (14)

Discussion: The Ecology of Alarm Recruitment

The author was at first baffled by the discovery of enemy specification. However, further consideration of the ecology of *P. dentata* removed the mystery, and the following explanation now seems reasonably well established. The distribution of the native fire ant *S. geminata*, to which *P. dentata* responds so strongly, broadly overlaps that of *P. dentata* through the southern United States. The two species occur together in many of the same habitats, particularly open mixed pine-hardwood forests. To some extent they even utilize the same nest sites, principally logs and stumps in an advanced stage of decay. *S. geminata* forms the largest, most aggressive colonies of any potential competing native ant species. It also employs a swift, precise trail system which is initiated by scouts when they discover food or new nest sites (Wilson, 1962).

When *S. geminata* colonies are given close access to *P. dentata* colonies in the laboratory, they launch swift, overwhelming attacks. Each fire ant colony contains tens of thousands of workers—in nature, this number often exceeds 100,000—which enjoy a decisive numerical advantage over the several thousand workers that comprise a typical *P. dentata* colony.

On two occasions I allowed wars between Solenopsis and Pheidole colonies to proceed to a conclusion in the laboratory. The nest areas of the two species were connected by a glass tube 80 cm long supported on Erlenmeyer flasks which were in turn set alongside the nest tubes. In both cases *S. geminata* scouts quickly climbed the flasks, ran along the bridges, and descended to the Pheidole nests, all within 15 min and before Pheidole scouts could begin to climb the flasks on their own side. The Solenopsis laid odor trails back and forth, and the invading forces engaged the Pheidole minors and majors as the Pheidole colony proceeded through the first two phases of colony defense. In one case the Pheidole were quickly overwhelmed, and they absconded only 28 min after the bridge was laid in place. Unable to escape over the arena walls, the fleeing Pheidole were then methodically destroyed by the fire ants. Within 65 min all of the Pheidole adults, including the queen, were dead, and the fire ants were carrying off the captured brood. The fire ants subsequently ate the Pheidole brood, but they merely collected the Pheidole adult corpses in piles and abandoned them. They also occupied the deserted nest tubes. Hence the Solenopsis gained both food and nest space as the rewards of their assault. In the second experiment the Pheidole held their own for a while, destroying virtually all of the fire ants that descended to their nest area. However, within 2 h the tide of battle turned, and at 2 h 14 min the Pheidole absconded. The invaders were beginning to destroy the survivors and to carry away the brood when the experiment was halted in order to save the colony.

Clearly, it is essential for Pheidole colonies to halt invasions by fire ants in the earliest stages. It is of advantage to strike hard and fast whenever a fire ant scout is discovered near the nest. The danger is sufficient to commit major workers to destroy even a single intruder and to search the surrounding area for the presence of additional scouts. This observation is apparently sufficient to explain the seeming overreaction to single fire ants which has been observed in the first phase of colony defense (see Fig. 6).

The slight departures from genus specificity in the alarm-recruitment response also appear to have rational explanations. At an early stage in the study it was predicted that *P. dentata* would react to army ants of the genus *Neivamyrmex*, which are predators of other ants that occur in the same habitats as the Pheidole. This was subsequently shown to be the case, although the response did not prove to be as strong as that displayed toward fire ants (see Table 4). It was also anticipated that species of *Monomorium* might evoke the response, because they are phylogenetically the closest to Solenopsis of all the North American ants. This also proved to be true to a limited degree. The moderately positive response to *A. interjectus* was more surprising. *Acanthomyops* is a northern genus with a distribution that barely overlaps the northern fringes of the *P. dentata* range. It is possible that the relatively large size of these formicine ants and the large quantities of citronellal and other defensive secretions they expel are the key stimuli.

Finally, it should be noted that alarm-recruitment appears to be limited to other ants. When foraging minor workers are disturbed by human hands or inanimate objects they usually attempt to flee and only rarely attack. They have never been observed to recruit nestmates. When the nest is shaken or penetrated by human hands or an inanimate object, in a manner simulating an attack by a vertebrate predator, a large percentage of both the minor and major workers rush out, swarm over the offender, and attempt to bite it. The total effect is slightly painful to a human being and might serve as a deterrent to smaller vertebrates. Other minor workers seize pieces of brood and retreat deeper into the nest. If the disturbance continues and is serious enough, the colony leaves. There is no evidence of alarm recruitment during the entire process. Thus basically different defense strategies are employed against vertebrates as opposed to other ants.

It will be interesting to learn to what extent alarm-recruitment systems occur in other ant species in addition to pure recruitment systems, as is the case in *P. dentata*, and whether they are specifically directed at principal enemies. The significance of the present study is the demonstration that the entire defense strategy of an ant, including its alarm-recruitment system, is a sequence of complex events triggered by varying forms and intensities of stress. Also, the threshold of response varies according to the identity of the invading enemy in a way that appears appropriate to the ecology of the species.

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