Division of labor in *Ponera pennsylvannica* (Formicidae: Ponerinae)

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Summary

We examined division of labor and colony demography in the ant *Ponera pennsylvannica*. Observation of three colonies with individually marked workers revealed a high degree of interindividual behavioral variation and a rough but consistent division of labor between brood tenders and foragers. This division was present both in colonies consisting entirely of workers produced in the previous summer and in colonies containing freshly eclosed ants. Two colonies showed typical age-based polyethism, with young ants focusing on brood care and overwintered ants on foraging. No such age basis was detected in the third colony. This difference may relate to variability in brood production schedules. Colonies showing temporal polyethism had two peaks of brood production and thus had relatively large brood populations when the first young workers eclosed, while the third colony had only one peak and little brood for the young workers to tend. Even if young ants have a lower threshold for brood care, it may have been concealed in the latter situation. Demographic data indicate that natural colonies produce one brood per year and that workers typically eclose into colonies with relatively low brood care demands. This suggests that overwintered workers do most of a colony's work and that the division of labor among overwintered ants is the more important one under natural conditions. The basis of this division is as yet unknown. These results also suggest that small colony size, univoltine brood schedule and a close association between foraging and brood care do not preclude division of labor among specialized castes, as has been suggested for another ponerine species (Traniello 1978).

Introduction

The division of colony labor among specialized individuals is a central feature of insect eusociality (Wilson 1971). It is thought to contribute to the ecological success of social insects by enhancing the efficiency and reliability of colony responses to

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important contingencies (Oster and Wilson 1978). In most species studied to date division of labor is based on temporal or physical castes: i.e., groups of individuals distinguished by age or morphology which specialize on particular tasks for prolonged periods of time (Oster and Wilson 1978). In many cases an even finer division of labor is attained through significant interindividual variability in the task specialization of caste members (Fewell and Harrison 1991, Jeanne et al. 1988, Rissing 1981, Schmid-Hempel 1984, Traniello 1988).

Under the hypothesis of adaptive demography, the caste structure of a colony is species-specific and constitutes a direct adaptation to the local environment (Oster and Wilson 1978). At the same time, many species show considerable flexibility of caste behavioral profiles in response to changes in the colony's population structure or in the external environment (Calabi 1989, Calabi and Traniello 1989, Gordon 1989a, Lachaud and Fresneau 1987, Lenoir 1979, McDonald and Topoff 1985, Sorensen et al. 1984, Wingston and Fergusson 1985). This flexibility, as well as interindividual variability within castes, may complement programmed caste structures by molding a colony's labor profile to meet changing current needs. Indeed, the range of behavioral flexibility and variability exhibited by a particular caste may itself be a product of selection (Calabi 1989). The degree and kind of interindividual variability and behavioral flexibility seems to vary among species and among behaviors and individuals within species, but the reasons for this variation are as yet poorly understood (Gordon 1989b, Lenoir 1987, Robinson 1992). Progress on this question requires broader knowledge of division of labor patterns in different species, particularly in relation to each species ecological situation and social structure.

The subfamily Ponerinae offers a potentially interesting subject for comparative study of these questions. The limited research carried out to date has uncovered a considerable diversity of labor allocation patterns. Some ponerines exhibit temporal polyethism typical of species in higher subfamilies (Fresneau and Dupuy 1988, Fresneau, Garcia Perez and Jaisson 1982). On the other hand, *Amblyopone pallipes* is the only ant reported to completely lack temporal division of labor (Traniello 1978). This species could therefore represent an extreme in the direction away from caste. Traniello attributed this finding primarily to the species' small colony size (nine to sixteen workers) and multimodal age structure. Since only one brood matures per year, the workers eclose nearly simultaneously. Hence age differences cannot provide an adequate number of age ensembles to function as castes. In addition, direct provisioning of larvae with unprocessed food creates a close link between foraging and brood care.

Nonetheless, the organization of colony labor in *A. pallipes* remains somewhat unclear. Traniello's data show considerable variation among the behavioral profiles of individual workers, leaving open the possibility of castes based on factors other than age. In accord with this, subsequent work by Lachaud et al. (1988), on colonies of *A. pallipes* with individually marked workers, detected rough behavioral castes similar to those reported in other ponerines. These included specialists on brood care and on foraging, but the ages of the ants were unknown. In addition, Hölldobler and Wilson (1986) found a rough temporal polyethism in the related amblyoponine species *Prionopelta amabilis* and suggested that the larger size of *P. amabilis* colonies may account for this difference from *A. pallipes*.

Understanding the relationship of such social, ecological and phylogenetic factors to division of labor could benefit from further studies of related ponerines, particularly species with colony sizes and ecology similar to *A. pallipes*. *Ponera pennsylvannica* is a small hypogaeic ponerine occurring in the eastern deciduous forests of North America (Taylor 1967). Like *A. pallipes*, these ants form small colonies (< 60 workers), are nearly exclusively subterranean, hunt small arthropods, and raise only one brood per year (Traniello 1982, Wheeler 1900). We observed individually marked workers of known age in colonies of *P. pennsylvannica*, compiled behavioral repertoires, and looked for evidence of temporal division of labor and interindividual variability in this species. We also collected data on colony demography and brood production schedules in nature.

Materials and methods

Three queenright colonies were collected at Middlesex Fells Reservation and two at Blue Hills Reservation, near Boston, Massachusetts between April and June 1986. All colonies were found on slopes in open deciduous woods, nesting under stones in moist soil. Those collected in April (colonies 55 and 59) contained only queens and fully pigmented adult workers, while those collected in May and June (67, 69 and 79) contained eggs and small- to medium-sized larvae as well. Colonies were monogynous except for 55, which had two queens. Voucher specimens from these colonies were deposited at the Museum of Comparative Zoology at Harvard University. In order to acquire data on colony demography and brood production schedules, sixty-six additional colonies were collected between 25 April and 21 September 1985, and between 22 April and 17 August 1986. Most were collected in Blue Hills and Middlesex Fells, but some came from similar habitat at Beaver Brook Reservation in Belmont, Massachusetts.

Each observation colony was housed in a laboratory nest consisting of a plastic box (17 × 12 × 6 cm) floored with plaster. A clear glass cover (two 7.6 by 2.5 cm microscope slides) resting 2 to 3 mm above the floor on small pellets of aluminum foil gave the ants a suitable nesting site open to observation of the entire colony. A small pile of sand near the cover was provided as additional building material. The nest floor outside the glass cover constituted a foraging arena in which ant brood (primarily *Camponotus floridanus*) was provided as food. Nests were kept moist by regularly adding water to a small well in the floor.

Behavioral data were taken at two phases of colony ontogeny. In phase 1 colonies had plenty of brood, but no new workers had eclosed. All workers present at this point had been collected as adults and had presumably overwintered with the colony. In phase 2, at least six new workers had eclosed, but developing brood was still present. Phase 2 observations were not begun until at least one week had elapsed since the end of phase 1. The ages of all new workers were known to within one day; none were older than fifteen days at any time during phase 1 or phase 2. In colony 79, three workers eclosed during phase 2 and were immediately removed. In colony 67, one worker eclosed late in phase 1 and was not removed; it remained completely inactive for the duration of the observation period. Unfortunately, time constraints or colony condition permitted observations on both phases of only two colonies (67 and 79).

Table 1. Composition of observation colonies

Colony	Queens	Mature workers	Callow workers	Males	Eggs	Larvae	Pupae
55, phase 2	2	9	7	0	c. 25	8–10	6–8
67, phase 1	1	29	0	0	6–10	10–22	22–23
67, phase 2	1	29	17	1	7–8	c. 7	3
79, phase 1	1	13	0	0	0	40–55	7–12
79, phase 2	1	9	6	0	0	1–2	10–14

Colony 55 was observed only in phase 2 and Colonies 59 and 69 only in phase 1. Data from Colonies 55, 67 and 79 are analyzed and presented here. Worker and brood populations of these colonies are given in Table 1.

All workers were individually marked with small chits of colored plastic shaved from Lego™ blocks and attached with cyanoacrylate glue. Six colors (white, black, yellow, red, blue and green), two shapes of chit (triangle and square) and two gluing locations (pronotum and gaster) made possible 144 unique combinations, more than enough for these small colonies.

Behavioral profiles were determined by one of us (SCP) through repeated scanning of each colony. During a scan the behavior of each ant was noted and the information entered directly into a personal computer. No data were recorded for ants which were only walking or standing motionless during a scan. Because ants varied in the amount of time they spent idle, each ant did not receive an equal number of recorded observations. A colony could be completely scanned in three to nine minutes, depending on colony size and activity level. Observation sessions ranged in length from one-half to two hours, but typically lasted one hour. All data were collected between June and August 1986, usually between 1000 hours and 1800 hours, although some were taken as late as 2400 hours. Observation time totalled nine to fifteen hours per colony per phase, spread over two to six days. All observations were made through a dissecting microscope at 120 X or 250 X. Because these microscope scans were limited to the nest interior, the foraging arena was periodically scanned (six to eight times per one hour session) and the identity of ants present there was noted. Presence in the foraging arena was counted as foraging, regardless of specific activity there (e.g. walking, handling prey). Because these scans were made at lower frequency than those in the nest interior, the observed frequency of foraging can be considered an underestimate.

Colony and individual behavioral repertories were compiled from these data. In order to characterize the labor profiles of each ant, a relative frequency was calculated for each worker and each behavior:

$$R_{ij} = \frac{f_{ij}}{F_i}$$

where f_{ij} gives the observed frequency of behavior j by ant i, F_i gives the observed frequency of all tasks by ant i and R_{ij} gives the relative frequency of task j in the labor profile of ant i. Use of this relative value, rather than the actual observed frequencies

of each behavior by each ant, controlled for differences in the number of acts recorded for each ant. Such differences could be due to several factors, including variation in activity level among individuals and variation in the likelihood of being observed because of location within the nest (nest interior vs. foraging arena). Calculations of these values included only tasks, that is behaviors judged to serve some colony function (e.g. brood care, foraging and nest maintenance).

Mann-Whitney U-tests were used to detect differences in the behavioral profiles of age groups. Additional statistical analyses are described in the relevant sections of the results. Stat View II ™ was used for all statistical analyses except correspondence analysis, which was carried out on NTSYS (© Applied Biostatistics, Inc.).

Results

I. Nest organization

Workers used the provided sand to build partial or complete walls around the nest area. Pupae and larvae were scattered over distinct, although sometimes overlapping floor areas. The eggs lay in a few distinct clumps. Waste areas in the corners of the foraging arena or under the glass served as depositories for food remains, old cocoons, dead workers, feces and infrabuccal pellets. In some colonies defecation and trash areas were separate.

II. Description of behaviors

Table 2 shows the absolute frequencies of each behavioral act by old and young workers of each colony. This classification recognizes thirty-five distinct behaviors, some of which require more detailed explanation.

Table 2. Number of times each behavior was performed by workers of different ages at different phases of colony ontogeny

Behavior	Colony							
	55 phase 2		67 phase 1	67 phase 2		79 phase 1	79 phase 2	
	young	old		young	old		young	old
Egg Care								
Lick egg	10	1	12	3	1	0	0	0
Antennate egg	18	4	7	3	4	0	0	0
Handle egg	5	3	51	4	14	0	0	0
Larval Care								
Lick larva	92	33	560	100	121	557	10	76
Antennate larva	15	22	141	16	64	84	7	13
Handle larva	47	23	111	19	40	243	0	17
Feed larva	1	0	1	1	13	13	0	0
Pseudoreg. to larva	0	0	5	0	0	0	0	0

Table 2 (continued)

Behavior	Colony							
	55 phase 2		67 phase 1	67 phase 2		79 phase 1	79 phase 2	
	young	old		young	old		young	old
Pupal Care								
Lick pupa	0	2	37	0	1	16	0	0
Antennate pupa	23	14	203	15	6	41	9	16
Handle pupa	3	2	163	0	1	24	8	35
Help pupation	0	0	304	9	9	178	2	21
Help eclosion	0	0	1	0	0	0	0	3
Chew old cocoon	0	0	6	0	0	0	0	0
Social Grooming								
Groom worker	71	93	380	113	334	123	66	117
Groom male	0	0	0	6	0	0	0	0
Groom queen	1	0	1	3	0	0	0	0
Nest maintenance								
Handle nest material	21	168	84	13	70	410	9	86
Handle other material	9	19	16	0	2	3	0	2
Foraging								
Forage	14	269	570	29	617	178	32	40
Other Tasks								
Lay trophic egg	0	0	1	0	0	2	0	0
Handle trophic egg	0	0	5	1	3	1	2	1
Non-task Behaviors								
Eat prey	160	64	125	325	251	234	85	57
Eat dead brood	0	0	15	0	0	3	0	0
Handle food	31	20	29	43	92	110	15	48
Eat trophic egg	0	0	1	0	0	0	2	0
Self-groom	304	408	1050	362	659	706	130	247
Antennate worker	28	52	47	5	16	5	3	4
Antennate male	0	0	0	1	0	0	0	0
Antennate queen	1	2	1	1	0	1	0	0
Pseudoregurgitate								
to worker	11	3	9	11	5	1	3	7
to queen	4	2	1	1	0	0	0	0
Receive pseudoreg.	10	7	9	10	7	1	0	0
Drink larval drop	0	0	0	0	0	9	0	0
Antennal trip	46	3	15	42	5	5	11	1
Total	925	1214	3961	1136	2335	2948	394	791

Help pupation: Workers piled small bits of sand and debris on spinning larvae, apparently to provide them with a surface on which to spin the cocoon. This behavior also included removing these bits after the cocoon was complete.

Help adult eclosion: Workers eclosed from their cocoons with minimal assistance from their adult sisters, who simply cut open the anterior end of the cocoon at the appropriate time, allowing the callow ant to walk out on her own power. This limited degree of assistance is similar to the behavior of *Aneuretus simoni* (Traniello and Jayasuriya 1985) and unlike the completely unassisted eclosion of *A. pallipes* (Traniello 1978).

Chew old cocoon: After an eclosion, workers tore the old cocoon into shreds, compacted the shreds into balls with their mandibles and deposited the balls in the colony's waste area.

Lay, handle, and eat trophic egg: As in a wide variety of other ant genera (Hölldobler and Wilson 1990), workers occasionally laid small, sticky, fragile eggs which were subsequently eaten or fed to larvae. The eggs were laid in the same manner as queens laid viable eggs, with the gaster curved under the body and the sting extruded. Only old workers were seen laying these eggs.

Drink larval droplet: Workers drank droplets of opaque fluid emitted from the posterior end of larvae. Similar secretions have been reported in other ant species (LeMasne 1953) and may serve a nutritive function.

Antennal tipping: As described previously in several other ant species (e.g. Wilson 1976, Traniello 1982), a worker stood stiffly on outstretched legs, with its antennal flagella trembling and pointing at one another so that the tips touched. This occurred predominantly among young ants; its function is unknown.

Initiate and receive pseudoregurgitation, pseudoregurgitation with larvae: Although actual food exchange was never seen, workers sometimes engaged in a form of mouth-to-mouth contact that resembled regurgitation behavior in other ants. The initiator vigorously antennated the head of a nestmate, who reciprocated; both then extruded their mouthparts and rubbed them together, with mandibles held wide open. After a few seconds, they pressed their mouthparts together for about 30 seconds, but no drop of liquid passed between them. During this phase both partners remained still, except for a weak jittering of the antennae, with their heads slightly tilted relative to one another. Afterwards, the partners separated and walked slowly away, showing no evidence of excitement or tendency to engage in tandem runs. Most of these interactions involved young workers. Pseudoregurgitation with larvae was similar except that antennation and rubbing of the mouthparts were performed only by the adult ant. The significance of these behaviors is unknown.

Feed larvae: Larvae were fairly active and capable of moving short distances by pulling themselves along the substrate with their mandibles. Workers fed them by putting pieces of solid food next to them or directly on their mouthparts or ventral surfaces.

Some rare behaviors and others occurring predominantly in the foraging arena were not seen during these observation sessions and are therefore not included in Table 2. They were noted during pilot observations in the summer of 1985 and during separate observations of nest moving:

Lead tandem run and follow tandem run: One ant antennated the head of another, who reciprocated. One of these (usually the initiator) then tilted her head sideways, made a quick, tight turn and ran forward, her gaster presented to the follower. The follower ran close behind with mandibles open, maintaining antennal contact with the gaster of the leader. During many solicitations the initiator tugged sharply on the forelegs or mandibles of the other ant.

Most observed runs were very short and served little apparent purpose, since they occurred within the limited confines of the nest. They were never seen during foraging, but they occurred frequently when colonies were forced to change nest sites by removal of the nest cover and provision of a nearby alternate nest. Even during nest-moving, tandem runs were very short and rarely led all the way from the old to the new nest. Males were never led to the new nest, but rather dragged along by the leg or mandibles. Tandem runs also appeared in the context of returning apparently lost workers or queens to the nest.

Expel infrabuccal pellet: As in other ant species, workers occasionally discharged the contents of the infrabuccal pocket, a cavity beneathe the tongue which filters out solid material from food (Eisner and Happ 1962). The pellet was then deposited in the colony's waste area.

Leg-dragging: Workers wandering in the foraging arena sometimes adopted an unusual gait. They walked with the fore- and midlegs but dragged the rear legs behind them so that the distal end of the first tarsal segment rubbed along the substrate while the rest of the tarsus was held up from the ground. Although it suggested trail-laying, this behavior was not associated with recruitment of any kind, nor with the discovery of large food sources or changes of nest site. It was frequently observed in apparently healthy ants and in several colonies, indicating that it is not merely a pathological behavior. A similar behavior has been described for *P. amabilis* (Hölldobler and Wilson 1986); its significance in either species remains unclear.

Forage: Foraging was typically solitary. If several workers simultaneously moved a large item, they tended to work at cross-purposes and were very slow at retrieval. Recruitment was never observed, although the arrival of food in the nest was frequently followed by the arousal of some workers inside and an increase in the number of ants foraging. Nest ants fed themselves by cutting open the prey and licking the fluids. In the lab, foragers attacked prey over 1 cm in length (e.g. staphylinid beetles and centipedes) but were not able to capture or kill them. They bit, stung, retrieved and ate these same prey if they were presented freshly killed. They could readily capture small live prey (isotomids, psocids, and mites) in their mandibles after short, lightning-quick lunges.

III. Division of labor

Queens

Since queens showed little activity besides self-grooming, their labor profiles were not analyzed in detail. During phase 1 queens performed brood care at a low level (less than fifteen observations per queen). In phase 2 they very rarely tended brood (zero to one observation per colony) and never performed other task behaviors.

Old vs. young workers

Because of the infrequent occurrence of many behaviors, observed values were lumped into the eight general categories shown on Table 1. Only those categories identified as tasks were compared between age groups. Of these, behaviors associated with trophic eggs were too rare to analyze, leaving the following six categories: egg care, larval care, pupal care, social grooming, nest maintenance and foraging. Two workers were eliminated from the analysis of colonies 67 and 79 because they appeared unhealthy and died during the observation periods.

The three colonies which yielded data for phase 2 showed age-based division of labor to varying degrees (Figure 1). In colony 55 all tasks except nest maintenance differed significantly between age groups. Old workers showed higher than expected frequencies of foraging, while young workers showed higher than expected frequencies of brood care and of social grooming. The pattern in colony 67 was similar but less well-marked, with egg care and grooming not differing significantly between castes. In colony 79 no significant age differences were found. Even foraging, strongly age-dependent in other colonies, showed no difference in colony 79. This was due principally to the activity of worker 19, a young ant which specialized very strongly in foraging (Figure 2 E). When this ant was excluded from the analysis, a significant age difference ($p < 0.05$) was found for foraging, but not for the other behaviors. With the exception of this ant, the most consistent feature across colonies was the much higher rate of foraging among old workers.

Young ants in all three colonies performed significantly fewer task behaviors relative to their total repertory size than did old workers (Table 3). In addition, they performed fewer task behaviors than would be predicted assuming equal rates of activity per worker (Table 4).

Individual behavioral profiles

In order to examine behavioral variability among individual ants, we performed a correspondence analysis of the data from each phase of each colony. The same relative frequencies (R_{ij}) used in examining the differences between young and old ants were used in this analysis, but the data were not lumped together into age groups. Instead, each ant was characterized by six relative frequency values (one for each task), and the data for each colony treated as a cloud of points in a six-dimensional space. Correspondence analysis, (see Greenacre 1984 for details) was used to construct the most complete two-dimensional description of this space. The simplified description accounted for 78–89% of the total variance in the raw data.
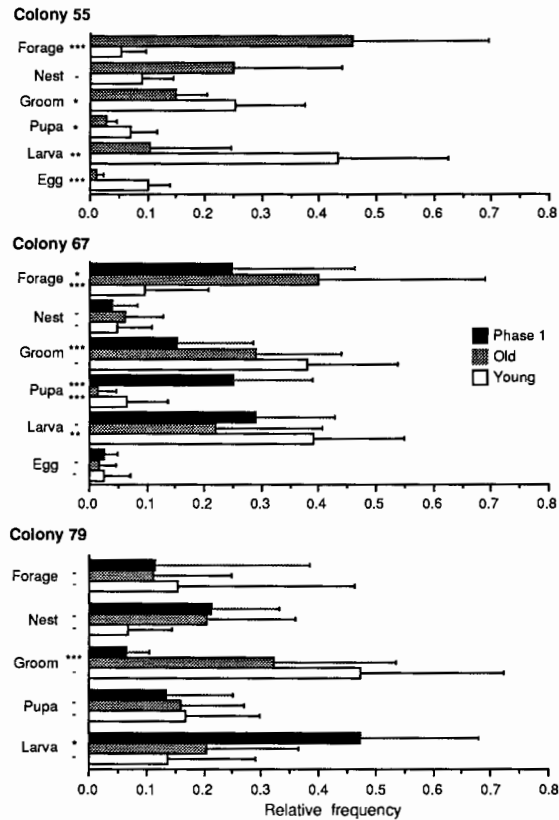
Figure 1. Behavioral profiles of age groups, by colony. For each ant the frequency of each task relative to the frequency of all tasks performed by that ant was calculated. Bar lengths give the mean values of these frequencies over all members of an age group. Brackets give the standard deviations. Symbols on the vertical axis give the significance of comparisons between old and young ants and between old and phase 1 ants. ***: p < 0.002; **: p < 0.01; *: p < 0.05; −: not significant (Mann-Whitney U)

Table 3. Observed and expected frequencies of task and non-task behaviors (as classified in Table 2) performed by old and young workers of each colony. Observed values are sums taken over all the members of each age group. Expected values are based on the assumption that tasks make up the same proportion of the behavioral repertories of old and young workers. Observed values are significantly different from expected in all colonies (p < 0.001, G test of independence)

Colony	Age	Non-task frequency		Task frequency		Total Observed	G
		Observed	Expected	Observed	Expected		
55	young	595	500	330	425	925	70.0
	old	561	656	653	558	1214	
67	young	801	601	335	535	1136	215
	old	1035	1235	1300	1100	2332	
79	young	249	204	145	190	394	31.4
	old	364	409	427	382	791	

Table 4. Observed and expected frequencies of task behaviors performed by old and young workers of each colony. Observed values are sums taken over all the members of each age group. Expected values are based on the assumption that task frequencies for each age group are proportional to the population of the age group. Observed values are significantly different from expected values in all colonies ($p < 0.001$, G test)

Colony	Age	Task frequency		Population	G
		Observed	Expected		
55	young	330	*430*	7	42.42
	old	653	*553*	9	
67	young	335	*604*	17	208.1
	old	1300	*1031*	29	
79	young	145	*229*	6	54.25
	old	427	*343*	9	

The values for each ant were used to make two dimensional plots of the data from each colony and phase, in which the distance between worker points was a function of the difference between their behavioral profiles.

Rather than present these plots, we reduced the data to one dimension by the following procedure. A line was drawn from the ant with the highest Factor 1 score to its nearest neighbor. The line was continued from this second point to its nearest neighbor possessing a lower factor 1 score than its own. The line was extended in this way until reaching the ant with the lowest factor 1 score. Points left off the line were then interpolated by placing them between their two nearest neighbors on the line. This yielded a non-linear one-dimensional scale connecting all of the points on the plot and along which ants with similar behavioral profiles were near to one another. In a few cases, particularly in colony 79, the position of some ants on the scale was shifted in order to bring them nearer to ants with similar profiles to their own. The order of points on this scale was used to arrange the behavioral profiles depicted in Figure 2.

These figures reveal considerable behavioral variation in all of the colonies, but they also indicate a fairly consistent division of labor in which ants appearing at the left end of the scale specialize in brood care, and those toward the right specialize in foraging. Ants in the center show more variable profiles, but typically include those with the highest relative frequencies of grooming and nest maintenance. In colonies showing significant age-based division of labor (55 and 67), young ants are found predominantly on the left-hand, brood-care side of the scale.

In addition to this general pattern, each colony had distinctive traits. In colony 55, which had the clearest differences in labor profiles between young and old ants, most old workers fell into two groups: nest maintenance workers (e.g. workers 10 and 11) and foragers (e.g. workers 14, 15 and 16). Although young workers performed nest maintenance at very low rates, the tests for age-based division of labor reported above did not detect a significant age difference for this behavior. This may be due to the fact that only three or four ants were nest work specialists, yielding a low average ranking for this behavior among old ants. The labor profiles of young ants were dominated by larval care and showed less individual variation.
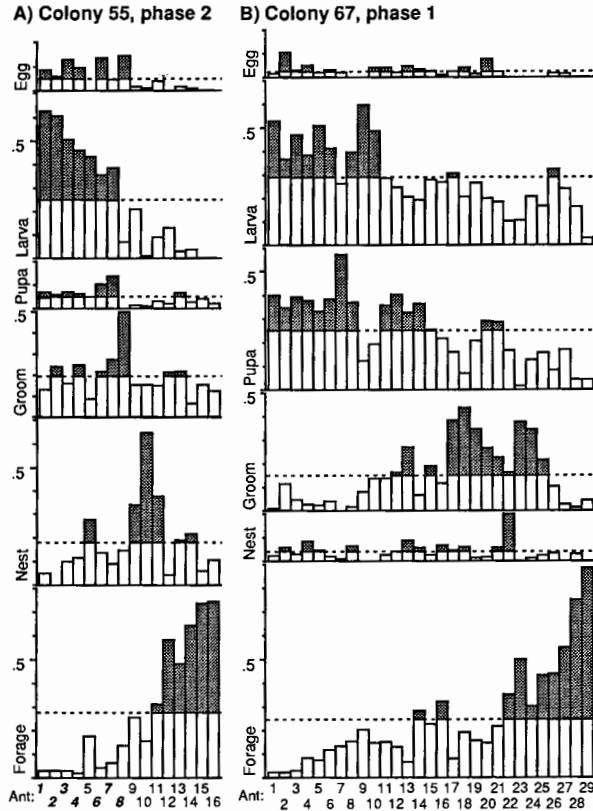
Figure 2 A–E. Behavioral profiles of individual ants, by colony and phase. Column heights give the frequency of each task relative to the frequency of all tasks performed by a given ant. Each dotted line shows the mean value of this relative frequency over all workers in a colony for each task. For ants with relative frequencies above this mean, the portion exceeding the mean is shown in gray. Ant labels shown in boldface italic script indicate young ants

Colony 67 during phase 2 had a similar variety of profiles as did colony 55, but the behavioral groups were not as clearly defined by age. Among workers with frequencies of foraging above the colony mean, some did little else besides forage, while others also showed high frequencies of brood care, grooming and nest maintenance. Only the specialist foragers included no young ants. Of a small number of workers doing either primarily grooming or some grooming and some nest maintenance (including workers 8, 20 and 46), all but one (46) were old. Most young ants focused on brood care and some showed appreciable frequencies of grooming and/or nest maintenance. Significant numbers of old workers (e.g. 1, 6 and 10) also displayed these sorts of labor profiles.

In colony 79 during phase 2, three of the six young ants (workers 15, 16 and 17) focused strongly on grooming. Another (14) showed a high frequency of brood care, the fifth (18) was more of a generalist, and the last one (19) focused almost exclusively
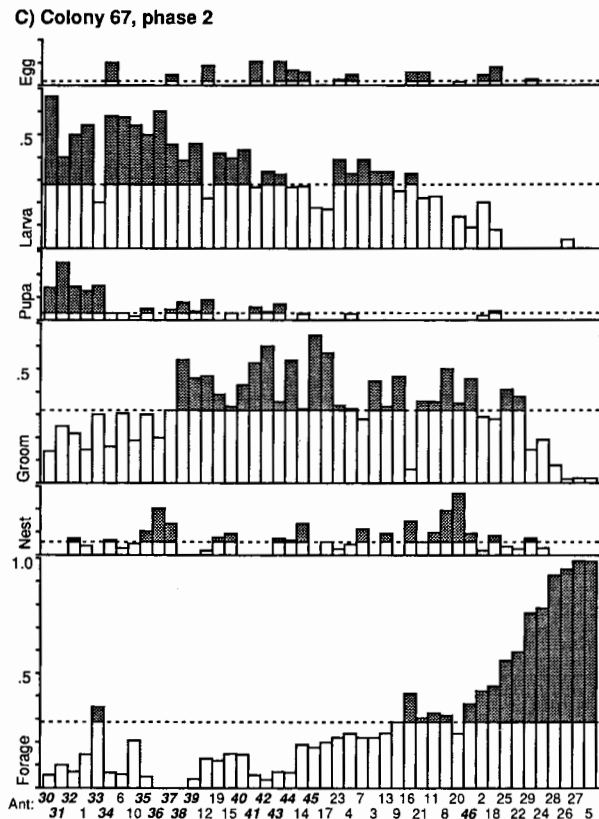
C) Colony 67, phase 2

Figure 2 (continued)

on foraging. The behavioral profiles of the old ants varied widely, with at least one worker specializing on each of the tasks.

Phase 1 vs. phase 2

In order to determine how the behavioral profiles of old workers changed when young workers entered the labor force, relative task frequencies of phase 1 workers were compared with the task frequencies of these same workers in phase 2. Two colonies provided data on both phases. In colony 67, eight days intervened between phases; in colony 79, twenty-one days intervened. Colony 67 showed significant differences between phases for foraging, grooming and pupal care, while colony 79 showed significant differences for grooming and larval care (Figure 1). For foraging and brood care, the differences were largely consistent with a shift away from the tasks dominating the profiles of young workers. That is, the old workers in phase 1 performed relatively more brood care and less foraging than these same workers later did in phase 2. Social grooming was an exception to this pattern, showing strong
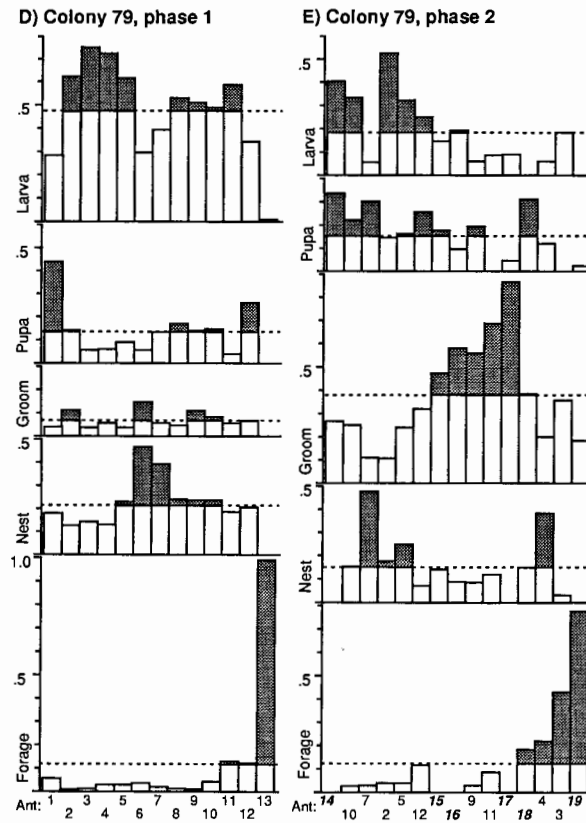
Figure 2 (continued)

increases in frequency among the old workers, although it formed a dominant portion of the repertory of young workers in both colonies.

Interpretation of these tests is hindered by the fact that any observed changes could result either from a new distribution of tasks across age castes or from altered labor demands on the entire colony. In particular, the amount and type of brood shifted between phases: phase 1 had large brood populations, composed primarily of larvae (colony 79) or pupae and larvae (colony 67), while phase 2 had smaller amounts of brood, consisting mainly of pupae (colony 79) or eggs and larvae (colony 67) (Table 1). Thus, the decline in the relative frequency of pupal care by old workers between phase 1 and phase 2 in colony 67 was probably largely due to a sharply lower pupal population in phase 2. Similarly, the strong increase in social grooming may reflect the presence of recently eclosed workers, which received exceptionally high rates of grooming.

As another approach to this question, we compared the relative rankings of old ants in phase 1 with their rankings in phase 2. Ants were ranked from left to right in the order in which they are presented in Figure 2, determined as described above.

Rankings in phase 2 were determined as though the younger ants were not present; ants which died between phases were not included in the analysis. A significant correlation was not found for colony 79 ($\tau = -0.167$, $p > 0.5$, Kendall's rank correlation) but was found for colony 67 ($\tau = 0.389$, $p < 0.01$). That is, for colony 67, ants which had low ranked, brood-related profiles in phase 1 tended to have low-ranked, brood-related profiles in phase 2. Examination of Figure 2 suggests that the specialized foragers in phase 1 remained particularly faithful to this task in phase 2.

IV. Demography

A total of seventy-one colonies were collected between 25 April and 21 September 1985, and between 22 April and 17 August 1986. Most were found in moist soil under stones embedded a few centimeters in soil, but one was nesting under a fallen rotten tree. All collecting sites were in relatively open woods and at the borders of woods and meadows. Thirty-six colonies (51 %) were queenright, typically with one queen, but with as many as thirteen (Figure 3 A). It is not clear, however, that all queens in a nest are fertilized or function as egg-layers. Conflict between queens was never seen in two polygynous nests which were observed closely. Worker populations were small (Figure 3 B) and did not differ significantly between queenless and queenright nests (Queenless: 18.0 ± 11.0, Queenright: 20.6 ± 18.2; $p > 0.9$, Mann-Whitney U). Brood populations were also similar (Queenless: 13.7 ± 14.5, Queenright: 17.6 ± 33.3; $p > 0.1$, Mann-Whitney U; figures give mean ± standard deviation).

Because the small, dark, slow-moving ants can be difficult to detect in disturbed nests, the completeness of collections is uncertain. Some or all of the queenless nests may have been portions of queenright colonies. Sex of brood in some collections suggests that many of the queenless groups came from colonies with a fertilized egg-layer. In twelve colonies the identity of some collected brood could be identified, because it consisted either of mature pupae which could be directly examined or of larvae sufficiently advanced that they matured bevore any eggs laid in the laboratory could catch up in development. Of seven queenless colonies in this group, two produced only males and five produced females as well. Of five queenright colonies, two produced only females, and three produced males as well.

Both dealate and ergatoid queens were found. Of forty-two queens examined, thirty (71 %) were dealate. In only four polygynous colonies could all the queens be identified as to type: three had all dealate queens and one had all ergatoid queens. Of the two largest queen groups, one had thirteen dealate queens and the other had six ergatoid queens.

Brood occurrence suggests a univoltine breeding schedule, as reported by Wheeler (1900). No apparently overwintered brood was found in early spring colonies. Eggs were seen only in late spring to early summer, while larvae, pupae, and newly eclosed workers appeared successively through the summer and early fall (Figure 3C). Newly eclosed workers were readily recognizable by their pale coloration. Captive young workers were usually still distinguishable from old ants two weeks after eclosion. Brood production seems only roughly synchronized, with multiple brood stages occurring simultaneously. Nonetheless, callow workers were never found in colonies still containing eggs or larvae.
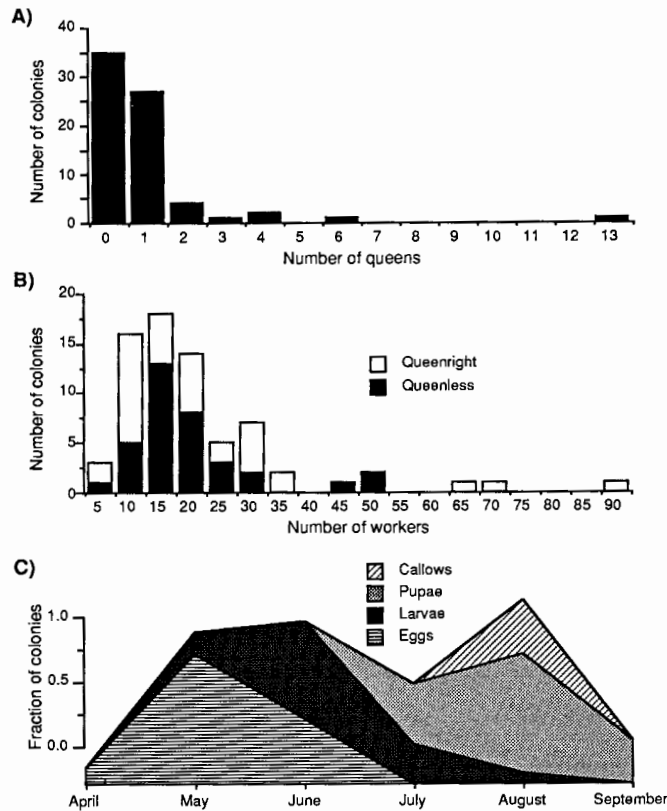
Figure 3. Demographic data on seventy-one colonies collected in 1985–1986. A) Frequency distribution of queen number per colony. B) Frequency distribution of worker number per colony. C) Time course of brood appearance. The height of each section gives the proportion of colonies collected in a given month that contained the brood type represented by that section

The three colonies maintained in the lab for behavioral observations differed from this schedule to varying degrees. Colony 55, collected on 29 April, showed two distinct peaks of egg production, the second one overlapping with the eclosion of callows from the first batch. Colony 67, collected on 26 May, had only one egg-laying peak, but continued a low level of production until late July, beyond the time at which eggs were found in field nests. Colony 79, collected on 29 June, had its peak egg population at collection and showed little or no new production afterwards. It is possible that the artificial early warming of colonies collected in spring hastened brood development and allowed a second egg batch. In addition, the light regime of indoor colonies was not carefully regulated and may have had disturbing effects on production schedules.

Discussion

All three colonies, at both phases of development, showed a rough classification of workers into brood tenders, foragers, and others performing varying degrees of grooming and nest maintenance. The colonies varied greatly, however, in the degree to which labor profiles correlated with age. In colony 67, and particularly in colony 55, a classic pattern of temporal polyethism emerged, with young workers tending brood and old workers foraging. In colony 79, virtually no age-based division of labor was detectable. Even in Colonies 55 and 67, the division was a rough one reminiscent of that in *P. amabilis*, with much variation of labor profiles within age groups. In particular, many old ants performed brood care at high frequencies. The pattern differed notably from that reported in *A. pallipes* in that young ants rarely foraged.

The basis of the division of labor observed in phase 1 colonies and in colony 79 is unknown. Age may be more important in colony 79, phase 2, than the data suggest, since the very small population size allowed even one unusual worker significantly to skew the results. Division of labor during phase 1 may reflect age differences among the old workers, or task fixation based on different experiences in the previous summer. In any event, the demographic data suggest that this situation, in which only overwintered ants are available to do all of a colony's labor, is the typical one in nature. Since colonies rear only one batch of eggs per year, there is little brood left to tend by the time young workers eclose.

Demographic differences may partly explain the variability in degree of temporal polyethism among the colonies. The experimental colony that came closest to the natural brood production schedule (79) also had the weakest division of labor, while the colony with the strongest bivoltine schedule (55) had the strongest division of labor. In all colonies, the young workers avoided foraging and focused on brood care, but in colony 55 this focus was narrower, and, more notably, old workers more completely avoided brood care. Thus, old workers in colony 55 may have become far more specialized in the presence of young workers, than they would have been able to do under typical natural conditions. In Colonies 67 and 79, old workers were active in all tasks.

While the more complete division of labor seen in colony 55 may be viewed as an artifact, it is nonetheless remarkable that temporal polyethism can be enhanced or diminished simply by adjusting the colony's brood structure, and thus its labor demands. It may be that young workers differ from old workers principally in having very low thresholds for brood care and very high thresholds for leaving the nest and foraging. This is to be expected if foraging is the most dangerous activity, since the mean worker lifespan, and thus ergonomic contribution to the colony, is maximized if older workers do the most dangerous tasks (Jeanne 1986). If enough young workers are available in the nest to tend the brood, then old workers may abandon brood care and focus on foraging simply by default. On the other hand, if little brood is present, young workers may be free to encounter stimuli for other tasks, including foraging and nest maintenance. Despite their higher thresholds for these tasks, they could come to perform them at relatively high rates. In this way, behavioral flexibility by individual ants can interact with age-specific behavioral tendencies to mold the

colony's labor profile to current demands (Calabi 1989). However, given the small amount of data gathered in these experiments, testing this scenario will require more thorough controlled experiments on the effects of brood population size on division of labor.

The features of small colony size, univoltine brood schedule and direct provisioning of larvae proposed by Traniello to account for the lack of behavioral castes in *A. pallipes* are here associated with a high degree of variability within castes, but not with the complete absence of castes. The division of colony labor among worker specialists, whatever its basis, may be so fundamental an advantage of social life that even the most rudimentary ant societies possess it.

Acknowledgments

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