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Research article

Variation in the transition from inside to outside work in the red harvester ant *Pogonomyrmex barbatus*

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Summary. In laboratory colonies of the red harvester ant, *Pogonomyrmex barbatus*, we observed the sequence of tasks performed by marked individuals. Observations of about 760 ants in three laboratory colonies indicate that ants often move from inside to outside work. However, there was a great deal of variation in the sequence. If trends in sequence were weak because ants do move from inside to outside work but the duration of our observations was too short to see the transition, ants should be observed to stay either inside or outside. There was no significant tendency for ants to persist in inside or outside work, indicating the variability in sequence is real. Ants tended to perform midden work before they died. Foraging activity is low in laboratory colonies, and it may be that ants that would be foragers in the field end up as midden workers in the laboratory. High variability in task sequence, in uniform laboratory conditions, contrasts with the apparently more consistent sequence from inside to outside work in the field. This suggests that requirements imposed by variable external conditions and colony needs in the field have a strong influence on task sequence.

Key words: Harvester ants, age polyethism, task allocation.

Introduction

In honeybees, workers shift tasks as they grow older, moving from tasks inside the nest to tasks outside. This sequence is well established (e.g. Robinson et al., 1994). The same sequence, from inside to outside work, is thought to be typical of ants (e.g. Hölldobler and Wilson, 1990). However, there are few data on any ant species showing that individuals consistently work inside the nest when young and outside the nest when older. Some combination of the following trajectories has been found in several ponerine species: workers that progress from interior to exterior work, workers that remain active inside the nest all their lives, workers that remain inactive all their lives, and workers that become foragers without previously performing brood care (Dejean and Lachaud, 1991; Nakata, 1995; Masuko, 1996). Similar variability, departing from the scheme often said to be typical, has been shown in formicine (Retana and Cerdá, 1991; Lenoir, 1979 for *Lasius niger*) and myrmicine (Beshers and Traniello, 1996) species.

How can we explain this diversity in ant behavior? The task a worker performs depends on colony needs, which are influenced by changing external conditions and the colony's reaction to those conditions. For example, transitions from one task to another are influenced by current colony composition and external events (Gordon, 1987, 1989). An individual's task also depends on physiological changes as individuals grow older. For example, age-related transitions in task are associated with physiological changes in brains, ovarioles and poison glands (Fénéron et al., 1996; Gronenberg et al., 1996). Recent work shows that harvester ant workers inside the nest differ in gene expression from foragers (Ingram et al., 2004).

Harvester ants (*Pogonomyrmex barbatus*) switch tasks in response to conditions such as food availability, disturbances and the need for nest maintenance work (Gordon, 1986, 1987, 1989). Gordon (1984) found that in laboratory colonies of *P. badius*, workers move from nest maintenance, performed partially inside the nest, to the more exterior tasks of midden work and patrolling. It appears that individual ants live a year or less (Gordon and Hölldobler, 1987). Evidence from field studies suggests, but does not confirm, that exterior workers are older in *P. owheei* (Porter and Jorgensen, 1981) and stay at the top of the nest near the nest entrance (MacKay, 1981). Gordon's (1986, 1987, 1989) field experiments with *P. barbatus* showed that ants switch tasks from nest maintenance to foraging, suggesting that nest maintenance generally precedes foraging.

A trajectory from inside to outside tasks seems to be typical for social Hymenoptera generally, including harvester ants in field colonies. It is not clear how much this trend for harvester ants results from the demands of the environment in the field, and how much from physiological changes in ants as they grow older. Here we investigate this by examining, in relatively uniform laboratory conditions, whether ants first work inside and then outside the nest. We do not consider how long an ant spends in each task. If workers first work inside the nest and later work outside the nest, observations of marked individuals should yield the following results: 1) at any time, an individual should tend to work either inside or outside the nest; and 2) over time, an individual's work inside the nest should tend to precede its work outside the nest.

Methods

Observations of marked individuals were made in 3 queenright laboratory colonies: Trillian (about 1500 ants), Luna (about 300–1000 ants), and Remedios (about 500–1000 ants). Brood was present in all colonies during observations. Trillian was collected in southeastern Arizona about 18 months before observations began in February 1998; Luna was collected at the same site about 18 months before observations began in October 1999; Remedios was collected at the same site about 12 months before observations began in June 2001.

Each colony was housed in plastic, plaster-filled nest boxes, arranged in rows of 6–8, covered with red Mylar to block some of the light, and connected to each other by transparent Tygon tubing. At any time, some nest boxes were empty. The nest boxes led to a single box, here called the "outer chamber", that was connected by tubing to a two-tiered foraging arena. Like the chamber just inside the nest entrance in natural nests, the outer chamber is where ants deposit food collected in the foraging arena and appear to wait between trips outside. The foraging arena was about 0.75 × 1.25 m (shown in Gordon and Mehdiabadi, 1999). Ants used a ramp to get from the lower to the upper tier of the arena.

Ambient temperature in the laboratory was about 29 °C. Food, artificial diet modified from Keller et al. (1989) and mixed birdseed, was placed in a watch glass on the upper tier of the arena on alternate days. Lights were on a light-dark schedule that varied from 12L-12D to 14L-10D schedule, with additional full-spectrum lights over the foraging arena for 4–5 h at midday.

Behavioral observations

Ants were given unique marks using Uni-Paint markers (Mitsubishi Pencil Co. for Eberhard Faber Inc). Previous work indicates that paint-marking does not influence the subsequent behavior of marked ants or the behavior of ants that interact with marked ants (Gordon, 1989; Brown and Gordon, 1997). Within 2 hours after marking, ants were returned to the location from which they were taken.

Observations were made once a day. For Trillian, observations of 54 marked ants were made on 80 of the 104 days between 20 Feb and12 June 1998. For Luna, observations were made of 101 marked ants on 24 of the 46 days between 7 October and 22 November 1999, and of 133 marked ants for 60 days between April 23 and July 27 2001. In Remedios, 475 ants were marked and observed for 23 days between 25 June and 27 July 2001, 4 days from 14 to 18 Aug 2001, and for 38 days between 19 Sept and 15 Nov 2001.

In each observation, the location and activity of each marked ant were recorded. An ant's location was defined as "outside" if it was anywhere in the arena, including the water tubes, midden, or food dish. Inside locations were any of the nest boxes. If an ant stood in a tube between boxes without moving, the nearest box was recorded as the location.

Activities were:
Manipulating food and foraging: Moving seeds or other food inside the nest; digging in a pile of food inside the nest; carrying a piece of food from the food dish towards the entrance to the nest; standing in the food dish while eating the food or cutting off a piece of food; bringing food from the arena to the outer chamber.
Midden work: Standing or piling refuse on the midden (which was always in one or more of the corners of the arena furthest from the nest entrance); carrying a dead ant or other refuse, such as dried food or seed husks.
Brood care: Standing over brood (eggs, larva, or pupa) and touching it with legs or antennae, licking it, turning it over, moving it; feeding a larva.

Data analysis

To test whether there were trends in the sequence of an ant's activities or locations, such that some tend to occur before others, we used a Mann-Whitney-Wilcoxon test. We considered three locations, the arena (outside), nest boxes other than the box containing the queen (inside), and the outer chamber (inside). Because midden work was the predominant activity outside the nest, we considered one activity, midden work, relative to the other two activities, brood care and foraging. For each ant we classified the location data into two types, the location being considered, which we will call the 'target location' (e.g. outside) and the other locations (e.g. outer chamber, inside). Similarly, for each ant we classified the activity data into midden work, the only target activity considered, and the other activities. We then found for each ant the Mann-Whitney value z; the null hypothesis if there is no trend in sequence is that the z-values for all of the ants will be normally distributed around 0.5. To test whether there was a trend, we used a sign test corrected for continuity.

Next we tested whether midden work is performed recurrently and whether ants tend to stay in certain locations day after day, using a Wald-Wolfowitz runs test (Siegel, 1956). This test was performed for two locations, inside (or specifically the outer chamber), and outside, and for one activity, midden work. For each activity or location, the data were converted into two types, the target activity or location and the other activities or the other location. We found for each ant the Ward-Wolfowitz value z, which is negative when the target activity is performed many times in a row, and positive when the target and other activity are more mixed than they would be if random. The null hypothesis is that successive observations, or runs, of the target activity (or location), are randomly mixed with runs of other activities (or locations); in this case the mean of the z-values for all ants would be 0. We tested this by finding the mean and standard deviation of the z-values; at the 0.05 significance level the average value of z would be more than 2 standard deviations from 0.

Results

If ants tend to move from inside to outside work, the trajectory would be from inside, in the nest boxes where the queen and brood were found, to a second stage, the outer chamber and the outside arena. The results show this trajectory, but it is weak. Usually ants were seen inside, in one of the nest boxes other than the outer chamber, before they were seen outside. This trend was significant for Trillian, Luna 2000 and Remedios (Table 1). However, in observations of 125 ants in

Table 1. A. Results of Mann-Whitney-Wilcoxon test of significant tendency to perform tasks in the indicated sequence. For each test, columns show z-value, p-value and number of ants. Tests 3 and 4 were not performed for Luna 1999 because there was no significant tendency to perform inside work before outside work, or to be in the outer chamber before other locations. B. Results of Wald-Wolfowitz runs test of significant tendency to persist in the indicated task or location. For each test, columns show z-value, p-value and number of ants

A) SEQUENCE	1. Inside before outside			2. Outer chamber before inside or outside			3. Inside before outer chamber			4. Midden work after other activities		
	z	p	n	z	p	n	z	p	n	z	p	n
Trillian	4.3	0.001	24	1.3	ns	21	–0.3	ns	15	2.6	0.005	21
Luna 1999	–2.2	0.05	125	–1.7	0.05	125	–	–	–	–	–	–
Luna 2000	6.1	0.001	74	3.8	0.001	52	–1.5	ns	50	6.2	0.001	67
Remedios	14.7	0.001	324	6.2	0.001	126	1.9	ns	148	11.5	0.001	322

B) PERSISTENCE	Inside = Outer Chamber			Outside			Midden Work		
	z	p	n	z	p	n	z	p	n
Trillian	1.3	ns	15–21	–1.9	0.1	24	–1.2	0.05	21
Luna 1999	–0.2	ns	124	–0.5	ns	107	–0.2	ns	104
Luna 2000	0.4	ns	57	1.3	ns	81	1.5	ns	74
Remedios	0.6	ns	201	2.4	ns	481	1.7	ns	419

Luna made in 1999, the opposite trend was significant: ants were seen outside before they went inside. To give the reader an impression of the variability in the data, Figure 1 shows some of the data from Trillian.

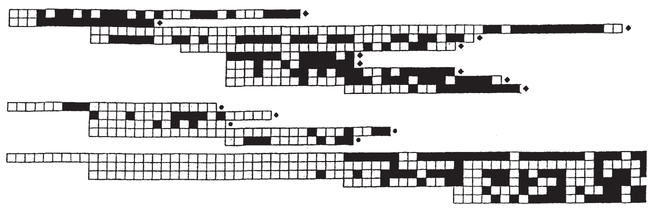
The complete trajectory from inside to outer chamber and outside arena was not observed in any colony. There was no significant tendency to be inside the nest before the outer chamber in Trillian, Luna 2000 or Remedios (Table 1A). This was not tested in Luna 1999 because the ants were outside before they were inside.

In the same observations in which ants tended to be inside before they were outside (Trillian, Luna 2000 and Remedios), they were also in the outer chamber before they were in the other inside nest boxes, or outside in the arena (Table 1A). In Luna 1999, this was not tested because ants tended to be outside before they were inside.

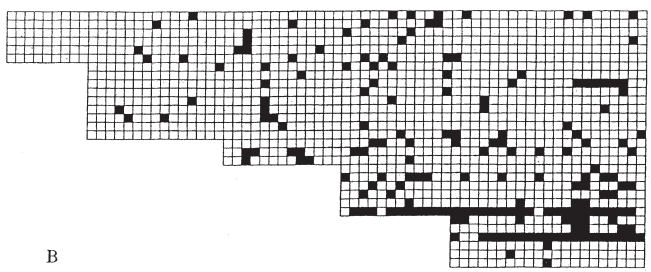
Taken together, these statistical results suggest that the tendency to be inside before outside, and in the outer chamber before the outside arena, was stronger than the tendency to be in the outer chamber before the other inside nest boxes.

There was no tendency for ants to persist in a certain location. The test for persistence was not significant for inside or outside for Trillian, Luna 1999, Luna 2000 or Remedios (Table 1B).

Ants tended to do midden work shortly before they died. In Trillian, all of the marked ants that died were midden workers. Of 21 midden workers, 10 died; of 33 ants that were not midden workers, 0 died. In Luna, there was no association in 1999 between midden work and dying; of 51 midden workers, 32 died; of 82 ants that were not midden workers, 31 died. However, of the 61 ants that died during the observations of Luna in 2000, 52 did midden work at least once during the week before they died, and 42 did midden work the day before they died. For Remedios, 315 of 332 ants that died did midden work at least once during the



A



B

Figure 1. Sequence of activities for individual ants. Each row shows data for an individual ant in observations of Trillian. Each column represents a particular day. Each cell shows the data from one morning observation. Only one activity is represented both in A and B. A. Midden work. Filled cells indicate the ant performed midden work; open cells indicate the ant performed other activities. Shown are 3 groups of rows: top, midden workers that died; middle, observations ended because the ant's paint was gone; bottom, midden workers still alive when observations ended. Diamond indicates the day the ant was found dead, Circles indicate the day the ant's paint was completely gone. B. Brood care. Filled cells indicate the ant performed brood care; open cells indicate the ant performed other activities.

week before they died, and 251 of these did midden work the day before they died.

Discussion

High variability in task sequence, in uniform laboratory conditions, contrasts with the apparently more consistent sequence from inside to outside work in the field. This suggests that requirements imposed by variable external conditions and colony needs in the field have a strong influence on task sequence.

Observations of about 760 ants in 3 laboratory colonies, kept in fairly uniform conditions, showed that ants tend to move from inside to outside work (Table 1A). However, there was a great deal of variation in the sequence. If trends in sequence were weak because ants do move from inside to outside work but the duration of our observations was too short to see the transition, ants should be observed to stay either inside or outside. There was no significant tendency for ants to persist in inside or outside work (Table 1B), indicating the variability in sequence is real.

Laboratory colonies of harvester ants perform fewer tasks than colonies in the field. In the field, patrollers search the foraging area each morning before the foragers emerge. Patrolling does not occur in the laboratory, perhaps because there is little variability in the location of food. Numbers of ants performing midden work are much higher in the laboratory than in the field. Midden material may be more abundant in the laboratory because there are no other species to remove refuse and dead ants, and because decomposition proceeds so slowly. It appears that midden material is a repository for colony-specific odour cues, both in the field (Gordon, 1984b) and in the laboratory (pers. obs.). More midden work may be needed to establish odour cues in a painted wooden arena than in soil. Numbers of ants foraging are much lower in the laboratory than in the field. Perhaps ants perform midden work in the laboratory that would otherwise perform foraging in the field. As a consequence, ants that would die as foragers in the field remain midden workers until their death in the laboratory.

However, evidence from field studies suggests that in natural conditions, ants tend to move from inside to outside work, which indicates that in the field, extrinsic factors are an important influence on task sequence. Such evidence includes the result from other *Pogonomyrmex* species that ants captured and marked while working outside the nest were found only at the top of the nest when nests were excavated (MacKay, 1981). Field studies of *P. barbatus* show that when new nest maintenance workers are needed, they are recruited from ants inside the nest (Gordon, 1989). Nest maintenance workers, patrollers or midden workers all switch to foraging when extra food is available, but this transition is irreversible: foragers do not switch back to nest maintenance work when needed. Thus in a colony in the field, the average age of exterior workers and the sequence of tasks an individual performs will depend on the colony's recent history. For example, if events have created a need for inside workers to do nest maintenance, individuals might remain inside longer and thus be older; however, if events have created a need for new foragers, foragers will be recruited and will tend to be younger. Our results here suggest that the recent history of conditions affecting task may be more important than intrinsic factors in determining the sequence from inside to outside work.

More generally, it may be typical of ants that age polyethism, the transition from inside to outside work, is extremely variable. For example, in their review of temporal castes, Hölldobler and Wilson (1990) cite only 16 species (including the *Formica rufa* group) with "typical age polyethism… the younger workers attend the brood and queen, with the older workers changing to nest work (usually) and then foraging" (Table 8–3, p. 320). We were able to read 21 of the 35 articles cited to support this, including at least one article for 13 of the16 species listed. Of these 21 only 2 present data showing that younger ants work inside and older ones work outside of the nest (McDonald and Topoff, 1985; Wilson and Hölldobler, 1986). Three of the 20 show that some ants behave in the "typical" way, but about as many do not, e.g. foraging when young or performing nest work when old (Dobrzañska, 1959; Calabi et al., 1983; Lenoir, 1979). Another 5 articles do not present data on younger intranidal and older extranidal behavior, but instead test a different hypothesis about the relation of age and behavior: Cammaerts-Tricot and Verhaeghe (1974) relates age and the distance an ant follows an extract of poison gland; Cammaerts-Tricot (1975) relates age and reaction to an ant of another species; Higashi (1974) relates mandibular wear and intranidal vs. extranidal nest construction; Rosengren (1977) compares behavior of younger and older foragers; Weir (1958a) compares nest construction activities in older and younger workers. A further 3 of the articles present suggestions, without data, on whether younger ants work inside the nest while older ones work outside (Gordon, 1984; Wilson and Brown, 1984; Freeland, 1958). The remaining 8 articles do not present any data on behavior as a function of age (Cammaerts-Tricot, 1974; Weir, 1958b, 1959; Hölldobler and Wilson, 1970; Perez-Bautista et al., 1985; Lenoir and Mardon, 1978; Wheeler, 1984; Lenoir and Ataya, 1983).

If the transition from work inside the nest to work outside is generally extremely variable in ants, this represents an important difference between ants and honeybees. Honeybees have much shorter lives than most ant workers. Moreover, they have been domestic animals, selected for foraging performance, for thousands of years. Artificial selection has clearly shaped their behavior and may have reduced variability in the sequence of tasks an individual performs.

The progression from one task to another is the product of interacting factors. The most obvious of these is spatial. Workers tend to eclose inside the nest; in fact, whatever the nesting arrangement, we would define the place where brood are found and thus where adults emerge from pupae as "inside the nest". Franks and colleagues (Franks and Tofts, 1994) have outlined clearly a process that would create a tendency for tasks inside to precede tasks outside the nest: ants eclose near the brood, and over time move farther from it. A second factor that contributes to shifts from inside to outside work is physiological changes in an individual as it ages (e.g, Billen, 1982; Fénéron et al., 1996; Robinson et al., 1994). A third factor is the current demands of the colony and the environment. For example, when workers are removed other workers change tasks (McDonald and Topoff, 1985). Fourth, some individuals are consistently more active, throughout their lives,than others, and these more active individuals are more likely to leave the nest (e.g. Retana and Cerda, 1991). Any empirical study of the sequence in which individuals perform tasks examines the combined outcome of these forces. It would be surprising if results did not vary.

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