



---

Encounter Rate and Task Allocation in Harvester Ants

Author(s): Deborah M. Gordon and Natasha J. Mehdiabadi

Reviewed work(s):

Source: *Behavioral Ecology and Sociobiology*, Vol. 45, No. 5 (Apr., 1999), pp. 370-377

Published by: [Springer](#)

Stable URL: <http://www.jstor.org/stable/4601616>

Accessed: 20/01/2012 12:29

---

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



Springer is collaborating with JSTOR to digitize, preserve and extend access to *Behavioral Ecology and Sociobiology*.

<http://www.jstor.org>

## ORIGINAL ARTICLE

Deborah M. Gordon · Natasha J. Mehdiabadi

**Encounter rate and task allocation in harvester ants**

Received: 1 July 1998 / Accepted: 15 November 1998

**Abstract** As conditions change, social insect colonies adjust the numbers of workers engaged in various tasks, such as foraging and nest work. This process of task allocation operates without central control; individuals respond to simple, local cues. This study investigates one such cue, the pattern of an ant's interactions with other workers. We examined how an ant's tendency to perform midden work, carrying objects to and sorting the refuse pile of the colony, is related to the recent history of the ant's brief antennal contacts, in laboratory colonies of the red harvester ant, *Pogonomyrmex barbatus*. The probability that an ant performed midden work was related to its recent interactions in two ways. First, the time an ant spent performing midden work was positively correlated with the number of midden workers that ant had met while it was away from the midden. Second, ants engaged in a task other than midden work were more likely to begin to do midden work when their rate of encounter per minute with midden workers was high. Cues based on interaction rate may enable ants to respond to changes in worker numbers even though ants cannot count or assess total numbers engaged in a task.

**Key words** Task allocation · Interaction rates · Ants · Social insects · *Pogonomyrmex barbatus*

**Introduction**

Social facilitation of behavior occurs when an animal is more likely to behave in a certain way in the presence of

other animals engaged in that behavior (Thorpe 1963). Social facilitation occurs in many taxa and affects many kinds of behavior, including foraging behavior in red-winged blackbirds (Mason and Reidinger 1981), habitat selection in anole lizards (Stamps 1991) and egg-laying behavior in fruit flies (Prokopy and Duan 1998). Social insects provide well-known examples of social facilitation (Wilson 1974), but in many cases, we do not know how workers perceive the behavior of others.

Interaction rates may contribute to social facilitation, by providing a cue to the numbers of animals currently engaged in some behavior. For many animals, signal rate is informative. In some cases, individuals vary the rate at which they produce a signal (e.g., Blumstein and Armitage 1997; Boinski and Campbell 1996; Jang and Greenfield 1996). In the present study, we consider the case when signal rate depends on some feature of a group, such as group size or density. For example, in a group of freely moving individuals, encounter rate will increase as a function of group size (Waser 1984).

Social facilitation and its opposite, socially induced inhibition of behavior, are crucial to task allocation in social insects. As conditions change, social insect colonies adjust the numbers of workers engaged in various tasks, such as foraging and nest work. Task allocation operates without central control; individuals respond to simple, local cues. One example of how social facilitation affects task allocation is the trail pheromone of some ant species; the more foragers there are returning to the nest from a food source, depositing pheromone on the ground, the more ants leave the nest to forage (Wilson 1962). Allocation of workers to foraging and to nest construction is relatively well understood for some social insect taxa (e.g., Seeley 1989 for nectar foraging in honey bees; Jeanne 1996 for nest construction in *Polybia* wasps). However, there are large gaps in our understanding of task allocation. First, most work so far is on foraging, and many other tasks have not been studied. Second, most studies of task allocation are on transitions between inactivity and a single task, such as foraging, rather than transitions between different tasks;

D.M. Gordon (✉) · N.J. Mehdiabadi<sup>1</sup>  
Department of Biological Sciences, Stanford University  
Stanford, CA 94305-5020, USA  
e-mail: gordon@ants.stanford.edu

Present address:

<sup>1</sup>Department of Zoology  
University of Texas, Austin, TX 78712, USA

though we know that workers switch from one task to another, we know little about when or why. Third, we often cannot specify which cues influence individual task decisions.

Here we investigate whether harvester ants use encounter rates as a cue in transitions between tasks. We consider one type of interaction among workers: brief antennal contacts. Ants engaged in tasks outside the nest meet as they go in and out of the nest entrance. When two ants meet, one ant often touches, with its antennae, the antennae or body of the other. Antennae are the organs of chemical perception, and when one ant touches another it can determine, for example, whether the other ant is a nestmate. Patterns of brief antennal contact occur in many social insect species (Cole 1991; Franks et al. 1990) and influence individual behavior in some (Gordon et al. 1993; Reeve and Gamboa 1987; Reznikova and Ryabko 1994).

We asked whether the probability that a harvester ant (*Pogonomyrmex barbatus*) performs a task is related to the recent history of its contacts with other ants. A social insect worker's task performance is influenced by its age, its hormonal state, and by genetic factors (Robinson and Page 1989). The task decisions of social insect workers are also based on cues from the environment or from the extent to which a task has been accomplished; examples are the amount of food or nest material available, which may elicit foraging or nest construction (Jeanne 1996). In addition, information from other workers affects an individual's task decisions; one example is the honeybee waggle dance. There is considerable indirect evidence that rates of interaction among workers have a role in task allocation: the number of individuals present, which partly determines interaction rate, influences a worker's task performance (Gordon 1986, 1987; Huang and Robinson 1992; Jeanne 1996; Kolmes and Winston 1988; Reeve and Gamboa 1987; Wilson 1984; Winston and Fergusson 1985).

Previous work on harvester ants showed that if the numbers engaged in one task (e.g., nest maintenance) change, numbers engaged in another task (e.g., foraging) will change as well (Gordon 1986, 1987). This would occur if an ant responds to its rate of interactions with nestmates engaged in a different task. Another finding that suggests that interaction patterns may be important is that the dynamics of task allocation depend on colony age and size (Gordon 1987, 1989); older, larger colonies (5 years or more) differ from younger, smaller ones (2 years). Since workers live only a year (Gordon and Hölldobler 1987), and all ants are the offspring of a single founding queen who lives 15–20 years (Gordon 1991), the difference between old and young colonies in task allocation seems to arise from the difference in colony size. Encounter rate may vary with colony size or the local density of ants (Gordon et al. 1993). If ants use cues based on encounter patterns in making task decisions, this could explain why task allocation depends on colony size.

This study was performed with laboratory colonies that devoted much of their effort to one task, midden

work. In the field, harvester ant colonies maintain a refuse pile, or midden, on their nest mounds. Middens of *P. barbatus* colonies consist of dead ants (which are quickly removed by scavenger species), husks of the seeds the ants eat, and bits of rock and soil. Middens, or some chemical signal in midden material, may function in colony defense (Gordon 1984).

We observed the activities and encounters of undisturbed ants in laboratory colonies. We then examined in three ways how encounters affected the probability that an ant performed midden work. The first two approaches define encounter rate as the proportion of all of an ant's encounters that are with midden workers. We asked (1) whether there is a correlation between the number of encounters an ant had with midden workers while it was away from the midden, and the time it spent performing midden work, and (2) whether an ant that stopped another activity to begin midden work had a higher proportion of encounters with midden workers than when it stopped midden work to begin another activity. The third approach was to test whether ants assess the rate of encounter with midden workers per unit time; such a rate would be correlated with the proportion of all encounters that are with midden workers. We asked (3) whether ants that switched to midden work from another activity had a higher rate of encounter (in encounters per minute) with midden workers than ants that did not switch.

## Methods

### General methods

Observations were made with four colonies, called Ingrid, Lilith, Hermione and Trillian, each collected from southeastern Arizona 6–30 months before it was used in this study. Each colony contained a queen. We do not know the ages of the colonies when collected. Once established in the laboratory, Ingrid, Lilith and Hermione each contained 500–1000 ants, which is probably the size of a large 1-year-old colony in the field. In the laboratory, Trillian contained about 1500 ants, which is about the size of a 2-year-old colony in the field (Gordon 1992).

Each colony was housed in a row of plastic, plaster-filled nest boxes, covered with red Mylar to block the light, and connected to each other by transparent Tygon tubing. One of the nest boxes was connected by tubing to a single box, here called the "outer chamber," which was connected to a foraging arena. For one colony, Ingrid, the outer chamber was connected by tubing to a large (22 × 30 cm) plastic box in which food (artificial diet modified from Keller et al. 1989) was placed in a petri dish on alternate days. For the other three colonies, the nest boxes and outer chamber were on a table, connected by tubing to a two-tiered foraging arena on another table (Fig. 1). Food was placed in a watch glass on the upper tier of the arena on alternate days. Ants used a ramp to get from the lower to upper tier of the arena. Lights were on a 12L-12D schedule. There were additional full-spectrum lights on for 4 h during the light period, placed over the foraging box of Ingrid, and over both tiers of the foraging arena of the other three colonies. All observations were conducted during the light period, and most during the time the full-spectrum lights were on.

Ants travelled between the outer chamber and the foraging arena, but rarely between the outer chamber and the nest boxes except to move food into the nest (A. Fullerton, unpublished data).

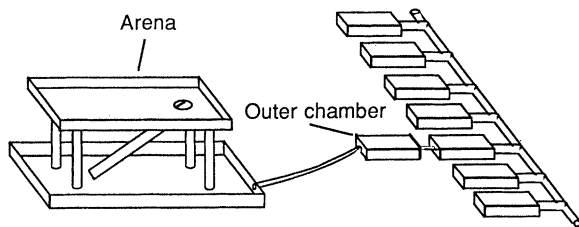


Fig. 1 Arena and nest boxes of laboratory colonies

In ants of the genus *Pogonomyrmex*, exterior workers, probably the oldest workers in the colony, rarely go down into the lower chambers of the nest (MacKay 1983). It appears that in the laboratory, use of the outer chamber was similar to that of the upper chambers of nests in the field.

Ants were marked with paint from Uni-Paint markers (Mitsubishi Pencil Co. for Eberhard Farber). 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 (Brown and Gordon 1997; Gordon 1989).

We recorded whether the focal ant entered any of the following locations: nest boxes; outer chamber and the tube connecting outer chamber to arena; arena, which included the lower tier of the arena except for the midden, the ramp to the upper tier of the arena, and the upper tier of the arena except for the food and midden; and the food dish. The other location was the midden, one or two piles of discarded food and dead ants, usually in the lower tier of the arena in the corners furthest from the entrance. The midden tends to be a discrete pile with a distinct edge generated by the piling activity of midden workers, so it is not difficult to decide if an ant is on or off the midden.

Three activities were observed. The first, foraging, consisted of carrying food or inspecting it with the antennae. The second, midden work, consisted of carrying or inspecting a refuse item such as a dead ant, either on the midden or anywhere in the arena, or standing on the midden pile. Midden workers often spent some time merely standing on the midden pile in between bouts of moving midden objects from one place to another. Any ant on the midden was considered to be a midden worker. The third activity, walk/stand/groom, consisted of any of the following, in which the ant could not be seen to perform any particular task: walking without carrying anything; standing somewhere away from any food or midden material; or self-grooming, usually wiping the antennae with the forelegs.

An encounter was considered to occur when the antennae of a focal ant touched any part of the body of another ant; almost always the focal ant touched the antennae of the other. Though chemicals on the body surface probably differ from one body part to another, we do not know enough about this to distinguish different types of antennal contact.

#### Time engaged in midden work and encounters off the midden with midden workers

Observations were made with three colonies, Lilith, Hermione, and Trillian. Observations of Lilith were made from April to December 1995. The behavior of the colony changed during this time. From April to August 1995, there was considerable brood production in Lilith and a great deal of foraging activity. From September to December 1995, brood production in Lilith almost ceased, many ants died, there was more activity on the midden, and foraging activity decreased. This may correspond to a seasonal cycle of brood production in the field (MacKay 1981). Observations of Hermione were made from January to March 1996. Observations of Trillian were made from March to June 1997. Data were analyzed in four sets: April to August 1995 (Lilith I; 93 ants observed), September 1995 to January 1996 (Lilith II; 41 ants observed),

January to March 1996 (Hermione; 62 ants observed), March to June 1997 (Trillian I, 16 ants observed). In total, 212 ants from three colonies were observed for about 2850 min.

About 10–15 ants were marked identically each week; the marks lasted about a week. At least 24 h elapsed between paint-marking and any observation. Ants marked for observation were collected while performing each of several activities. The purpose of marking was to make ants easier to follow visually during a single observation, not to track the behavior of specified individuals over successive observations. The same ant may have been observed more than once. However, the chances are small that we would choose the same one of 10 ants for observation on successive days, and even smaller that we would choose for marking on successive weeks the same 10 ants out of a colony of 500–1000, so it is unlikely that we observed the same ant week after week in any of the four separate studies of three different colonies.

For each observation, a marked focal ant was chosen haphazardly from among the marked ants that happened to be in the outer chamber or bottom of the arena. In Lilith I, all focal ants were in the outer chamber at the beginning of the observation; in Lilith II, Hermione, and Trillian I, 60%, 50%, and 20%, respectively, of focal ants were chosen when in the outer chamber, and the remaining focal ants were in the arena at the beginning of the observation. The length of time the focal ant was observed changed over the course of the study. In the first data set (Lilith I), the ant was observed for 5 min or until lost from sight by the observer if it did not leave the outer chamber, and for 20 min or until lost from sight if it entered the foraging arena. In the other three data sets (Lilith II, Hermione, and Trillian I), all ants were observed for 20 min or until lost from sight.

We recorded each change of activity or location by the focal ant and the time it occurred, each encounter with another ant and the time it occurred, and the activity of the ant encountered. Observations were made by two people: one person observed the ants and the other typed the data into a computer, using a program that recorded the time of each data entry.

We examined whether the probability an ant performs midden work is related to the number of encounters it has with midden workers while it is away from the midden. As a measure of the probability a focal ant performs midden work, we used the proportion of each ant's time, out of the total time that ant was observed, that it spent engaged in midden work. We then found the proportion of all encounters the focal ant had off the midden (i.e., excluding all encounters on the midden) that were with midden workers, who were likewise not on the midden but were carrying a dead ant or other refuse item in their mandibles. We tested for a correlation between the proportion of time an ant spent engaged in midden work, and the proportion of all its encounters off the midden that were with midden workers. Spearman's rank correlation tests were performed separately for each of the four data sets, with *ns* corresponding to numbers of ants observed.

#### Encounters with midden workers before beginning and before stopping midden work

We next tested whether an ant had more encounters with midden workers when it began or when it stopped midden work. If the probability an ant performs midden work were related simply to the number of encounters it has with midden workers, then ants that switched to midden work might have more such encounters than ants that stopped performing midden work. However, ants performing midden work are more likely to have encounters with midden workers than ants engaged in other activities. A midden worker was defined either as an ant on the midden or an ant away from the midden carrying refuse. An ant that was performing midden work and then stopped usually had many opportunities for encounters with midden workers; if it was on the midden, it could meet only other ants on the midden, who were by definition midden workers. An ant that was performing another activity and then began midden work was an ant away from the midden with few opportunities for encounters with midden workers.

The test was performed separately with three of the data sets, Lilith II, Hermione, and Trillian I, described in the previous section. In the other data set, Lilith I, so few ants had performed midden work (see Fig. 2) that this test would not be meaningful.

The data on each focal ant were divided into segments, each consisting of a portion of an observation during which the focal ant performed one activity. The number of segments per observation is one plus the number of transitions between activities: if an ant performed only one activity throughout an observation, that observation provided one segment; if an ant changed activities once, that observation provided two segments, and so on. This analysis compared, for the same ant, its encounters before it began and before it stopped midden work, so the analysis used data only for those ants that changed activities enough to have at least three segments or at least two transitions in and out of midden work. We classified segments as being either of midden work or of another activity (foraging or walk/stand/groom). For each segment, we found the proportion of all encounters that were with midden workers. (In a segment in which the focal ant had no encounters, the proportion of encounters that were with midden workers could not be calculated, so such segments were eliminated from the data). For each ant, we calculated the average proportion of encounters with midden workers over all of its segments of midden work, and the average proportion over all of its segments of other activities. Using a paired *t*-test, we compared for each ant the average proportion of its encounters that were with midden workers in the two types of segments, midden work and other. We thus tested whether an ant had a higher proportion of encounters with midden workers before it stopped or before it switched to midden work.

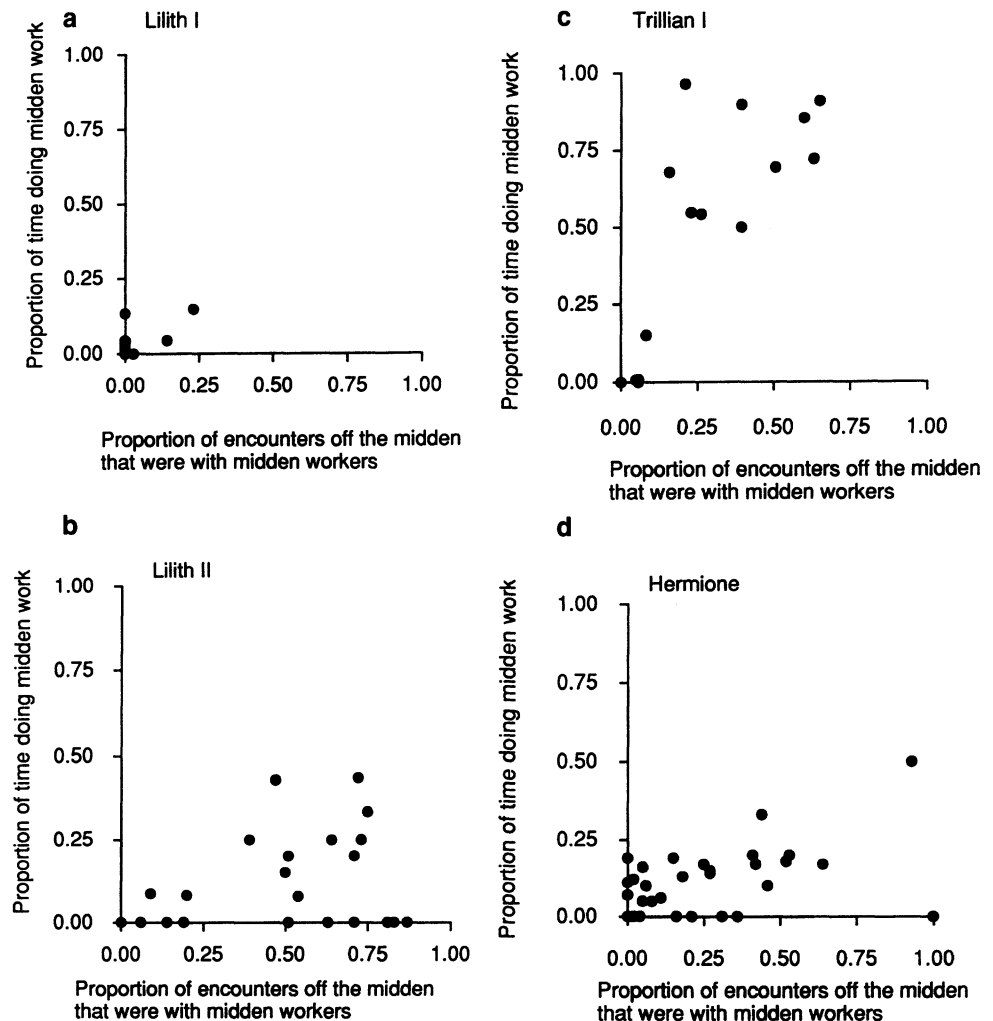
Encounter rate and probability of beginning midden work

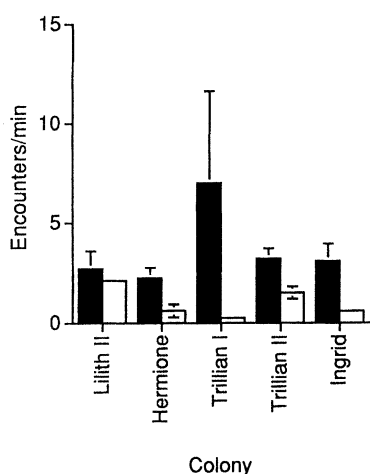
We next tested whether ants in another activity besides midden work (foraging or walk/stand/groom) that later switched to midden work had a higher rate of encounter with midden workers than ants that did not switch to midden work.

First, using the data described above, from Lilith II, Hermione, and Trillian I, we found all observations of ants which, while engaged in some other activity besides midden work, encountered a midden worker. If an ant met these criteria more than once during an observation, we chose only the first instance from the observation of that ant. For each ant, we found the total number of contacts with midden workers and the time elapsed until either it began to do midden work or the observation ended. We then found for each ant the rate, in encounters/min, of encounters with midden workers, and compared this rate in ants that began to perform midden work and ants that did not, using a Mann-Whitney *U*-test performed separately for each data set. This comparison was not made for Lilith I because few ants performed midden work or encountered midden workers (Fig. 2).

Second, using a slightly different procedure for data collection, observations were made with Ingrid and again with Trillian (data set called Trillian II in the following). For Ingrid, 31 ants were observed on 15 days in May 1996; for Trillian, 38 ants were observed on 10 days in May 1997. Each focal ant observed in Trillian was marked immediately after observation, which made it possible to ensure that no ant was observed more than once. Ants from Ingrid were not marked and may have been observed more than once; however, the results indicate that variation among ants in

**Fig. 2a–d** Proportion of time spent performing midden work, as a function of the proportion of an ant's encounters, while it was away from the midden, with midden workers. Each point represents data from one ant. **a** Lilith I ( $n=93$ ; most of the data points overlap in a cluster near the origin). **b** Lilith II ( $n=40$ ). **c** Trillian I ( $n=16$ ). **d** Hermione ( $n=62$ )





**Fig. 3** Rates of encounter with midden workers for ants that subsequently began to do midden work (filled bars) and ants that did not do midden work (open bars). Error bars show SE of the mean

Ingrid was similar to that of Trillian II, in which each ant was observed only once (Fig. 3). A total of 69 ants from two colonies were observed for about 750 min.

In Ingrid and Trillian II, focal ants were chosen as follows. We observed a haphazardly chosen midden worker that was carrying refuse off the midden, until it encountered an ant that was not engaged in midden work. The latter ant became the focal ant. The focal ant was observed for 15 min or until it began to perform midden work, was lost, or left the foraging arena to return to the nest. During the observation we recorded, using a tape recorder, the activity of the focal ant, the occurrence of an encounter, the activity of the ant encountered, and the location of the encounter. In these data, activities were defined as above. Locations were the midden, the food dish, or elsewhere in the foraging arena besides the midden or food dish.

These data were analyzed as described above. For each ant, we found the total number of contacts with midden workers and the time elapsed until either it began to do midden work or the observation ended. We then found for each ant, the rate, in encounters/min, of encounters with midden workers, and compared this rate in ants that began to perform midden work and ants that did not, using a Mann-Whitney *U*-test performed separately for each data set.

## Results

Table 1 shows encounter rates and activity counts for the first four data sets, Lilith I, Lilith II, Hermione, and Trillian I.

### Time engaged in midden work and encounters off the midden with midden workers

The more midden workers an ant encountered while it was away from the midden, the more of its time was spent engaged in midden work (Fig. 2). In all four data sets, the proportion of time ants spent performing midden work was significantly correlated with the proportion of encounters off the midden with midden workers (Lilith I:  $\rho = 0.38$ ,  $Z = 3.64$ ,  $P = 0.0003$ ,  $n = 93$ ; Lilith II:  $\rho = 0.56$ ,  $Z = 3.49$ ,  $P = 0.0005$ ,  $n = 40$ ; Her-

mione:  $\rho = 0.67$ ,  $Z = 5.21$ ,  $P = 0.0001$ ,  $n = 62$ ; Trillian I:  $\rho = 0.81$ ,  $Z = 3.12$ ,  $P = 0.002$ ,  $n = 16$ ; Spearman's rank correlation test,  $\rho$  and  $Z$  corrected for ties).

### Encounters with midden workers before beginning and before stopping midden work

The proportion of an ant's encounters that were with midden workers was similar, whether it performed midden work and then began another activity, or the reverse. There was no significant difference in average proportions of encounters with midden workers in the two types of segments, midden work to another activity or another activity to midden work, in two of three data sets: Lilith II ( $t = -1.139$ , n.s.,  $n = 19$ , paired *t*-test; mean difference  $-0.071$ , 95% confidence intervals  $-0.202$ ,  $0.061$ ) and Hermione ( $t = -1.036$ , n.s.,  $n = 26$ , paired *t*-test; mean difference  $-0.088$ , 95% confidence intervals  $-0.266$ ,  $0.09$ ). In the remaining data set, Trillian I, ants had a significantly higher proportion of encounters with midden workers while performing midden work before beginning another activity than they did when performing another activity before beginning midden work ( $t = -2.699$ , one-tailed  $P = 0.01$ ,  $n = 13$ , paired *t*-test; mean difference  $-0.223$ , 95% confidence intervals  $-0.405$ ,  $-0.041$ ). Proportions of encounters that were with midden workers ranged from 0 to 0.97. Ants on the midden could meet only midden workers, since all ants on the midden were considered to be midden workers.

### Encounter rate and probability of performing midden work

Ants engaged in tasks other than midden work who switched to perform midden work had met midden workers at a higher rate than ants who did not switch. Figure 3 shows the results on encounter rates for all five data sets in which this comparison was made. In Lilith II, only one ant that met a midden worker did not eventually begin to do midden work, so the statistical test could not be performed. The result was clear: all the ants that began midden work met midden workers at a higher rate than the one that did not begin midden work. In Hermione, the encounter rates for the 9 ants that began to do midden work were all higher than the rates for the 2 that did not do midden work ( $U = 18$ , one-tailed  $P = 0.02$ , Mann-Whitney *U*-test). In Trillian I, rates for the 16 ants that began to do midden work were significantly higher than those for the 6 ants that did not ( $Z = 2.54$ , one-tailed  $P < 0.005$ , Mann-Whitney *U*-test). In the data in which focal ants were chosen upon encounter with a midden worker, the results were the same: ants who began to do midden work after performing another activity had met midden workers at a higher rate than ants which did not do midden work (Ingrid,  $Z = 2.68$ , one-tailed  $P = 0.004$ , 21 began to do midden work, 10 did not; Trillian II,  $Z = 2.39$ , one-tailed

**Table 1** Comparison of four data sets. A segment is a portion of an observation during which the focal ant performed one activity. For counts of encounters per segment, foraging and walk/stand/groom were counted as a single segment when they occurred consecutively

	Lilith I	Lilith II	Hermione	Trillian I
Number of ants observed	93	48	62	16
Segments per ant				
Range	1–3	1–45	1–32	52
Mean (SD)	1.1 (0.4)	6.1 (8.9)	4.7 (6.5)	15.3 (16.8)
Segments of each activity				
Foraging	22	3	34	11
Midden work	6	453	350	331
Walk/stand/groom	155	208	239	132
Encounters per ant				
Range	0–157	0–49	0–87	0–148
Mean (SD)	35.2 (28.8)	16.0 (12.9)	21.6 (16.9)	80.4 (36.5)
Encounters per segment				
Range	0–157	0–43	0–87	0–107
Mean (SD)	32.1 (27.7)	2.4 (5.7)	4.6 (9.5)	5.3 (11.4)

$P=0.01$ , 26 began to do midden work, 12 did not; Mann-Whitney  $U$ -test).

## Discussion

The probability an ant will begin to do midden work is associated with its recent interaction history. The more midden workers an ant meets while it is away from the midden, the more likely it is to perform midden work. This positive correlation was significant in four data sets from three colonies (Fig. 2). In one of these data sets, Lilith I, the correlation persisted with low values of both variables; when contact with midden workers was rare, ants did little midden work.

How an ant reacts to interaction with midden workers is related to its rate of interaction, in encounters per minute. Ants engaged in some other task were more likely to begin to do midden work when their rate of encounter with midden workers was high (Fig. 3). Ants may assess encounter rate using the interval between encounters. The interval that elapses between interactions influences activity in honeybee foragers (Seeley and Tovey 1994) and nest builders of *Polybia* wasps (Jeanne 1986, 1996).

To distinguish the task of the ants it meets, an ant may use the odor of objects carried by another ant, such as dead ants or refuse. In addition, harvester ants of different task groups differ in cuticular hydrocarbons (Wagner et al. 1998). Task-specific cuticular hydrocarbon profiles have also been reported in other ant species (Bonavita-Cougordan et al. 1993) and termites (Howard et al. 1982). Cuticular hydrocarbons are the source of colony-specific odors used by social insects in kin recognition (Arnold et al. 1996). An ant can detect in the course of a brief antennal contact whether another ant is a nestmate, presumably by its cuticular hydrocarbon profile. Perhaps an ant can also detect the task of another ant during brief antennal contact.

Our results do not show how many of an ant's recent encounters contribute to its task decisions. In many theoretical models of task allocation, individuals begin to perform a task at a threshold value of a variable which is reset to zero after every response (e.g., Gordon et al. 1992; reviewed in Beshers and Robinson, in press). In the present case, such a rule would be that when an ant accumulates  $x$  encounters in a given time interval it begins to do midden work, and once it begins doing midden work the number of encounters is set to zero and a new time interval begins. Our results here are not consistent with a model like this, because ants that stopped performing midden work often had as many encounters with midden workers as ants that left another activity to take up midden work. If such a model is correct, ants must employ different threshold rules in different situations, so that the threshold encounter rate required to take up midden work differs from the threshold required to leave it. Another possibility is that such models are incorrect, and an ant's task decision depends on information accumulated over more than one activity. For example, encounter rate might influence the probability of performing midden work over many transitions in and out of midden work. This is consistent with our results.

Whatever the correct model for individual task decisions, it seems unlikely that ants behave in a completely deterministic way or that their responses are calibrated to a narrow range of stimuli. Such behavior would be appropriate for animals that reliably make precise assessments and inhabit a predictable environment, and neither seem to be the case for ants. For example, a task decision that depends in a fully deterministic way on a threshold of four encounters would require ants to count reliably to four and would be most useful if ants reliably experience exactly four encounters in particular situations; both seem unlikely. Theoretical work shows that the rules that individuals use in task decisions may be stochastic or imprecise, yet still lead to predictable dynamics at the level of the colony (e.g., Deneubourg et al. 1986; reviewed in Gordon 1996).

We found that ants away from the midden, not engaged in midden work, began to perform midden work when they met many other ants carrying refuse. Ants away from the midden were not constrained to go to the midden. However, ants which were somehow predisposed for midden work and were moving toward the midden, which we would classify as walking, would probably encounter midden workers as they approached the midden. There are two reasons why this effect probably does not contribute greatly to our results. First, large numbers of ants were observed walking around, relative to numbers on the midden, and ants walking around were dispersed throughout the arena. Thus it is unlikely that most ants walking around were already headed for the midden. Second, the focal ants we observed off the midden encountered midden workers all over the arena, and the number and locations of midden piles changed many times during the course of the study. Thus most contacts between focal ants and midden workers off the midden did not occur near the midden.

If encounters with midden workers tend to elicit more midden work, why do all workers not end up doing midden work? The positive feedback from other workers may be countered by a tendency to stop performing a task when the environment does not provide opportunities to perform it (as in the model of Pacala et al. 1996). Environmental cues provide negative feedback for other tasks of harvester ants. The rate at which successful foragers return to the nest is probably linked to food availability. When this rate declines, foragers are more likely to remain inactive inside the nest (Gordon 1991).

Similarly, negative feedback from the environment may curtail midden work. The amount of midden work performed is probably linked to the amount of midden material present. In the field, dead ants are often taken far from the nest where they are removed by other, scavenging species (personal observations), and the majority of time spent in midden work is in the collection, sorting, and rearrangement of pebbles and seed husks. Midden workers in *P. barbatus*, as in *P. badius* (Gordon 1984), may help prevent intrusion on the nest mound by other ant species by transferring some scent mark to midden material. Perhaps when the midden is not sufficiently permeated with this scent-marking chemical, a few ants may respond to a lack of midden scent, and begin midden work, and their encounters with other ants will elicit more midden work. Then, midden workers might become more likely to return to the nest when they do not encounter midden material that requires scent-marking. In laboratory colonies, midden work is mostly the futile attempt of the colony to dispose of dead ants. We found that midden workers stop performing midden work despite encounters with other midden workers; the proportion of recent encounters with midden workers for ants beginning or stopping midden work was equally high. We do not know what environmental cues provide negative feedback; some possibilities are insufficient midden material to occupy ants, or competing cues that elicit other tasks. In Lilith I,

when numbers of dead ants were relatively low, few ants performed midden work (Table 1).

The task an individual worker performs is the outcome of many influences (Gordon 1996). A worker's activity at any instant depends on its physiological state; both genetic variation and hormonal state lead individuals to differ in the propensity to perform tasks (Robinson and Page 1989). A worker's activity further depends on the current status of the environment relevant to the task it is performing; for example, a forager's activity is affected by the availability of food (Seeley 1989). This study shows correlations between an ant's task and its short-term accumulation of brief encounters with its nestmates. Manipulative experiments are needed to establish a causal link between encounters and task decisions; we are currently performing such experiments using extracts of task-specific cuticular hydrocarbons (Wagner et al. 1998).

An ant's brief encounters with others could provide a cue to the numbers of ants currently engaged in a task. Cues based on interaction rate may enable ants to respond to changes in worker numbers even though ants cannot count or assess total numbers engaged in a task. As conditions change, social insect colonies adjust the numbers of workers engaged in various tasks. This task allocation operates without central control; individuals respond to simple, local cues. Encounter rate can translate overall changes in group size into a simpler, local index. Each ant's assessment of its recent interaction history may contribute to the complex process of task allocation in the colony.

**Acknowledgements** Many undergraduate research assistants contributed their enthusiasm and hard work to this project. Many thanks to Justin Augustine, Sonya Elder, Michelle Forgy, Meghan Hagerty, Robert Hung, Lindsay Kiriakos, Anthony Liu, Meghan Rollins, Eric Saxon, Erika Marin-Spiotta, and Paul Wright for their help with data collection, and special thanks to Anne Fullerton who contributed greatly to the beginning of the project and who made Fig. 1. We are enormously grateful to Lincoln Moses and Lynn Gale for help with statistical analysis. Michael Lachmann and Dennis Chao wrote computer programs we used for data entry. We thank David Hall, Larry Gilbert, Ben Kerr, Henrique Pereira, Noa Pinter, Nathan Sanders, Diane Wagner, Clare Wuellner, and Jennifer Yeh for comments on the manuscript. Data analysis was done while D.M.G. was a Fellow of the Stanford Center for Advanced Studies in Behavioral Sciences; the fellowship was supported in part by NSF SBR 9601236. The research was supported by NSF grant no. 9603639.

## References

- Arnold G, Quenet B, Cornuet J, Masson C, De Schepper B, Estoup A, Gasque P (1996) Kin recognition in honeybees. *Nature* 379:498
- Beshers S, Robinson GE (in press) Response thresholds and division of labor in insect colonies. In: Pasteels JM, Deneubourg J-L, Detrain C (eds) *Information processing in social insects*. Birkhäuser, Basel
- Blumstein DT, Armitage KB (1997) Alarm calling in yellow-bellied marmots. I. The meaning of situationally variable alarm calls. *Anim Behav* 53:143–171



- Boinski S, Campbell AF (1996) The huh vocalization of white-faced capuchins: a spacing call disguised as a food call. *Ethology* 102:826–840
- Bonavita-Cougourdan A, Clement JL, Lange C (1993) Functional subcaste discrimination (foragers and brood-tenders) in the ant *Camponotus vagus* Scop: polymorphism of cuticular hydrocarbon patterns. *J Chem Ecol* 19:1461–1477
- Brown MJF, Gordon DM (1997) Individual specialisation and encounters between harvester ant colonies. *Behaviour* 134:849–866
- Cole BJ (1991) Short-term activity cycles in ants: generation of periodicity by worker interaction. *Am Nat* 137:244–259
- Deneubourg JL, Aron S, Goss S, Pasteels JM, Duernick G (1986) Random behavior, amplification processes and number of participants: how they contribute to the foraging properties of ants. *Physica D* 22:176–186
- Franks NR, Bryant S, Griffiths R, Hemerik L (1990) Synchronization of the behaviour within nests of the ant *Leptothorax acervorum* (Fabricius). I. Discovering the phenomenon and its relation to the level of starvation. *Bull Math Biol* 52:597–612
- Gordon DM (1984) Harvester ant middens: refuse or boundary? *Ecol Entomol* 9:403–412
- Gordon DM (1986) The dynamics of the daily round of the harvester ant colony. *Anim Behav* 34:1402–1419
- Gordon DM (1987) Group-level dynamics in harvester ants: young colonies and the role of patrolling. *Anim Behav* 35:833–843
- Gordon DM (1989) Dynamics of task switching in harvester ants. *Anim Behav* 38:194–204
- Gordon DM (1991) Behavioral flexibility and the foraging ecology of seed-eating ants. *Am Nat* 138:379–411
- Gordon DM (1992) How colony growth affects forager intrusion in neighboring harvester ant colonies. *Behav Ecol Sociobiol* 31:417–427
- Gordon DM (1996) The organization of work in social insect colonies. *Nature* 380:121–124
- Gordon DM, Hölldobler B (1987) Worker longevity in harvester ants. *Psyche* 94:341–346
- Gordon DM, Goodwin B, Trainor LEH (1992) A parallel distributed model of ant colony behavior. *J Theor Biol* 156:293–307
- Gordon DM, Paul, REH, Thorpe K (1993) What is the function of encounter patterns in ant colonies? *Anim Behav* 45:1083–1100
- Howard RW, McDaniel CA, Nelson DR, Blomquist GJ, Gelbaum LT, Zalkow LH (1982) Cuticular hydrocarbons of *Reticulitermes virginicus* (Banks) and their role as potential species and caste-recognition cues. *J Chem Ecol* 8:1227–1239
- Huang Z-Y, Robinson GE (1992) Honeybee colony integration: Worker-worker interactions mediate hormonally regulated plasticity in division of labor. *Proc Natl Acad Sci USA* 89:11726–11729
- Jang YW, Greenfield MD (1996) Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. *Anim Behav* 51:1095–1106
- Jeanne RL (1986) The organization of work in *Polybia occidentalis*: The costs and benefits of specialization in a social wasp. *Behav Ecol and Sociobiol* 19:333–341
- Jeanne RL (1996) Regulation of nest construction behavior in *Polybia occidentalis*. *Anim Behav* 52:473–488
- Keller L, Cherix D, Ulloa-Chacon P (1989) Description of a new artificial diet for rearing ant colonies as *Iridomyrmex humilis*, *Monomorium pharaonis* and *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Insectes Soc* 36:348–352
- Kolmes SA, Winston ML (1988) Division of labour among worker honey bees in demographically manipulated colonies. *Insectes Soc* 35:262–270
- MacKay WP (1981) A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Psyche* 88:25–74
- MacKay WP (1983) Stratification of workers in harvester ant nests (Hymenoptera: Formicidae). *J Kans Entomol Soc* 56:538–542
- Mason JR, Reidinger RF (1981) Effects of social facilitation and observational learning on feeding behavior of the red-winged blackbird. *Auk* 98:778–784
- Pacala SW, Gordon DM, Godfray HCJ (1996) Effects of social group size on information transfer and task allocation. *Evol Ecol* 10:127–165
- Prokopy RJ, Duan JJ (1998) Socially facilitated egg-laying behavior in Mediterranean fruit flies. *Behav Ecol Sociobiol* 42:117–122
- Reeve HK, Gamboa GJ (1987) Queen regulation of worker foraging in paper wasps: a social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behavior* 102:147–167
- Reznikova ZI, Ryabko BYA (1994) An experimental study of ants' language and cognitive aptitude based on ideas of the information theory. *Sib J Ecol* 4:347–359
- Robinson GE, Page RE Jr (1989) Genetic basis for division of labor in an insect society. In: Breed MD, Page RE Jr (eds) *Genetics of social evolution* Westview, Boulder, Colo
- Seeley TD (1989) Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. *Behav Ecol Sociobiol* 24:181–199
- Seeley TD, Tovey CA (1994) Why search time to find a food-storer bee accurately indicates the relative rates of nectar collecting and nectar processing in honey bee colonies. *Anim Behav* 47:311–316
- Stamps JA (1991) The effect of conspecifics on habitat selection in territorial species. *Behav Ecol Sociobiol* 28:29–36
- Thorpe WH (1963) *Learning and instinct in animals*. Methuen, London
- Wagner D, Brown MJF, Brown P, Cuevas W, Moses LE, Chao DL, Gordon DM (1998) Task-related differences in the cuticular hydrocarbon composition of harvester ants, *Pogonomyrmex barbatus*. *J Chem Ecol* 24:2021–2037
- Waser PM (1984) "Chance" and mixed-species associations. *Behav Ecol Sociobiol* 15:197–202
- Wilson EO (1962) Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith). 2. An information analysis of the odour trail. *Anim Behav* 10:148–158
- Wilson EO (1974) *The insect societies*. Belknap, Cambridge, Mass
- Wilson EO (1984) The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 16:89–98
- Winston ML, Fergusson LA (1985) The effect of worker loss on temporal caste structure in colonies of the honeybee (*Apis mellifera* L.). *Can J Zool* 63:777–780

Communicated by R.H. Crozier