

Research article

## Resources and the flexible allocation of work in the desert ant, *Aphaenogaster cockerelli*

N.J. Sanders\* and D.M. Gordon

Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020, USA

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**Summary.** Social insect colonies can respond to changes in resource availability by altering their foraging behavior. Colonies of the desert ant, *Aphaenogaster cockerelli*, responded to experimental changes in the distribution and type of available resources by adjusting the numbers of ants engaged in foraging and other tasks outside the nest, and by adjusting the temporal patterns of these activities. Colonies foraged more intensely for protein resources than for seed resources, and for high-density resources more than for low-density resources. This flexible allocation and resource use may promote coexistence with interspecific competitors such as ants in the genus *Myrmecocystus*.

**Key words:** Foraging, behavioral plasticity, task allocation, desert ants, *Aphaenogaster cockerelli*.

### Introduction

Social insects dominate many terrestrial ecosystems, perhaps because of their flexible division of labor (Hölldobler and Wilson, 1990). Initial theory and data suggested that internal factors, such as body size, determined the task that a worker performed (Oster and Wilson, 1978). However, more recent theoretical and empirical work shows that the allocation of workers to tasks is dynamic: the task that an individual performs can change hourly, and the distributions of workers among tasks change as environmental conditions change (Robinson, 1992; Gordon, 1996). But, for most social insect species, we lack information on the dynamics of task allocation or the environmental cues which influence the numbers of workers engaged in tasks (Gordon, 1996).

Ant colonies, like other social insect colonies (e.g., Cartar, 1992; Fewell and Page Jr., 2000; Robinson, 1992;

Schmid-Hempel, 1992; Seeley, 1986, 1989), can adjust their foraging behavior in response to changes in resource availability and forage more intensely for closer, better, or more abundant resources (e.g., Breed et al., 1987; Crawford and Rissing, 1983; Crist and MacMahon, 1992; Davidson, 1978; de Biseau and Pasteels, 2000; Detrain et al., 2000; Fewell and Harrison, 1991; Fewell et al., 1992; Gordon, 1991; Hölldobler, 1976; Taylor, 1977; Traniello, 1989). But foraging behavior is only one of the tasks that colonies perform each day, and diverse colony tasks may be related and affect each other (Gordon, 1987). For example, if the number of ants engaged in foraging increases, the numbers engaged in other tasks may decrease.

We have two aims in this paper. First, we examine how the intensity of foraging behavior in the desert ant *Aphaenogaster cockerelli* depends on both the distribution of resources and the interaction between resource type and distribution. Davidson (1977) suggested colonies may forage more efficiently for dispersed resources. However, *A. cockerelli*'s preference for protein over seeds (Hölldobler et al., 1978) may affect its response to the spatial distribution of resources.

Second, we ask how the temporal patterns of several tasks performed outside the nest, including foraging, depend on the distribution and type of resources available. As in other species (Gordon, 1984a), in *A. cockerelli*, there is a temporal pattern of tasks performed outside the nest (Sanders and Gordon, 2000) which has been called the 'daily round' of colony activities (Gordon, 1986). Such tasks include foraging, nest maintenance, midden work, meandering, and loitering (defined in Table 1). Tasks other than foraging may be important to colony fitness. For example, nest maintenance behavior may protect the colony from flooding and extremes in air temperature, and it may also be necessary for storing resources inside the nest and increasing the size of the nest as colonies grow larger. Chew (1995) suggested that *A. cockerelli* colonies at his nearby site are especially susceptible to flooding and extremes in surface temperatures because the

\* Current address: Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA, e-mail: njs12@humboldt.edu

**Table 1.** Classification of behaviors within 0.5 m radius of nest entrance**Foraging**

- Ants travel to nest entrance carrying food item such as seed, plant matter, or other insect

**Nest maintenance**

- Ants move rocks around on nest mound
- Ants carry out inorganic material from nest

**Midden work**

- Ants carry out midden items from the nest entrance such as dead nestmates, seed husks, or insect parts
- Ants stand on midden pile or move midden items around

**Meandering**

- Ants walk with frequent stops in a zig-zag pattern around the nest mound with nothing in their mandibles

**Loitering**

- Ants convene in the nest entrance

hard layer of caliche soil below the surface may limit how deep colonies can go into the ground. Colonies that are able to devote more workers to nest maintenance may be better able to penetrate the caliche. Midden workers, by removing organic matter from the nest, may prevent fungal and bacterial infections (Chew, 1977). Midden piles around the periphery of the nest may be the site of colony-specific scent marks, as in *Pogonomyrmex badius*, and deter workers from other nests (Gordon, 1984b). The behavior of meanderers may inform the rest of the colony about the environment outside the nest. Loiterers may be workers forced to stay inside the nest because of increased activity of neighbors or reduced resource availability.

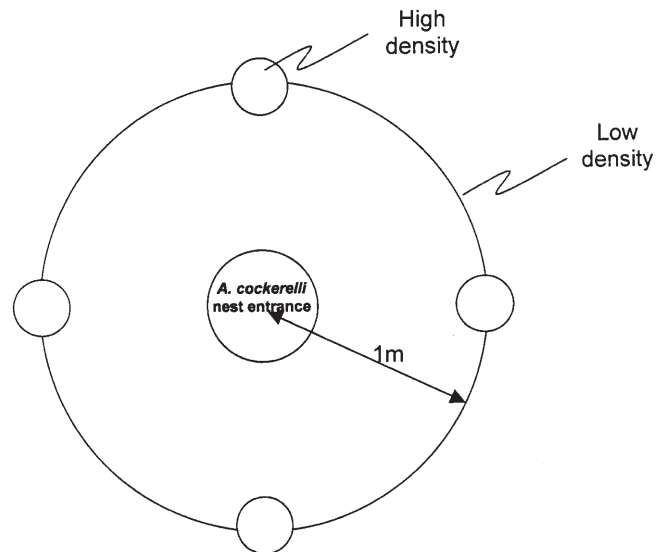
**Methods***Study site and natural history*

We conducted this study in a *Prosopis-Acacia* dominated community, approximately 3 km north of Portal, Arizona, USA. The 3 ha site is on an alluvial fan, and the vegetation varies from bare ground with small bunches of grass to primarily shrubs such as *Acacia constricta*, *Prosopis glandulosa*, *Gutierrezia sarothrae*, and *Ephedra* spp.

*Aphaenogaster* (formerly *Novomessor*) *cockerelli* is distributed throughout the deserts in the southwestern U.S. from eastern California to western Texas and into northern Mexico (Johnson, 2000; Wheeler and Creighton, 1934). *Aphaenogaster cockerelli*, which can form polydomous nests, forages for seeds and other plant matter, dead arthropods, termites, and occasionally homopteran honeydew (Chew and De Vita, 1980; Whitford et al., 1980).

*Resources and foraging rate*

To examine how the intensity of colony foraging behavior depends on the density and distribution of food resources, we did an experiment with three treatments following Davidson's (1977) experimental design. In each treatment, one nest of each of 10 *A. cockerelli* colonies was surrounded with a ring of food resources as depicted in Figure 1. Each high-density patch and low-density arc consisted of approximately 60 mL of resources. To determine which distribution of resources work-

**Figure 1.** Schematic of the experimental design for foraging intensity experiment. Small circles represent the high-density resources, and the biggest circle represents the ring of low-density resources

ers visited, high-density patches were colored red or green using vegetable dye and the low-density arcs were not colored. In a pilot cafeteria experiment, the numbers of foragers returning to the nest with food items from colored and non-colored resource patches did not differ.

In the first treatment, we used the same kind of food resources, a 1 : 1 mixture by volume of crushed Pecan Sandies (Keebler Corporation, Elmhurst, Illinois, USA) and wild bird seed, as both the high- and low-density resources. In the second treatment, we used tuna as the high-density resource and crushed wild birdseed as the low-density resource to determine if a colony's response to resource density depended on resource type. In the third treatment, we used tuna as both the high- and low-density resource, and manipulated only density. We used Pecan Sandies in the first experiment because they are an ideal food item for ants because they are rich in fats, proteins, and carbohydrates (e.g., Kaspari et al., 2000). We used tuna as a standardized protein resource to represent insects, as many other studies have, and wild birdseed as standardized seed resource to represent naturally occurring seeds (Lynch et al., 1980; Fellers, 1987; Bestelmeyer et al., 2000; Yanoviak and Kaspari, 2000).

We recorded the color of the food items that the first 100 foragers carried back to the nest from the experimental distribution of resources in each treatment. We counted as a forager each individual that was carrying either a high-density or low-density resource from the experimental distribution of resources into the nest. We also recorded the time elapsed until 100 of these foragers entered the nest. The presence of other resources, besides those we experimentally added, may have influenced the time it took for 100 foragers to return to the colony. However, the effect of naturally occurring resources should average across colonies and thus would not affect the results from our experiment.

To determine statistically the effect of the density and distribution of resources on *A. cockerelli* foraging behavior, we used t-tests to compare the numbers out of 100 ants returning to the nest with either high-density or low-density resources in each treatment. We also compared the times it took for 100 foragers to return in each treatment using a one-way ANOVA. In the model, time, in minutes, was the response variable, and the treatment effect corresponded to the three resource distributions described above.

*Resources and colony activity patterns*

We performed two experiments to examine the effect of the density distribution and type of food resources on the numbers and temporal pat-

tern of ants performing exterior tasks. In the first experiment, we manipulated the density and distribution of food resources. Each morning twelve randomly selected colonies received one of three treatments: 1) high-density resources (HD colonies), 2) low-density resources (LD colonies), or 3) no resources. The colonies that received no resources served as control colonies. The high-density resources were arranged in 4 patches of 60 mL each and placed at cardinal directions. The low-density resources were scattered in a circle around the nest in a band approximately 10 cm wide. Resources were a 1 : 1 mixture by volume of crushed wild bird seed and Pecan Sandie cookies placed 1 m away from the nest entrance. Each colony, except the control colonies, received approximately 240 mL of resources. Since we were not interested in resource type per se in this experiment, we used the mixture of seeds and Pecan Sandies because 1) we could easily and accurately manipulate density, and 2) the ants were attracted to the resources.

In the second experiment, we manipulated the type of food resources available. There were three treatments in this experiment: 1) protein (P colonies), 2) seed (S colonies), and 3) no resources as a control. Protein resources were 4 clumps of approximately 60 mL of tuna placed 1 m away from the nest entrance in each cardinal direction. Seed resources were 4 clumps of approximately 60 mL of crushed wild bird seed placed 1 m from the nest entrance in each cardinal direction.

For both experiments, we visited every colony in each experiment in a haphazard order each morning for seven mornings between 0600 and 0630. We counted the number of ants engaged in each of the 5 tasks described in Table 1 for two minutes, and then put out the food resources. We visited each colony one hour later and at one-hour intervals until 1100. During each visit, we counted the numbers of ants performing each task. To normalize for differences in colony sizes, all observations for each colony were converted to proportions of the maximum number of ants ever active outside the nest in that colony, which we call the OSmax.

Because we divided each count of workers in task *i* at time *t* for colony *j* by the OSmax, the sum of the proportions for colony *j* at time *t* do not sum to one. Thus, the proportions for different tasks are independent of each other; for example, when the proportion for task *i* decreases, the proportion for another task may not change.

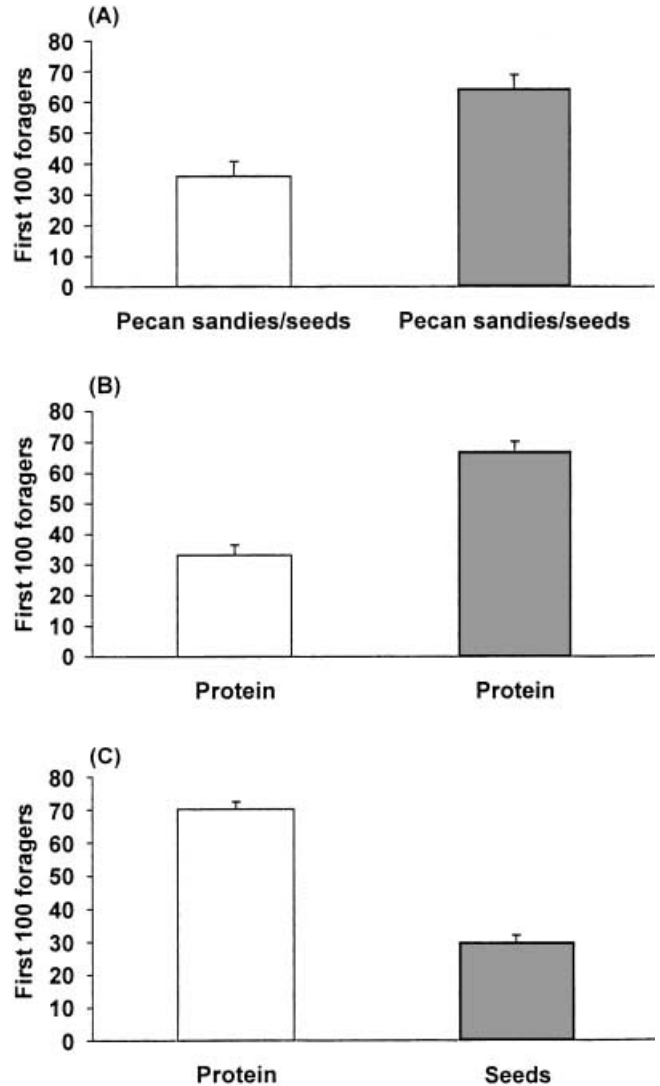
In the density experiments, we observed 70 randomly chosen colonies. Fourteen of the 70 colonies were observed in two treatments. In the food type experiments, we observed 70 randomly chosen colonies. Twelve of the 70 colonies were observed in two treatments and one colony was observed in all three treatments. If a colony was observed in more than one treatment, at least two days separated the observations in each treatment. For each hour of each treatment, there were 28 observations (4 colonies × 7 days).

To determine statistically the effect of resource distribution and type on colony task activity patterns, we first performed a multivariate analysis of variance (MANOVA) on each set of colonies in each treatment. In both the resource distribution and type experiment, the MANOVA detected strongly significant effects of both time and treatment on colony task activity. Here, we report only the results from examining each behavior (Table 1) independently using a two-way ANOVA. In the ANOVA model, treatment and time were main effects, and the arcsin-transformed proportion of ants engaged in task *i* was the response variable. To determine the influence of resource distribution and type on the total number of ants outside the nest, we used unpaired t-tests to compare the maximum number of ants ever observed outside the nest.

**Results**

*Resources and foraging rate*

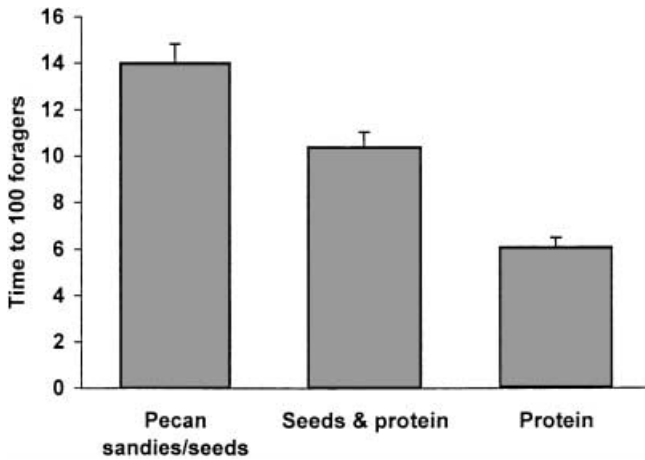
When both high-density and low-density food resources were the same type, almost twice as many foragers returned with the low-density resources (Fig. 2a,  $t_{18} = 4.21$ ,  $P =$



**Figure 2.** Response of *A. cockerelli* foraging behavior to resource density distribution. The bars ( $\pm$  SEM) represent the mean number out of the first 100 foragers to return with high-density-resources (open bars) or low-density resources (shaded bars) from the experimental setup

0.0003; Fig. 2b,  $t_{18} = 7.59$ ,  $P < 0.0001$ ). When the high-density resource was tuna and the low-density resource was seeds, more than twice as many foragers returned with the high-density resources than with the low-density resources (Fig. 2c,  $t_{18} = 10.17$ ,  $P < 0.0001$ ).

The type of resource distributed around nests influenced how long it took 100 foragers to return with a food item (Fig. 3,  $F_{2,27} = 37.28$ ,  $P < 0.0001$ ). When both high-density and low-density resources were the mix of Pecan Sandies and seeds, it took colonies approximately 14 min for 100 foragers to return to the nest with resources from the experimental setup. When high-density resources were tuna and low-density resources were seeds, it took an average of 10 minutes for 100 foragers to return to the nest. When both high and low-density resources were tuna, it took an average of 6 minutes.



**Figure 3.** The response time of colonies stocked with different kinds of resources. The bars ( $\pm$  SEM) show the mean time in minutes for 100 foragers to return with resources from the experimental setup

### Resources and colony activity patterns

The distribution of food resources influenced the proportions of *A. cockerelli* workers engaged in tasks outside the nest (Table 2, Fig. 4). As expected, there was a significant effect of time on the proportion of ants engaged in each task. This reflects the daily round of colony behavior: colonies tend to perform certain behaviors at certain times during the morning (Sanders and Gordon, 2000).

There was a significant effect of the density distribution of resources on each task except midden work (Table 2). The

proportion of workers devoted to foraging was much higher, sometimes as much as four times higher, in HD (high-density) colonies than in control colonies (Fig. 4a). HD and LD (low-density) colonies both devoted more workers to nest maintenance work than did control colonies (Fig. 4b). HD and LD colonies devoted significantly fewer workers to meandering and loitering than did control colonies (Fig. 4d, 4e).

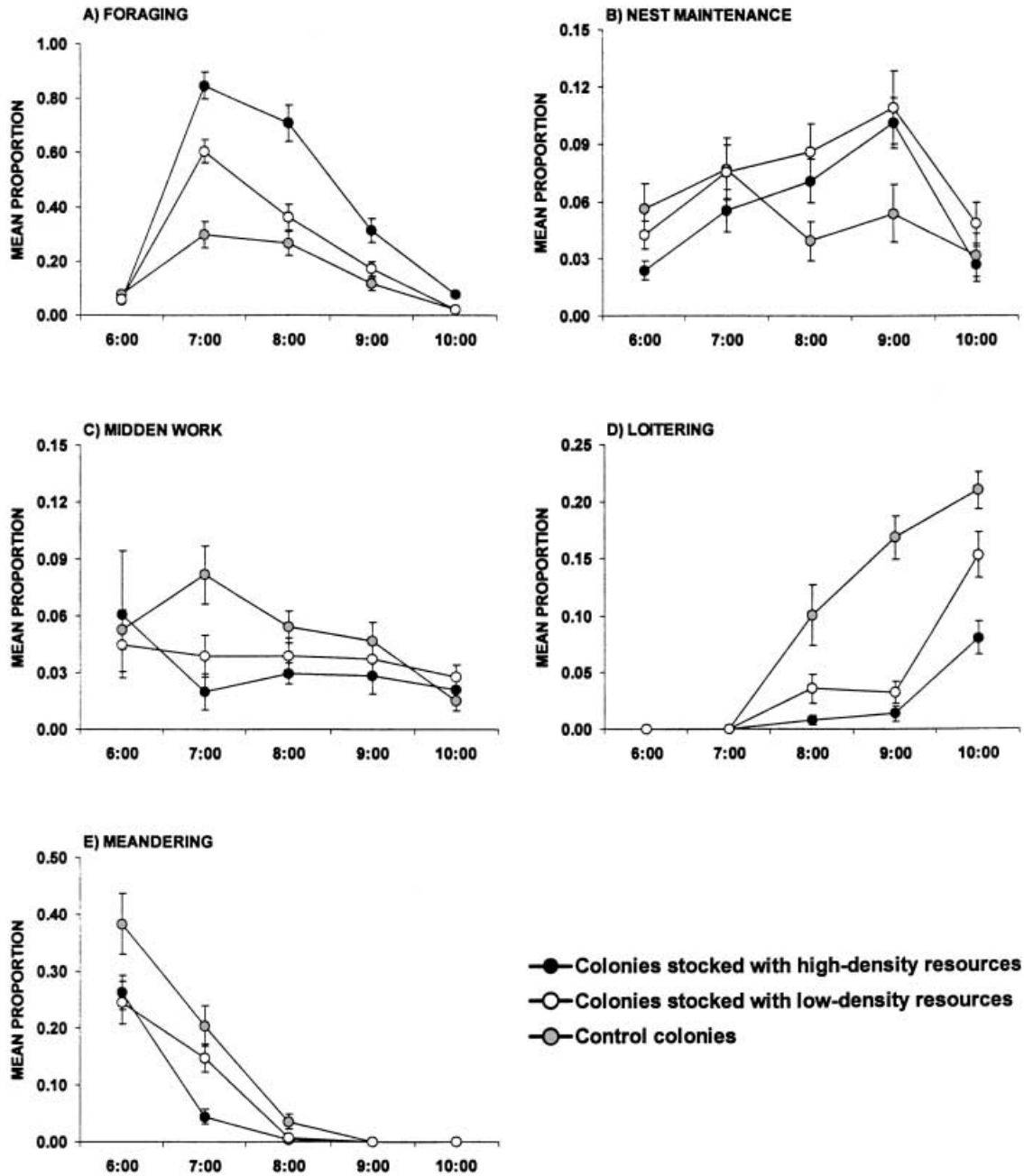
The significant time  $\times$  resource density effect indicates that the density distribution of resources influenced the temporal pattern of activities (Table 2). For example, HD colonies devoted more workers to foraging, and they did so for longer into the morning activity period than did LD or control colonies (Fig. 4a). Both HD and LD colonies devoted more workers to nest maintenance work than control colonies, with a late peak at 9:00 (Fig. 4b). HD and LD colonies devoted fewer workers to midden work immediately after resources were added between 6:00 and 7:00, but by the end of the morning, colonies in all three treatments devoted about the same amount of workers to midden work (Fig. 4c). Loitering did not increase as rapidly in HD and LD colonies as it did for control colonies (Fig. 4d). After resources were added to the experimental colonies, meandering decreased more rapidly than it did for control colonies (Fig. 4e).

The type of resources available to *A. cockerelli* colonies influenced the proportions of workers engaged in tasks outside the nest (Table 3, Fig. 5). P (protein) colonies devoted more workers to foraging, and fewer workers to nest maintenance and loitering than did S (seed) or control colonies (Fig. 5a, b, d). S colonies devoted more workers to nest maintenance

**Table 2.** ANOVA for the effects of time and density distribution and their interaction on the proportion of ants engaged in each task

	df	SS	MS	F	P
<b>Foraging</b>					
Time	4	32.42	8.10	101.24	< 0.0001
Density distribution	2	10.68	5.34	66.71	< 0.0001
Time $\times$ Density distribution	8	3.34	0.42	5.22	< 0.0001
Error	405	32.42	0.08		
<b>Nest maintenance</b>					
Time	4	0.71	0.18	7.51	< 0.0001
Density distribution	2	0.54	0.27	11.64	< 0.0001
Time $\times$ Density distribution	8	0.37	0.05	1.96	0.05
Error	405	9.50	0.02		
<b>Midden work</b>					
Time	4	0.18	0.04	2.85	0.02
Density distribution	2	0.06	0.03	2.06	0.13
Time $\times$ Density distribution	8	0.27	0.03	2.17	0.03
Error	405	6.25	0.02		
<b>Loitering</b>					
Time	4	34.74	8.68	127.56	< 0.0001
Density distribution	2	5.93	2.96	43.57	< 0.0001
Time $\times$ Density distribution	8	6.01	0.75	11.03	< 0.0001
Error	405	27.57	0.07		
<b>Meandering</b>					
Time	4	30.92	7.73	263.15	< 0.0001
Density distribution	2	0.41	0.21	6.98	0.001
Time $\times$ Density distribution	8	1.22	0.15	5.21	< 0.0001
Error	405	5.60	0.01		





**Figure 4.** The effect of the density distribution of resources on *A. cockerelli* colony task activity patterns. Each panel shows the mean number of ants observed performing task *i* in colony *j* at time *t*/the maximum number of ants ever active for colony *j* at any time. Symbols represent the mean ( $\pm$  SEM)

nance work than did control or P colonies. S colonies also devoted more workers to foraging, and fewer workers to loitering and meandering than did control colonies (Fig. 5d, e).

For each task except meandering (Fig. 5e), there was a significant time  $\times$  treatment effect, indicating that resource type influenced the temporal pattern of colony activity (Table 3, Fig. 5). Foraging increased more rapidly in P colonies than in S or control colonies, and colonies foraged for longer in the day than did S or control colonies (Fig. 5a). S colonies devoted a higher proportion of workers to nest maintenance

work, and did so more rapidly than either P or control colonies (Fig. 5b). Loitering did not increase as rapidly in P and S colonies as it did for control colonies (Fig. 5d).

There were approximately 15% more workers active outside of HD colonies (mean  $\pm$  SEM,  $23.40 \pm 0.98$ ) than LD colonies ( $20.21 \pm 1.24$ ), though this result was only marginally significant (two-tailed *t*-test,  $t_{51} = 2.01$ ,  $P = 0.05$ ). There were approximately 25% more workers active outside the nests of P colonies ( $22.14 \pm 1.12$ ) than S colonies ( $17.46 \pm 0.96$ ) (two-tailed *t*-test,  $t_{53} = 3.16$ ,  $P = 0.003$ ).

**Table 3.** ANOVA for the effects of time and resource type and their interaction on the proportion of ants engaged in each task.

	df	SS	MS	F	P
<b>Foraging</b>					
Time	4	13.70	3.42	60.71	< 0.0001
Resource type	2	4.29	2.14	38.02	< 0.0001
Time × Resource type	8	1.78	0.22	3.94	0.0002
Error	405	22.84	0.06		
<b>Nest maintenance</b>					
Time	4	0.20	0.05	5.82	0.0001
Resource type	2	0.62	0.31	36.09	< 0.0001
Time × Resource type	8	0.32	0.04	4.59	< 0.0001
Error	405	3.49	0.01		
<b>Midden work</b>					
Time	4	0.04	0.01	1.87	0.12
Resource type	2	0.03	0.02	3.18	0.04
Time × Resource type	8	0.08	0.01	1.97	0.05
Error	405	2.12	0.01		
<b>Loitering</b>					
Time	4	1.54	0.39	36.48	< 0.0001
Resource type	2	0.79	0.40	37.36	< 0.0001
Time × Resource type	8	0.57	0.07	6.73	< 0.0001
Error	405	4.28	0.01		
<b>Meandering</b>					
Time	4	6.59	1.65	122.45	< 0.0001
Resource type	2	0.03	0.01	1.02	0.36
Time × Resource type	8	0.06	0.01	0.56	0.81
Error	405	5.45	0.01		

## Discussion

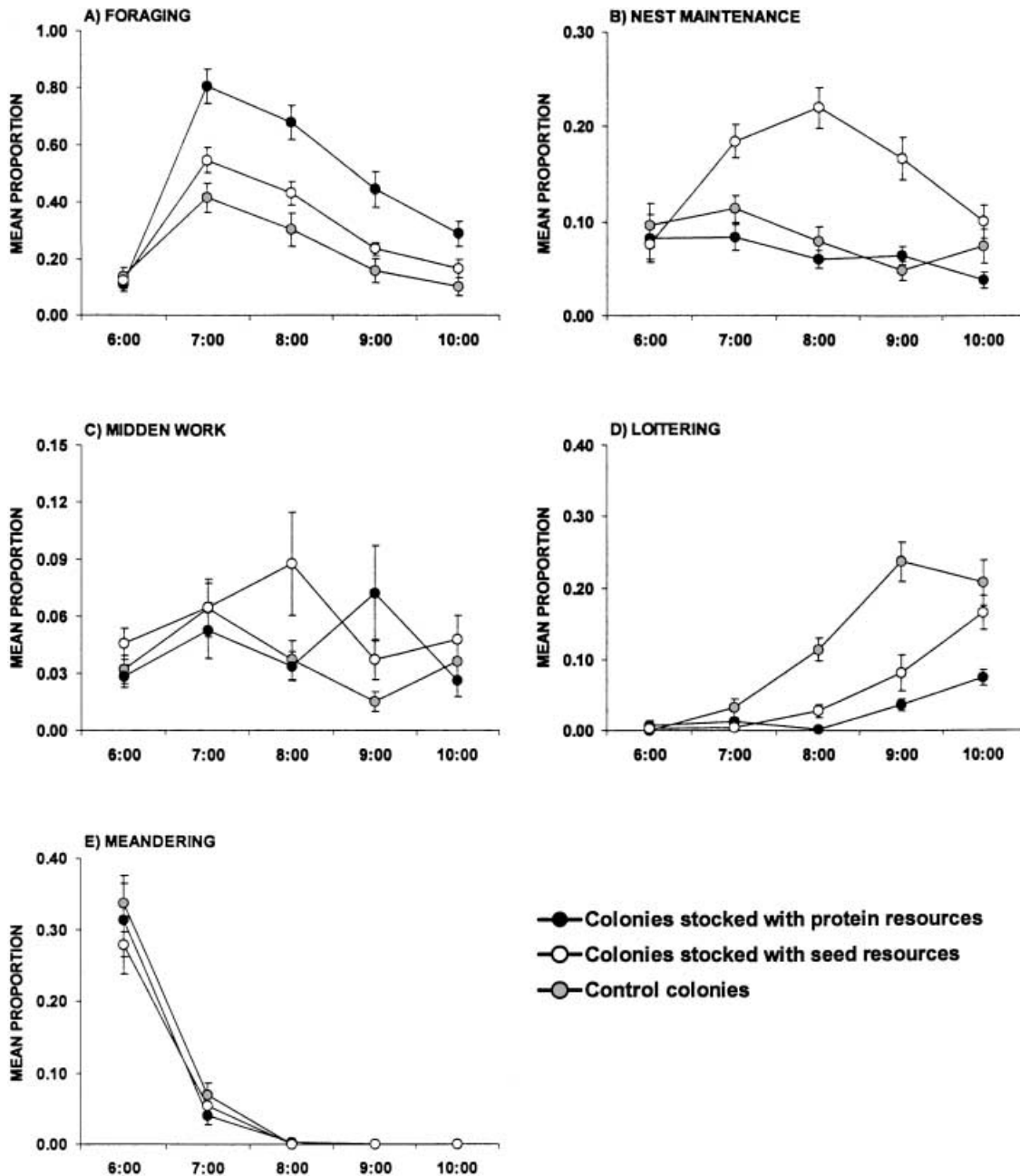
The distribution and type of food resources available clearly influence the behavior of *Aphaenogaster cockerelli* colonies. *Aphaenogaster cockerelli* colonies respond to variation in the distribution and availability of resources by adjusting their foraging behavior. When clumped and dispersed resources were the same, either protein or seeds, *A. cockerelli* foraged solitarily, and collected more dispersed than clumped resources. This is consistent with the results of Davidson (1977). However, when the high-density, clumped food resource was protein and the dispersed, low-density resource was seeds, *A. cockerelli* collected more high-density than low-density resources. Our results suggest that both the density and type of resources are important.

When *Aphaenogaster cockerelli* colonies responded to changes in resource availability and distribution by altering their foraging behavior, the proportions of workers performing other tasks changed. Colonies in all treatments devoted a higher proportion of workers to nest maintenance than did control colonies. This probably occurred because colonies with a resource windfall must create or clear out more nest chambers to store their bounty, and this may explain why nest maintenance peaked immediately after the peak in foraging between 7:00 and 8:00. S colonies did more nest maintenance than did colonies in any other treatment. This may be because protein is stored in the brood, whereas seeds are stored in nest chambers. Another explanation might be that the extra food resources coming into the colony from our experimental addi-

tions signaled the colonies that times are good and they could devote more effort to nest maintenance work.

In *Pogonomyrmex barbatus*, there seems to be a reciprocal relationship between foraging and nest maintenance such that an increase in one is accompanied by a decrease in the other (Gordon, 1987). When both tasks are perturbed, mature colonies choose foraging instead of nest maintenance (Gordon, 1987). This does not appear to be the case in *A. cockerelli*. Previous experiments showed that temporarily removing interspecific competitors led to increases in both foraging and nest maintenance work in *A. cockerelli* (Sanders and Gordon, 2000), and the work presented here shows that an increase in foraging is followed by an increase in nest maintenance. Our preliminary hypothesis is that foraging and nest maintenance are of equal priority, but manipulative experiments are needed to test explicitly this hypothesis.

Increases in foraging and nest maintenance for experimental colonies may be due to task switching by loiterers and meanderers or new workers may come from a pool of inactive workers inside the nest. Once recruitment to a resource begins, meanderers may stay inside the nest or switch tasks to become foragers. Loiterers, rather than convening in the nest entrance late in the morning activity period, may also forage. Loitering was substantially lower in P and HD colonies than in S and LD colonies. Previous experiments also suggested that loiterers are potential foragers (Sanders and Gordon, 2000). Increases in the proportion of workers performing foraging and nest maintenance may have also come from the increased level of overall activity: there were 15% more



**Figure 5.** The effect of resource type on *A. cockerelli* colony task activity patterns. Each panel shows the mean of the number of ants observed performing task *i* in colony *j* at time *t*/the maximum number of ants ever active for colony *j*. Symbols represent the mean ( $\pm$  SEM)

workers outside the nests of P colonies than S colonies, and 25% more outside of HD colonies than LD colonies. There is no *a priori* reason to think that new workers must come from either task switching or from inside the nest. Future experiments will determine where new workers come from.

The distribution and type of resources available also influenced the temporal pattern of tasks in *A. cockerelli* colonies, as indicated by the significant time  $\times$  treatment effects (Table 2, 3). Temporal patterns in overall activity exist in many ant species, and colonies of several species exhibit a

daily round of several tasks (Gordon, 1984a). For control colonies, meandering precedes foraging, and foraging and nest maintenance precede loitering (Fig. 4, 5). The same is true for the experimental colonies, but the rates of changes in the proportions of workers performing the tasks differed among treatments. For example, when food resources were added after the 6:00 observation, the proportion of workers foraging increased more quickly in experimental than control colonies (Fig. 4, 5). Loitering increased more slowly, late in the morning activity period, in experimental than in control

colonies, probably because experimental colonies continued to forage and do nest maintenance work.

Although differences among treatments in resource availability and density distribution influenced the temporal patterns of some activities, some patterns did not change. Foraging behavior peaked generally between 7:00 and 8:00. Loitering increased only after meandering and foraging decreased. Meandering generally peaks before foraging, perhaps because the behavior of meanderers signals the rest of the colony about the abiotic environment, the activity of neighbors, or the distribution of resources that day. In *Pogonomyrmex barbatus*, foraging is always preceded by patrolling (Gordon, 1986). Similarly, meandering precedes foraging in *A. cockerelli*, perhaps because meandering behavior functions to inform the colony of the environment outside the nest.

This study leaves open two sets of questions. First, at the behavioral level, what cues lead to changes in the numbers of workers in particular tasks? In honeybees, when less food is brought in, foragers become more active (Seeley, 1986). This is not the case in *P. barbatus* colonies (Gordon, 1986; 1987; 1991). In *A. cockerelli*, more food coming into the nest may be the signal for both increased foraging and nest maintenance, and less food may signal decreased foraging and nest maintenance, and more loitering.

Second, at the ecological level, our work shows how colonies can modulate their behavior to take advantage of changes in resource type and distribution. Several studies have shown that exploitative competition can affect the distribution and abundance of resources, and thereby influence the foraging behavior of colonies (Fellers, 1987; Human and Gordon, 1996; Lynch et al., 1980), and exploitative competition may be an important mechanism of competition employed by *Myrmecocystus* colonies (Sanders and Gordon, 2000). *Myrmecocystus* colonies locate and exploit high-quality resources more quickly than *A. cockerelli* colonies do (NJ Sanders, unpublished data). Once high-quality resources are discovered, *Myrmecocystus* foragers are likely to displace *A. cockerelli* foragers (NJ Sanders, unpublished data). Long-term studies are needed to determine if the behaviorally plastic response of *A. cockerelli* colonies promotes coexistence with *Myrmecocystus* or negatively influences *A. cockerelli* persistence at the site.

Finally, we suggest that studies of foraging behavior, especially those aimed at understanding how natural selection operates on foraging behavior, consider the myriad other behaviors that animals are engaged in. Our work shows that when foraging behavior changes in response to changing environments, other behaviors also change. Understanding the ecological and evolutionary consequences of changes in a suite of potentially linked behaviors should be a focus of future research, especially in the social insects.

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