

Nathan J. Sanders · Deborah M. Gordon

The effects of interspecific interactions on resource use and behavior in a desert ant

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Abstract We examined how interspecific competition in ants affects resource use and behavior. To test how neighboring *Myrmecocystus* colonies influence the desert ant *Aphaenogaster cockerelli*, we placed temporary enclosures around *Myrmecocystus* spp. colonies and recorded the resources collected by *A. cockerelli* and the numbers of *A. cockerelli* ants engaged in various tasks outside the nest. When neighbors were enclosed, *A. cockerelli* colonies collected a significantly higher proportion of termites and significantly less plant matter than when neighbors were active. The numbers of *A. cockerelli* ants engaged in foraging behavior and nest maintenance work increased when *Myrmecocystus* colonies were enclosed. Interspecific interactions thus can affect the behavior and resource use of *A. cockerelli* colonies and may influence colony fitness.

Key words *Aphaenogaster cockerelli* · *Myrmecocystus* · Resource use · Colony behavior · Niche shift

Introduction

Interspecific competition can influence the organization of communities by altering the resource use and behavior of individuals. Convincing evidence for this comes from perturbation experiments, in which the densities of one or more species are altered. Such perturbations show that the presence of competitors can affect resource use (e.g., Werner and Hall 1976; Kincaid and Cameron 1982; Persson and Greenberg 1990; Luo and Fox 1995; Beckerman 2000), and foraging activity (e.g., Englund et al. 1992; Haemig 1996) in a variety of taxa.

Experimental manipulations have shown that interspecific competition is an important influence on ant community structure (Hölldobler and Wilson 1990). Ecologists have employed two experimental approaches

to assess the effects of interspecific competition in ant communities: (1) examining how competitors alter the intensity of foraging at experimental baits (Lynch et al. 1980; Fellers 1987; Savolainen 1991; Vepsäläinen and Savolainen 1990; Andersen and Patel 1994; Human and Gordon 1996; Cerdá et al. 1998b), and (2) testing how competitors affect the total number of ants active outside the nest (Ryti and Case 1988; Andersen and Patel 1994).

Several questions relating interspecific competition to the resource use and behavior of individuals remain to be addressed. First, few studies of ants have tested the effects of interspecific competition on the use of naturally occurring resources, and these few studies have arrived at different conclusions. Manipulations of granivorous desert ants demonstrated that the removal of neighbors did not influence the kinds and amounts of naturally occurring resources collected by *Veromessor pergandei* or *Pogonomyrmex californicus* colonies (Ryti and Case 1988). In contrast, experiments performed in the taiga biome showed that a subordinate ant species shifted its diet to less preferred resources in the presence of the dominant species at experimental bait stations (Savolainen and Vepsäläinen 1988; Savolainen 1991).

Second, the use of bait stations may not be an adequate tool to assess the extent to which interspecific competition reduces or shifts foraging activity of ant colonies. In natural habitats, there may be considerable variation in the distribution of resources, and certain species may specialize on resources of a particular density (Davidson 1977). Since baits are clumped resources, species that employ recruitment systems to exploit such resources may be preferentially sampled, while those species that tend to exploit widely dispersed resources may be under-represented. A second problem with bait is that recruitment rate of a colony to experimental baits can depend on the other activities in which a colony is engaged (Gordon 1983a). For example, if a colony is engaged in behavior other than foraging while bait is offered, it may not respond to the bait. Finally, the type of resource offered at an experimental bait affects the intensity of foraging response (Cerdá et al. 1998a). In most

N.J. Sanders (✉) · D.M. Gordon
Department of Biological Sciences, Stanford University,
Stanford, CA 94305-5020, USA
e-mail: sanders@ants.stanford.edu

Table 1 Classification of behaviors (observed within 0.5 m radius of nest entrance)

Behavior	Description
Foraging	Ants travel to nest entrance carrying food item such as seed, plant matter, or other insect
Nest maintenance	Ants move rocks around on the nest mound Ants carry out inorganic material from nest
Midden work	Ants stand on midden pile or move midden items around Ants carry out midden items from the nest entrance such as dead nestmates, seed husks, or insect parts
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

studies, tuna or millet is offered, so species that utilize other types of resources may be under-represented.

Behavior other than foraging may be important to a colony's ecological success. In the desert ant, *Aphaenogaster cockerelli*, such behavior includes nest maintenance work, repairing the physical structure of the nest; midden work, carrying out dead insects, seed husks, or other organic matter; loitering behavior, when workers convene in the nest entrance; and meandering, in which ants walk around on the nest mound in a zig-zag pattern (see Table 1). Midden work may prevent fungal or bacterial infection of food stored inside the nest (Chew 1977). Furthermore, midden piles may be the site of colony-specific scent marks used in *Pogonomyrmex badius* (Gordon 1984b) and could be important in *A. cockerelli* as well. Nest maintenance workers clear the nest mound for foragers and ants performing other tasks, and meanderers might serve to inform the colony of the abiotic environment.

In this study, we investigate the interspecific interactions and nest distributions of *Myrmecocystus mimicus* and *M. depilis* colonies (hereafter jointly called *Myrmecocystus*) and *A. cockerelli*. At a long-term study sites near our site, *A. cockerelli* has gone locally extinct, while *Myrmecocystus* populations have persisted (Chew 1995; Brown et al. 1997). Although other factors may have contributed to the extinction of *A. cockerelli* at this site (Chew 1995), competition for food may be important in the decline of *A. cockerelli*. To investigate the mechanisms of interactions between *A. cockerelli* and *Myrmecocystus*, we temporarily enclosed *Myrmecocystus* colonies and examined the effects on resource collection and colony behavior of *A. cockerelli*.

Methods

Natural history and study site

Aphaenogaster (formerly *Novomessor*) *cockerelli* is widely distributed throughout the deserts in the southwestern U.S. from eastern California to western Texas and into northern Mexico (Wheeler and Creighton 1934; Creighton 1955; Snelling and George 1979). *A. cockerelli* can form polydomous colonies of one to five nests and forages for seeds and other plant matter, dead arthropods, termites, and occasionally homopteran honeydew (Snelling 1976; Chew and De Vita 1980; Whitford et al. 1980; Hölldobler 1981). *A. cockerelli* colonies are generally active at all times except the hottest parts of the day (Whitford 1978a), and *M. mimicus* and *M. depilis* reach peak activity levels during mid-morning and forage

intermittently throughout the afternoon (Snelling 1976; Hölldobler 1981). Interestingly, *A. cockerelli* workers forage both individually (Whitford 1976; Davidson 1977) and collectively (Hölldobler et al. 1978; Markl and Hölldobler 1978; Fowler and Whitford 1983).

We conducted this study in July–August 1998 in the Chihuahuan Desert 5 km east of Portal, Arizona (31°54'N, 109°05'S) at an elevation of approximately 1300 m. The 3-ha site is on an alluvial fan, and the vegetation varies from open ground with small bunches of grass to shrubs such as *Acacia constricta*, *Prosopis glandulosa*, *Gutierrezia sarothrae*, and *Ephedra* sp.

We mapped the locations of every *A. cockerelli*, *M. mimicus* and *M. depilis* colony and gave each colony an identification code painted on a rock. In both 1997 and 1998, we located nests by walking parallel paths approximately 3 m apart. There are approximately 100 colonies of *A. cockerelli* and 200 colonies of *Myrmecocystus* at the 3-ha site. *A. cockerelli* colonies are often polydomous (multiple nests per colony). We decided nests belonged to the same colony if they were located within 5 m of one another and if we observed workers exiting one nest and entering another.

Distribution of nests

Colonies of many species have overdispersed patterns of nest distribution (Levings and Traniello 1981; Rytí and Case 1984; Hölldobler and Wilson 1990) in which colonies are spaced more regularly than would be expected if they were placed at random. Overdispersion of ant colonies is generally regarded as evidence of competition between colonies, although exceptions to the rule have been reported (Gordon 1991). To measure the spatial distribution of colonies at the site, we found the distance and direction of each nest entrance in relation to a reference point in a grid system set up at the site. For a colony with more than one nest entrance, we used the average x and y coordinates of all the nests as the colony's location. To test whether *A. cockerelli* colonies were distributed at random with respect to *Myrmecocystus* colonies, we used the method of Pielou (1961). Using this method, an index of segregation, S , is generated and can range from -1 to $+1$. S is positive when nests are aggregated intraspecifically, zero when patterns follow a Poisson distribution, and negative when nests are interspecifically aggregated.

Enclosures

We observed 12 *A. cockerelli* colonies, each approximately 40 m away from the nearest conspecific neighbor, of similar nest size (nest disc diameter about 0.50 m) and local interspecific density (about 7 *Myrmecocystus* colonies within 25 m). We made observations during three periods of 11 days each: before, during, and after the enclosure of neighboring *Myrmecocystus* colonies.

For six *A. cockerelli* colonies, we enclosed all *Myrmecocystus* nests within 25 m of the nest entrance. For the other six *A. cockerelli* colonies, no neighboring *Myrmecocystus* nests were enclosed; these six colonies served as controls. Enclosures were made of aluminum flashing dug approximately 5 cm into the soil around the edge of the nest, secured with nails driven into the soil, and coated with a ring of a sticky tree-banding compound (Tanglefoot

Company, Grand Rapids, Mich., USA) around the top to prevent workers from escaping. Each morning before observations began, we made sure all enclosures were secure. We left the enclosures up for 11 days. On alternate days, we fed enclosed colonies one-half of a crumbled Pecan Sandie cookie.

Activity of *Myrmecocystus* colonies

To estimate the time of day that *Myrmecocystus* colonies were active, we observed 20 nearby *Myrmecocystus* colonies that were not enclosed. Observations were made each hour from 0600–1100 hours on six mornings during the 11 days that other *Myrmecocystus* colonies were enclosed. Colonies were classified as active if there were more than 20 workers outside within 0.5 m of the nest entrance. Each of the 20 colonies was visited five times each morning for six mornings, for a total of 600 observations.

Resource use

To determine the effect of neighboring *Myrmecocystus* colonies on resource use by *A. cockerelli*, we collected returning *A. cockerelli* foragers and identified the food items in their mandibles on any 4 days during each of the 3 11-day periods. We identified 200 food items in each period, approximately 100 each from control and experimental colonies, brought back to randomly chosen *A. cockerelli* colonies. We identified a total of 600 food items. Food items were classified as termite, other insect or insect part, or plant matter (leaves, stems, flower petals, and seeds).

Measures of *A. cockerelli* daily round

To measure the effects of *Myrmecocystus* neighbors on the colony behavior of *A. cockerelli*, we observed each of the 12 *A. cockerelli* colonies (6 with neighbors enclosed and 6 controls) for 2 min each hour from 0600 to 1100 hours during the morning activity period. We observed the 12 colonies on seven mornings of each 11-day period, for a total of 1260 observations in 33 days. Observations of each colony were separated by at least 1 h. For each colony, we recorded the numbers of ants within a 0.5-m radius of the main nest entrance engaged in each of the five activities listed in Table 1. The sum of the five numbers, the observation sum (OS), is the total number of ants active during one observation. In a polydomous colony (occupying more than one nest), the largest nest entrance was considered to be the main entrance.

Data analysis

Resource use

To examine the effect of neighbors on the proportion of each resource type (termite, other insect or plant matter) collected by *A. cockerelli* colonies, we defined an index of carnivory, $C_j^{(i)}$, for colony j during period i as $(I^*-P^*)/(I^*+P^*)$, where I^* is the number of returning foragers with either an insect or termite, and P^* is the number of returning foragers with either a piece of plant matter or seed. To compare resource use during enclosure (period 2) with resource use before (period 1) and after enclosure (period 3), we then calculated a contrast value, D_j , for each colony as $D_j = C_j^{(2)} - (C_j^{(1)} + C_j^{(3)})$. We compared the contrast values (D_j) for control and experimental colonies using a two-sample t -test. We compared our results from experimental colonies and control colonies to ensure that any effect we observe was not due to changes in weather conditions, day length, or other day-to-day variation. We then performed the same analysis using the insects-termite contrast calculated as $(I-T)/(I+T)$, where I is the number of returning foragers with a non-termite insect, and T is the number of returning foragers with a termite. We calculated the plant matter-seed contrast calculated as $(P-S)/(P+S)$, where P is the number of returning foragers with plant matter, and S is the number of returning foragers with a seed.

To test how neighboring colonies influenced the diversity of food items *A. cockerelli* colonies brought back to the nest, we calculated a Shannon-Wiener diversity index, H , as $H' = -\sum_{i=1}^k p_i \log p_i$, where k is the number of categories (here, $k=4$) and p_i is the proportion of the observations found in category i during period 2. We then tested whether the diversity indices of the experimental colonies and the control colonies differed using a two-sample t -test following Hutcheson (1970).

Daily round of *A. cockerelli*

To examine whether interactions with *Myrmecocystus* influenced total activity (the total number of ants active each morning) of *A. cockerelli* colonies in each of the three periods, we performed an analysis of variance for the six experimental colonies, with time period as the main effect.

To determine whether interactions with *Myrmecocystus* affected the daily round of *A. cockerelli* behavior, we examined each of the five activities (foraging, nest maintenance, loitering, midden work, and meandering) separately. To normalize for differences in the numbers of workers among colonies, we divided each observation for a particular colony by the maximum OS ever obtained for that colony. For each of the six control and six experimental colonies and for each period i , we defined $S_j^{(i)}$ for a given task as the sum of the proportions (observed number of ants performing task/OS) of the 5 h counts for colony j . To compare behavior during enclosure (period 2) with behavior before (period 1) and after enclosure (period 3), we then calculated a contrast value for each colony as $B_j = S_j^{(2)} - (S_j^{(1)} + S_j^{(3)})$. To test whether the proportions of ants devoted to each activity changed in the absence of *Myrmecocystus*, we compared the B_j values for control and experimental colonies using a two-sample t -test.

Results

Distribution of nests

A. cockerelli colonies and *Myrmecocystus* colonies were distributed randomly at our site ($S=0.985$, $\chi^2=0.18$, $df=1$, $P>0.50$). Though Meagher and Burdick (1980) warn against obtaining a chi-square value when making multiple reciprocal comparisons, our chi-square value is so far from the critical value that we were not at risk of assigning statistical significance when none existed. Table 2 shows the mean nearest interspecific and intraspecific neighbor distances for *A. cockerelli* and *Myrmecocystus* at our site. On average, nearest intraspecific neighbors were more distant than nearest interspecific neighbors.

Activity of *Myrmecocystus* colonies

The mean proportions (\pm SEM) of *Myrmecocystus* colonies active during each hour were 0.59 ± 0.05 , 0.73 ± 0.02 ,

Table 2 Distance to nearest neighbors. Values are the mean distance to the nearest neighbor (m) \pm SEM

	<i>Aphaenogaster cockerelli</i>	<i>Myrmecocystus</i>
<i>A. cockerelli</i>	1.14 \pm 0.23	0.95 \pm 0.10
<i>Myrmecocystus</i>	0.76 \pm 0.05	1.04 \pm 0.07

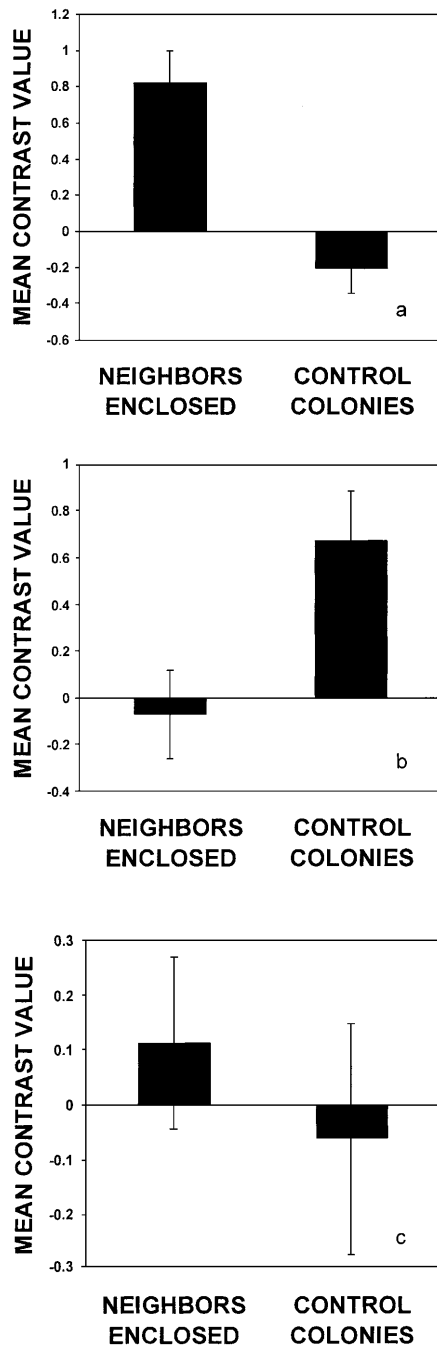


Fig. 1a–c The effect of neighboring *Myrmecocystus* colonies on *Aphaenogaster cockerelli* resource use. Each graph shows the mean contrast value comparing the proportion of resources collected by undisturbed *A. cockerelli* colonies and those with neighbors enclosed. **a** Insect/plant contrast. **b** Other insect/termite contrast. **c** Plant/seed contrast. Bars show mean±SEM. A positive value means that the proportion of the food item in the diet was greater in period 2, when neighbors were enclosed, than in the average of periods 1 and 3, before and after enclosure

0.84±0.01, 0.86±0.03, and 0.89±0.02 for the hours beginning 0600, 0700, 0800, 0900, and 1000 hours respectively. The activity periods of *Myrmecocystus* colonies overlap with those of *A. cockerelli* (data for *A. cockerelli* are given below).

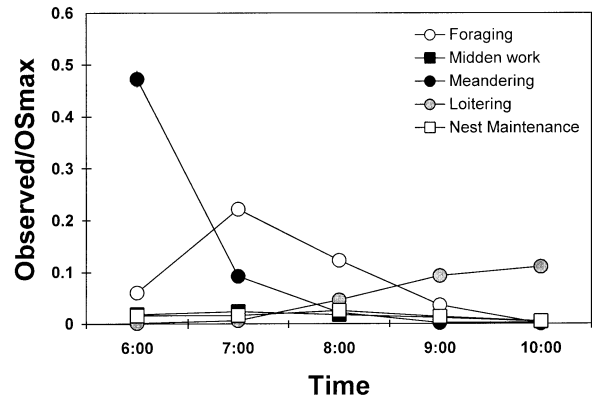


Fig. 2 The daily round of *A. cockerelli*. The value for each hour and activity is the mean observed number of ants performing that activity divided by the maximum number of ants active at one time (OS_{max}). Bars show mean±SEM (mostly concealed by symbols)

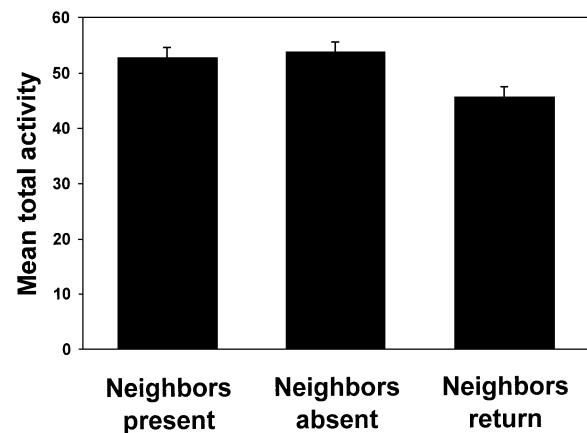


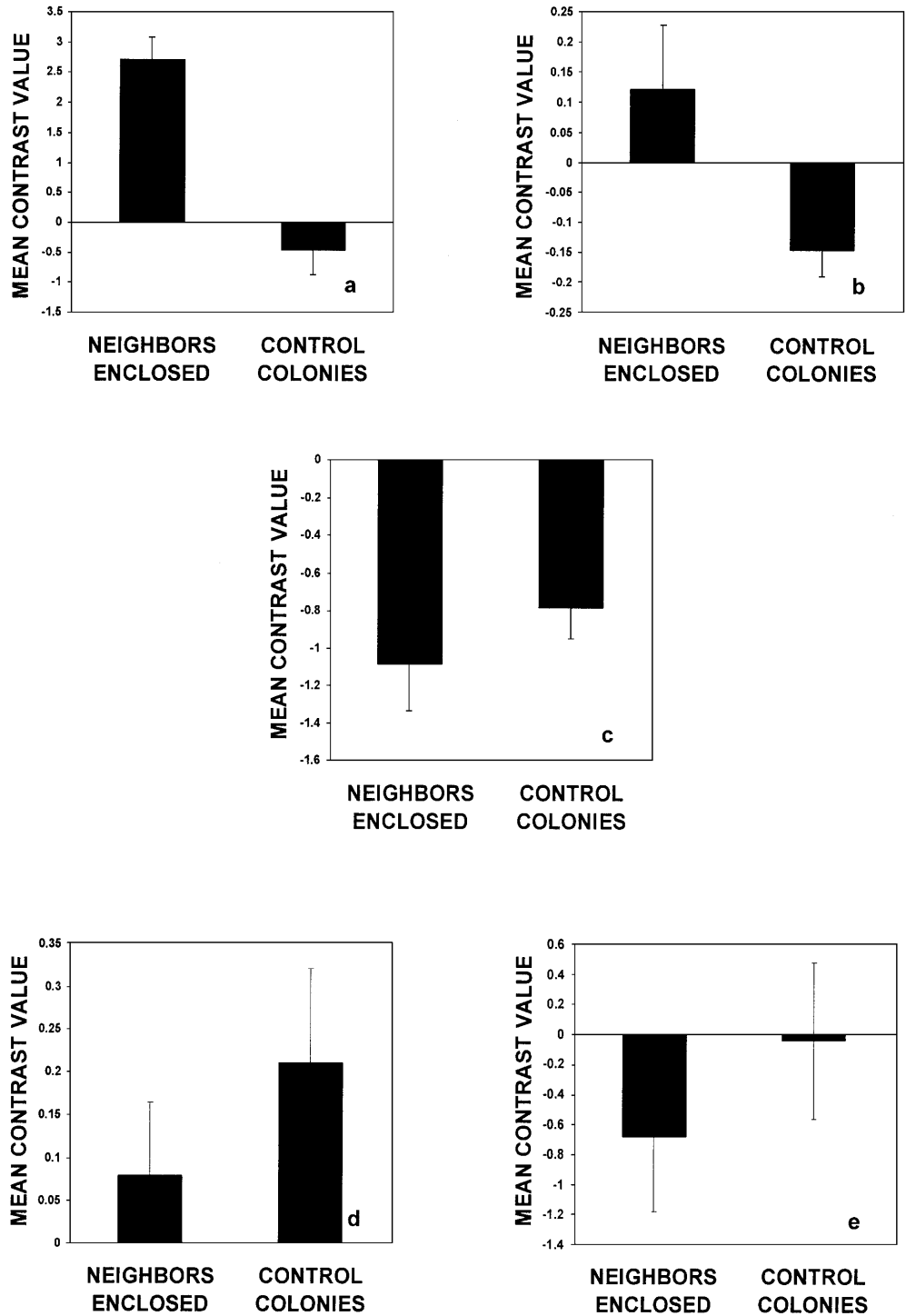
Fig. 3 The effect of neighboring *Myrmecocystus* colonies on the overall activity of *A. cockerelli* colonies. Bars show the mean sum of ants active each morning ±SEM

Resource use

Myrmecocystus neighbors influenced the resource use of *A. cockerelli* colonies (Fig. 1). When neighboring *Myrmecocystus* colonies were enclosed, *A. cockerelli* colonies collected a significantly higher proportion of termites and other insects than they did seeds and other plant matter ($t=4.65$, $df=9$, $P<0.001$). When neighboring *Myrmecocystus* colonies were enclosed, *A. cockerelli* colonies also collected a significantly higher proportion of termites than they did other insects ($t=2.62$, $df=10$, $P=0.01$). The enclosure of neighboring *Myrmecocystus* colonies did not affect the proportion of seeds out of all plant matter collected ($t=0.66$, $df=9$, $P=0.26$).

Myrmecocystus neighbors also affected the diversity of food items *A. cockerelli* colonies collected ($t=7.27$, $df=199$, $P<0.001$). Compared to control colonies, experimental colonies with neighbors enclosed collected a higher diversity of food items ($H'=1.56$ for control colonies and 3.07 for experimental colonies).

Fig. 4a–e The effect of neighboring *Myrmecocystus* colonies on *A. cockerelli* behavior. Each graph shows the mean contrast value comparing the proportion of ants engaged in each behavior for undisturbed *A. cockerelli* colonies and those with neighbors enclosed: **a** foraging, **b** nest maintenance, **c** loitering, **d** midden work, and **e** meandering. The graphs differ in scale. Bars show mean \pm SEM. A positive value indicates that the proportion of workers engaged in the indicated task was greater in period 2, when neighbors were enclosed, than the average of periods 1 and 3, when neighbors were not enclosed. A negative value indicates that the proportion of workers engaged in the indicated task was lower in period 2 than in the average of periods 1 and 3



Daily round of *A. cockerelli*

In *A. cockerelli*, there is a daily temporal pattern, or daily round of behavior, as in other ant species (e.g., Gordon 1983b, 1984a, 1986) (Fig. 2). A large proportion of workers perform meandering behavior early in the morning. Then foraging peaks between 0700 and 0800 hours. After foraging behavior declines, loitering behavior increases, and colony activity stops. Nest maintenance and

midden work are relatively constant throughout the morning activity period.

Effects of interactions with *Myrmecocystus* on daily round of *A. cockerelli*

Interactions with *Myrmecocystus* colonies significantly affected the activity of *A. cockerelli* colonies (ANOVA,

$df=2$, 123 , $F=5.52$, $P=0.005$). There were fewer workers outside the nests of *A. cockerelli* colonies when enclosures were removed from neighboring colonies (period 3) than in either period 1 or 2 (Fig. 3).

Neighboring *Myrmecocystus* colonies influenced the numbers of *A. cockerelli* workers engaged in specific tasks (Fig. 4). When neighbors were enclosed, a higher proportion of *A. cockerelli* workers outside the nest performed foraging behavior ($t=5.92$, $df=10$, $P<<0.0001$), and a higher proportion of workers performed nest maintenance behavior ($t=2.36$, $df=7$, $P=0.03$). The enclosure of *Myrmecocystus* colonies did not affect the numbers of *A. cockerelli* performing loitering behavior ($t=1.02$, $df=9$, $P=0.17$), midden work ($t=0.95$, $df=9$, $P=0.18$), or meandering behavior ($t=0.89$, $df=10$, $P=0.20$).

Discussion

Interactions with neighboring *Myrmecocystus* colonies led to shifts in resource use by *A. cockerelli* colonies and in the numbers of workers engaged in some tasks. Interestingly, interspecific competitive interactions did not lead to regular spacing of colonies as is often reported in studies of intraspecific competition in ants (e.g., Levings and Traniello 1981; Hölldobler and Wilson 1990).

When *Myrmecocystus* colonies were active, *A. cockerelli* colonies collected mostly seeds and other plant matter. When *Myrmecocystus* colonies were temporarily enclosed, *A. cockerelli* colonies switched to collecting mostly termites and other insects. Interestingly, our results suggest that competition with neighbors led to a decrease in the diversity of food items collected by *A. cockerelli* colonies. By contrast, Schoener (1982) predicted that competition should lead to a more diverse diet, and Whitford (1978b) observed that the seed harvester, *Pogonomyrmex desertorum*, collected a more diverse diet in the presence of competing species. *Myrmecocystus* foragers may interfere with *A. cockerelli* foragers while foraging, or may deplete the pool of available dead arthropods and termites. The changes in *A. cockerelli* resource use when *Myrmecocystus* was enclosed may thus reflect the absence of interference, or greater resource availability, or both. The diet of *A. cockerelli* is extremely variable (Chew and De Vita 1980; Whitford et al. 1980), sometimes changing over the course of a year and between years (Chew and De Vita 1980). This variation in resource use may be caused by the combination of fluctuations in resource availability and competitive interactions with heterospecific neighbors.

The daily round of *A. cockerelli* may be influenced by competitive interactions with neighboring colonies. Foraging behavior reaches its peak each morning between 0700 and 0800 hours. Colonies forage throughout the evening and into the early morning, and cease activity when air temperatures get high by late morning (Whitford and Ettershank 1975; Whitford et al. 1980). Our observations suggest that *A. cockerelli* colonies at our site forage throughout the night, though less intense-

ly than in the morning. Interactions with nocturnal species such as *M. mexicanus* might also influence the foraging behavior of *A. cockerelli*. Foraging of *A. cockerelli* colonies may peak between 0700 and 0800 hours because competing species are least active at that time. After foraging intensity decreases, the proportion of ants engaged in loitering behavior increases. Loiterers may be foragers that do not leave the nest, perhaps because of rising temperatures. *A. cockerelli* foragers may return to the nest to avoid interactions with *Myrmecocystus*. Experiments with marked workers might indicate whether loiterers and foragers are the same individuals. Experimental manipulations could also determine if temperature influences the dynamics of the daily round of colony behavior.

When we experimentally removed *Myrmecocystus* neighbors, *A. cockerelli* colonies devoted a larger proportion of workers to foraging than when neighbors were active. Interactions did not lead to a shift in the peak foraging period of *A. cockerelli*, which was between 0700 and 0800 hours throughout the experiment. Instead, the peak increased in magnitude; foraging intensity of *A. cockerelli* was higher when *Myrmecocystus* colonies were enclosed. How do interactions with neighboring *Myrmecocystus* reduce foraging intensity in *A. cockerelli*? There may be direct interference. Foragers from *A. cockerelli* colonies forage at distances of up to 30 m from the nest (N.J. Sanders, unpublished work). Within its foraging range a forager of *A. cockerelli* might encounter ants from several conspecific and heterospecific ant colonies. There were about 7 *Myrmecocystus* colonies and 5 conspecific colonies within 25 m of each of the 12 *A. cockerelli* colonies in this study. *Myrmecocystus* may employ some form of chemical interference to deter heterospecifics, as reported in other species (Baroni Urbani and Kanno 1974; Adams and Traniello 1981). On several occasions, we witnessed encounters between *A. cockerelli* and *Myrmecocystus* workers. Afterwards, most of the *A. cockerelli* foragers immediately returned to their home nest without collecting any food. Although we saw no aggression between *A. cockerelli* and *Myrmecocystus mimicus* or *M. depilis*, we often saw *Myrmecocystus* workers returning to the nest with dead *A. cockerelli* workers. It seems plausible that these interactions, which led to reductions in foraging intensity, also led to changes in resource use by *A. cockerelli*.

Interestingly, when *Myrmecocystus* neighbors were removed, the proportion of *A. cockerelli* workers engaged in nest maintenance work increased. If nest maintenance workers serve to keep the nest free of debris and thereby facilitate foraging, then factors that mediate the numbers of ants engaged in nest maintenance might also affect the ecological performance and survival of the colony. Other behaviors may be equally important to *A. cockerelli*'s ecological performance, but our results suggest that other behaviors are not influenced by competitive interactions with *Myrmecocystus*.

What is the mechanism by which interactions with *Myrmecocystus* colonies affect the numbers of *A. cockerelli*

elli workers engaged in behaviors other than foraging, like nest maintenance? Changes in foraging behavior may lead to changes in other colony tasks, or the numbers in each task may be affected independently by interactions with *Myrmecocystus*. Experiments using marked workers are needed to distinguish these possibilities.

The ecology of ant populations and the resource use and behavior of individual colonies are tightly linked. We have demonstrated that interspecific interactions lead to a niche shift along a food resource axis and alter foraging and nest maintenance behavior. Competition for resources, mediated by behavior, could affect the reproductive potential and survivorship of *A. cockerelli* colonies and ultimately influence the structure of the ant community.

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