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RESOURCE-DEPENDENT INTERACTIONS AND THE ORGANIZATION OF DESERT ANT COMMUNITIES

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Abstract. Resources influence consumer physiology, behavior, population growth, interspecific interactions, and community structure. To understand fully the influence of resources on interactions among consumer populations and community structure, it may be necessary to understand the influence of resources on individual behavior. In the first part of this study, we examined how resource type influenced foraging behavior and interactions in a guild of omnivorous desert ants. Cafeteria experiments showed that *Myrmecocystus depilis*, *M. mimicus*, and *Aphaenogaster cockerelli* prefer protein resources to seed resources. However, *A. cockerelli* collects mostly seed resources, and *M. depilis* and *M. mimicus* collect mostly protein resources when faced with competition from one another. A temporary removal experiment showed that the effect of *M. mimicus* and *M. depilis* on *A. cockerelli* depended on resource type. At protein resources, *Myrmecocystus* foragers tended to displace *A. cockerelli* foragers, but at seed resources, there was no effect of one species on the other.

In the second part of this study, we tested how resource availability may influence the arrangement of species in ecological dominance hierarchies. We found that there was considerable variation among sites in the arrangement of species, and that variation could be attributed to variation in resource availability and in the effect of particular species among sites. Our results suggest that the outcome of interactions between individuals are resource dependent, because individuals respond to resources in different ways. Furthermore, resource-dependent interactions and behavior can lead to communities that are arranged in intransitive dominance hierarchies, which may promote biodiversity at regional scales.

Key words: Aphaenogaster cockerelli; *Arizona; community structure; competition; desert ants; dominance hierarchy;* Myrmecocystus; *resources.*

INTRODUCTION

Both individual foraging behavior and interactions between consumer populations can depend on the kinds and amounts of resources available (e.g., Morse 1977, Pimm and Pimm 1982, Toft 1984). Thus resource variation, through its effects on foraging behavior, links the behavior of individuals to the organization of communities (Brown 1989, Kotler and Brown 1999). However, studies linking resources to individual foraging behavior, interactions between populations, and the organization of communities are rare. In this paper, we first examine how the foraging behavior of, and interspecific interactions between, two species of *Myrmecocystus* ants and *Aphaenogaster cockerelli* depend on resources. We then examine how community organization is influenced by such resource-dependent interactions among species.

In ants, foraging behavior can depend on the size and distribution of resources (Davidson 1977*a*, *b*, Chew and De Vita 1980, Fellers 1987, Cerdá et al. 1998*a*), and several species choose resources based on food quality (e.g., Taylor 1977, Crawford and Rissing 1983, Breed et al. 1987, Fewell and Harrison 1991, de Biseau and Pasteels 2000). Such differential responses to resources can lead to variation in competitive outcomes and promote coexistence between species (Chase 1996*a*, *b*). For example, Cerdá et al. (1998*a*) showed that small, mass-recruiting species were better able to exploit large food items than were larger, solitary foraging species.

In a previous study, we found that both resource use and diverse colony behaviors of *A. cockerelli* were influenced by interactions with *Myrmecocystus depilis* and *M. mimicus* (Sanders and Gordon 2000). These species compete for a wide variety of resources (Chew 1977, 1995, Chew and De Vita 1980). Because these species use a wide variety of resources, and our previous study indicated that competition is important, we focus here on their foraging behavior and the mechanisms of interactions between them.

At the community level, there is general agreement that competition is important in structuring ant communities (Hölldobler and Wilson 1990). Here we define an ant community as the ant populations at the same place at the same time. We use ''organization'' to mean the arrangement of species in a dominance hierarchy, where dominance results from asymmetric pairwise interactions. Many animal communities are organized in

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dominance hierarchies, including hummingbirds (Des Granges 1979), honeycreepers (Pimm and Pimm 1982), bumblebees (Thomson et al. 1987), bee flies (Toft 1984), and fish (Werner 1976). In ants, one way to define ecological dominance is to use the ratio of numbers present at food resources to numbers present in pitfall traps, that is, the ratio of foraging success to abundance (Andersen 1992). The organization of a dominance hierarchy is usually considered to be the ranked order of these ratios.

Though many studies show dominance hierarchies are common in ant communities (Vepsäläinen and Pisarski 1982, Fellers 1987, Savolainen and Vepsäläinen 1988, Savolainen et al. 1989, Andersen 1992, 1997), it is not clear whether such hierarchies are robust under varying conditions. For example, Cerdá et al. (1997, 1998*b*) showed that temperature can disrupt the organization of dominance hierarchies. In this paper, we examine whether the organization of transitive dominance hierarchies depends on resource availability.

METHODS

Resources and behavior

Natural history.—*Aphaenogaster* (formerly *Novomessor*) *cockerelli* and *Myrmecocystus depilis* and *M. mimicus* are widely distributed throughout the deserts in the southwestern USA, from eastern California to western Texas and into northern Mexico (Wheeler and Creighton 1934, Creighton 1955, Snelling 1976, Johnson 2000). The two *Myrmecocystus* species, *M. mimicus* and *M. depilis*, are hereafter referred to as *Myrmecocystus* because they are ecologically similar and indistinguishable in the field. Both *A. cockerelli* and *Myrmecocystus* forage for seeds and other plant matter, dead arthropods, termites, floral nectar, and homopteran honeydew (Snelling 1976, Chew and De Vita 1980, Whitford et al. 1980, Hölldobler 1981). *Aphaenogaster cockerelli* is generally active at all times except the hottest parts of the day (Whitford 1978), and *Myrmecocystus* reaches peak activity levels during mid-morning and forages intermittently throughout the afternoon (Snelling 1976, Hölldobler 1981). We did the experiments examining interactions between *A. cockerelli* and *Myrmecocystus* in the Chihuahuan desert near Portal, Arizona at the same site as described in Sanders and Gordon (2000).

Resource preference.—We measured the resources *A. cockerelli* and *Myrmecocystus* colonies used when the threat of competition with neighbors was minimal. We placed food baits 1 m from the nest entrances, so close that ants of neighboring colonies were unlikely to forage there. We placed two food baits, one protein and one seed, at five randomly chosen nests of *A. cockerelli* and of *Myrmecocystus* on five days, for a total of 25 pairs of baits for each. Each bait consisted either of 15 mL of tuna or 15 mL of crushed wild bird seed in a 9 cm diameter petri dish lid placed flush with the soil and painted white to help us see the ants. After placing the baits, we waited 30 min and then counted the numbers of ants foraging at each bait for 30 s.

We calculated the average number of foragers at protein and seed baits, for each colony, over five days and used a two-way ANOVA with average number of foragers as the response variable, and species and resource type as the main effects in the model.

Resource use.—We observed which naturally occurring resources were collected by undisturbed colonies. We collected 313 food items from *A. cockerelli* foragers returning to six colonies on nine days. We collected 193 food items from foragers returning to 20 *Myrmecocystus* colonies on three consecutive days. We classified food items as either plant matter (stems, leaves, flower petals), seeds, termites, or other insect matter (whole insects, insect parts), four major categories of resources used by these species (Snelling 1976, Chew and De Vita 1980, Whitford et al. 1980, Hölldobler 1981). We were often unable to determine if foragers of *A. cockerelli* were returning with liquid resources such as extrafloral nectar or homopteran honeydew, so we ignored this resource for both species.

To compare the use of naturally occurring resources by undisturbed *Myrmecocystus* (n = 20) and *A. cockerelli* (n = 6) colonies, we used a two-way ANOVA, with species and resource type as the main effects in the model, and the mean proportion of the diet of each colony that each resource type made up as the response variable.

Enclosure experiment.—To test how the influence of interactions with *Myrmecocystus* on *A. cockerelli* depended on resource type, we manipulated the presence of *Myrmecocystus* and resource type in a 2 × 2 factorial design. We temporarily enclosed all of the *Myrmecocystus* colonies within 18 circles of radius 25 m and manipulated resource availability; we call this the ‘‘neighbors absent’’ treatment. Enclosures were sheets of aluminum flashing dug ~5 cm into the soil around the edges of the *Myrmecocystus* nests, secured with nails driven into the soil, and coated with a ring of Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan, USA) around the top to prevent workers from escaping. For another 18 circles, we did not enclose *Myrmecocystus* colonies, but we did manipulate resource availability; we call this the ‘‘neighbors present’’ treatment. These 36 circles were similar to one another in the densities of both *A. cockerelli* and *Myrmecocystus* colonies.

One day after the enclosures were erected, we began to manipulate resource type using standardized protein and seed baits, as in many studies of ant interspecific interactions (e.g., Culver 1974, Lynch et al. 1980, Fellers 1987, Savolainen and Vepsäläinen 1988, Andersen 1992, 1997, Andersen and Patel 1994, Cerdá et al. 1997, 1998*b*, Yanoviak and Kaspari 2000). In the centers of half of the circles, we placed protein baits, and in the other half we placed seed baits. Protein baits consisted of ~15 mL of tuna, and seed baits were ~15 mL of crushed wild bird seed. We placed baits on four mornings between 0530 and 0700.

One hour after the bait had been placed, we recorded the number of *A. cockerelli* and *Myrmecocystus* foragers on the petri dish lid for 30 s. We also recorded the number of times *A. cockerelli* foragers retreated when encountering a *Myrmecocystus* forager at the bait station. A retreat occurred when an *A. cockerelli* forager contacted a *Myrmecocystus* forager, then jumped backwards and left the bait station without collecting any resources. We did not count the number of contacts that did not lead to retreats, but such contacts were rare.

To examine statistically how resource type and the presence of neighboring *Myrmecocystus* colonies influenced *A. cockerelli* foraging behavior, we used an ANOVA with resource type and presence of neighbors as main effects in the model. The response variable in the model was the average log-transformed number + 1 of *A. cockerelli* foragers in each circle over the four days of observations. Thus, for each combination of treatments, there were a total of nine observations.

We examined the relative numbers of *A. cockerelli* and *Myrmecocystus* foragers at protein and seed baits to determine if the effect of the number of one species on the number of the other species at a bait depended on resource type. We used data from the neighbors present plot ($n = 72$ observations at baits over four days) and from baits at the eight sites in the ecological dominance experiment described below ($n = 320$ observations). We excluded data from baits to which neither *A. cockerelli* nor *Myrmecocystus* species recruited, leaving 276 observations ($n = 106$ for protein baits, $n = 170$ for seed baits). For each resource type, we performed a correlation analysis of the number of *Myrmecocystus* foragers and of *A. cockerelli* foragers to examine the effect of numbers of one species on the numbers of the other. We report Spearman's rank coefficient (r_S) because the numbers of foragers of each species at baits were not normally distributed.

To test whether *A. cockerelli* foragers were more likely to retreat when encountering *Myrmecocystus* foragers on protein than on seed resources, we compared the proportions of retreats on each bait type using a goodness-of-fit test following Zar (1999).

Resources and community organization

We tested the influence of resource type on the organization of dominance hierarchies at eight sites. The eight sites were along a transect and near the site of the *A. cockerelli–Myrmecocystus* experiments. Each site was 200 m from the site nearest to it. Sites 200 m apart were used because they were similar, at least to human observers, in slope, soil type, elevation, and plant community composition, all of which potentially influence ant community organization. However, it is highly unlikely that colonies separated by 200 m interacted with each other. Thus, sites were independent of one another.

At each site, numbers of ants at baits were used as a measure of foraging success, and numbers of ants in pitfall traps were used as a measure of forager abundance. Pitfall traps provide a good estimate of the relative numbers of workers foraging on the ground, especially in open habitats (Bestelmeyer et al. 2000). For example, Andersen (1991) found that pitfall trapping and more intensive methods yielded similar results.

We arranged a 2 × 5 grid of bait stations with 10 m spacing at each of the eight sites. Baits consisted either of protein (tuna) or seeds (crushed wild birdseed). We placed 15 mL of tuna or crushed birdseed on a plastic petri dish lid (as described previously) each morning before peak foraging activity began. We alternated daily, over 4 d, the type of bait placed on each petri dish. We placed baits in random order at each site each morning. From 45 min to 1 h after baits were stocked, we recorded the numbers of ants of each species foraging at each bait for 30 s. There were a total of 320 observations (8 sites × 10 baits at each site × 4 days). Species that could not be identified in the field were collected after observations ended and identified later at the nearby Southwestern Research Station (SWRS, Portal, Arizona).

To measure the abundances of ant species at each site, we placed a 2 × 5 grid of pitfall traps, spaced by 10 m, and picked them up 72 h later. Each pitfall trap was a plastic cup with a diameter of 10 cm partially filled with Sierra brand propylene glycol (Old World Industries, Northbrook, Illinois, USA) and placed flush with the ground. Pitfall traps were sorted at SWRS. For each site, we determined the total ant species richness, S; the Shannon-Wiener diversity index, H'; and a measure of evenness, J.

For each site, we divided the number of each species at baits by that species' abundance in pitfall traps at the site. We use this ratio as the ecological dominance score, though there are other ways to estimate ecological dominance. A species with a higher score, with more ants at food baits relative to its abundance, ranked higher in a dominance hierarchy. We constructed, for each site, ecological dominance hierarchies based on these scores.

We used a multifactorial ANOVA to evaluate the influence of resource type on ecological dominance. In the model, the main effects were species, site, and resource type and the response variable was the ecological dominance score of species x at bait type y at site z ($n = 320$; 20 species × 8 sites × 2 resource types). Thus, the response is a composite score for each species at each site for each resource type. We also determined if the average ecological dominance score of species x competing for resource type y was concordant among our eight sites using Kendall's coefficient of concordance, W. The value of W ranges from 0, when there is no similarity among species' average ecological

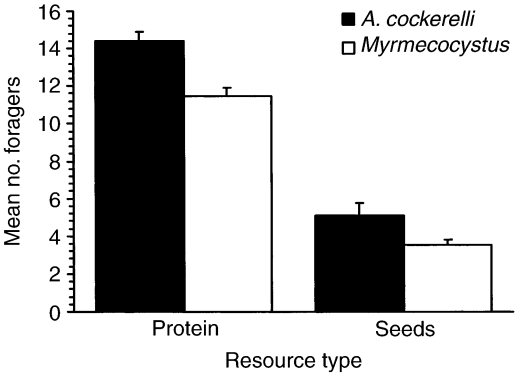

FIG. 1. Resource preferences of *A. cockerelli* and *Myrmecocystus* when resources were 1 m from nest entrance and there was no threat of competition with neighbors. Bars represent the mean number (+1 SE) of foragers visiting bait stations 1 m from the nest entrance.

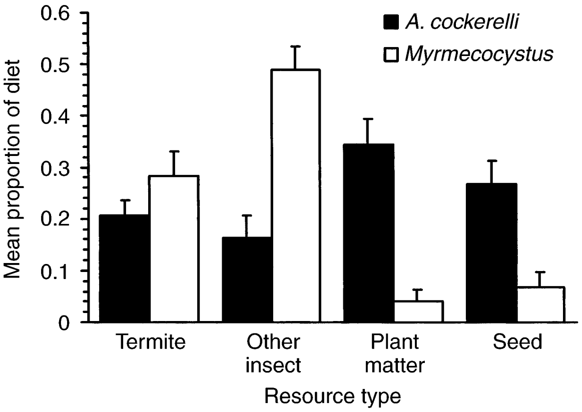

FIG. 2. Use of naturally occurring resources by undisturbed colonies of *A. cockerelli* and *Myrmecocystus*. Bars represent the mean proportion (+1 SE) of diet.

dominance scores among sites, to 1, when there is perfect agreement among all species' ecological dominance scores among sites. If a species either did not show up at baits (0 in the numerator of the ecological dominance ratio) or in pitfall traps (0 in the denominator of the ecological dominance ratio), its score was considered to be a zero for both the ANOVA and concordance analysis.

RESULTS

Resources and behavior

Resource preference.—When the threat of competition with neighbors was minimal, both *A. cockerelli* and *Myrmecocystus* significantly preferred protein to seed resources ($F_{1,16} = 301.35$, $P < 0.0001$, Tukey test: $P < 0.05$, Fig. 1), and the species × resource interaction was not significant, indicating that species did not differ in the preference of protein to seed resources ($F_{1,16} = 1.99$, $P = 0.18$, Fig. 1).

Resource use.—There was significant species × resource interaction, indicating that species differed in the proportion of naturally occurring termites, other insects, plant matter, and seeds that they collected (Fig. 2, Table 1). *Myrmecocystus* colonies collected mostly termites and other insects, whereas *A. cockerelli* colonies collected mostly seeds and plant matter.

Enclosure experiment.—*Aphaenogaster cockerelli* foraging behavior was influenced by the presence of *Myrmecocystus* neighbors and resource type. There was also a significant neighbor presence × resource type effect, indicating that the influence of *Myrmecocystus* was not independent of resource type (Fig. 3, Table 2). When neighboring *Myrmecocystus* colonies were temporarily enclosed, 2.3× as many *A. cockerelli* foragers recruited to protein baits as to seed baits (Tukey test, $P < 0.05$).

There was a significant negative relationship between the numbers of *Myrmecocystus* foragers and *A. cockerelli* foragers at protein resources ($r_S = -0.64$, $P < 0.001$, Fig. 4). There was no significant relationship between the numbers of foragers of each species at seed resources (Fig. 4, $r_S = 0.074$, $P = 0.54$).

Aphaenogaster cockerelli foragers retreated 3× more often when they encountered *Myrmecocystus* foragers at protein baits than at seed baits ($Z = 36.19$, $P < 0.001$).

Resources and community organization

We identified a total of 20 ant species at the eight sites (Table 3). The eight sites had similar species richness, Shannon-Wiener diversity indices, and evenness scores (Table 3). Ecological dominance, the ratio of a species' abundance at baits to its abundance in pitfall traps, did not depend on resource type alone when averaging across all species and sites (Table 4). Species differed in their ability to recruit to baits, as indicated by the significant species × resource interaction (Table 4). Furthermore, both ecological dominance and the effect of resources varied among sites (Table 4). There

TABLE 1. Results of ANOVA on the proportion of resource collected by *Aphaenogaster cockerelli* and *Myrmecocystus*.

Source	df	SS	MS	*F*	*P*
Species	1	0.011	0.011	0.447	0.506
Resource type	3	0.269	0.090	3.603	0.016
Species × Resource type	3	1.119	0.373	14.984	<0.0001

Notes: Error df = 96. The Species × Resource type interaction indicates that the resource use of *A. cockerelli* and *Myrmecocystus* differed.

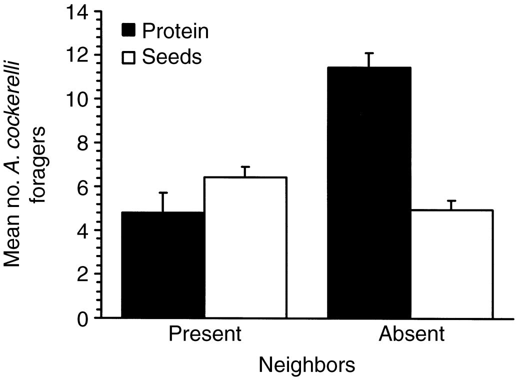

FIG. 3. The effects of resource type and presence of neighboring *Myrmecocystus* colonies on foraging activity of *A. cockerelli* during the enclosure experiment. Bars represent the mean (+1 SE) numbers of *A. cockerelli* foragers at bait stations.

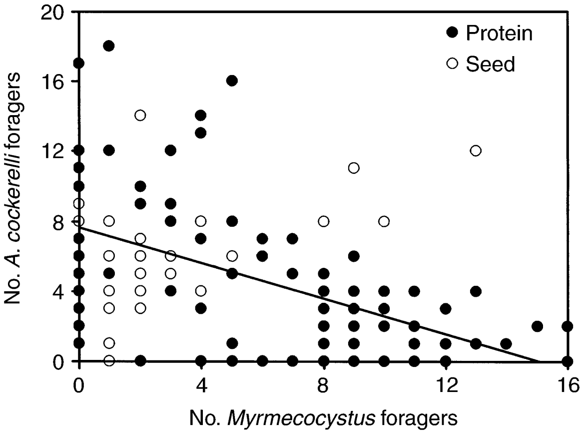

FIG. 4. The numbers of *A. cockerelli* and *Myrmecocystus* foragers at bait stations. Each symbol represents one observation at one bait station. The line shows the correlation between *A. cockerelli* and *Myrmecocystus* foragers on protein baits. There was no relationship between the numbers of foragers on seed baits.

was significant, though weak, similarity in the ranks of species in the ecological dominance hierarchy among all eight sites ($W = 0.23$, $\chi^2 = 68.80$, df = 19, $P < 0.001$, Table 5).

DISCUSSION

At the behavioral level, our results show that resource use by *A. cockerelli* was strongly affected by competition with *Myrmecocystus*. Though *A. cockerelli* colonies preferred protein to seed resources (Fig. 1), and collected protein resources when neighboring *Myrmecocystus* colonies were temporarily enclosed (Fig. 3, Table 2), colonies collected mostly plant matter and seeds when *Myrmecocystus* colonies were active (Fig. 2, Table 1). We take this as strong evidence for competitive release in *A. cockerelli*.

Studies in several taxa have shown that competitive interactions can alter the resource use of individuals (e.g., fish, Werner and Hall 1976; rodents, Kincaid and Cameron 1982, Luo and Fox 1995; grasshoppers, Beckerman 2000). In ants, results are equivocal, sometimes showing the effects of competition on resource use (e.g., Savolainen and Vepsäläinen 1988, Savolainen 1991), and sometimes not (e.g., Ryti and Case 1988). This study and previous work on these species (Sanders and Gordon 2000) show that resource use by *A. cockerelli* is strongly influenced by interactions with neighboring *Myrmecocystus* colonies.

When *A. cockerelli* and *Myrmecocystus* competed for protein resources, *Myrmecocystus* foragers displaced *A. cockerelli* foragers, and there was a negative correlation between the numbers of *Myrmecocystus* and *A. cockerelli* foragers. But when the two species competed for seed resources, there was no correlation between the numbers of foragers of each species (Fig. 4). In contrast, in tropical canopies and leaf litter communities, interactions between ant species seem to be independent of resource type (Yanoviak and Kaspari 2000).

What is the mechanism underlying these resource-dependent interactions? Perhaps *A. cockerelli* can assess the risk of competition with *Myrmecocystus*, and the relative rewards of protein and seed resources, and alters its foraging behavior to reduce risk (e.g., Nonacs and Dill 1988, 1990). We observed no overt aggression of *Myrmecocystus* foragers toward *A. cockerelli* foragers. However, our results suggest that *Myrmecocystus* may use some form of chemical interference to displace *A. cockerelli* from protein resources, as in other species (Adams and Traniello 1981, Hölldobler 1982, Hölldobler and Wilson 1990), but not at seed resources. This may indicate that *Myrmecocystus* employs a resource-dependent mechanism of interference competition.

At the community level, when we analyzed ecological dominance (i.e., the ratio of numbers of ants at baits to the numbers of ants in pitfall traps), there was a strongly

TABLE 2. Analysis of variance on the log (n + 1) number of *Aphaenogaster cockerelli* foragers.

Source	df	SS	MS	F	P
Neighbors	1	0.187	0.187	12.22	0.001
Resource type	1	0.103	0.103	6.748	0.014
Neighbors × Resource type	1	0.660	0.660	43.160	<0.0001

Notes: Error: df = 140. The Neighbors × Resource type indicates that the effect of interactions with neighboring *Myrmecocystus* colonies on *A. cockerelli* foraging depends on resource type.

TABLE 3. Community characteristics of eight sites.

Site	S	H'	J
A	20	2.49	0.80
B	17	2.35	0.83
C	20	2.34	0.78
D	19	2.41	0.82
E	19	2.36	0.80
F	18	2.36	0.82
G	18	2.36	0.82
H	19	2.42	0.82

Note: Key to characteristics: S, species richness; H', Shannon-Wiener diversity index; J, evenness.

significant effect of species (Table 4). For a given resource type, the rank ordering of some species in dominance hierarchies was consistent at all eight sites. For example, *A. cockerelli* and *Myrmecocystus* are generally near the middle of the dominance hierarchy for all sites. Our analysis of concordance among sites was low, but statistically significant. This suggests that the same set of factors acts to organize communities similarly at all sites; otherwise the ecological dominance ranks of species would vary haphazardly among sites. In a similar study, Andersen (1997) examined the organization of several ant communities in a variety of habitats near our site and found consistent patterns in the arrangement of functional groups among sites. Taken together, these results suggest that there may be a set of general rules that determine ant community organization (Andersen 1997, Yanoviak and Kaspari 2000).

Though there are similarities in organization among sites, species positions in dominance hierarchies differ between resource types, indicated by the significant species × resource type interaction in Table 4. For some species, rank order varies consistently with resource type (Table 5). This makes sense because species differ in how they respond to resources. For example, the seed harvesters (e.g., *Pogonomyrmex barbatus*) tend to use seeds more than they do other resources (e.g., Gordon 1993). We found that *P. barbatus* is near the top of dominance hierarchies when competing for seed resources, but near the bottom when competing for protein resources. Scavengers such as *Forelius* spp. and *Dorymyrmex* spp. tend to forage for dead insects and insect parts (Chew and De Vita 1980, Hölldobler 1982) more than they do for seeds and plant matter. We found that *Dorymyrmex* and *Forelius* are always near the top of the dominance hierarchy when competing for protein resources, but near the bottom when competing for seed resources.

Differences among colonies can explain the significant species × site interaction. For example, the density of *Dorymyrmex* spp. colonies may have been lower at site D than at the other seven sites (Table 5), and its response to protein resources may have been reduced. Or, individual colonies of particular species could have varied among sites. Young, growing colonies might require more protein and behave more aggressively at protein baits than do older colonies (e.g., Gordon 1992). Even if there is no competition for resources among species, the number of foragers recruited to baits can depend on colony size or age, or a colony's specific nutritional needs (Hölldobler and Wilson 1990). Thus, the position of species in dominance hierarchies does not necessarily depend on competitive interactions. Variation in factors other than competition can lead to variation in the arrangement of species in dominance hierarchies (e.g., Cerdá et al. 1997). Nevertheless, as resources change so does the arrangement of species in dominance hierarchies.

Our results from the *Results: Resources and behavior* section illustrate that the kinds of resources available, and how species respond to them, can influence the mechanisms and outcome of competition between *Aphaenogaster cockerelli* and *Myrmecocystus*. These species are embedded in a community of interacting species, and, despite variation among sites, *Aphaenogaster cockerelli* and *Myrmecocystus* are always in the middle of the dominance hierarchy. Furthermore, *A. cockerelli* is generally higher than *Myrmecocystus* for seed resources, but lower for protein resources. The same is generally true for other species in these communities: their positions in dominance hierarchies do not vary substantially among sites, when competing for one resource. However, when resource availability changes, so does the structure of dominance hierarchies.

Thus, our results at the community level, showing that the organization of communities is influenced by resources, are consistent with the more detailed study of the interactions between *A. cockerelli* and *Myrmecocystus*. Whether variation among sites in community organization is driven by variation in population densities, the nutritional status of individual colonies, or the be-

TABLE 4. Results of ANOVA on the effect of resource type, site, and species on ecological dominance of ant species.

Source	df	SS	MS	F	P
Site	7	0.365	0.052	3.60	0.001
Species	19	8.643	0.455	31.41	<0.0001
Site × Species	133	3.031	0.087	1.57	0.005
Resource type	1	0.087	0.023	6.02	0.015
Site × Resource type	7	0.127	0.018	1.26	0.277
Species × Resource type	19	6.790	0.357	24.68	<0.0001

Note: Error df = 133.

TABLE 5. Competitive ranks of ant species for each resource type at eight sites.

	Site															
	A		B		C		D		E		F		G		H	
Species	P	S	P	S	P	S	P	S	P	S	P	S	P	S	P	S
Aphaenogaster cockerelli	8	5	7	4	7	6	8	3	7	4	5	4	5	4	5	4
Camponotus ocreatus															7	
Crematogaster depilis	4	3	4	6	3	5	1	2	3	5	3	1	4	3	3	5
Dorymyrmex spp.	1	11	1	9	1	9	3	8	1	9	2	8	1	5	2	8
Ephebomyrmex imberbiculus	7	4		3		2	10	4		7		3				6
Forelius spp.	2	10	2	7	2	10	2	9	2	10	1		3	7	4	
Formica gnava		7				7										
Formica perpilosa	9						9				9	10			10	7
Leptothorax neomexicanus																
Monomorium peninsulatum	3	6	4	5	5	7	4	6	4	6	4	7	2	2	1	3
Myrmecocystus mexicanus		9			6		7	7	8			9	6	6		
Myrmecocystus spp.	6	11	6	8	8	12	6	10	5	8	7	11	8	9	6	9
Pheidole desertorum	5	1	3	2	4	1	5	5	9	3	6	5	7	7	9	2
Pheidole rugulosa						11										
Pheidole sciophila																
Pheidole tucsonica																
Pogonomyrmex barbatus		2		1		4		1	6	1		2		1	8	1
Solenopsis aurea		8				2					8	6				
Solenopsis xyloni										2						
Tetramorium hispidum							11									

Notes: A low number indicates a high rank in the dominance hierarchy. Key to abbreviations: P, protein resources; S, seed resources. If a cell is blank, that species did not occur in either the pitfall traps or at bait stations at that site.

havioral responses of individuals, our results suggest that the concept of rigid dominance hierarchies, in which the ecological roles of species are the same at all locations and for all resources, is inadequate to explain the variation among sites in community organization (Cerdá et al. 1997). Just as environmental variability can promote coexistence among species (Chesson 1986), so can differences in the behavioral response of species to resources. We suggest that combined studies of behavior and community organization can illuminate how behavioral factors affect population dynamics and help determine the maintenance of diversity in communities, and how that diversity is organized.

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LITERATURE CITED

Adams, E. S., and F. A. Traniello. 1981. Chemical interference competition by *Monomorium minimum* (Hymenoptera: Formicidae). Oecologia **51**:265–270.

Andersen, A. N. 1991. Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. Australian Journal of Ecology **16**:273–279.

Andersen, A. N. 1992. Regulation of momentary diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. American Naturalist **140**: 401–420.

Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography **24**:433–460.

Andersen, A. N., and A. D. Patel. 1994. Meat ants as dominant members of Australian communities: an experimental test of their influence on the foraging success and forager abundance of other species. Oecologia **98**:15–24.

Beckerman, A. P. 2000. Counterintuitive outcomes of interspecific competition between two grasshopper species along a resource gradient. Ecology **81**:948–957.

Bestelmeyer, B. T., D. Agosti, L. E. Alonso, C. R. F. Brandao, W. L. Brown, J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. Pages 122–144 *in* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, editors. Ants: standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press, Washington, D.C., USA.

Breed, M. D., J. H. Fewell, A. J. Moore, and K. R. Williams. 1987. Graded recruitment in a ponerine ant. Behavioral Ecology and Sociobiology **20**:407–411.

Brown, J. S. 1989. Desert rodent community structure: a test of four mechanisms of coexistence. Ecological Monographs **59**:1–20.

Cerdá, X., J. Retana, and S. Cros. 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. Journal of Animal Ecology **66**:363–374.

Cerdá, X., J. Retana, and S. Cros. 1998*a*. Prey size reverses the outcome of interference interactions of scavenger ants. Oikos **82**:99–110.

Cerdá, X., J. Retana, and A. Manzaneda. 1998*b*. The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. Oecologia **117**:404–412.

Chase, J. M. 1996*a*. Differential competitive interactions and the included niche: an experimental analysis with grasshoppers. Oikos **76**:103–112.

Chase, J. M. 1996*b*. Varying resource abundances and competitive dynamics. American Naturalist **147**:649–654.

Chesson, P. L. 1986. Environmental variation and the coexistence of species. Pages 240–256 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Chew, R. M. 1977. Some ecological characteristics of the ants of a desert-shrub community in southeastern Arizona. American Midland Naturalist **98**:33–49.

Chew, R. M. 1995. Aspects of the ecology of three species of ants (*Myrmecocystus* spp., *Aphaenogaster* sp.) in desertified grassland in southeastern Arizona, 1958–1993. American Midland Naturalist **134**:75–83.

Chew, R. M., and J. De Vita. 1980. Foraging characteristics of a desert ant assemblage: functional morphology and species separation. Journal of Arid Environments **3**:75–83.

Crawford, D. L., and S. Rissing. 1983. Regulation of recruitment by individual scouts in *Formica oreas* Wheeler (Hymenoptera, Formicidae). Insectes Sociaux **30**:177–183.

Creighton, W. S. 1955. Studies on the distribution of the genus *Novomessor* (Hymenoptera: Formicidae). Psyche **62**: 89–97.

Culver, D. C. 1974. Species packing in Caribbean and north temperate ant communities. Ecology **55**:974–988.

Davidson, D. W. 1977*a*. Species diversity and community organization in desert seed-eating ants. Ecology **58**:711–724.

Davidson, D. W. 1977*b*. Foraging ecology and community organization in desert seed-eating ants. Ecology **58**:725–737.

de Biseau, J.-C., and J. M. Pasteels. 2000. Response thresholds to recruitment signals and the regulation of foraging intensity in the ant *Myrmica sabuleti* (Hymenoptera, Formicidae). Behavioural Processes **48**:137–148.

Des Granges, J. L. 1979. Organization of a tropical nectar feeding bird guild in a variable environment. Living Bird **17**:199–236.

Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. Ecology **68**:1466–1478.

Fewell, J. H., and J. F. Harrison. 1991. Flexible seed selection by individual harvester ants, *Pogonomyrmex occidentalis*. Behavioral Ecology and Sociobiology **28**:377–384.

Gordon, D. M. 1992. How colony growth affects forager intrusion between neighboring harvester ant colonies. Behavioral Ecology and Sociobiology **31**:417–427.

Gordon, D. M. 1993. The spatial scale of seed collection by harvester ants. Oecologia **95**:479–487.

Hölldobler, B. 1981. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology **9**:301–314.

Hölldobler, B. 1982. Interference strategy of *Iridomyrmex pruinosum* (Hymenoptera: Formicidae) during foraging. Oecologia **52**:208–213.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Johnson, R. A. 2000. Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. Sociobiology **36**:83–122.

Kincaid, W. B., and G. N. Cameron. 1982. Effects of species removal on resource use in a Texas rodent community. Journal of Mammalogy **63**:229–235.

Kotler, B. P., and J. S. Brown. 1999. Mechanisms of coexistence of optimal foragers as determinants of local abundances and distributions of desert granivores. Journal of Mammalogy **80**:361–374.

Luo, J., and B. J. Fox. 1995. Competitive effects of *Rattus lutreolus* presence on food resource use by *Pseudomys gracilicaudatus*. Australian Journal of Ecology **20**:556–564.

Lynch, J. F., E. C. Balinsky, and S. G. Vail. 1980. Foraging patterns in three sympatric forest ant species, *Prenolepis imparis*, *Paratrechina melanderi* and *Aphaenogaster rudis*. Ecological Entomology **5**:353–371.

Morse, D. H. 1977. Resource partitioning in bumble bees: the role of behavioral factors. Science **197**:678–679.

Nonacs, P., and L. M. Dill. 1988. Foraging response of the ant *Lasius pallitarsis* to food sources with associated mortality risk. Insectes Sociaux **35**:293–303.

Nonacs, P., and L. M. Dill. 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. Ecology **71**:1886–1892.

Pimm, S. L., and J. W. Pimm. 1982. Resource use, competition, and resource availability in Hawaiian honeycreepers. Ecology **63**:1468–1480.

Ryti, R., and T. J. Case. 1988. Field experiments on desert ants: testing for competition between colonies. Ecology **69**: 1993–2003.

Sanders, N. J., and D. M. Gordon. 2000. The effects of interspecific interactions on resource use and behavior in a desert ant. Oecologia **125**:436–443.

Savolainen, R. 1991. Interference by wood ant influences size selection and retrieval rate of prey by *Formica fusca*. Behavioral Ecology and Sociobiology **28**:1–7.

Savolainen, R., and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos **51**:135–155.

Savolainen, R., K. Vepsäläinen, and H. Wuorenrinne. 1989. Ant assemblages in the taiga biome: testing the role of territorial wood ants. Oecologia **81**:481–486.

Snelling, R. R. 1976. A revision of the honey ants, genus *Myrmecocystus* (Hymenoptera: Formicidae). Los Angeles County Museum of Natural History Bulletin **24**:1–163.

Taylor, F. 1977. Foraging behavior of ants: experiments with two species of Myrmecine ants. Behavioral Ecology and Sociobiology **2**:147–167.

Thomson, J. D., S. C. Peterson, and L. D. Harder. 1987. Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency. Oecologia **71**:295–300.

Toft, C. A. 1984. Resource shifts in bee flies (Bombyliidae): interactions among species determine choice of resources. Oikos **43**:104–112.

Vepsäläinen, K., and B. Pisarski. 1982. Assembly of island ant communities. Annales Zoologici Fennici **19**:327–335.

Werner, E. E. 1976. Species interactions in freshwater fish communities. Pages 344–357 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science **191**:404–406.

Wheeler, W. M., and W. S. Creighton. 1934. A study of the ant general *Novomessor* and *Veromessor*. Proceedings of the American Academy of Arts and Sciences **69**:340–387.

Whitford, W. G. 1978. Structure and seasonal activity of Chihuahuan desert ant communities. Insectes Sociaux **23**: 79–88.

Whitford, W. G., E. Depree, and P. Johnson. 1980. Foraging ecology of two Chihuahuan desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus*. Insectes Sociaux **27**:148–156.

Yanoviak, S. P., and M. Kaspari. 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos **89**:259–266.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey, USA.