

Mark J.F. Brown · Deborah M. Gordon

## How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant

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**Abstract** We examined how the foraging ecology of the seed-harvesting ant *Messor andrei* depends upon the distribution of resources and the presence of conspecifics. Bait experiments showed that colonies can recruit to high-density patches of seeds. However, at the seasonal scale, natural resource distribution did not affect the distribution of foraging activity. We conducted the study in years of high rainfall and thus seed availability may not have been a limiting factor. Colonies always preferred to forage in areas closer to their nest, which may reduce travel time between the nest and foraging sites. On a day-to-day scale, encounters between neighboring colonies at a site increased the probability that colonies would return to forage at that site; this was true both for natural and experimental encounters. In the summer, this resulted in colonies foraging at the sites of intraspecific encounters on more days than in areas where no encounter had occurred. Encounters between colonies included fighting, and there was little overlap between the foraging areas of neighboring colonies: both results suggest that one function of encounters is to defend foraging space. The high probability of return to the site of an encounter between colonies suggests that encounters may have a second function: to indicate the presence of resources.

**Key words** Resource distribution · Encounters · Territoriality · Central-place forager · Seed-harvesting ant

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M.J.F. Brown (✉)<sup>1</sup> · Deborah M. Gordon  
Department of Biological Sciences, Stanford University, Stanford  
CA 94305-5020, USA

*Present address:*

<sup>1</sup> Experimentelle Ökologie, ETH-Zürich  
ETH Zentrum NW, CH-8092 Zürich, Switzerland  
e-mail: brown@eco.umnw.ethz.ch  
Tel: +41-1-6326935, Fax: +41-1-6321271

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### Introduction

How animals use space for foraging determines their access to resources, and may ultimately affect reproductive success and population demography (Gordon 1997). Central-place foragers and territorial animals operate within a restricted foraging area, limited by distance from the central place (e.g., Chase 1998) or territorial boundaries (e.g., Gill and Wolf 1975; Kugler 1984). How foraging activity is distributed within this area can affect the rate of resource acquisition (e.g., Davies and Houston 1981), depending on spatial and temporal variation in the distribution of resources (reviewed in Stephens and Krebs 1986).

Encounters with conspecifics should also affect foraging activity (Ydenberg et al. 1986; Ydenberg and Houston 1986; Giraldeau et al. 1994). Animals might avoid foraging at encounter sites in order to minimize the foraging time lost to encounters or to reduce the effects of exploitative competition (e.g., Gordon and Kulig 1996). Alternatively, foraging at encounter sites might increase, either because animals return to these sites to defend territorial boundaries and forage when active territorial behavior is not required, or because encounters are used as a cue to the location of resources (Reznikova 1982; Stamps 1994).

Harvester ants are a conspicuous component of many desert and grassland ecosystems (Brown and Davidson 1977; Davidson 1977; Hölldobler and Wilson 1990) and they have frequently been used to test optimal foraging theory (Rissing and Pollock 1984; Bailey and Polis 1987; Baroni Urbani and Nielsen 1990; Crist and Macmahon 1991; Fewell and Harrison 1991; Johnson 1991; Weier and Feener 1995). Few studies have examined how the foraging activity of a colony relates to resource distributions (Hahn and Maschwitz 1985; Gordon 1993; Lopez et al. 1993, 1994). Harvester ant species exhibit a variety of territorial behaviours (e.g., Hölldobler 1976), and encounters with conspecifics may both alter the foraging behavior of colonies (Gordon 1991, 1992; Gordon and Kulig 1996) and define territorial bound-

aries, limiting potential foraging space (Hölldobler 1976; Harrison and Gentry 1981; Jorgensen and Porter 1982; Gordon 1992). To our knowledge, no study has examined how encounters and resource distribution interact to determine the foraging strategy of seed-harvesting ant colonies.

*Messor andrei* is a seed-harvesting ant species native to the western United States (Creighton 1953), which collects resources that are locally and currently produced (Brown 1997). In this study, we aim to investigate the combined effects of encounters and resource distributions on foraging by addressing three questions. First, how likely are colonies to revisit foraging space, both from one day to the next and within a season? Second, how do encounters with conspecifics affect the day-to-day use of space? Finally, how do resource distributions and encounters interact to determine the use of foraging space across a season?

## Methods

### Study site and study organism

The study was conducted on a serpentine grassland at Jasper Ridge Biological Preserve, Stanford University, Calif. (122°12' W, 36°25' N, elevation about 180 m). The area has a mediterranean-type climate, with most rainfall occurring between November and April. Vegetation at this site is a mixture of native annual forbs, native and exotic annual grasses, and a few perennial bunchgrasses (McNaughton 1968; Brown and Human 1997).

Foraging activity by *M. andrei* at the study site begins in late March and ends in mid-October/early November (Brown 1999a, 1999b). Colony activity appears to be light and temperature related (McCluskey 1963). Colonies forage every day during the foraging season, except on particularly cold days in the spring. At the beginning of the season there is one foraging period each day, lasting approximately 5 h from 9:00 a.m.–2:00 p.m. As the season progresses and daily temperatures rise, the morning foraging period starts just before dawn and lasts until mid-morning (5:00–10:00 a.m.). An evening foraging period starts a few hours before dusk and continues for about an hour after dusk (5:00–9:00 p.m.). On warm nights, colonies continue to forage throughout the night and into the morning period.

Ants leave their nest to forage for seeds in the surrounding grassland along well-defined columns (Wheeler and Creighton 1934; Creighton 1953) that may be up to 20 m long. At the end of the column, ants disperse and search for food items individually before returning to the nest along the column. In this paper, we refer to the area at the end of a column in which ants search for food as a “foraging fan” or “fan.” A colony may have more than one foraging column, and thus more than one foraging fan, on a given day. The area covered by all the foraging fans used on one day is the “daily foraging area.”

### Data collection

#### Space use by colonies of *M. andrei*

The use of space by all *M. andrei* colonies in a 40×30 m area of grassland was recorded in 1994 and 1995 during three 25-day periods at the beginning, middle and end of the March–November foraging season; we refer to these as the spring, summer, and autumn observation periods. There were 17, 15, and 14 colonies in 1994, and 17, 14, and 12 colonies in 1995; colony numbers changed due to nest relocation (Brown 1999a), the emergence of new colonies, and colony death. In 1994, we mapped the daily for-

aging areas of every colony on every day of each 25-day period. In 1995, we collected seeds from foraging colonies on 5 days dispersed evenly across the 25-day observation period, and mapped daily foraging areas for all colonies on all other days. On the 5 days that seeds were collected, we mapped only those colonies that either encountered another colony on that day, or had an encounter on the previous day.

Foraging maps were made using a 1×1 m grid system and graph paper. A foraging column was defined as a stream of ants leaving the nest, when more than five ants crossed an imaginary line approximately 25 cm from the nest in 30 s. A foraging fan was the area within which ants from a particular foraging column searched for forage items. Fan edges were considered to be 25 cm beyond where the farthest foragers were observed. Each colony was observed two or three times in a morning foraging period, and the final map for each day showed the maximum area used by the colony.

Encounters between colonies occurred when foraging fans from different colonies impinged on each other and individual ants from the two colonies were seen to interact. We refer to a foraging fan that impinged on that of another colony as an “encounter fan;” a foraging fan that did not meet one from another colony is a “non-encounter fan.” At the site of encounters, we observed the behavior of ants that met non-nestmates, and recorded the number of fighting ants. In the absence of fighting, non-nestmates engaged in intense antennation, and the colony to which an individual belonged could be determined by the direction travelled after the end of the interaction.

#### Encounter experiment

We performed an experiment in which we induced encounters, to test for a causal link between encounters and the day-to-day use of space. Every day in September 1996, at the start of the morning foraging period, we observed eight colonies that were similar in nest mound size and in extent of daily foraging area. If a colony had at least two foraging fans it was used in the experiment. The experiment lasted 2 days. On the first day, we mapped the daily foraging area of the colony, and then added 50 non-nestmates to an arbitrarily chosen foraging fan. On the second day, we remapped the daily foraging area. The experiment was done twice for each of the eight colonies, with at least 7 days elapsed between successive experiments with the same colony. To examine the effect of encounters, we calculated the difference in the probability of returning on the second day to an experimental encounter fan versus the probability of returning to a non-manipulated fan with no encounter, for each colony. We used these difference data in a one-sample *t*-test to determine whether encounters changed the probability of reusing a foraging area.

#### Bait recruitment experiment

To determine whether colonies of *M. andrei* respond to areas of higher seed density, we carried out a baiting experiment in 1993. The experiment lasted for 2 days and used 28 colonies. Each colony was assigned an experimental site, approximately 3.5 m from the nest (mean=3.36 m, SD=1.678 m; there was no difference between experimental and control colonies in the distance to the experimental site, *t*-test, *n*=28, *df*=26, *t*=-0.96, *P*=0.347). On the first day, we mapped the daily foraging area of each colony. After all foraging activity had ceased we placed bait, consisting of 50 ml of *Microseris douglasii* seeds, which are selectively harvested by *M. andrei* (Hobbs 1985; Brown 1997), at the experimental site of 18 colonies. The 10 control colonies were not given bait, but to control for human disturbance we walked to the experimental site for each of these colonies. On the second day, we again mapped the daily foraging area of each colony. To test whether bait made a colony more likely to return to an experimental site, we compared the number of colonies that foraged at their experimental site on day 1 and day 2 of the experiment for the control and the baited colonies, using *G*-tests of independence with Williams' correction.

### Resource distribution

Colonies of *M. andrei* harvest locally produced resources from the current-year seed production (Brown 1997). Thus, seed production of the vegetation in a given area corresponds to the availability to ants of seed resources in that area. Seed plants were heterogeneously distributed over most of our study site. The spatial scale at which ant colonies recognize heterogeneity in resource distributions is not known. We measured resource distribution using a grid with one square equivalent in size to the median area of a foraging fan (1 m<sup>2</sup>).

Seed production in 1995 was estimated for each of nine plant species that together constituted more than 80% of the annual forage of *M. andrei* (Brown 1997). We divided the study area into 1200 1×1 m plots and in April and July recorded the percent cover of the nine plant species in each plot. Previous work had shown that surveys in April and July are sufficient to estimate accurately plant cover of these nine species throughout the year (Brown and Human 1997). One percent cover is equal to a 10×10 cm area. To convert percent cover values into numbers of plants, we calculated the average density of plants of each species that would cover a 10×10 cm area, and used this as the number of plants corresponding to each 1% of cover. Average density was calculated from three high-density and three low-density plots for each species. For each species we calculated average seed production by counting the seed set of 12 randomly chosen plants from the study site (standard errors of these means ranged between 1 and 8% of the mean, suggesting that they are relatively accurate estimates of actual seed production). Seed production (*S*) for each species in each 1×1 m plot was calculated as follows:  $S = (\% \text{ cover}) \times (\text{number of plants in a } 10 \times 10 \text{ cm area}) \times (\text{mean seed production})$ .

### Statistics

#### Basic foraging data

The effects of year and season on the daily foraging area of colonies were analysed using a two-way ANOVA, with Scheffé tests for post hoc comparisons. Data (mean daily foraging area of a colony in a season) were log-transformed to meet the assumptions of the analysis.

#### Space use

We first considered whether colonies use exclusive foraging areas throughout a season or from one season to the next. Foraging maps were digitized using MTV software (DataCrunch Inc.). The study site was divided into 50×50 cm cells. A colony was deemed to have foraged in a 50×50 cm cell if a foraging fan covered at least 50% of the cell. The sum of all the cells used by a colony in a 25-day observation period is its seasonal foraging area. For each colony and each 25-day observation period, we determined the number of days on which the colony foraged in each cell. The seasonal foraging area weighted by the number of times each cell was used gives the total foraging area of a colony.

To determine whether colonies had exclusive total foraging areas during a season, we determined asymmetrical weighted overlap values for pairs of colonies, and for each colony versus all other colonies, as in Smith and Dobson (1994). The weighted overlap value of one colony relative to another is the proportion of the total foraging area of one that is shared with the other. That is:  $\text{overlap} = [\text{total use (in days) of all cells that colony 1 shared with colony 2}] \div [\text{total use (in days) of all cells foraged by colony 1}]$ .

To determine whether each colony used the same foraging area from one season to the next, we calculated the same overlap values for the total foraging area of each colony in one 25-day observation period with its total foraging area in the next observation period.

#### The effect of encounters

*Day-to-day effects.* An encounter on one day may change the probability that a foraging area is used on the following day. The

probability of the return of a colony to an encounter (or a non-encounter) fan was the proportion of fans of that type to which the colony returned on the following day, over a 25-day period. For each colony in each of the six 25-day observation periods, we calculated the difference between the probabilities of returning to the site of an encounter and to a site where no encounter occurred. Positive values indicate that encounters increased the probability of returning to foraging areas. To test whether there was a significant effect of encounters on the probability of returning to a foraging area, we used the difference values from each 25-day period (one value per colony) in a one-sample *t*-test (once for each period).

#### Resource abundance, distance, encounters, and the use of space.

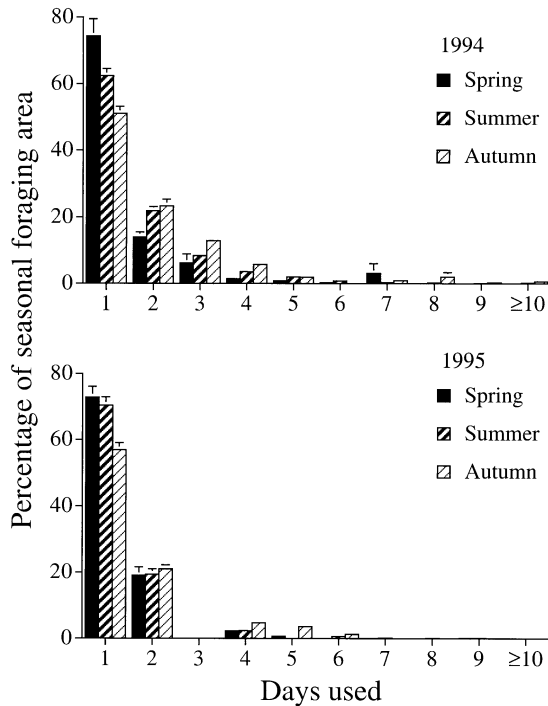
To determine the relationship between resource distribution and the use of foraging area, we first calculated the resource abundance in each 1×1 m plot for each 25-day observation period in 1995. Analysis of seeds taken from *M. andrei* colonies in 1995 showed that the seed species harvested change as the year progresses (Brown 1997), so for each observation period we calculated the distribution of only those plant species that were harvested during those 25 days. Next we used the foraging map data to count the number of days on which each 1×1 m plot was used by a colony in an observation period.

We tested how distance of an area from a colony and the number of encounters that occur in an area, in combination with resource density, affect how often the area is foraged. For each 1×1 m plot foraged by a colony, we calculated the amount of resources (using the resource distribution data, described above), distance from the nest, and number of encounters. If a colony relocated its nest entrance during the 25-day period, distance from the nest was determined with respect to the active nest entrance. If, during an observation period, a plot was used from more than one nest entrance, the plot was included in the analysis only if all uses bar one were from a single nest entrance; distance was calculated using this nest entrance. For each colony, we calculated a multiple linear regression (SPSS 6.1), using the resource, distance, and encounter data for each plot as the independent variables and the number of days each plot was used as the dependent variable. Resource data were log transformed and distance, encounter, and foraging-use data were square-root transformed to meet the assumptions of the regression. Inspection of variance inflation factor values showed that estimates of partial regression coefficients were not affected by multicollinearity between independent variables (Neter et al. 1985, pp. 391–393). One-sample *t*-tests were used to determine whether partial regression coefficients of independent variables were significantly different from zero for all three 25-day observation periods from 1995.

## Results

### Foraging areas

Daily foraging areas were larger in the summer and autumn observation periods than in the spring [daily foraging area in m<sup>2</sup>, mean±SE(colony days), spring, summer, and autumn 1994: 1.5±0.07 (318), 4.7±0.20 (349), 5.5±0.19 (325); and 1995: 1.9±0.11 (184), 4.6±0.24 (223), 3.1±0.13 (207)]. There was a significant effect of season on daily foraging area (two-way ANOVA, adjusted  $r^2=0.37$ , season: MS=0.911,  $F_{2,83}=24.564$ ,  $P<0.001$ , partial  $\text{ETA}^2=0.372$ ; Scheffé comparisons among seasons,  $P<0.001$ , spring<summer=autumn), but no effect of either year (MS=0.04,  $F_{1,83}=1.078$ ,  $P=0.302$ , partial  $\text{ETA}^2=0.013$ ) or the interaction of year and season (MS=0.104,  $F_{2,83}=2.816$ ,  $P=0.066$ , partial  $\text{ETA}^2=0.064$ ).



**Fig. 1** Frequency of use of foraging areas. The bars show the percent foraging area that was used on a specific number of days (mean $\pm$ SE for all colonies in a season)

### Revisiting foraging areas

Most cells were used by foragers of a given colony on just one day in a 25-day observation period (Fig. 1). However, whether cells were used more than once depended significantly on season (1994:  $G=310.71$ ,  $df=2$ ,  $P<0.001$ ; 1995:  $G=68.48$ ,  $df=2$ ,  $P<0.001$ ); the percentage of cells that were used on just one day declined from spring to autumn in both years (Fig. 1). Furthermore, the maximum number of days in which a cell was foraged increased from spring to autumn, ranging from 7 to 20 days.

Colonies rarely shared foraging area within a day (see Encounter section below). However, in the course of a 25-day observation period, pairs of neighboring colonies shared about 7.5% of their total foraging area (Table 1). On average, a colony shared 20% of its total foraging area with all its neighbors (range 0–100%; Table 1).

Foraging area overlap between successive observation periods was determined for the 18 colonies that re-

mained present in the study area for all three observation periods (11 in 1994, 7 in 1995). Colonies varied widely in the proportion of the total foraging area of one season that was incorporated in the total foraging area of the next season (spring to summer, mean=38.8%, SD=30.77, range=0–92.5%; summer to autumn, mean=29.6%, SD=21.25, range=0–65.1%). Similarly, the proportion of the total foraging area of a season that was part of the total foraging area of the previous season varied widely among colonies (summer, mean=11.8%, SD=7.29, range=0–26.3%; autumn, mean=33.9%, SD=26.84, range=0–70.7%).

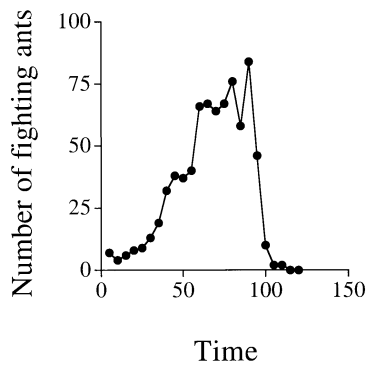
### Encounters

Encounters between colonies occurred in all six observation periods. There were significant effects of year, season, and the year by season interaction on the frequency of encounters (two-way ANOVA, multiple  $r^2=0.372$ , year: MS=1.59,  $F_{1,140}=34.983$ ,  $P<0.001$ , partial  $\eta^2=0.2$ ; season: MS=0.756,  $F_{2,140}=16.641$ ,  $P<0.001$ , partial  $\eta^2=0.192$ ; year $\times$ season: MS=0.317,  $F_{2,140}=6.976$ ,  $P=0.001$ , partial  $\eta^2=0.091$ ). Encounter frequency was higher in 1994 than in 1995 (Scheffé comparison between years,  $P<0.001$ ), and higher in the summer and autumn than in the spring (Scheffé comparisons among seasons,  $P<0.001$ ; number of encounters per day, spring, summer, and autumn 1994:  $1.2\pm 0.25$ ,  $4.7\pm 0.47$ ,  $3.6\pm 0.35$ ; and 1995:  $1.0\pm 0.22$ ,  $2.8\pm 0.43$ ,  $1.3\pm 0.21$ ). Encounters generally occurred at the edge of foraging fans, with little overlap between the two foraging fans. The number of fighting ants at encounter sites increased from the start of the encounter and did not decrease until approximately 10 min before the end of a daily foraging period, when fights broke up and the ants returned to their nests (Fig. 2). Only occasionally did one ant return to its nest with a non-nestmate in tow and there was little evidence for mortality during encounters: few, if any, dead ants were seen at encounter sites after colonies had stopped foraging. The number of fighting ants at encounter sites varied between zero and 660 (ranges in spring, summer and autumn 1994: 2–267, 2–469, 0–660; and 1995: 0–312, 0–231, 0–250), but approximately 75% of encounters had fewer than 20 fighting ants (median number of fighting ants, spring, summer and autumn 1994: 10, 8, 6; and 1995: 5, 4, 5).

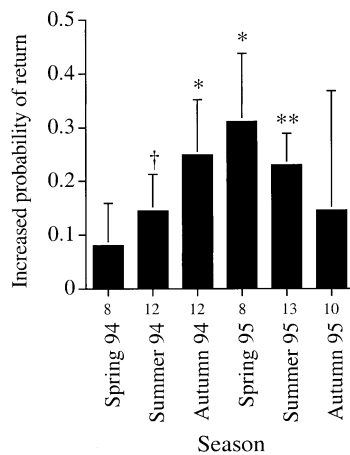
**Table 1** Overlap between colonies in the use of foraging areas within the six 25-day observation periods. Values are the percentage of cells that were shared (mean $\pm$ SE of asymmetric weighted

overlap values) between neighboring colony pairs and between each colony and all other colonies combined. Values in parentheses are the numbers of colony pairs

	Spring 1994	Summer 1994	Autumn 1994	Spring 1995	Summer 1995	Autumn 1995
Overlap between pairs	4.8 $\pm$ 0.78 (28)	7.3 $\pm$ 1.31 (26)	12.0 $\pm$ 3.1 (17)	8.5 $\pm$ 2.52 (20)	8.4 $\pm$ 1.42 (26)	5.6 $\pm$ 1.17 (15)
Range	0.6–23.7	0.1–44	0.2–33.7	0.4–100	0.2–44.6	0.3–25.7
Overlap with all other colonies	15.4 $\pm$ 2.62 (17)	23.8 $\pm$ 4.50 (15)	28.5 $\pm$ 7.10 (14)	19.3 $\pm$ 5.71 (17)	26.8 $\pm$ 4.27 (14)	11.9 $\pm$ 2.84 (12)
Range	0–44.7	0–57.7	2.6–100	0–100	2.3–50.4	0–28.7



**Fig. 2** The dynamics of fighting at an encounter site. The graph shows data for one representative fight. The abscissa shows time in minutes from the beginning of the fight to the end of the daily foraging period. The ordinate axis shows the number of fighting ants, from both colonies, at the encounter site



**Fig. 3** Encounters increase the probability of returning to a foraging fan. Bars show the mean (with associated SE) difference between the probability of returning to an encounter fan on the following day and the probability of returning to a non-encounter fan ( $\dagger P < 0.1$ ,  $* P < 0.05$ ,  $** P < 0.01$  from one-sample *t*-tests). Values below bars show numbers of colonies

#### The effects of encounters: day-to-day

Sites where an encounter occurred were used more often on the next day than sites that were not associated with an encounter. In all 25-day observation periods in 1994 and 1995, the probability of returning to an encounter fan was greater than the probability of returning to a non-encounter fan (sign test,  $n=6$ ,  $P=0.016$ ; Fig. 3). Furthermore, this difference was significantly greater than

**Table 2** The effect of distance, resource abundance, and encounters on the frequency of foraging in  $1 \times 1$  m plots. Values given are the mean  $\pm$  SE of the partial regression coefficients across all colo-

	Distance	<i>t</i> -value	Encounters	<i>t</i> -value	Resources	<i>t</i> -value
Spring	$-0.37 \pm 0.077$ ( $n=13$ )	4.75***	$0.04 \pm 0.058$ ( $n=13$ )	0.73 n.s.	$0.14 \pm 0.094$ ( $n=13$ )	1.54 n.s.
Summer	$-0.22 \pm 0.065$ ( $n=12$ )	3.46**	$0.33 \pm 0.079$ ( $n=12$ )	4.21**	$0.21 \pm 0.206$ ( $n=12$ )	1.01 n.s.
Autumn	$-0.25 \pm 0.105$ ( $n=12$ )	2.40*	$0.25 \pm 0.167$ ( $n=12$ )	1.49 n.s.	$0.35 \pm 0.268$ ( $n=12$ )	1.32 n.s.

zero for three of the six observation periods, once in each season (Fig. 3).

Experimentally induced encounters also increased the probability that a foraging site was used again the next day. Colonies that had non-nestmate foragers added to one of their fans were significantly more likely to return to that fan than to a fan without an encounter (to which the mean probability of return =  $0.469 \pm 0.1$ ) from the same day ( $n=8$  colonies, two experiments each, mean increase  $\pm$  SE =  $0.4 \pm 0.09$ ,  $df=7$ ,  $t=4.33$ ,  $P=0.003$ ).

#### Bait experiment

The colonies recruited to experimental bait. Out of 18 experimental colonies, 4 foraged at the bait site on the day before bait was added, while 13 foraged at that site after the addition of bait ( $G_{adj}=9.08$ ,  $P < 0.005$ ). Out of 10 control colonies, 4 foraged at the bait site before the manipulation and 5 foraged there on the following day ( $G_{adj}=0.19$ ,  $P > 0.5$ ).

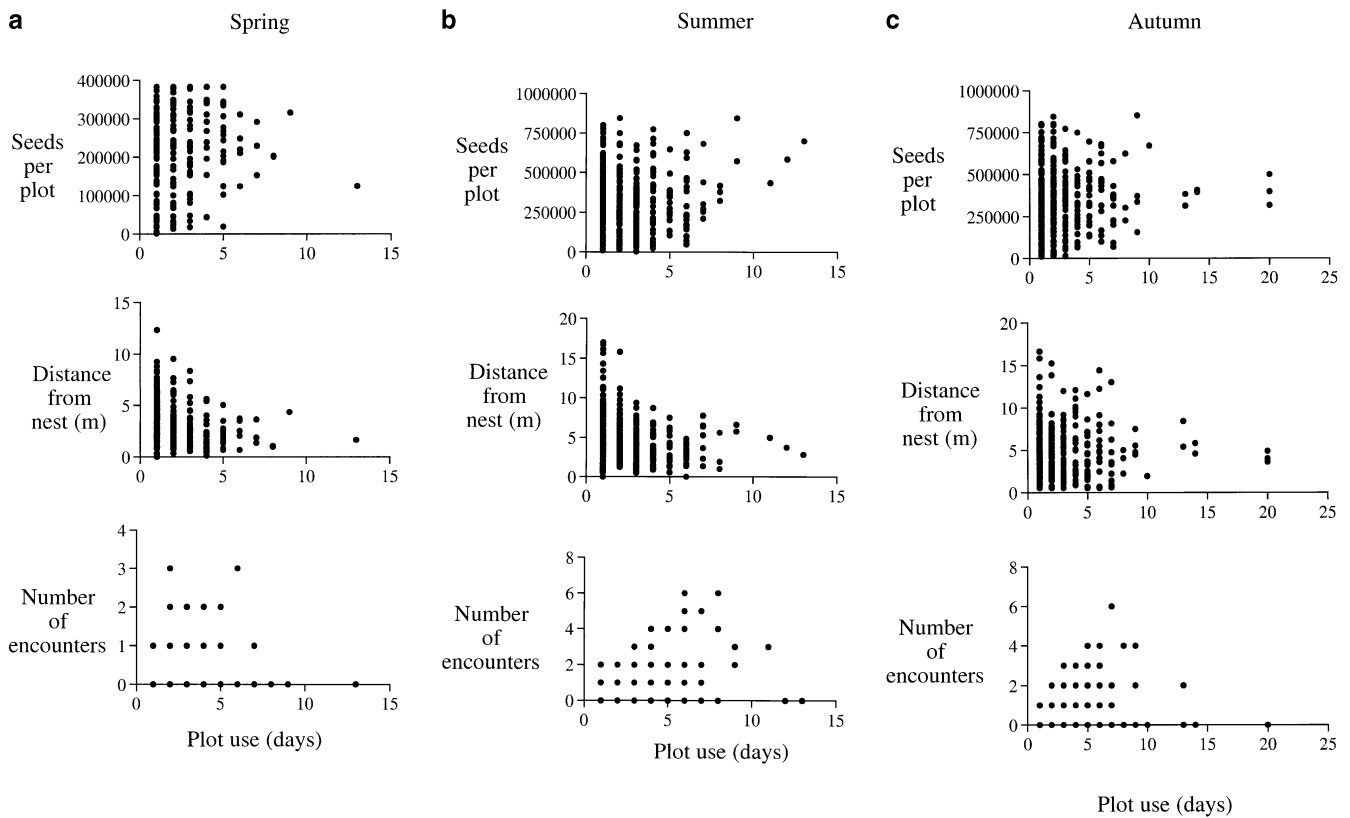
#### Resource abundance, distance, encounters and the use of space

Distance from the nest and encounters affected the use of space by colonies. The closer a plot was to the nest, the more likely it was to be foraged on multiple days (Fig. 4). The average partial regression coefficients for distance were negative, indicating a decrease in plot use with an increase in distance, and significantly different from zero in all three observation periods (Table 2). Foraging distances ranged up to 12.3, 16.7, and 17 m in the spring, summer, and autumn observation periods, respectively. In spring, 80% of total foraging area was within 10 m of the nest, and in summer and autumn this proportion was 60%.

In the summer observation period, the more encounters that occurred at a plot, the more likely it was to be foraged on multiple days (Fig. 4). While the average partial regression coefficients for encounters were positive in all three observation periods, indicating an increase in plot use with an increase in the number of encounters, only in the summer was this average significantly greater than zero (Table 2).

In contrast, despite 1000-fold variation among plots in resource abundance (Fig. 5), the amount of resources in a plot never significantly affected the number of days on which that plot was foraged (Table 2, Fig. 4). Our re-

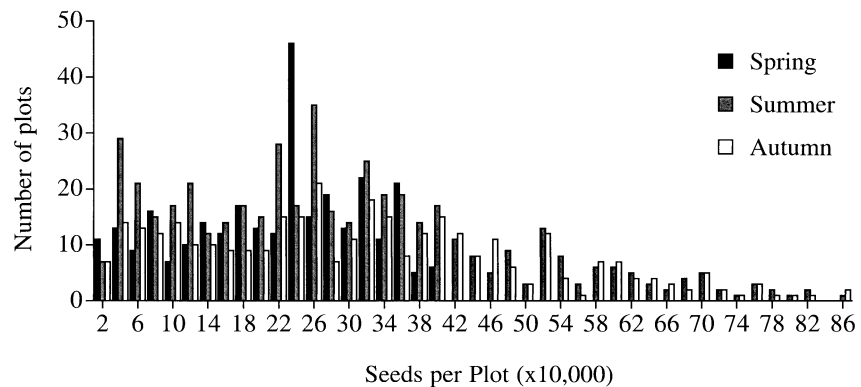
gressions in a season, for each of the independent variables in the regression (see text for description of the multiple regression; *n.s.*  $P > 0.05$ ,  $* P < 0.05$ ,  $** P < 0.01$ ,  $*** P < 0.001$ )



**Fig. 4a–c** The relationship between space use and resources, distance from the nest, and encounters. Each point corresponds to a 1×1m plot. The abscissas show the number of days on which a 1×1m plot was used. Ordinate axes show resource abundance, distance from the nest, and number of encounters for individual plots.

Note the absence of a relationship between plot use and resource abundance, the consistently negative relationship between plot use and distance, and the positive relationship between plot use and encounters in the summer. For statistical relationships, see text

**Fig. 5** Resource abundance in foraged plots. Bars show the frequency of plots which fall within the indicated range of seed abundance



source calculations, which did not account for potential differences in the seed production of individual plants due to differences in plant density, may have underestimated variation among plots. However, foraged plots were still distributed quite evenly across a very broad range of estimated resource availability (Fig. 5), so a relationship between foraging and resource abundance is unlikely to have been hidden by our resource calculation method. On average, foraged 1×1 m plots contained about 250,000 seeds [mean±SD, spring, summer and autumn 1995: 207,216±102,756.8 ( $n=282$ ), 279,487±

182,020.5 ( $n=475$ ), 306,840±191,644 ( $n=343$ )], and seed density varied between 606 and 851,209 seeds in a plot.

## Discussion

Encounters between conspecific colonies increased the probability that associated foraging space was revisited by foragers at both the day-to-day and the seasonal scale. In contrast, where a colony chose to forage did not reflect the distribution of resources, despite experimental

evidence that colonies can recruit to high-density patches of seeds.

Encounters between colonies of *M. andrei* occurred frequently: nearly all colonies observed had several encounters during each 25-day observation period. Encounter frequency is known for only two other species of seed-harvesting ants. Harkness and Isham (1988) studied a population of *Messor wasmanni* with a nest density similar to that of the population studied here, but saw only one encounter in 3 months of observation. In contrast, Gordon and Kulig (1996) reported that colonies of *Pogonomyrmex barbatus* encounter on average about two other colonies per day. Our results for *M. andrei* fall between these two extremes. There were significantly more encounters in the summer and autumn than in the spring, reflecting similar significant seasonal changes in the size of daily foraging areas. As colonies exploit larger foraging areas, they are likely to impinge on the foraging areas of their neighbors more frequently.

Encounters in this study invariably involved fighting between pairs of ants. However, less than 20 ants fought in most encounters; this is a small proportion (about 1%) of the daily foraging force. In many ant species, encounters that involve fighting serve to defend foraging areas (e.g., Adams 1990; reviewed in Hölldobler and Wilson 1990). By returning to encounter sites, *M. andrei* colonies may defend their day-to-day foraging space. This may explain the low level (7.5% on average) of overlap in the foraging areas of neighboring colonies. In addition, fighting at encounters may present a living barrier to foragers, and thus reduce scramble competition for resources within a day. Fights frequently formed a band where the two colonies met, and foragers that tried to cross this band invariably joined in the fight. The foraging area of a colony in one season shows little overlap with its foraging area in the next, which suggests that foraging space may only be defended for a short period. Similarly, in *P. barbatus*, foraging area around the nest is used repeatedly at the scale of weeks, but from year to year the area is not conserved (Gordon 1992, 1995).

Encounters between colonies of *M. andrei* may serve an additional function. In summer, when encounters were frequent, areas where encounters had occurred were foraged more frequently. An encounter provides information about where neighboring colonies are foraging, and thus potentially about the distribution of resources. Territorial *Anolis* lizards also use encounters both to demarcate territories and as resource cues (Stamps 1994).

Colony foraging decisions were not influenced by the distribution of resources. In serpentine grasslands, this distribution is spatially and temporally heterogeneous (Hobbs and Mooney 1995; Brown and Human 1997); in 1995, numbers of seeds in a square meter ranged from 500 to 850,000. Our bait experiment showed that colonies can respond to resource distributions. This suggests either that resources were not a limiting factor for *M. andrei* colonies in 1995, or that other factors were more important in that year. Our data indicate that in 1995, colo-

nies were not competing for a limited resource. For example, a 1×1 m plot containing the average number of seeds (about 250,000) would be depleted after 70 days of foraging (about 3,500 foraging trips/day), but most plots were foraged for only about 10 days in a year. In fact, annual precipitation for the 1995 observation periods was nearly twice as high as the previous 20-year average (N Chiariello, personal communication), presumably resulting in a correspondingly high level of seed production.

If resources were not limiting, and most foraging areas were used on just a few days, why do encounters affect the use of space? In a long-lived organism, foraging behavior might be adapted to “crunch” periods, when selection for foraging efficiency is highest. *M. andrei* colonies in northern California must survive years of drought when seeds are scarce (Hobbs and Mooney 1995). If foraging behavior is similar in drought and non-drought years, as it is in the congener *Messor pergandei* (Rissing 1988), then defense of foraging areas, and the potential use of encounters as cues about resource distribution, may be adaptations to times when resources are less abundant. To test these hypotheses, data from drought years are needed.

In the rufous hummingbird (*Selasphorus rufus*), the pattern of territory use is also determined mainly by encounters with intruding conspecifics, rather than by the distribution of resources (Paton and Carpenter 1984). The immediate return of territory holders to flowers at encounter sites (usually at the periphery of the territory) was interpreted as territory defense by exploitation, where depleting the territory edges discourages competitors from intruding on the resource-rich territory core (Lucas and Waser 1989). This appears to be very similar to the behavior of *M. andrei* colonies, albeit on a shorter time scale. However, it seems unlikely that *M. andrei* behavior is an example of such territorial defense. The total foraging area of a colony is highly irregular and, unlike those of birds, the foraging areas of neighboring colonies interdigitate. Consequently, the exploitation of encounter sites is unlikely to deter neighboring colonies from approaching the rest of the foraging area of a colony.

Distance from the nest had a striking effect on foraging behavior. In all seasons, plots closer to the nest were foraged more often. By reducing travel time to foraging fans, a colony may increase the rate at which resources are brought back to the nest. *P. occidentalis* and *Messor capitatus* colonies adjust foraging intensity similarly with respect to distance (Crist and MacMahon 1992; Diaz 1992), suggesting that at least in this way harvester ant colonies may adopt an optimal foraging strategy (Stephens and Krebs 1986).

Most of the foraging area used by a colony was exploited only once in a 25-day period. The use of foraging space by harvester ants often changes from one day to the next. For example, a colony of *P. barbatus* uses each of its habitual foraging directions just once in 8 days (Gordon 1991). We found a seasonal change in the frequency with which foraging space is used. From spring

to summer to autumn, foraging areas were visited more often by *M. andrei* colonies. This can be explained by two non-exclusive factors. One, an increase in the frequency of encounters from spring to summer increased the rate at which ants returned to the same plot on successive days. Two, by autumn there may be fewer resource patches from which to choose.

While numerous studies have examined foraging strategies with respect to artificial resource distributions, we still know little about how animals respond to resource distributions in natural systems. Recent theoretical work (Dolman and Sutherland 1997) has shown that incorporating interference between animals into foraging models increases our understanding of herbivore-imposed patterns of resource depletion. Our results show that the choice of foraging area by a *M. andrei* colony depends upon proximity to the nest, encounters with neighbors and, surprisingly, not on resource distributions. Testing spatially explicit foraging models, which incorporate both interactions with conspecifics and resource distributions, is the next important step toward an understanding of how animals use foraging space.

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