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The spatial scale of seed collection by harvester ants

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Abstract. Colonies of the seed-eating ant, *Pogonomyrmex barbatus,* compete with neighboring colonies for foraging areas. In a conflict over foraging area, what is at stake? This depends on how resources are distributed in time and space: if certain regions consistently provide particularly nutritious seed species, or especially abundant seeds, such regions will be of greater value to a colony. During the summer, seeds were taken from returning foragers in colonies located in 4 different vegetation types. There was no relation between the vegetation currently growing in the foraging area, and the species of seeds collected by ants. During the summer, ants collect mostly seeds produced in previous seasons and dispersed by wind and flooding. In 1991, colonies in all vegetation types collected mostly *Bouteloua aristidoides;* in 1992, *Eriastrum diffusum* and *Plantago patagonica.* There was no relation between colony density and numbers of seeds collected. Seed species collected by ants were compared in different colonies, and on different foraging trails within a colony. The results show that seed patches are distributed on the scale of distances between nests, not the smaller scale of different foraging trails of one colony. It appears that colonies are competing for any space in which to search for seeds, not competing for certain regions of consistently high value.

Key words: Territorial behavior – Foraging – Seed-eating ants – Seeds – Intraspecific competition

Desert granivores compete for food (Brown and Davidson 1977; Davidson 1977, 1985). The foraging ecology of seed-eating ants depends on resource use at several spatial scales, from large areas of seed-producing vegetation (on the scale of hectares), to distances between colonies (tens of meters), to the tiny patches from which ants on a particular foraging trail collect seeds (Wiens 1989; Crist et al. 1992). There are two outstanding questions about the spatial scale of resource use by seed-eating ants. First, how does the distribution of food influence an individual colony's foraging behavior? Second, how does the distribution of food influence competition among neighboring colonies for foraging space?

There has been much research on the foraging ecology of seed-eating ants, but some crucial assumptions have never been tested. It is often assumed that resource use reflects current production by nearby plants, either on the scale of nests or of foraging patches; some authors have suggested this explicitly (e.g. Bernstein and Gobbel 1979; Davidson 1980; Hansen 1978; Ryti and Case 1986; Ryti 1991). More generally, the assumption that resource use is local is a common starting point for models of spatial distributions and territory sizes (e.g. Fretwell and Lucas 1970; Schoener 1983). But if resources and consumers do not overlap in space and time, such models predict very different outcomes (e.g. Charnov et al. 1976; Pacala 1988). The assumption that resource use is local often guides empirical work as well, with measures of local resource abundance taken to be measures of resource use.

Studies of plant ecology seem to suggest that harvester ants could use local, currently-produced seeds. In plant species whose seeds are often collected by harvester ants, survivorship and germination rates are density-dependent (Davidson 1985; Inouye 1980), which indicates that plants distribute at least some seeds nearby. However, the majority of seeds collected by ants may have already dispersed some distance from the parent plants, and considerable time may elapse between seed production and collection by ants. It is difficult to measure seed distribution directly (Kemp 1989; Nelson and Chew 1977; Reichman 1984; Price and Reichman 1987). Here I test whether ants collect seeds that are produced by local vegetation currently growing in their foraging area, by comparing seeds collected by colonies foraging in different vegetation types.

Where a colony forages each day is presumably influenced by the distribution of food. A mature colony of the red harvester ant, *Pogonomyrmex barbatus,* has a set of about 8 habitual foraging directions. Only 3–5 of these are used each day (Gordon 1991). A colony's decision about which foraging direction to use is made early each morning by the patrollers, a distinct group of workers that search the foraging area before the foragers become active (Gordon 1983, 1989a, 1991). In the absence of human intervention, colonies rarely engage in recruitment, in which large numbers of ants travel directly to a food source and retrieve it, a process that ends abruptly when the food is gone. Instead, the usual foraging trail consists of smaller numbers of dispersed, slowly moving ants searching for seeds over a wide area. Each ant continues searching until it finds a food item (Gordon 1991), and foraging continues until high midday temperatures drive all ants back into the nest. Foraging trails are often fan-shaped rather than linear (illustrations in Gordon 1991, 1992a). The area covered by searching foragers usually becomes more elongated, with a linear trail-shaped base, in the course of a day and also over the course of a summer foraging season, probably because areas closer to the nest become depleted. If particular regions of foraging area consistently yield particular species of seeds, this could influence a colony's choice of foraging direction. Here I examine whether the species of seeds collected differ among the foraging trails used by a single colony.

Where a colony forages is influenced by the behavior of its conspecific neighbors (Gordon 1991, 1992a). A *P. barbatus* colony usually remains at a single nest site throughout its lifespan of 15–20 years (Gordon 1991, 1992b), and ants distinguish workers of neighboring and more distant colonies (Gordon 1989b). Colonies compete with their neighbors for foraging area: when one colony is prevented from foraging, the foraging trails of its neighbors will enter its foraging area within 10 days (Gordon 1992a). Each summer, after the rains, there is a period of several weeks during which foraging trails intersect and fighting erupts between neighboring colonies. (One colony never invades the nest of another).

What is at stake in interactions of neighboring colonies? Territories provide their occupants with a resource, and the distribution of resources can shape territorial behavior (Monaghan and Metcalfe 1985; Carpenter 1987; Grant and Kramer 1992). For ant colonies, territories usually provide a region in which to search for food (Holldobler and Lumsden 1980; Traniello and Levings 1986). If particular regions consistently offer more abundant or nutritious seeds, these regions may be more valuable as foraging area. The timescale on which a region of foraging area maintains its value, could determine the timescale of territorial conflict between colonies. In a harvester ant colony, territorial behavior develops over the course of many years. Young, growing colonies (2–5 years old) are more likely to engage in sustained conflict over foraging areas than older, larger colonies of stable size (5 years or more) (Gordon 1991, 1992a). The distribution of seeds, in time and space, will determine how consistently certain regions provide abundant or nutritious seeds. This in turn will determine the prospective value of a foraging area for a young colony.

Methods

The study was conducted in Jul–Aug 1991 and 1992 near Rodeo, New Mexico (elevation c. 1400 m). The 12-hectare study site contains approximately 250 *P. barbatus* colonies (Gordon 1991). There tend to be two annual bouts of plant flowering, following the winter rains in January–February, and following the much heavier summer rains in July–August (e.g. Nelson and Chew 1977; Davidson et al. 1985).

The study was conducted during the summer, when fighting between neighboring colonies is likely. Summer resource use is relevant to competition for foraging area because, if ants are fighting with neighbors over local resources, the contested resources may be available at the time the ants are fighting.

1. Seeds collected by ants and local vegetation

This section describes how data were collected in 1991. Individual plants of all species encountered in repeated walks around the study site in July and August were collected and identified. Seven markers were placed at 30 m intervals in one E–W row across the study site, and 6–8 markers in each of four N–S columns. At each marker, my assistants and I measured the percent of plant cover along a line 3 m long, and counted all plants inside a circular quadrat covering a region of 1 m^2. This survey was performed twice in 1991 (18–19 Jul and 5–6 Aug), with similar results; a briefer survey in 1992 showed little change.

Small shrubs of *Gutierrezia* sp., *Isocoma tenuisecta*, and *Ephedra trifurca* are distributed throughout the site, except in places covered by a dense perennial grass, *Hilaria mutica*. Four main vegetation types were identified. Percent cover is given for bare ground and *Hilaria mutica*, and percentages in numbers of plants for herbaceous plants and other grasses:

1) Bare: $>75\%$ bare ground, $<10\%$ *H. mutica*, no other plants.
2) Broad-leafed herbaceous plants: $<50\%$ bare ground, $<10\%$ *H. mutica*, $>50\%$ broad-leafed herbaceous, $<25\%$ other grasses.
3) Grasses: $<50\%$ bare ground, $<10\%$ *H. mutica*, $<25\%$ broad-leafed herbaceous, $>50\%$ other grasses.
4) *Hilaria mutica*: $<20\%$ bare ground, $>75\%$ *H. mutica*, $<10\%$ broad-leafed herbaceous, $<10\%$ other grasses.

The most common plant species (besides the shrubs listed above) found in the Broad-leafed Herbaceous and Mostly Grasses vegetation types are listed in Table 1. A vegetation map (Fig. 1) was constructed using an existing map on which all *P. barbatus* colonies were marked and labelled with an identifying number. Boundaries between vegetation types were drawn by eye, using marked colonies as points of reference, and are less distinct than they appear on the map.

For each vegetation type, 2 districts were chosen, representing two levels of ant density: 'not crowded' (≤ 3 colonies per 20 m^2), and 'crowded' (≥ 5 colonies per 20 m^2). Three colonies were observed in each of the 8 vegetation/ant density districts [4 vegetation types, each crowded and not crowded (see Tables 1 and 2)], for a total of 24 colonies. Colonies were chosen that seemed rarely to make foraging trails (up to 30 m long) leading into other vegetation types. Colony ages ranged from 3 to 10 years; in each district, the three colonies included one 3–4 year-old colony and two at least 5 years old, except for one district (Broad-leafed Herbaceous, not crowded) in which all 3 colonies were at least 5 years old.

Each week during the summer of 1991, 100 foragers were collected from each of the 24 colonies as they returned to the nest on a foraging trail. Returning foragers were collected whether or not they visibly carried a food item; previous work shows that foragers rarely return to the nest without a food item (Gordon 1991). "Food items" in this paper refers only to plant parts; foragers carrying termites or (more rarely) other insects were not included in the counts of 100. The proportion of successful foragers carrying termites rather than plant parts ranges from about 1 in 25 ants in dry weather to about 1 in 8 the day after rain (pers. obs.). Four col-

Table 1. Plant species growing on study site, and species collected by ants. Species found on the site are listed by vegetation type. * = species that were both found growing on the study site, and had seeds collected by ants. Species collected by ants, listed in the third column, are listed near the related species found on the study site, but were not necessarily collected by colonies in the corresponding vegetation type

Family	Found on site in July–August	Species collected by ants
Vegetation type 2:		
Broad-Leafed Herbaceous Plants		
Amaranthaceae:		*Amaranthus fimbriatus*
		Guilleminea densa
Asteraceae:	*Baileya multiradiata*	*Chaenactis* sp
	Machaeranthera pinnafitida	*Centaurea mellitensis*
	Acourtia nana	
Brassicaceae:		*Lepidium lasiocarpum*
Chenopodiaceae:		*Monolepis nuttalliana*
		Atriplex elegans
Convolvulaceae:	*Evolvulus sericeus**	*Evolvulus sericeus**
		Ipomoea costellata
Cyperaceae:		*Carex eleocharis*
Euphorbiaceae:		*Euphorbia (Chamaecye) florida*
		Europhorbia (Chamaecye) albomarginata
Fabaceae:	*Hoffmanseggia glauca*	*Chamaecrista nictitans*
		Lupinus sp
Geraniaceae:		*Erodium texanum*
Hydrophyllaceae:		*Phacelia crenulata*
Krameriaceae:	*Krameria lanceolata*	
Malvaceae:	*Sphaeralcea* sp	
Nyctaginaceae:	*Allionia incarnata*	
Onagraceae:		*Oenothera* sp
Polygonaceae:	*Eriogonum wrightii*	
Portulacaceae:	*Portulaca suffrutescens**	*Portulaca suffrutescens**
	*Talinum aurantiacum**	*Talinum aurantiacum**
Solanaceae:	*Solanum elaeagnifoluim*	
Vegetation type 3: Mostly grasses		
Plantaginaceae:	*Plantago patagonica**	*Plantago patagonica**
Poaceae:	*Aristida purpurea**	*Aristida purpurea**
	Aristida ternipes subsp. *hamulosa*	
	Aristida adscensionis L	
	Bothriochloa laguroides subsp. *torreyana*	
	Bouteloua barbata	*Bouteloua aristidoides*
	Bouteloua curtipendula	*Chloris virgata*
	*Digitaria californica**	*Digitaria californica**
	Eragrostis lehmanniana	
	*Erioneuron pulchellum**	*Erioneuron pulchellum**
	Hilaria mutica	*Hilaria belangeri*
	Muhlenbergia arenicola	
	Panicum obtusum	
Polemoniaceae:	*Eriastrum diffusum**	*Eriastrum diffusum**

Table 2. Variation among colonies and among foraging trails within colonies. Results of an ANOVA using log-transformed numbers of seeds collected in 1992

	Mean squares			Colonies		Trails within colonies	
	Colony	Trails Within Colonies	Days Within Trails	$F_{8,25}$ (Colonies, Trails Within Colonies)	p	$F_{25,168}$ (Trails Within Colonies, Days Within Trails)	p
Monolepis nuttalliana	10.90	1.72	0.32	9.08	0.001	5.38	0.001
Eriastrum diffusum	4.53	1.03	0.72	4.4	0.01	1.43	NS
Plantago patagonica	6.14	1.30	0.48	4.72	0.01	2.71	0.001
Bouteloua aristidoides	6.99	2.38	0.32	2.94	0.05	2.38	0.001
Lepidium lasiocarpum	3.38	0.80	0.43	4.21	0.01	1.88	0.05
Other	1.04	0.76	0.28	1.37	NS	2.70	0.001

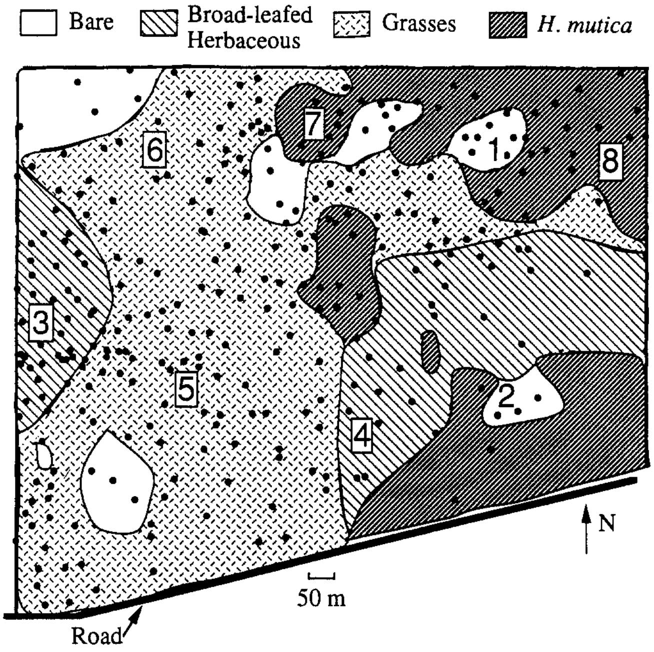

Fig. 1. Vegetation map of study site. Each filled circle shows the location of one colony of *Pogonomyrmex barbatus* in 1991. Numbers indicate the 8 vegetation/ant density districts: *1* Bare, crowded; *2* Bare, not crowded; *3* Broad-leafed Herbaceous, crowded; *4* Broad-leafed Herbaceous, not crowded; *5* Grasses, crowded; *6* Grasses, not crowded; *7 Hilaria mutica*, crowded; *8 H. mutica*, not crowded. In each district, seeds were taken from returning foragers in 3 colonies. Table 1 lists plant species found in districts 3–6

lections were made at weekly intervals (Jul 25–26; Aug 1–2; Aug 8–9; and Aug 15–16). The foragers were collected by aspirator and allowed to leave the vial and return to the nest when they had dropped their food items. Food items were taken back to the laboratory for identification and counting. Dry fruits and seeds are both referred to here as "seeds". Ants occasionally carried parts of seeds, especially the husks of grasses; each husk was counted as 1 food item. [In 1992, using identical collection methods, the average proportion of plant parts collected by ants that were not complete seeds was 0.08 (± 0.08, $n = 175$ trail-days)]. Numbers of food items per colony sometimes exceeded 100, perhaps because seeds were aspirated from the ground when ants were collected, or because an ant was carrying more than one seed. Approximately 1200 seeds were collected by us per vegetation/ant density district (100 seeds per colony for 3 colonies × 4 weeks per colony).

Numbers of food items of each plant species were totalled over all 4 weeks of sampling, tabulated by vegetation/ant density district, and then converted to proportions out of all food items collected by the 3 colonies in that district. Results for the 3 colonies in each vegetation/ant density district were thus pooled in analysis of the 1991 data; variation among colonies was considered in analysis of the 1992 data, discussed in the next section. In 1991 18 species of seeds were collected, as well as a category called "miscellaneous" of unidentified seeds each collected less than 3 times. Of these 19 seed types, only the 9 collected by ants in proportions $>1\%$ were considered in the analysis of the 1991 data.

Standard errors were calculated for proportions using the usual method for a Poisson process (e.g. SE for a proportion of 12%, 60/512, is $\sqrt{60/512}$). Then to correct for overdispersion (in the probabilistic, not spatial sense) caused by vegetation type, density, or week-to-week changes, standard errors were multiplied by a correction factor $\Sigma\chi^2/K$, where K is degrees of freedom of the χ^2's (McCullagh and Nellder 1989, p. 174–175). To calculate the correction factor, I found values of χ^2, each using the weekly totals for one plant species and one vegetation type, for each of the 11 plant species for which the highest numbers of seeds were taken in some vegetation type. These 11 values were combined as above to obtain an overall correction factor of 2.79. The resulting standard errors are referred to as 'corrected standard errors' of proportions. To determine whether a difference between two proportions was statistically significant, I divided it by the corrected standard error of the difference, and referred the resulting z-statistic to the normal distribution (Moses 1986).

2. Variation among colonies and among foraging trails in seeds collected

In 1992, 9 colonies were chosen to examine differences among foraging trails in seed species collected. Two of the 9 were among the 24 observed in 1991. Of the 9 colonies, 5 were 3–4 years old, and 4 were 5–11 years old. In each colony, on a given day, seeds were collected as described above from 20–45 returning foragers on each of 2 foraging trails. Seeds were taken from ants on the same 2 trails on 2–3 consecutive days. This was repeated 4 or 5 times, at weekly intervals, for each of the 9 colonies, for a total of 26 trails, 202 colony-days, and 5495 seeds.

Thirty-six species of seeds were collected. Only 5 species ever represented more than 10% of the intake on at least 2 days of some trail of some colony; these species are listed in Table 2. In the analysis of the 1992 data, I considered these 5 species, plus a sixth category, "other", consisting of the total numbers of seeds in the remaining 31 categories. The log-transformed numbers of seeds of each of the 6 types from a particular colony, day and trail were used in an ANOVA, with colony and trails within colonies as main effects, and days within trails as the error term.

Results

1. Seeds collected by ants and local vegetation

Seeds collected did not reflect current local vegetation. Table 1 shows plant species found on the study site in July–August and those for which seeds were collected. There is little correspondence between the two lists.

There was no relation between the vegetation type in which colonies were located, and the species of seeds they collected. Figure 2 shows the proportions collected in 1991 (out of all seeds of all species) by the 3 colonies in one vegetation/ant density district, for the 9 plant species taken by the ants in the greatest abundance.

Most of the seeds collected by ants during the summer are not produced by vegetation currently in fruit. In 1991, colonies in all vegetation types mostly collected the seeds of *Bouteloua aristidoides*. For each of the 8 vegetation/ant density districts, I compared the proportion of *B. aristidoides* to the proportion of the next most frequently collected species. Proportions of *B. aristidoides* were greater in most districts; the difference was highly significant ($p < 0.01$) for districts 3, 4, 5, 6, 7; significant ($p < 0.05$) for district 1, and not significant for districts 2 and 8 (Fig. 2). *B. aristidoides* sets seed and releases seeds at this site in September, 10–11 months before the study was made (Davidson et al. 1985). In 1992, the species collected in largest quantity were *Eriastrum diffusum* and *Plantago patagonica*. *E diffusum* is a winter annual (Davidson et al. 1985); *P. patagonica* sets seed in the spring (Kearney and Peebles 1960).

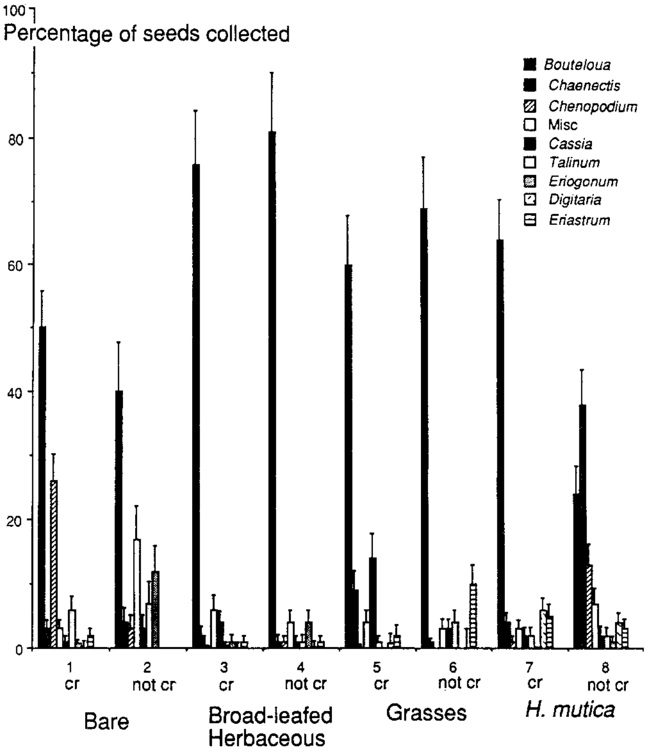

Fig. 2. Proportion of seeds collected, in each vegetation/ant density district. Each group of bars shows the proportions taken of 9 plant species, by 3 colonies in one district, over the 4 weeks of the 1991 study. Proportions are out of total numbers of seeds of all plant species (about 1200 per vegetation/ant density district); each group of bars adds to 100. 'Misc' refers to seeds of unidentified species, of which not more than 3 seeds were collected by ants throughout the summer. Error bars show corrected Poisson standard errors (details in text). 'cr' is 'crowded', 'not cr' is 'not crowded'

Seeds collected by ants and temporal patterns in seed production. Over the course of the summer of 1991, the proportion of *B. aristidoides* collected decreased. From week 1 to week 4, the proportion of *B. aristidoides* collected decreased in 7 of the 8 vegetation/ant density districts (except district 1, 'Bare, crowded'). The decrease in the proportion of *B. aristidoides* collected from week 1 to 4 was highly significant ($p < 0.001$, using the test described in the last paragraph of section 1 of the Methods section) in 3 districts. These districts are listed with mean per cent, for weeks 1 and 4, of all seeds collected that were *B. aristidoides* (± corrected Poisson standard error of the mean): 'Broad leafed Herbaceous, crowded' (wk 1: 92 ± 17.5, wk 4: 60 ± 13.7); 'Grass, not crowded' (wk 1: 93 ± 20.1, wk 4: 53 ± 15.2); '*H. mutica*, crowded' (wk

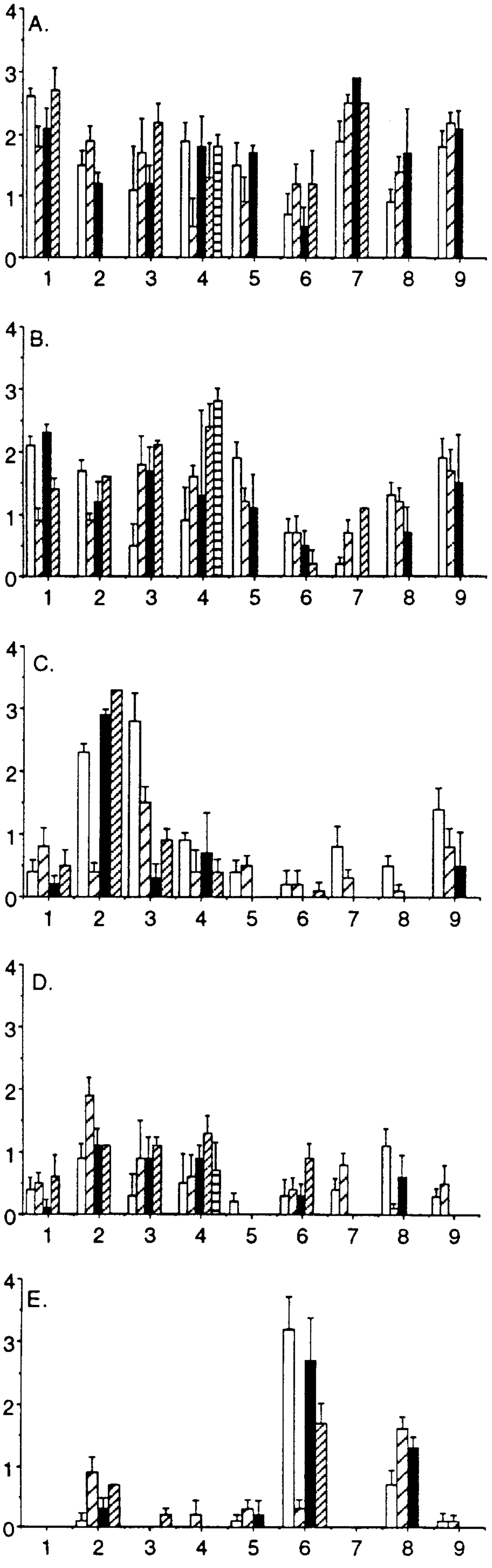

Fig. 3A–E. Colonies and foraging trails differ in species of seeds collected. Each graph shows the results from 1992 for one plant species: **A** *Eriastrum diffusum*, **B** *Plantago patagonica*, **C** *Bouteloua aristidoides*, **D** *Lepidium lasiocarpum*, **E** *Monolepis nuttalliana*. In each graph, the abscissa represents the 9 colonies; the ordinate is mean log-transformed numbers of seeds. Each bar shows results for one foraging trail. Error bars show standard error of the mean. Each shading design represents a different trail; e.g. filled bar is trail 2, etc. Trails are numbered arbitrarily in each colony; there is no correspondence among similarly shaded bars in different colonies

1: 91 ± 14.8, wk 4: 47 ± 10.8). There was a significant decrease ($p < 0.05$) in district 4 'Broad-leafed Herbaceous, not crowded' (wk 1: 95 ± 21.4, wk 4: 65 ± 14.3), and no significant decrease in the other 4 districts. Proportions of other species collected, such as *Eriogonum abertianum, Digitaria californica* and *Chaemaecrista nictitans,* appeared to increase from weeks 1 to 4. Numbers of species collected by one colony in one week ranged from 1 to 13. In all but 2 of the 8 districts, there was an increase, from week 1 to week 4, in the mean number of different seed species collected.

Temporal patterns in seed collection in 1991 sometimes, but not always, reflected plant phenology. Five of the species collected by ants set seed during the summer. For these 5 species, no seeds (from a previous season) were collected by ants before the plant had flowered. For these species, the ants seemed to be tracking immediate seed availability. However, for most other plant species, there were similar, inexplicable temporal peaks in collection, with the majority of seeds of most species collected in only 1 or 2 of the 4 weeks of the study.

Over the 5 weeks of study in 1992, there were no apparent temporal patterns in species of seeds collected. The residuals of the ANOVA, in which days within trails was used as the error term (with colonies and trails within colonies as main effects), were plotted against calendar time. There were no observable patterns.

Numbers of seeds collected and colony density. There was no significant relation in the 1991 data between the number of food items collected by 100 foragers of a colony, and the density of nearby colonies. Colonies in more crowded regions sometimes took larger numbers of seeds; this was true for the Bare, Broad-leafed Herbaceous and *H. mutica* vegetation types. Mean (± SE) numbers of seeds collected for 'crowded' and 'not crowded' districts, respectively, were: Bare 398.7 ± 70.6, 171.3 ± 31.8; Broad-leafed Herbaceous 293.3 ± 44.3, 226.3 ± 35.1; Mostly Grasses 256.7 ± 28.3, 264.7 ± 24.5; *H. mutica* 379.7 ± 43.9, 308.3 ± 10.9. There was no significant difference between the total numbers taken (over all 4 weeks) for seeds of the 9 most frequently collected species (species shown in Fig. 2) in the crowded and not crowded districts (mean total number per seed species for crowded, 104.2 ± 32.4 seeds; for not crowded 75.9 ± 24.2; two-tailed t-test: $t = 0.69$, df = 70, $p = 0.48$).

2. *Variation among colonies and among foraging trails in seeds collected*

The species of seeds a colony collects depends more on the location of its nest than on its choice of foraging trail. Though differences among colonies in seeds collected do not reflect the species of plants growing nearby, colonies still differ in the species of seeds they collect. For the 5 seed species most frequently collected in 1992, colonies differed significantly in numbers collected (Table 2). For 4 of the 5 plant species (the exception was *Plantago patagonica*), foraging trails within a colony differed significantly in numbers collected. However, variation among colonies was always 2–10 times greater than variation among trails within colonies (cf. MS values for colonies and trails within colonies in Table 2). Figure 3 illustrates that differences among colonies in seeds collected tend to exceed differences among the foraging trails of one given colony. In each graph, representing one plant species, heights of bars vary more among different colonies (1–9), than within each cluster of bars representing the different trails of a single colony.

Discussion

During the summer, while colonies are in conflict over foraging area, ants do not collect locally and currently produced seeds. There was no relation between the species of seeds collected, and the species composition of vegetation in which ants were foraging (Fig. 2). Previous work shows that both the shape of foraging trails and the type of bait chosen in recruitment experiments vary with the density (not species) of surrounding vegetation (Fewell 1988; Crist et al. 1992). However, I know of no work providing direct evidence that harvester ants collect locally produced seeds. The present study is the first investigation of intraspecific resource use in harvester ants to employ such a large sample (15,000 seeds, 31 colonies on a 12-hectare site).

In both years of this study, ants collected seeds produced months before which were dispersed by wind or flooding. In 1991, ants foraging during July and August collected mostly seeds of *Bouteloua aristidoides,* which sets seed in September and October. In 1992, ants foraging during the summer collected mostly seeds of *Eriastrum diffusum* and *Plantago patagonica. B. aristidoides* was among the 5 most commonly collected species in 1992; *E. diffusum* and *P. patagonica* were among the 8 most commonly collected species in 1991. Yearly fluctuations in quantity of seeds produced (Price and Reichman 1987) probably led to year-to-year differences in quantities of seeds collected by ants.

Colonies differ in the seed species they collect, though this variation cannot be explained by the distribution of local vegetation (Table 2). In addition, different foraging trails of the same colony tend to yield different seed species (as in Crist and MacMahon 1991a). However, differences among trails within a colony are much weaker than differences among colonies (Fig. 3). Local variation in microtopography, especially the extent to which particular sites can trap wind-blown seeds (Reichman 1984), greatly affects patterns of seed distribution. There is enormous spatial and temporal variability in the location of seeds, and seed densities do not correlate well with plant densities (Kemp 1989; Nelson and Chew 1977). Seeds of different species, which vary in shape and size, may disperse in characteristic ways (Harper et al. 1970) leading to patches of particular species. This would lead to spatial autocorrelation in seed distribution: two nearby sites would be more likely to contain similar seed species than two more distant sites. For the seed species used by *P. barbatus,* there seem to be patches on the spatial scale of tens of meters, corresponding to distances among colony foraging areas. Further work in other seasons is needed to examine how seed collection reflects production by local vegetation.

How does the distribution of seeds influence ant foraging ecology? What seeds ants collect is an expression of both preference and availability. In studies of interspecific competition in seed-eating ants, efforts to measure either preference or availability independently have generally shown instead how the two factors interact. Seed-eating ants show species-specific preferences for seeds of a particular size or type (Bailey and Polis 1987; Chew and DeVita 1980; Fewell and Harrison 1991; Hansen 1978), but interspecific overlap in resource use depends on availability (Briese 1982; Davidson 1980; Gordon 1980; Mehlhop and Scott 1983; Rissing and Wheeler 1976; Rissing 1988). Caution is needed in interpreting results of experiments involving unusual conditions (e.g. recruitment) or unusual seeds (as Price 1983; Kelrick et al. 1986 and others have suggested). However, it seems clear that individual ants may specialize on particular seed types or species (Davidson 1978; Fewell and Harrison 1991; Rissing 1981), but that an individual ant's preferences may also be affected by availability (Crist and MacMahon 1991a).

Some authors have suggested that trail-specific seed use is a consequence of patch fidelity on the part of individual ants (Crist and MacMahon 1991b). But individual choice cannot fully determine differences among trails in seed species collected, because there is turnover of ants on trails. An individual forager tends to use the same trail for a few days (Holldobler 1976; Crist and MacMahon 1991b; Fewell 1990; Gordon 1991). However, if there is recruitment to an abundant food source, the ant will leave its usual trail and join the recruitment trail (Gordon 1991), and ants that previously performed other tasks will switch tasks to forage (Gordon 1989a). Moreover, a colony does not use the same trails every day (Gordon 1991). Thus two factors can lead to turnover of ants on trails: first, when a trail is not in use, the foragers that habitually use that trail may use another; and second, ants may respond to natural fluctuations in food abundance as they do when recruiting to bait, by switching tasks and changing trails.

An intriguing question in behavioral ecology is how the spatial and temporal dynamics of forager allocation reflect preference, availability, and food requirements, and studies of social insects are beginning to address these problems (Seeley 1989; Gordon et al. 1992; Cartar 1992). In an optimal system, the turnover rate of foragers on a given trail, the degree to which individuals specialize on particular seeds, and turnover in the colony's use of different trails, would all be calibrated to the patchiness, in space and time, of nutritious seeds. How colonies actually operate remains to be discovered.

Variation among colonies in seed species collected may be influenced by competition between neighboring colonies. However, more crowded colonies did not obtain fewer seeds; in fact, they often obtained more. There are at least three plausible explanations. First, a more sensitive index of crowding may be required to show the effect of colonies on the foraging rates of their neighbors. Second, colonies may have achieved the ideal free distribution: more crowded colonies may persist in areas of more abundant seeds, perhaps because of variation in the numbers of wind-blown seeds that collect on the ground. Third, crowding could affect the nutritive value, rather than the numbers, of seeds collected. Further work is needed to to determine how spacing patterns of nests affect resource use.

Temporal patterns of seed collection suggest how preference and availability may interact in intraspecific competition. As the proportion of *Bouteloua aristidoides* collected declined from week 1 to week 4 of the 1991 study, a greater diversity of species was taken. It may be that *B. aristidoides* was the most abundant seed available in the early summer of 1991 (as in Mehlhop and Scott 1983), but its depletion by *P. barbatus* forced conspecific colonies gradually to accept a more diverse array of species. These results parallel previous studies of interspecific competition (e.g. Whitford 1978). Such patterns would be subject to yearly fluctuations in seed production. I found no temporal patterns in seeds collected in the second year of this study.

The results presented here suggest that colonies partition space in which to search for seeds, and that the value of a foraging area does not depend on the seed-producing vegetation it contains. Each summer's burst of overt conflict may be elicited by the elimination by flooding of chemical cues that mark established trails or foraging areas. In deserts, most seeds in soil seed banks tend to be within 2 cm of the surface, where they are exposed by rain (Kemp 1989). Another stimulus to conflict may be that rain uncovers seeds previously buried in the upper layer of soil, causing a sudden increase in food abundance, and flooding may leave behind concentrated small patches of seeds. Whatever the proximate cause of conflict between neighboring colonies, the results of this study eliminate one hypothesis about what is at stake in such conflict. Colonies are not fighting over currently productive patches of vegetation.

The quality of a foraging area at one time, and a colony's tendency to fight over it later on, could be linked in this way: food abundance could be correlated with colony size, and colony size could be correlated with intensity of conflict. That is, more food could enable a colony to produce more workers (the development of an adult worker from an egg takes about 6 weeks), and larger colonies might have more workers available to fight with neighboring colonies. However, studies of conflict between colonies show that smaller, frowing colonies are more likely to continue a conflict with a neighbor (Gordon 1991), and more likely to retain newly-gained areas than are larger, older ones (Gordon 1992a). Thus larger colonies are less, not more, likely to engage in sustained conflict with neighbors. While more food may produce larger colonies, it appears that more food does not lead in this way to more conflict with neighbors.

During the time that colonies are fighting to partition foraging areas, resource use is not based on seeds currently produced by local vegetation. Thus the resources obtained in a foraging area do not depend on the presence of particular seed-producing plants. A particular region may be a valuable foraging area for a short time because wind-dispersed seeds have recently accumulated there. Whether a seed accumulates in a particular place depends on seed shape, the directions of wind and flooding, and the details of microtopography. Seed production varies greatly from year to year, so seeds of the same shape are not likely to be abundant in successive years. For these reasons, it seems unlikely that the same site would yield abundant patches of the same seeds over the 15–20 year lifespan of a colony. However, this remains to be tested.

Like a spider's web, a colony's foraging range changes in location and form. Colonies compete to partition space in which to search for seeds dispersed by wind and rain. Theoretical work shows that when resources are patchy and ephemeral, territorial behavior may be concerned with establishing a searching area, rather than defending local resources (Covich 1976; Carpenter 1987; Schoener 1983). The results here suggest this is how we should interpret neighbor interactions in seed-eating ants.

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