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Harvester ant response to spatial and temporal heterogeneity in seed availability: pattern in the process of granivory

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Abstract The influence of temporal and spatial heterogeneity in seed availability on the foraging behaviour of the harvester ant *Messor arenarius* was studied in an arid shrubland in the Negev Desert, Israel. The study investigated the implications of behavioural responses to heterogeneity in seed availability for the seed predation process and the potential for feedback effects on vegetation. Vegetation and seed rain were monitored across two landscape patch types (shrub patches and inter-shrub patches) in 1997. Shrub patches were shown to have higher plant and seed-rain density than inter-shrub patches. Patch use and seed selection by *M. arenarius* foragers were monitored through the spring, summer and autumn of 1997. After a pulse of seed production in the spring, the ants exhibited very narrow diet breadth, specialising on a single annual grass species, *Stipa capensis*. At this time, ants were foraging and collecting seeds mainly from inter-shrub patches. In the summer, diet breadth broadened and use of shrub patches increased, although the rate of seed collection per unit area was approximately equal in the two patch types. The increase in the use of shrub patches was due to colony-level selection of foraging areas with relatively high shrub cover and an increase in the use of shrub patches by individual foragers. In the autumn, a pulse of seed production by the shrub species *Atractylis serratuloides* and *Noaea mucronata* led to a reduction in diet breadth as foragers specialised on these species. During this period, foragers exhibited a large increase in the proportion of time spent in shrub patches and in the proportion of food items collected from shrub patches. The seasonal patterns in foraging behaviour showed linked changes in seed selection and patch use resulting in important differences in the seed predation process between the two landscape patch types. For much of the study period, there was higher seed predation pressure on the inter-shrub patches, which were of relatively low productivity compared with the shrub patches. This suggests that the seed predation process may help maintain the spatial heterogeneity in the density of ephemeral plants in the landscape.

Keywords Animal-landscape interactions · Israel · Negev Desert · Seed predation

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Introduction

Ecosystems are not homogeneous; materials and organisms are distributed heterogeneously in space and time. Spatial and temporal patterns in resource availability propagate through ecosystems in accordance with the distributions of constituent organisms and processes. The way in which patterns are propagated and modified through ecosystems depends on how organisms respond to spatial and temporal heterogeneity. Thus, the investigation of how organisms respond to pattern in the environment, and how this translates into patterns in ecological processes, is vital to our understanding of ecosystem dynamics (Wiens et al. 1993). While landscapes are often perceived and studied at the scale of kilometers, our understanding of animal-landscape interactions and the implications for ecosystem dynamics can be facilitated by the use of experimental model systems in which organisms operate over smaller and replicable spatial scales (Wiens et al. 1993). We employ harvester ants in an arid shrubland as one such model system.

In arid environments, primary production tends to occur in pulses in response to seasonal patterns in rainfall

(Noy-Meir 1973), and is spatially variable since water is often redistributed unevenly within the landscape (Yair and Danin 1980; Yair and Shachak 1982; Tongway and Ludwig 1994; Shachak and Pickett 1997; Aguiar and Sala 1999). These conditions force primary consumers to track primary production in space, to restrict their activity to periods when primary production occurs, or to specialise on long-lived resources, such as seeds. Specialisation on seeds dampens the spatial and temporal heterogeneity in food availability and may, to some extent, release granivores from the need to track patterns of seed production (see Gordon 1993). However, total seed availability and the composition of the available seed pool varies in space and time, reflecting patterns of primary production. Since the foraging behaviour of granivores is sensitive to the relative densities of seed species (Davidson 1982; Mehlhop and Scott 1983; Hobbs 1985; Crist and MacMahon 1992; Kunin 1994), spatial and temporal patterns in primary production are likely to impose spatial and temporal pattern on the process of granivory.

Granivores have been shown to have controlling effects on the structure of plant communities in deserts (Brown et al. 1979; Reichman 1979; Rissing 1986; Samson et al. 1992; Davidson 1993). The marked heterogeneity of vegetation in arid areas, and the influence of granivory on vegetation, make arid lands ideal systems in which to study consumer response to heterogeneity in primary production and feedback effects on heterogeneity. This study was undertaken in an arid shrubland of the Negev Desert in Israel, with the harvester ant, *Messor arenarius*, a common inhabitant of the region that feeds mainly on seeds (Steinberger et al. 1991).

The effect of seed harvesting by ants on plant communities depends primarily on seed choice and the spatial pattern of seed collection (Crist and MacMahon 1992). Spatial and temporal patterns in seed availability are likely to have a marked impact on both these characteristics of ant foraging behaviour. Thus, in an arid shrubland where seed production is spatially and temporally heterogeneous, we expect patterns in seed collection to occur through space and time. Generally, harvester ants exhibit selectivity among seeds species (Carroll and Janzen 1973; Traniello 1989) and, consistent with the predictions of optimal foraging theory, tend to be more selective when the availability of their favoured food items is high (Davidson 1982; Mehlhop and Scott 1983; Hobbs 1985; Crist and MacMahon 1992). Therefore, where seed production is pulsed (a seasonal pattern in seed availability) we expect ants to display relatively higher levels of specialisation during and shortly after pulses of seed production, and the diet breadth to increase as seed availability decreases.

Harvester ants also respond to the spatial pattern of food distribution. Colonies have been shown to concentrate their foraging effort on areas of high food availability (López et al. 1993; Crist and Haefner 1994), though in some situations space use may also be affected by inter-colony interactions (Brown and Gordon 2000). Some species have been shown to track seed production through time, switching diet and patch use in relation to the phenology of plant species (Hahn and Maschwitz 1985), or, conversely, space and seed use may not reflect current seed production, but the distribution of previously produced seeds (Gordon 1993). Responses to spatial pattern occur on two levels: in group foragers, recruitment processes result in colony level decisions over foraging area, whereas in individual foragers, individual ants select their foraging area. In practice, ants display a range of behaviours between these two extremes (Traniello 1989). However, the foraging mode employed is related to resource dispersion (Bernstein 1975) and conversely, foraging mode may strongly influence the effect of ants on their resource organisms (Rissing 1981; Fewell 1990).

Hence, in an arid shrubland we expect temporal and spatial pattern in seed availability to have a marked impact on the diets of harvester ants and their foraging patterns in space. At a particular point in time, diet breadth will be dependent on seed availability, and the spatial distribution of the preferred items will determine the spatial pattern of foraging. Since landscape-wide seed availability is temporally variable, we expect diet composition to change through time and, as the spatial distributions of the different food types are unlikely to be perfectly correlated, we expect spatial foraging patterns to shift in response to diet change. Such patterns should result in marked spatial patterns in the seed predation process, hence, in the potential for seed predation to alter plant community composition. These hypotheses were tested by monitoring, concurrently, seed availability, landscape patch use and seed collection by the harvester ant *M. arenarius* in an arid shrubland in southern Israel.

Materials and methods

The study was undertaken at Sayeret Shaked Park, an area of arid shrubland in the northern Negev Desert of Israel (31°17′N, 34°37′E). The experimental area covers approximately 7 ha and encompasses north-, south- and east-facing slopes that have been fenced to exclude grazing sheep since 1987. Precipitation at the site is restricted to the winter months (October to April) and is highly variable in time and space, with a long-term mean of *c*. 200 mm per annum. Vegetation at the site includes several small shrub species including *Noaea mucronata*, *Atractylis serratuloides* and *Thymelaea hirsuta* (Feinbrun-Dothan and Danin 1991), and a rich community of annuals and geophytes (Boeken and Shachak 1994). The soil surface of the inter-shrub spaces is consolidated by a biological crust containing cyanobacteria, algae, mosses and lichens (Zaady and Shachak 1994). No soil crust exists in the understorey of shrubs. Peak biomass of vegetation occurs towards the end of the rainy season in April, and the main period of seed production (for the majority of annual plant species) occurs in late April and May. Two of the common shrub species, *N. mucronata* and *A. serratuloides*, and a small number of annuals, e.g. *Gymnarrhena micrantha*, set seed in the late summer/early autumn.

The harvester ant *M. arenarius* is widespread at the site with a nest density of approximately 19 ha^{-1} (A. Wilby, unpublished work). This species feeds predominantly on fruits and seeds ranging in size from 1 to 100 mg, and is active throughout the year (Steinberger et al. 1992). Hereafter, the term “seed” is used loosely to describe the fruits and seeds dispersed as propagules by the plant species at the site. Colonies of *M. arenarius* comprise up to 5000 ants (Steinberger et al. 1992) which usually forage in groups. Cleared trails are often used by foragers to travel between the nest entrance and foraging areas.

Pattern in vegetation and seed rain

In common with many arid shrublands (Klemmedson and Barth 1975; Garner and Steinberger 1988), vegetation at Sayeret Shaked tends to be more productive in the understorey of shrubs than in open areas. Therefore, we describe the landscape at Sayeret Shaked as comprising a matrix of crusted soil in the inter-shrub spaces (inter-shrub patches) and areas of loose soil under the shrub canopy (shrub patches). Our sampling of vegetation and seed rain was designed to quantify and characterise differences in plant species composition and density between the two patch types, and how these differences are translated into differences in the seed rain. The transition from crusted soil to loose soil was employed to demarcate shrub and inter-shrub patches throughout the study.

In early 1997, vegetation sampling plots were established, each of which included a shrub patch and an inter-shrub patch up-slope of the shrub. A 40 cm×40 cm quadrat was placed in each patch type within each plot. Four blocks, each containing eight plots, were positioned in different areas of the watershed in which there was a locally high density of *M. arenarius* colonies. In April 1997, approximately the period of peak biomass, every individual herbaceous plant in each quadrat was identified and recorded.

In each of the areas established for vegetation recording, six extra shrubs were selected. A seed trap was placed in the understorey of each shrub, and a second was placed in an adjoining inter-shrub area. For consistency, each inter-shrub trap was placed approximately 30 cm up-slope of the shrub. The up-slope positioning of the traps is unlikely to have introduced bias into the data as further shrub patches usually occurred at a similar distance up-slope of the inter-shrub trap. Each trap consisted of a petri dish lid (90 mm diameter, *c.* 5 mm depth), which was sunk into the ground so that the rim was level with the soil surface. A PVC disc (90 mm diameter) was coated in a sticky substance, Rimiput (Yavnim Yafeh Ltd., Tel Aviv, Israel) on the upper surface and placed in the sunken dish lid. Since the traps were set level with the soil surface, they collected seeds in the process of primary and secondary dispersal, and therefore, they measured fresh seed input at the soil surface resulting from primary and secondary dispersal. The traps were originally set in early May 1997, at the beginning of the main period of seed dispersal. Seed rain was monitored using these traps until early August 1997. Since dust accumulated on the sticky traps, reducing their efficiency, the discs were collected and replaced at 4-week intervals. All seeds embedded in the sticky surface layer of the collected disc were identified and recorded.

Foraging observations

Patch choice and seed selection by *M. arenarius* were monitored to enable comparison of ant behaviour with the vegetation and seed rain data. Four colonies of *M. arenarius* were selected for study; each was selected at random from one of four areas of the watershed that roughly corresponded to the four areas identified for the vegetation recording. These colonies were used to monitor the composition of the diet and use of shrub and inter-shrub patches by foragers. At monthly intervals, from May to December 1997, samples were taken of the food items collected by foragers from each of the selected colonies. Returning foragers were intercepted as they approached the nest entrance. If they were observed to be carrying a food item, they were dispossessed before being released. Food items were retained until 50 items had been collected (preliminary studies during periods of low activity suggested that this was approximately the maximum number collectable per colony in a single foraging period). This process was repeated for each colony, during two foraging periods (two separate days), in each month.

The same four colonies were used for observations of patch use to allow direct comparison of patch use with seed collection. Individual foragers were tracked from the moment they left the nest mound to the moment they located a food item. During these foraging events, the cumulative time spent in shrub patches and in inter-shrub patches was recorded. If the foragers used a foraging trail, the time spent on the trail (not active foraging time) was discounted, as was the handling time between encounter of the food item and the return journey. Although time spent in the two patch types does not allow assessment of patch preference by foragers (as the patches differ structurally, imposing different constraints on ant movement), it does allow assessment of seasonal changes in relative preference for the two patch types through time, since the structural characteristics do not change in the short term.

As well as the time-based measure of relative patch use, the patch type from which each forager collected a food item was also recorded. This allowed calculation and analysis of a binary, collection-based index of patch-use by the foragers, in addition to the time-based index described above.

For each foraging trip, shrub cover was measured in order to give a local measure of patch cover for comparison with the patch-use data of individual foragers. This was done by measuring shrub and inter-shrub cover along a line transect between the point where foraging began (the nest entrance or the point where the ant left the foraging trail) and the point where the food item was found. Approximately ten foraging trips were recorded in the above manner for each colony, in each of the periods: May–June 1997 (henceforth, spring), July–August 1997 (summer) and October–November 1997 (autumn).

In order to give a measure of patch cover in the vicinity of each nest, which was independent of the foraging routes of the ants, the percentage cover of shrub under-storey was measured in the vicinity of each observation nest. Eight 9-m transects were taken from the edge of each nest mound along the main compass bearings. Along each transect, percentage cover of shrub patches was recorded.

Analysis

All analyses employed generalized linear models (GLIM 3.77, Royal Statistical Society, London). Hypothesis testing was done by removal of terms from the maximal model (Crawley 1993, p. 195); i.e. terms were reintroduced to the model before deletion of the next term. All models were checked for mis-specification (that they conformed to the assumptions about the distribution of errors) by inspection of residual plots (Crawley 1993, p. 13).

The monthly collections of seed dishes were summed to give the total seed number of each species and total number of species collected in each dish during the monitoring period. These variables and the vegetation data (total plant density and total number of plant species) were analysed with patch type as a split-plot factor within plot (each shrub and inter-shrub pair). All of the vegetation and seed-rain data met the assumptions of ANOVA and were therefore analysed using a normal error structure and identity link function (directly analogous to ANOVA).

The seed collection data were converted to proportions of the total number of items collected from each colony within each sample period. Time-based patch-use data (percentage of foraging time spent in shrub patches) were arc-sin transformed prior to analysis. Collection-based patch-use data (patch types from which food items were collected) were analysed as a binary response variable with binomial error structure and a logit link function. This test employs maximum likelihood methods to estimate parameters; therefore, deviance portions associated with model terms are tested against the χ^2 distribution (Crawley 1993). In each of these patch-use analyses, local percentage shrub cover of each foraging trip was included as a covariate. This allowed separation of the effect of the areas foraged (a colony-level decision in group-foraging species) and patch-use by individual foragers. For example, a significant effect on patch-use after inclusion of local shrub cover would suggest that there was an effect of individual

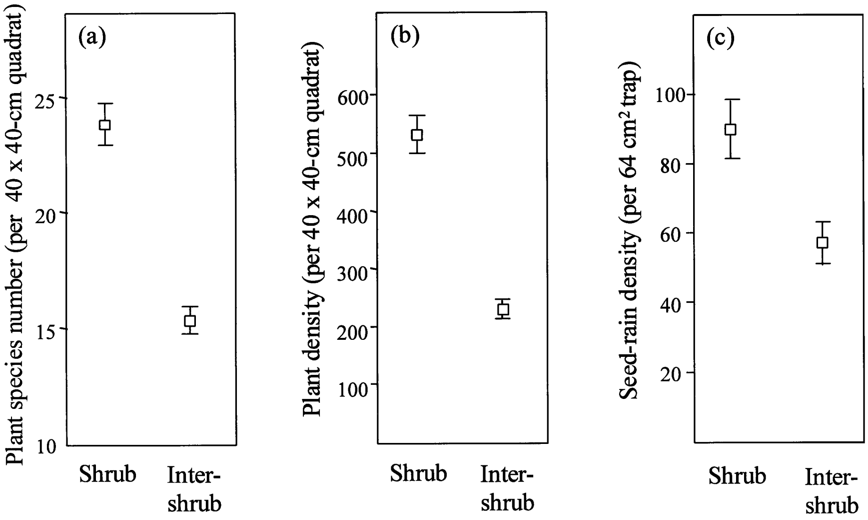

Fig. 1 Differences in **a** plant species richness, **b** plant density, and **c** seed-rain density between shrub patches and inter-shrub patches. *Bars* denote SEMs

patch choice beyond that imposed on individuals by the colony's choice of foraging area.

Results

Vegetation and seed rain

Significantly more species of herbaceous plant occurred in the shrub patches than in the inter-shrub patches ($F_{1,28}=87.4$; $P<0.001$; Fig. 1a) and a similar pattern was observed for total plant density ($F_{1,28}=79.0$; $P<0.001$; Fig. 1b). However, species composition in the shrub and inter-shrub patches was very similar; across the experiment as a whole, 71 species were recorded in the shrub patches as opposed to 59 in the inter-shrub patches. Of the 59 species recorded in the inter-shrub patches, all but one were also recorded under the shrubs. Thus, 13 species were recorded only in the shrub patches. Most of the annual plant species occurred at higher density in the shrub patches than the inter-shrub patches (Fig. 2a). The most commonly recorded species (*Stipa capensis*) showed the opposite trend, with higher plant density in the inter-shrub patches, as did the less common species *Onobrychis crista-galli* and *Leontodon laciniatus*.

During the seed-trapping period, significantly more seeds were trapped in the shrub patches compared with the inter-shrub patches ($F_{1,20}=14.1$; $P=0.001$; Fig. 1c). The distribution of seed rain reflected the distribution of plants as most of the common seed species were trapped at higher density in the shrub patches compared with the inter-shrub patches (Fig. 2b). The distribution of the seed rain was less heterogeneous than that of the plants, probably reflecting net dispersal of seeds out of the shrub patches and into the inter-shrub patches. Of the common species, *S. capensis* exhibited significantly higher seed rain density in the inter-shrub patches compared with the shrub patches ($F_{1,12}=7.48$; $P=0.018$), whereas seed rain of the other common species (*Bromus fasciculatus*, *Avena barbata* and *Rostraria cristata*) was more dense in the shrub patches (Fig. 2b).

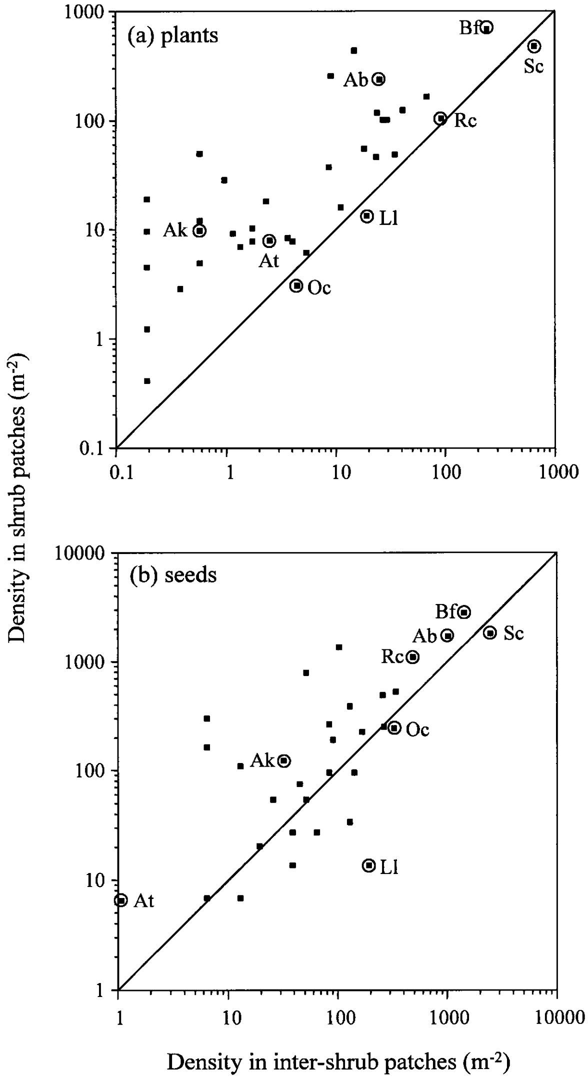

Fig. 2 Comparisons of **a** plant and **b** seed-rain density between inter-shrub (*x*-axis) and shrub patches (*y*-axis). Each *point* represents the mean of 32 plots for an individual species. Notable species are labelled: *Ab Avena barbata, Ak Aegilops kotschyi, At Astragalus tribuloides, Bf Bromus fasciculatus, Ll Leontodon laciniatus, Oc Onobrychis crista-galli, Rc Rostraria cristata, Sc Stipa capensis*

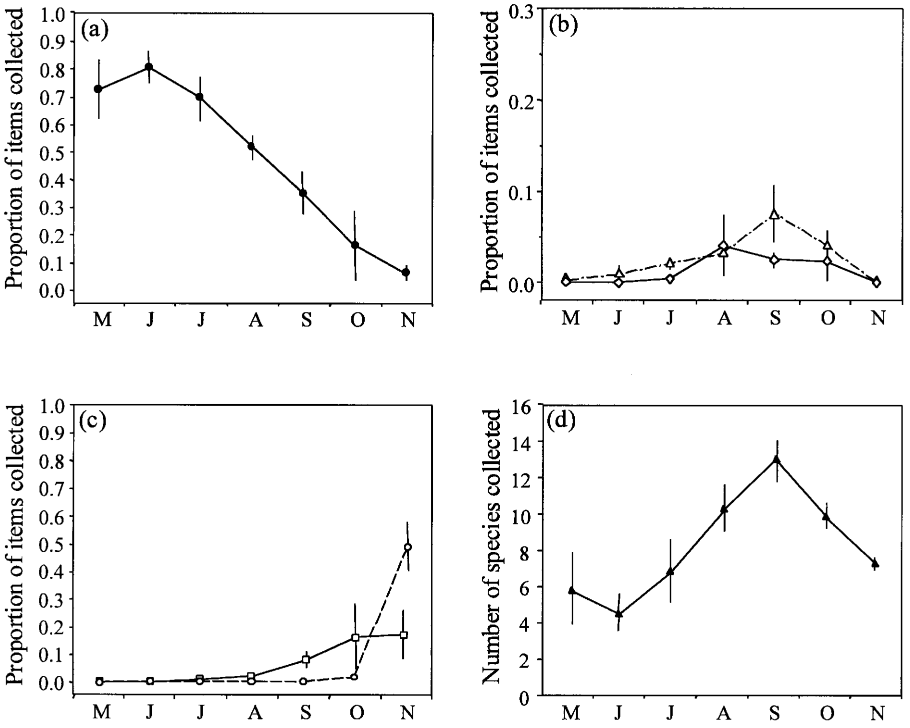

Fig. 3a–d Collection of seed species through the period May–November 1997. *Points* denote the mean proportion of all items collected across the four study colonies. Plots are grouped to show different trends: **a** *Stipa capensis*, favoured in the spring, **b** *Astragalus tribuloides* (*diamonds*) and *Aegilops kotschyi* (*triangles*), collected mainly in the summer, **c** *Atractylis serratuloides* (*squares*) and *Noaea mucronata* (*circles*), collected mainly in the autumn. **d** Diet breadth is represented as the mean number of species collected per 100 food items among the four study colonies. All *bars* denote SEMs

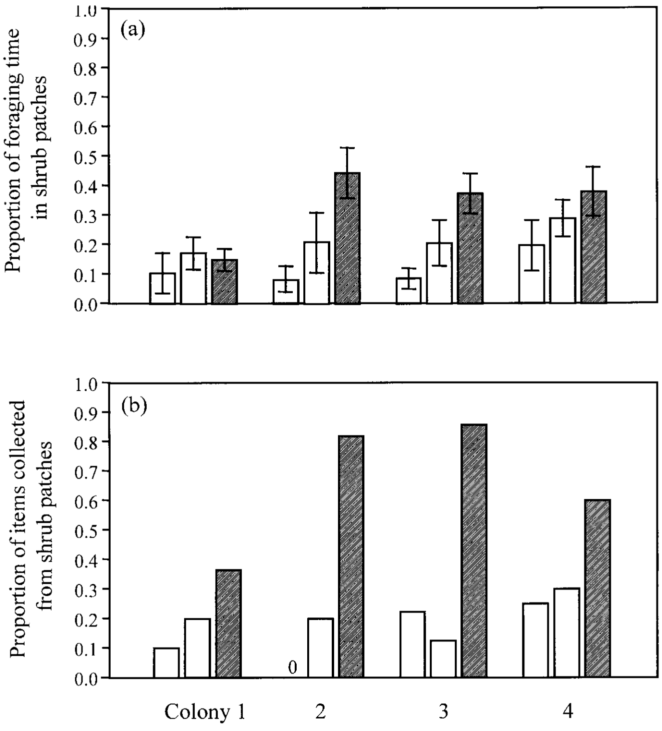

Fig. 4 **a** Time-based, and **b** collection-based, indices of patch use by *Messor arenarius* foragers of the four study colonies during the three study periods, spring (*open bars*), summer (*shaded bars*) and autumn (*hatched bars*). *Bars* denote SEMs

The relative availability of seed species in the landscape as a whole is the appropriate measure with which to compare seed selection by ants. Relative seed availability was estimated by weighting seed rain data from the shrub and inter-shrub patches by the proportional cover of the patch types in the landscape, as measured in the assessment of shrub patch cover around the ant colonies. The most common seeds were those of the annual grasses, just six species contributing more than 70% of the seed rain. The two most common species were *S. capensis* and *B. fasciculatus* which contributed 24.4% and 18.5% of the seed rain, respectively, followed by *A. barbata* (12.5%), *B. alopecurus* (5.9%), *R. cristata* (5.8%) and *B. rubens* (2.2%).

Seed collection

During the study, the ant colonies exhibited marked changes in diet composition and diet breadth. In the spring, 70–80% of the items collected were *S. capensis* seeds, but as the summer progressed, the proportion of *S. capensis* in the diet steadily declined to almost zero by the autumn (Fig. 3a). Concurrent with this decline in collection of *S. capensis* was an increase in diet breadth (species number collected, per 100 seeds, per month, per nest), which reached a peak in late summer (Fig. 3d). The rates of collection of several species, including *Aegilops kotschyi* and *Astragalus tribuloides*, increased markedly during the summer period of increasing diet breadth (Fig. 3b). Diet breadth was then observed to decline through the autumn (Fig. 3d). During this decline phase, two late-summer flowering shrub species, *N. mucronata* and *A. serratuloides*, became substantial components of the diet. Together, seeds of these shrubs constituted 63% of the items collected in November (Fig. 4c).

Table 1 Analysis of variance of the time-based index of patch use (percentage of foraging time spent in shrub patches, arc-sin transformed) with and without the inclusion of local shrub patch cover as a covariate

Source	Without shrub cover as covariate				With shrub cover as covariate			
	df	SS	*F*	*P*	*df*	SS	*F*	*P*
Season (S)	2	1.266	6.734	0.029	2	0.732	4.692	0.059
Colony (C)	3	1.100	3.904	0.073	3	0.780	3.333	0.097
S×C (error for S and C)	6	0.564	1.424	0.215	6	0.467	1.258	0.286
Local shrub cover	–	–	–	–	1	0.479	7.726	0.007
Residual	86	5.667			85	5.285		

Table 2 Analysis of deviance of the collection-based index of patch use (patch types from which seeds were collected) using a logit link function and binomial error structure. Analyses are presented with and without local shrub patch cover as a covariate

Source	Without shrub cover as covariate			With shrub cover as covariate		
	df	Deviance (χ^2)	*P*	*df*	Deviance (χ^2)	*P*
Season (S)	2	22.15	<0.001	2	16.33	<0.001
Colony (C)	3	4.10	>0.05	3	3.01	>0.05
S×C (error for S and C)	6	7.85	>0.05	6	5.79	>0.05
Local shrub cover	–	–	–	1	12.93	<0.001
Residual	86	91.11		85	87.15	

Patch use

Patch use by *M. arenarius* also varied considerably during the study period. Individual foraging trips lasted between 2 and 56 minutes, and seeds were collected from between 1.3 and 23.6 m from the nest entrance. Shrub cover in the vicinity of the nests did not differ significantly among the study colonies. Overall mean shrub cover was 20.2%±0.9 (SEM) of the surface area. The colonies did not differ significantly in the proportion of foraging time spent in shrub patches (Table 1). However, there was significant variation among seasons in the proportion of time spent in the shrub patches. As the study progressed from spring to autumn, ants tended to spend more foraging time in the shrub patches (Fig. 4a). When the local shrub patch cover of each foraging trip was included as a covariate in the analysis, the effect of season became marginally significant (Table 1). Local shrub patch cover itself was a highly significant explanatory variable of the percentage of foraging time spent in shrub patches (Table 1). The influence of local shrub patch cover on the percentage of time spent by foragers in shrub patches was also tested for each tracking period individually. In spring ($F_{1,24}$=5.03, P=0.034) and autumn ($F_{1,32}$=10.89, P=0.002), there was a significant effect of local patch cover, whereas the effect was insignificant in summer ($F_{1,27}$=0.01, P=0.02).

The collection-based patch use data are more indicative of the impact of the ants on the seed assemblage. These data showed the same pattern as the time-based measure of patch use (Fig. 4b, Table 2). That is, as the season progressed, an increasing proportion of food items was collected from the shrub patches, rather than the inter-shrub patches. The effect of season remained highly significant when local shrub patch cover was included in the analysis as a covariate. Across all the colonies, only 0.14±0.06 (SEM) of food items were collected from the shrub patches in the spring, and this rose to 0.21±0.04 (SEM) in the summer and 0.66±0.11 (SEM) in the autumn.

Discussion

Our data revealed a patchy distribution of herbaceous plants that is commonly found in arid shrublands (Klemmedson and Barth 1975; Garner and Steinberger 1988). Plant density in the shrub patches was more than twice that of the inter-shrub patches. Although plant size was not measured in this study, previous studies in this system have shown that total biomass of herbaceous plants in shrub patches can be up to four-fold that of similar areas of inter-shrub patch (A. Wilby, unpublished work). The marked spatial heterogeneity in the distribution of the herbaceous plant community was reflected in a heterogeneous distribution of the seed rain. The shrub patches and inter-shrub patches received seed rain with a very similar species composition, but there were marked differences in total seed density and in the relative densities of the constituent species, and this affected the foraging behaviour of *M. arenarius*.

In the spring, foragers were strongly selective for seeds of the annual grass, *S. capensis*. This species contributed only 24% to the seed rain in the landscape as a whole, yet constituted 70–80% of the diet during the spring period. By contrast, the second most common seed species, *B. fasciculatus*, which is also an annual grass and is of similar size to *S. capensis*, was never recorded in the collections of the four colonies.

As well as differentiating among seed species, foragers exhibited spatial pattern in their foraging behaviour. During the spring period, ants foraged more in the inter-shrub patches than the shrub patches, despite higher total seed rain density in the shrub patches. The relative rates of collection from the two patch types (86:14, inter-shrub:shrub) showed a bias towards inter-shrub patches that was larger than the bias in their relative cover in the landscape (80:20, inter-shrub:shrub), indicating a slight patch bias towards inter-shrub patches as seed sources. By weighting the collection figures by the relative cover of the two patch types, we arrive at a harvest rate ratio of approximately 3:2; that is, for every three seeds collected from an inter-shrub area, 2 seeds were collected from a shrub area of equal size. These data are consistent with other studies, which failed to show a preference for resource-rich shrub patches by harvester ants (Abramsky 1983; Crist and MacMahon 1991; Crist and Weins 1994). This apparent discrepancy is probably explained by the seed preferences of the ants. The favoured seed species, *S. capensis* was significantly more dense in the inter-shrub patches, not the shrub patches. Very similar time-based and collection-based patch-use estimates reveal that acceptable seeds were encountered at approximately equal rates in the two patch types. Thus, a combination of food selectivity and differences in structure between the two patch types seem to have negated the effect of higher seed density in the shrub patches.

The initial patterns of seed preference and patch use were not consistent through the study period. During the summer, the proportion of *S. capensis* in the diet diminished, presumably reflecting depletion of this species. As predicted by optimal foraging theory (Charnov 1976; Schoener 1979), the diet breadth increased as the availability of the preferred species declined. As the ants became more generalist in their diet choice, we observed a change in patch-use behaviour, with an increase in the proportion of foraging time spent in the shrub patches. The representation in the diet of several species (e.g., *A. kotschyi* and *A. barbata*) increased markedly in the mid-summer period and these species occurred at higher density in the shrub patches than the inter-shrub patches. Again, this suggests that seed preferences were a major factor governing patch choice.

Although the use of shrub patches increased in the summer period, relative to the spring, the proportion of seeds collected from the shrub patches was approximately equal to the proportion of shrub-patch cover in the landscape; i.e. the harvest rate ratio, standardised for area, was approximately 1:1 during the summer recording period. Hence, although the diet was relatively broad during the summer, and shrub patches were being used to a greater extent, there was no absolute bias towards shrub patches. As in the spring, time-based and collection based indices of patch use were approximately equal, indicating that the rate of encounter of acceptable seeds was approximately equal in the two patch types.

At the end of the summer, further changes in patch use and diet were observed. There was a reduction in diet breadth as seeds of the shrubs *Atractylis serratuloides* and *N. mucronata* became major constituents of the diet, and the increased rate of collection of shrub seeds was paralleled by an increased use of shrub patches during foraging. The bias towards shrub patches as measured by seed collection was much stronger than that measured by time allocation. In contrast to the spring and summer periods, it is clear that acceptable seeds were encountered at a higher rate in the shrub patches than in the inter-shrub patches. Presumably, this resulted from marked differences in seed availability between the two patch types during the autumn pulse of seed production by the shrubs themselves.

The general increase in the use of shrub patches through the season may have resulted from two separate effects, reflecting different levels of control and operating at different spatial scales. A group foraging effect, involving colony-level decisions about the directions of foraging trails and the foraging area, would likely result in spatial patterns of foraging at larger scales than our recognised scale of shrub and inter-shrub patches. There is evidence from North American harvester ants that such colony-level decisions over foraging area are made by a distinct group of workers which patrol the foraging area of the colony before each foraging period and make decisions about the direction of the foraging column (Gordon 1991). A significant positive relationship between shrub patch use and local shrub patch cover indicates that there was a colony level effect; colonies selected to forage in areas with higher shrub cover as the season progressed. However, this effect was insufficient to explain all the increase in shrub patch use, particularly as measured by the collection-based index of patch use. This suggests that individual ants were also increasing their use of shrub patches within the constraints of the colony foraging areas, i.e. at the scale of shrub and inter-shrub patches. It has been argued that individual foraging is an adaptive behaviour in situations where resources are at low density and well distributed, as opposed to group foraging which is adaptive where resources are at high density or highly clumped (Davidson 1977; Traniello 1989). Our data support this hypothesis and show that the relative importance of colony versus individual control can change within a colony as resource availability changes. The analyses show that local shrub cover was an insignificant covariate of shrub use in the summer when seed density was at its lowest, indicating increased importance of individual foraging decisions relative to colony choice of foraging area. The converse occurred during the spring and autumn periods of relatively high seed availability.

Since patch use changed concurrently with seed use, seed predation may have feedback effects on the spatial structure of vegetation. During the spring, inter-shrub patches were submitted to much higher rates of seed predation than shrub patches in terms of the proportion of the total surface seed pool harvested. During the summer months, when diet breadth was maximal, harvest rates were approximately equal in the two patch types, again suggesting a greater impact of seed predation on inter-shrub patches, where seed-rain density was lower. In the autumn, foraging became strongly biased towards shrub patches, but most of the seeds collected were those of the shrubs. Thus, the evidence from the spring, summer and autumn suggests that there was probably relatively little impact on the surface seed pool of herbaceous species in the understorey of shrubs compared with those in the inter-shrub patches. Seed predation may, therefore, have a greater influence on the composition of ephemeral vegetation in inter-shrub patches than in shrub patches. Potentially, these effects could be redressed during the remainder of the winter for which we do not have data. However, we consider this unlikely, as foraging activity is relatively low outside the periods of seed production (Steinberger et al. 1992). Currently, experiments are in progress to investigate whether the observed patterns in seed predation have any effect on plant community structure.

Our study highlights how pattern in resource distribution can influence distribution of ecosystem processes via modification of animal behaviour. In this case, interactions between seed preferences and seed availability resulted in variation in the characteristics of the seed predation process in different seasons, and in different patch types in the landscape. This result emphasises the importance of studying organisms and ecological processes at appropriate spatial and temporal scales (Goodwin and Fahrig 1998). In the present study, it was shown that *M. arenarius* used shrub seeds in the autumn, when the seeds of most ephemeral plants were depleted. The pulse of shrub seeds may be a vital resource input that would not have been identified if studies focussed on the main activity period in the spring and early summer.

A second implication of our study concerns the role of feedbacks between landscape structure and ecological processes. If ecological processes involving heterogeneously distributed organisms or resources vary qualitatively between landscape patch types, then some modification of the pattern of heterogeneity will occur. Taking our case study as an example, if seed predation rates were higher in areas of high seed density then seed predation would be a homogenising force tending to equalise seed density across patch types in the landscape. However, we found that the opposite was true, seed predation rates being higher in the less productive patches. The seed predation process may therefore play a role in the maintenance or extenuation of shrub:inter-shrub patchiness in the landscape.

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