Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands

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The scavenging of arthropod carrion by ants can be an important mechanism of nutrient redistribution in grasslands. By removing materials to nests over different sized areas, scavenging ants may contribute to differences in ecosystem patchiness. We asked how variation in overall ant foraging activity among three desert/grassland Long-Term Ecological Research sites creates differences in the distances that scavenged material is laterally redistributed. Generally, species with large-bodied workers and thermophilic species removed baits the farthest. Overall, this resulted in a positive relationship between removal distance and vapor pressure deficit. Mean removal distance across all ants increased from the shortgrass steppe to the Chihuahuan desert grassland, creating a seven-fold variation in the spatial scale of nutrient concentration by ants. The dominant species creating this pattern are inconspicuous and little-known when compared to the harvester ants that have been emphasized in ecosystem studies.

Introduction

Ants and termites are colonial, nesting insects, and the activity of tens to thousands of individuals concentrates on both materials and other changes around nest sites. Consequently, ants and termites can have important influences on ecosystem structure. For example, it has been shown that termite activity is the primary determinant of variation in soil organic matter status in many arid and semi-arid environments (Nash & Whitford, 1995). Although less well documented, ants may also have important effects on environmental heterogeneity by altering soil nutrient properties near nests (Whitford & DiMarco, 1995; Dean *et al.*, 1997; Wagner *et al.*, 1997). In particular, harvester ants (*Pogonomyrmex* spp.) have figured prominently in

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such studies due to their large nests and their habit of redistributing and consuming seeds (Kaspari, 1993a; Crist & Wiens, 1994; Andersen & Morrison, 1998) and creating patchiness in vegetation (Coffin & Lauenroth, 1991).

Most ant species, however, are scavengers (Carroll & Janzen, 1973) and the redistribution of material by these ants may have profound influences on soil nutrient levels (Petal et al., 1992; Laakso & Setälä, 1998). Scavenging ants are active throughout the day and night and may consume as much as 59–100% of dead arthropod material from the ground (Jeanne, 1979; Fellers & Fellers, 1982, Retana et al., 1991). Ants consume vertebrate carrion as well (Clark & Blom, 1991). Animal carrion is rich in nutrients such as nitrogen and phosphorus, which are often limiting to plants in arid and semi-arid zones (Noy-Meir, 1985; Schlesinger et al., 1990; Burke et al., 1997). Depending upon the duration that individual nests are inhabited by ants (Smallwood, 1982), these nutrients may accumulate in nest mounds in the form of waste products and result in locally increased plant growth (Gentry & Stiritz, 1972; Wagner, 1997).

Despite the potentially important roles that scavenging ants play in North American semi-arid and arid habitats (MacKay, 1991), no studies have yet examined how differences in species foraging behavior may mediate the impacts of ant communities on nutrient redistribution patterns. Similar work on granivorous ants suggests that patterns of material removal vary strongly among species (Hughes & Westoby, 1992; Gorb & Gorb, 1999). Both body size and microclimate use may determine these differences. Larger ant species may remove items over larger distances, on average, because they are able to move more directly and rapidly in a given environment (Kaspari & Weiser, 1999). Variation in microclimate determines which species of ants forage successfully at different times and in different places (Cerda et al., 1997; Bestelmeyer, 2000a), and so may indirectly affect patterns of material removal. Furthermore, ants may move faster at higher temperatures (Marsh, 1985; Morehead & Feener, 1998) and, therefore, farther. Thermophilic species may possess adaptations, such as long legs, that promote rapid movement (Cerda & Retana, 2000).

We asked, can differences in the combined foraging behaviors of ant species contribute to differences in nutrient patchiness? To address this, we documented the composition and behavior of ants scavenging small arthropod carrion placed on the ground surface and the distances that this material was laterally redistributed to nests in three semi-arid grassland sites. These grasslands lie along a north–south gradient from shortgrass steppe to Chihuahuan desert grassland. These sites differ greatly in ecosystem characteristics such as plant cover, patchiness and functional group representation (Hochstrasser et al., in press), and also differ in ant composition (Bestelmeyer & Wiens, 2001a).

We examined the roles of microclimate use and body size in mediating the redistribution of scavenged material by observing the removal of small insect baits that were placed on the ground at different times of day. By focusing our attention on the fate of food items, rather than on detailed studies of the nests of individual ant species, we can efficiently evaluate the relative importance of numerous ant species in discovering and removing material. This approach is especially useful for ant species that are small and have cryptic nests that are difficult to locate and study. By placing carrion during different times of day, we can evaluate the role of microclimatic variation in determining the roles of various species. We used this approach to ask: (1) which ant species are the dominant scavengers of insect carrion at each site, (2) how do these species differ in the distances that they remove food items to their nests, and (3) are these differences related to body size and microclimate? We integrate the answers to these questions to look for some general relationships between the ant traits and redistribution patterns. Finally, we consider the combined effects of foraging by all ant species to ask if there are differences in the spatial scale of redistribution among the sites.

Materials and methods

Study areas and design

We examined ant scavenging in several areas within three grassland Long-Term Ecological Research (LTER) sites. These sites lie along a N–S latitudinal gradient along which mean annual temperature increases and mean annual precipitation decreases (see Bestelmeyer & Wiens, 2001a). The northernmost site is the Shortgrass Steppe LTER (hereafter SGS), located in the USDA-ARS Central Plains Experimental Range and Pawnee National Grasslands near Nunn, Weld County, CO, U.S.A. Mean annual precipitation (MAP) is 320 mm and mean monthly temperature (MMT) ranges from –4°C to 22°C. Vegetation is classified as shortgrass steppe, and the dominant plant cover is blue grama grass, *Bouteloua gracilis*. The middle site is the Sevilleta LTER (SEV), located in the Sevilleta National Wildlife Refuge and on an adjacent privately owned land in Socorro County, NM, U.S.A. MAP is 265 mm and MMT ranges from 2·5°C to 25°C. This site harbors a biome transition from shortgrass steppe to Chihuahuan desert grassland (Gosz, 1992). The dominant grass cover in most areas is black grama, *B. eriopoda*, which is characteristic of desert grassland. Blue grama also occurs in large areas on coarse soils, and creosotebush (*Larrea tridentata*) dominates on relatively fine or shallow soils here (Bestelmeyer, 2000b). The southern site is at the Jornada LTER (JRN), located largely in New Mexico State University's Chihuahuan Desert Rangeland Research Center and Bureau of Land Management land near Las Cruces, Doña Ana County, NM, U.S.A. MAP is 232 mm and MMT ranges from 13°C to 36°C. This site is mostly desert grassland, and creosotebush-dominated shrublands occur in areas of coarse sand and gravel.

To approximate a regional characterization, ant scavenging observations were stratified across the four most common habitat types in each site including varying grazing treatments within grassland habitats and dominant shrubland habitat types (see Bestelmeyer and Wiens, 2001b). Study areas were randomly located along road segments assigned to each habitat type. Within each study area (centered on transects discussed in Bestelmeyer and Wiens, 2001b), from 9–12 baits were placed at different times (see below) at haphazardly selected points (where a pin flag thrown up into the air fell to the ground), provided that these locations were not within 40 m of one another. Given the high degree of patchiness in plant and ant communities in this scale, each bait was treated as an independent replicate.

Scavenging observations

We used halves of freshly killed termite workers (Rhinotermitidae, Termitidae) or whole fruit flies (*Drosophila*) as baits to simulate small arthropod carrion of a size that typically occurs in these areas and that most ant species in this study could gather individually (following Fellers & Fellers, 1982; Retana *et al.*, 1991). Baits were always *ca.* 1 mm in length. Baits were observed during June–August 1997. By observing ants during the summer–wet season, we ensured that the maximum levels of ant activity at each site would be encountered. This is also likely to be the period in which the majority of scavenging occurs.

We observed 2–6 baits in each study area (28–40 baits in each site) during each of three time periods during which microclimates differed and different ant species may be active: morning or afternoon (soil-surface temperatures 20–30°C), midday (33–45°C), and night (10–25°C). Baits were dusted with chemically inert orange fluorescent powder (Radiant Color, Richmond, CA, U.S.A.) to facilitate observations during the day and at night with the use of a fluorescent lantern outfitted with an

ultraviolet bulb (General Electric Company, #F6T5). Preliminary observations suggested that the powder did not affect the response of ants to the baits. Upon bait placement, soil-surface temperature (HH-23 Digital Thermometer, type J thermocouple, Omega Engineering, Inc., Stamford, CT, U.S.A.), and relative humidity at the soil surface (RH-30C Digital Humidity Meter with RH-30-3 Humidity Sensor, Omega Engineering, Inc., Stamford, CT, U.S.A.) were recorded adjacent to baits. The observer then sat motionless on a stool watching the bait continuously until the bait was discovered and removed or until 20 min elapsed, at which point observations ceased. This time limit was selected because preliminary trials suggested that if baits were not recovered within 20 min, they would usually not be recovered within the time period, perhaps because they were away from ant foraging routes. Upon bait discovery and removal, the observer followed the focal ants to their nests. Some ants never arrived at nests with baits because the ants were disturbed or their location lost by the observer, their baits robbed by other ant species (Hölldobler, 1986), or they were preyed upon by spiders. During nocturnal trials, observers were careful not to occlude view of the sky from ants at baits because this appeared to cause disorientation in nocturnally foraging ant species (i.e. *Myrmeco-cystus navajo, Dorymyrmex* c.f. *flavus*).

Upon arrival at the destination nest, a voucher specimen was collected at the nest to confirm field identification. Focal ants that were disturbed or preyed upon were collected. Focal ants that were lost en route were identified based on field observations only, which were generally reliable at the taxonomic levels considered in this study. Upon arrival to a nest, the distance from the nest entrance to the point of bait placement was recorded. Body lengths (measured from the frons to the tip of the outstretched gaster) of voucher specimens ($n = 3–10$) were measured using a stereo microscope outfitted with an ocular micrometer.

Data analysis

Because small arthropods such as ants are sensitive to variation in both temperature and humidity, microclimate was quantified by vapor pressure deficits (VPD) that measure the drying power of the air (Kaspari, 1993b). VPDs were calculated from temperature and relative humidity using formulae given by Campbell (1977). In this study, soil-surface temperature was highly correlated with VPD.

We examined relationships among species and removal distance to nests (disturbed/lost-ant observations excluded), VPD, and body size using general linear models (Proc GENMOD, SAS Institute, Inc., 1996). Natural log-transformation of distance and VPD values were required to normalize the data for this analysis. We used quantile (i.e. least absolute deviation) regression (Blossom software; Slauson *et al.*, 1994) to examine the relationship between removal distance to nest and microclimate. In contrast to least-squares regression approaches, quantile regression may be used to investigate relationships at the limits of the distribution of two variables (Cade *et al.*, 1999). We selected the quantile regression approach because the constraints to the distances that baits were removed were of interest, given the differing magnitude of variation along the abscissas. Quantile regression using the median (50th) quantile is analogous to traditional least-squares regression but with the advantage of de-emphasizing extreme outlying data points and performing well with sparse data sets (Scharf *et al.*, 1998). In addition to the 50th regression quantile, we examined patterns at the limits of the microclimate–distance relationship using the 80th and 20th quantiles. These quantiles were chosen because more extreme quantiles would have given unreliable estimates of variance for regression coefficients given our sample sizes (see Scharf *et al.*, 1998). Statistical tests for non-zero slope were performed using Monte Carlo permutation test procedures.

Results

Scavenger species composition

Of the 123, 112, and 114 baits observed at SGS, SEV, and JRN, respectively, 70·3% (SGS), 53% (SEV), and 60·5% (JRN) were removed by ants within 20 min. Almost all of the remainder went undiscovered within this period. From 10 to 16 ant species removed these baits in each site, but the dominant scavenger removed no more than about one-third of the total baits removed in each site (Table 1). At SGS, *Myrmica emeryana*, *Formica neogagates*, *Dorymyrmex insanus*, and *F. obtusopilosa* together removed 71·4% of the removed baits. At SEV, *Pheidole* spp. (mostly *longula*), *Forelius* spp., and *D. insanus* removed 76·7% of the removed baits, and at JRN *Forelius* spp., *D. bicolor*, *D. c.f. flavus*, and *Pheidole* spp. (mostly *xerophila*) removed 73·3% of removed baits. Species occurrence at baits among habitats was very patchy, so the analysis of

Table 1. *The number of baits removed by ant groups. Groups are displayed in descending rank of the number of baits that they removed in a site*

	Number (%) of baits removed
Shortgrass steppe	
Myrmica emeryana (Cole)	29 (32)
Formica neogagates gp.	15 (17)
Dorymyrmex insanus (Buckley)	10 (11)
Formica obtusopilosa (Emery)	10 (11)
Lasius crypticus (Wilson)	5 (6)
Leptothorax sp. C1	5 (6)
Pheidole coloradensis (Emery)	5 (6)
Tapinoma sessile (Say)	4 (4)
Pogonomyrmex occidentalis (Cresson)	3 (3)
Formica obscuripes (Forel)	2 (2)
Monomorium minimum (Buckley)	2 (2)
Sevilleta	
Pheidole sp.	18 (31)
Forelius sp.	14 (24)
Dorymyrmex insanus (Buckley)	13 (22)
Aphaenogaster cockerelli (André)	8 (14)
Myrmecocystus sp.	4 (7)
Crematogaster sp.	2 (3)
Jornada	
Forelius sp.	19 (28)
Dorymyrmex bicolor (Wheeler)	15 (22)
Dorymyrmex c.f. flavus (McCook)	9 (13)
Pheidole sp.	9 (13)
Pogonomyrmex desertorum (Wheeler)	5 (7)
Myrmecocystus sp.	4 (6)
Aphaenogaster cockerelli (André)	4 (6)
Monomorium minimum (Buckley)	2 (3)
Pogonomyrmex imberbiculus (Wheeler)	1 (1)
Tetramorium spinosum (Pergande)	1 (1)

□ 0-4, ▦ 4-8, ▨ 8-12, ■ 12-16 kPa
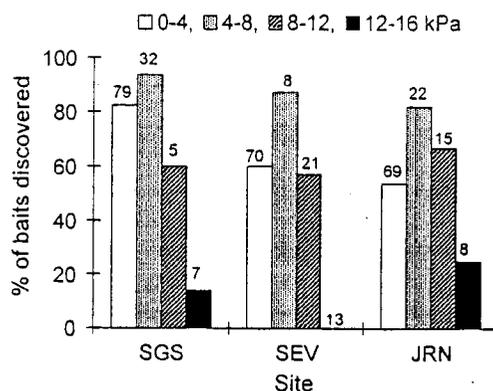
Figure 1. The percentage of baits discovered by ants in different vapor pressure deficit (VPD) classes at each LTER site. The number above bar is the number of observations in each VPD class.

habitat effects on species (analyses below) was not possible (see Bestelmeyer & Wiens, 2001*b* for ant–habitat relationships).

### Bait discovery under different microclimate conditions

Overall, baits were most often discovered by ants within 20 min of placement when VPD values were intermediate (from 4 to 8 kPa; Fig. 1). Bait discovery rates were quite low at very high VPDs (12–16 kPa). In all sites, different groups of ant species scavenged baits under different microclimatic conditions ($p < 0.0001$ for all sites; Fig. 2). At SGS, *F. obtusopilosa* removed baits at higher VPDs than did *F. neogagates*, *M. emeryana*, *Lasius crypticus*, and *D. insanus*. *Formica neogagates*, *Leptothorax* sp. C1, and *Pogonomyrmex occidentalis* foraged at intermediate VPD values. At SEV, *Forelius* spp. took baits at relatively high VPDs and *Pheidole* spp., *D. insanus*, and *Aphaenogaster cockerelli* foraged at lower VPDs. At JRN, *Forelius* spp. and *Myrmecocystus* spp. were active at high VPDs, *P. desertorum* and *D. bicolor* foraged at intermediate VPDs, and *Pheidole* spp., *D. c.f. flavus*, and *A. cockerelli* foraged at the lowest VPDs.

There was no significant relationship between the body length of species and the average VPD at which species removed baits ($F = 0.17$; df. $= 2,14$; $p = 0.69$). Inspection of Fig. 2, however, suggests that, with the exception of *Forelius*, species removing baits at high VPDs were often large.

Differences in removal distance among species

Controlling for variation in VPD, species in each site differed strongly in the distances that they removed baits to their nests (species term significant at $p < 0.01$ for all sites using Type III sums of squares; Fig. 2). At SGS, *P. occidentalis* removed baits the farthest, *F. obtusopilosa*, *F. neogagates*, *D. insanus*, and *M. emeryana* removed baits over intermediate distances, and *L. crypticus* and *Leptothorax* sp. C1 removed baits over the shortest distances. At SEV, *A. cockerelli* removed baits over the longest distances (but values were highly variable), *Forelius*, and *D. insanus* removed baits over intermediate distances and *Pheidole* sp. removed baits over the shortest distances. At JRN, *A. cockerelli* and *Myrmecocystus* sp. removed baits over the longest distances, and *P. desertorum*, *Forelius*, *D. c.f. flavus*, *Pheidole*, and *D. bicolor* removed baits over intermediate-to-short distances.

Part of the among-species differences can be attributed to differences in body length; there was a positive relationship between average worker length and the
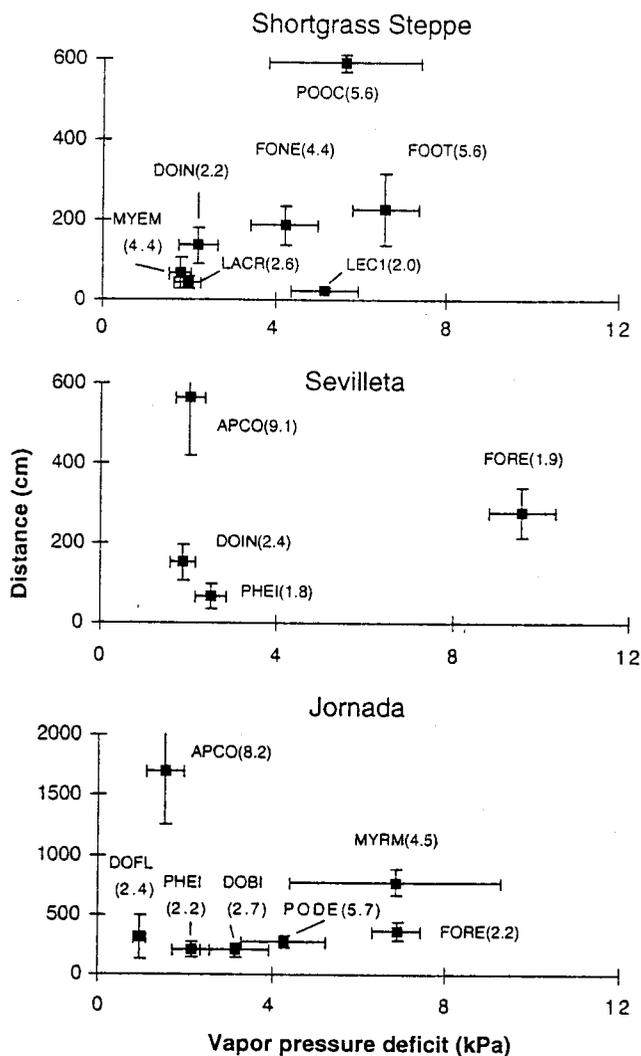
Figure 2. Means and standard errors for removal distances and vapor pressure deficits at which baits were removed for ant taxa. Body length values are given in parentheses. APCO=*Aphaenogaster cockerelli*, DOIN = *Dorymyrmex insanus*, DOFL = *D.* c.f. *flavus*, FONE = - *Formica neogagates*, FOOT = *F. obtusopilosa*, FORE = *Forelius* spp., LACR = *Lasius crypticus*, LEC1 = *Leptothorax* sp. C1, MYEM = *Myrmica emeryana*, MYRM = *Myrmecocystus* spp., PHEI = *Pheidole* spp., PODE = *Pogonomyrmex desertorum*, and POOC = *P. occidentalis*.

distance that species removed baits ($r^2 = 0·45$; $F = 13·49$; df. = 1, 14; $p = 0·003$). The large *P. occidentalis* at SGS and *A. cockerelli* at SEV and JRN removed baits over the longest distances, whereas smaller species such as *Lasius* or *Pheidole* removed baits only over short distances.

General relationships between removal distance and microclimate

Given that bait discovery by a species was microclimate dependent, and that removal distance varied among species, we asked how these effects combine to determine

overall relationships between microclimate and removal distance. The median (50th) quantile regressions all revealed significant, positive relationships between VPD and the distance baits were removed (Fig. 3). These relationships were highly variable; the coefficient of determination for SGS was 0·06, 0·20 for SEV, and 0·08 for JRN. Regressions at more extreme quantiles revealed that the relationships between VPD and the limits of removal distance differed depending upon whether the lower or upper limits were considered. At SGS, a significant positive slope was observed at the 80th quantile but not at the 20th quantile. At SEV and JRN, positive slopes were observed only at the 20th quantile. Thus, the maximum distance that baits were
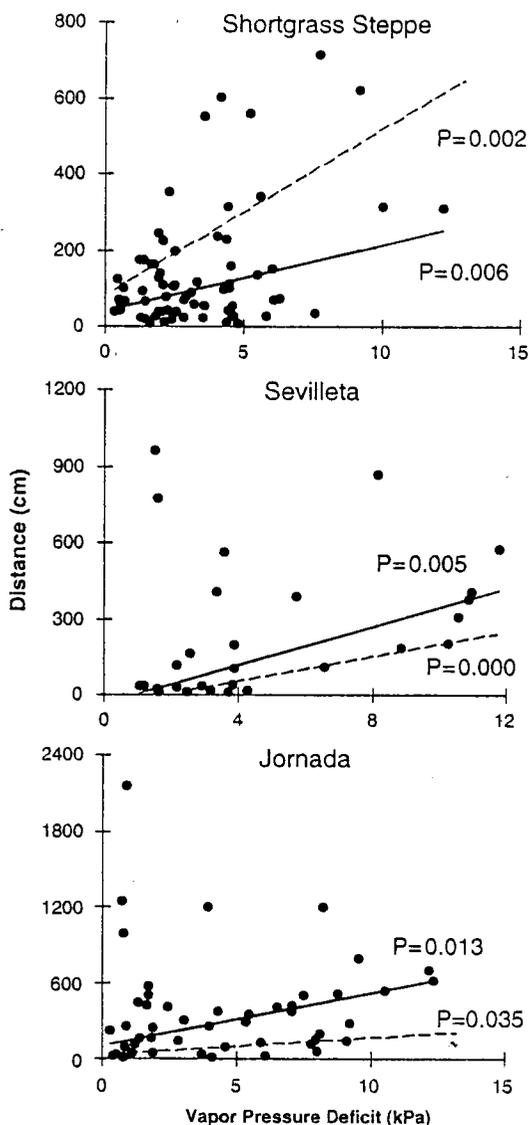
Figure 3. Quantile regressions of bait removal distance on vapor pressure deficit in each region. The solid lines are the 50th regression quantile estimates, dashed lines above the solid line are the 80th regression quantile estimates, and dashed lines below the solid line are the 20th regression quantile estimates (only estimates from statistically significant regressions are shown).
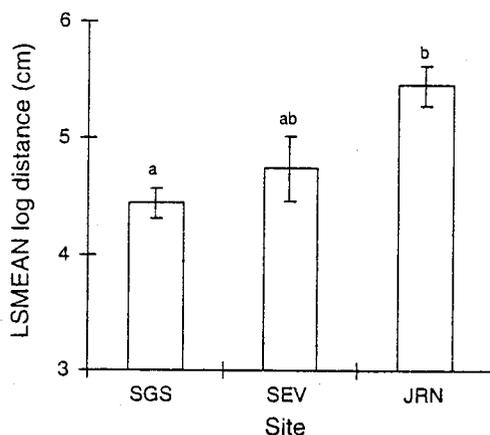
Figure 4. Least-squares estimates (+1 S.E.) of ln-transformed bait-removal distance values adjusted for habitat composition and between-site variation in vapor pressure deficit (VPD). Regions with differing letters above the bar differed significantly in *post hoc* contrasts of least-squares means (LSD).

removed increased with VPD at SGS, whereas the minimum distance baits were removed increased with VPD at SEV and JRN.

Species in each region for which there were >5 distance observations were tested individually to assess the effect of VPD on the distance moved by individuals within species. Of nine tests, only *Forelius* at SEV exhibited a significant, positive relationship at the Bonferroni-adjusted alpha level of 0·0055 ($r^2 = 0·96$; $F = 137·63$; df. = 1,6; $p = 0·0001$). Thus, VPD can affect the distance that baits are moved by affecting the composition and characteristics of species removing baits as well as by affecting the behavior of individuals of certain species.

Regional differences in removal distances across all ants

The distance baits that were removed by ants to nest sites differed among sites (controlling for habitat variation; $F = 4·05$; df. = 2, 9; $p = 0·055$). Contrasts of least-squares means (Fig. 4) revealed that mean removal distances at SGS (85 cm) were lower than at JRN (233 cm); SEV (114 cm) was intermediate. This pattern remained significant when differences in VPD during the study were controlled among regions ($F = 5·10$; df. = 2, 9; $p = 0·033$). If we assume that ants across a site concentrate materials from circular areas defined by their average foraging radius, then ants at SGS concentrate materials from an area of $2·27 m^2$, ants at SEV from $4·08 m^2$, and ants at JRN from $17·05 m^2$.

Discussion

Determinants of ant scavenging behavior

Our results show clear differences among ant species in the environmental conditions in which they scavenge and the distances that they redistribute scavenged material. Scavenging ant species partition foraging times due to differential tolerance of microclimate conditions and interference competition (Cerdá *et al.*, 1997; Bestelmeyer, 2000a). Microclimatic variation in time therefore affects species activity patterns and, consequently, the distances that material discovered at different times of

day is removed. Overall, relatively few baits were removed by ants at the highest VPDs (Fig. 1) in this study because conditions were too harsh for much activity by even thermophilic species such as *Forelius* or *F. obtusopilosa*. In contrast, Retana *et al.* (1991) found that removal rates increased at relatively high soil-surface temperatures due to increased activity by highly specialized scavenging species. At high VPDs in shortgrass steppe and desert grassland, relatively thermophilic species forage or move upon vegetation that provides cooler microclimates (Kay & Whitford, 1978), which may decrease foraging efficiency for baits located on the ground.

Species that removed baits at high VPDs tended to remove baits over longer distances than most species active at lower VPDs (Fig. 2). Consequently, we observed positive relationships between VPD and removal distances in all three regions (Fig. 3). Body size may, in some cases, mediate this relationship. Larger ant species tended to move baits farther (see also Crist *et al.*, 1992). Furthermore, Kaspari (1993*b*) found that larger ant species were generally more tolerant of higher VPDs than were smaller ones. In contrast, we did not observe an overall relationship between species body length and the VPDs at which species removed baits.

The relationship between species body length, VPD, and removal distance depends upon whether the maximum or minimum distance values are considered (Figs 2 & 3). The minimum distances (20th quantile) that baits were moved by ants increased with VPD only at SEV and JRN, and this pattern was not related to increasing body size (Fig. 2). No relationship between VPD and removal distance was observed at the 80th quantile at SEV or JRN because a large-bodied species (*A. cockerelli*) removed baits over long distances at low VPD values. These patterns were inverted at SGS. The lack of a VPD-removal distance relationship at the 20th quantile can be attributed to the effects of species that removed baits over short distances across a range of VPD values. The significant positive relationship at the 80th quantile is due to the activity of larger species (in particular, *P. occidentalis*) at high VPDs (see also Crist & MacMahon, 1991).

Part of the positive relationship between VPD and removal distance at SEV was caused by an increase in removal distance by *Forelius* individuals with increasing VPD. Morehead & Feener (1998) showed that the running speed of *Pogonomyrmex* increased with increasing temperature, which may explain why both thermophilic ant species and *Forelius* individuals foraging at high VPDs (at SEV) removed baits over longer distances in this study. We could not, however, detect any effects of temperature on variation in removal distances within other taxa, perhaps due to low sample sizes.

Large body size, thermophily, and the effects of increasing VPD on individual behavior have similar effects on removal distance, but different factors are important in different cases. Species active at high VPDs may or may not have large body sizes, and VPD may or may not increase removal rates by individual species. Nonetheless, the emergent community-wide pattern is a general increase of removal distance with increasing VPD. This indicates that the spatial scale over which ants, taken as a whole, forage increases systematically with VPD.

Inter-site differences in redistribution patterns

Mean bait removal distances were lowest at SGS and SEV because many baits at these sites were removed by species that forage over short distances, such as the heat-intolerant *M. emeryana* and *Pheidole* spp., respectively. At JRN, many baits were removed by species that moved baits over larger distances, such as the thermophile *Forelius*. The persistence of this relationship when among-site differences in VPD are taken into account indicate that variation in average VPD during the study did not contribute to the pattern. Nonetheless, differences in the overall activity of thermophilic species among the sites may determine much of the pattern.

Alternatively, among-site differences in removal distance may be caused by overall differences in the ant nest densities among the sites. The maximum number of ant nests along transects that intersect different habitat types at the SGS is higher than at either SEV or JRN (M. Kaspari, pers. comm.). Another possibility is that differences in vegetation cover among the sites directly affect foraging behavior. In Great Basin shrub steppe, for example, Fewell (1988) found that *P. occidentalis* traveled farther to search for seeds on routes with lower vegetation cover. Grass cover was highest in SGS habitats, intermediate in SEV habitats, and lowest in JRN habitats (Bestelmeyer & Wiens, 2001b). Thus, the decreasing vegetative complexity from SGS to JRN may have resulted in increasing ant foraging distances along the gradient.

Our results suggest that nutrients are, on average, redistributed by ants at a much finer spatial scale at SGS than at JRN. Vegetation patchiness in the relatively mesic SGS appears to be more finely textured than in desert grassland (i.e. smaller patches of both grass and bare ground; see Ludwig et al.,1999; pers. obs.) and this may generate relatively finer nutrient redistribution via fluvial runoff–runon processes (Ludwig & Tongway, 1995). The effects of this abiotic process may be mirrored and amplified by ant foraging activity. The rates of concentration and the amount of material concentrated by ants will depend on several factors including the longevity of nests at particular points in space (Smallwood, 1982) and the availability of animal carrion with respect to the daily and seasonal activity patterns of ant species.

Conclusions

Our results demonstrate that variation in ant species composition and foraging behavior can produce significant variation in the scale of material redistribution between sites. This variation may have a number of causes, although differences in the relative contributions of thermophilic ant species appear to be critical. For the purposes of including ants in the modeling of nutrient budgets within these ecosystems, ant functional groups will need to be based on body size as well as microclimate use. Of perhaps greater significance, our study demonstrates the overwhelming importance of non-harvester ant species such as *M. emeryana*, *Forelius* spp., and *Pheidole longula* in determining the redistribution of scavenged materials across the LTER sites. These ants and their nests are inconspicuous when compared to the large-bodied species that have been the subjects of intensive ecosystem studies such as *P. occidentalis* (Coffin & Lauenroth, 1990; MacMahon et al., 2000) or *P. rugosus* (Whitford & DiMarco, 1995). Although arthropods may comprise a significant proportion of the diets of large harvester ants (Mackay, 1985), our work indicates that relatively small but abundant species may better define the overall role of ants in nutrient cycling at the LTER sites.

The obvious next step is to quantify the consequences of these ant species for ecosystem properties. Specifically, what is the proportion of fine-scale variance in nutrient concentrations that can be attributed to dominant ants? Here, we have focused only on the lateral transport of materials and not on vertical transport within the soil column. How do ant species vary with respect to vertical transport? Given variation in the vertical disposition of the materials, how do the nutrients concentrated by different ant species differ in their availability to decomposers or plants? Ant colonies vary widely in worker population size and dispersion due to factors such as nest-site availability (Herbers & Greico, 1994) or social structure (e.g. polygyny; Porter & Savignano, 1990); how do ant worker population size and nest dispersion affect the concentration of nutrients by ant colonies? Finally, do ant foraging activities contribute to the retention of nutrients in ecosystems? Such studies are needed to clarify and model the roles of scavenging ants in the functioning of semi-arid ecosystems.

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