Influences of Spatial Attractors on *Pogonomyrmex rugosus* Nest Distributions in the Chihuahuan Desert, New Mexico

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Abstract

The spatial distributions of desert harvester ant (Pogonomyrmex rugosus) colonies were studied to examine edge influences along the margins of semi-desert grassland alluvial fan channels as a function of changes in landform scale. Detailed measurements were made of nestto-channel distances in two areas with differing channel sizes and densities, using transects, tape measures, and GPS. While nest densities reached as high 80 ha⁻¹ in Area 1, they only reached 17.78 nests ha⁻¹ in Area 2, which is similar to previous reports of approximately 20 ha⁻¹. In the low drainage density (0.010 m/m²), large channel setting (~20 m wide) of Area 1, a spatial statistical test of distance index of dispersion showed that nest densities clustered nearest the channel edges and decreased away from the banks. With smaller (0.5-2.0 m wide) channels and a higher drainage density (0.049 m/m^2) in Area 2, the dispersion index and an asymmetry ratio demonstrated a similar edge effect, but with counteracting effects from adjacent channels acting as opposing spatial attractors.

Keywords: ants, spatial distribution, edges, Pogonomyrmex rugosus, harvester ant.

Introduction

Previous research in the Chihuahuan desert of southern New Mexico has shown that desert harvester ant (*Pogonomyrmex rugosus*) colonies occur in a clustered spatial pattern along the edges of large alluvial fan drainage channels (arroyos). Statistical spatial pattern analysis shows that nest densities increase nearest the edges of large (~20 m wide) channels (arroys) and decrease away from the banks (Dugas 2001). This study addresses whether this effect also occurs along smaller (0.5-2.0 m wide), higher density, channels (gullies) in a similar alluvial fan location. How does reduced landform size modify the edge effect of nest clustering? Studying the distribution of nests in such a setting also adds to a better understanding of the relative effect of extrinsic geomorphic factors versus intrinsic colony behaviors.

Changes in the scale of landscape influences are widely recognized as being important in fully understanding biological spatial patterns and edge effects (Forman 1995; Phillips 1999; Turner, Gardner, and O'Neill 2001). Environmental factors, such as habitat boundaries, influence ant nest distributions. For instance, the edge effect, i.e. higher population densities and diversities of species along the outer portions of ecological patches, is a wellrecognized phenomenon in landscape ecology studies (Forman 1995). Greater ant biomasses have been measured along vegetation edge zones at the contact between different plant communities, as opposed to lower densities within each adjacent plant community (Levings and Traniello 1981; Helle 1985; Hammond 1987; Scougall, Majer, and Hobbs 1992; Whitford and Eldridge, forthcoming). Environmental influences, however, must also be considered within the contexts of ant behavior.

Ant colony distributions can be an important indicator of intraspecific and interspecific competition. The most common type of nest distribution among ants is overdispersion; a uniform, non-random spatial arrangement believed to be the outcome of territorial behavior with mutual exclusion by either active aversion by colony emigration, mutual annihilation of colonies until one remains in the minimal defensible space, or through preemption by destruction of incoming foundress queens by previously established colonies (Levings and Traniello 1981; Hölldobler and Wilson 1990). Overdispersion patterns exhibit regular nest arrays, spaced so that the distances between them are too uniform to have been randomly set. Levings and Traniello (1981) provided an important review of the literature on local distributions of ant colonies where 67 of the 80 data sets examined indicated overdispersion nest patterns, including examples among P. rugosus populations. Bernstein and Gobbel (1979) found that among all species of ants, including Pogonomyrmex spp., at ten study sites in the Mojave and Great Basin deserts of western North America, overdispersion patterns were common. Hölldobler (1976) found that among P. rugosus, P. barbatus, and P. maricopa colonies the spatial distribution was overdispersed.

This study examines some of these issues by measuring how smaller sized, higher density, environmental edges may be influencing spatial patterning of ant nests through statistical comparisons of detailed, field-mapped nest distributions in two analogous yet different alluvial fan areas. Both similarities and differences in spatial distributions resulting from the variations in the size and densities of channel edges are demonstrated. Some speculation as to the causes of the observed patterns is discussed although final causes are still undetermined.

Methods

This study encompasses two areas (Figure 1): a previously examined location along a large arroyo (Area 1) (Dugas 2001), and an area comprised of small gullies, but lacking larger arroyos (Area 2). Area 1(Figure 2) is located

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approximately 10 km west of Las Cruces, Doña Ana County, New Mexico, USA (UTM coordinates 347410mE / 3580330mN, Zone 13), at 1,520 m elevation. This location is on a west-facing alluvial fan piedmont fronting the Organ Mountains, a granitic/rhyolitic volcanic area that is the main upland feature generating storm runoff. The fan surface is a gravelly sandy loam soil (Pinaleno-Nolam association, Soil Survey Staff 1977). Mean annual rainfall in both areas is approximately 230 mm, with most occurring in late summer. Vegetation in both areas is characterized by sparse honey mesquite (*Prosopis glandulosa*), snakeweed (*Gutierrezia sarothrae*), mormon tea (*Ephedra trfur-ca*), creosote bush (*Larrea tridentata*), black grama grass (*Bouteloua eriopoda*) and bush muhly grass (*Muhlenbergia porteri*).

Area 2 (Figure 3) is located on a homologous alluvial fan surface 4.6 km northeast of Area 1 (UTM coordinates 348050mE / 3584850mN, Zone 13), at 1480 m elevation. It consists of the same slope, soil type, and vegetation as Area 1, but lacks large arroyos due to differences in upstream catchment size.



Figure 1. Location map and aerial photo of study areas 1 and 2.

Nest distribution measurements in Area 2 were made amidst several small (0.5 to 2.0-meter width) gully channels incised (0.25 to 1.25 meters) into the alluvial fan surface (Figure 3). This provided a significant decrease in size from the approximately 6 m depth x 20 m width channels of Area 1 (Dugas 2001).

The channel reaches in both areas were mapped using measuring tapecontrolled walking transects. There are a total of 1,600 m of channel edge in the 80,000 m² Area 1 and 4,725 m in the 48,460 m² Area 2. Drainage density in Area 1 is 0.010 m/m². Area 2 is notably higher at 0.049 m/m² (Table 1).



Figure 2. Map of stream channels and nest distribution in Area 1.

Colonies of *P. rugosus* are easily identified on the desert surface, with individual nest disks having single entrances centered on 0.5-2 meter-radius, flat, circular areas cleared of vegetation and armored with approximately 4 mm



Figure 3. Map of stream channels and nest distribution in Area 2.

size gravel (Whitford, Johnson, and Ramirez 1976; Taber 1998). To assure that all of the nests were identified, a grid of 5 m-interval transects (parallel and perpendicular to the drainage trend) were traversed across the entire measured area. Channel edges are defined by the abrupt margin at the upper convex shoulder of the slope located between the upper fan surface and the channel (Figure 4). Distances from nest locations to the nearest (shortest distance)

channel edge and the second nearest edge on the adjacent channel were recorded using measuring tapes (+/-1.0 cm accuracy). GPS reference points for the channels and each nest were also collected for additional mapping purposes (+/ - 10.0 cm accuracy). A total of 74 nests were recorded in Area 1 and 66 in Area 2. The average nest densities of Area 1 and Area 2 were 9.25/hectare and 13.62/hectare, respectively (Table 1).

Nest densities relative to total channel edge lengths and nest distances to the channel edges provide the basis for examining the influences the channels as spatial attractors (Dugas 2001). Prior to spatial statistical analysis, data sets



Figure 4. Illustration of channel edge-to-nest configuration at Area 2.

Parameters	Area 1 (n=74)	Area 2 (n=66)
Area	80,000 m ²	48,460 m ²
Total Channel Length	800m	2362m
Total Edge Length	1600 m	4725 m
Drainage Density	0.010 m/m ²	0.049 m/m ²
Density per channel length	0.04625 nests/m	0.01397 nests/m
Average Nest Density	9.25.0 n / hec.	13.62 n / hec.
Area within 5 m of channel	0.80 hec.	2.36 hec.
Density within 5 m of channel	80 nests/hec.	17.78 nests/hec.
<i>I</i> - index value	4.7877	15.0362

Table 1. Spatial measurements for areas 1 and 2.

from all channel reaches in Area 2 were combined and treated as a single group of nest-to-edge measurements. As discussed in Dugas (2001), a spatial statistical test of dispersion from the channel edge is provided by a "distance index of dispersion" (Johnson and Zimmer, 1985; Ludwig and Reynolds, 1988). The distance index of dispersion (I) equation is:

$$I = (N+1) \frac{\sum_{i=1}^{N} (x_i^2)^2}{\left[\sum_{i=1}^{N} (x_i^2)\right]^2}$$

This is a ratio of the sum of the squares of the squared nest-to-edge distances to the square of the sum of the squared nest-to-edge distances. I has an approximate expected value of 2 for a random pattern, less than 2 for a uniform pattern, and greater than 2 for an edge-clustered pattern. Johnson and Zimmer (1985) have also shown that I converges to normality at moderate sample sizes (i.e. N=100)

As noted above, the smaller channel sizes in Area 2 compared to Area 1 coincided with a much higher drainage density in Area 2 (Table 1). To examine the potential effect of this higher density, a measurement of "asymmetry" for the nest locations relative to nearest adjacent channels is introduced. This measurement is obtained by determining the distance of each nest to the two nearest but separate, channel reaches on either side. The shortest nest-to-edge distance for each nest is divided by the total distance between adjacent channel edges at the location of each nest to establish a ratio. The ratios are then averaged for the entire sample. A near-centered clustered distribution (i.e. nest placements tending to be as far from the channels as possible) produce an average value nearing .50. Average asymmetry ratio values are lower (i.e. below .125) if the clustering pattern is shifted toward one of the channel edges. A more evenly dispersed (uniform) distribution produces values in the midranges around .25. This asymmetry measurement is significant in the final interpretation of results from this study, as discussed below. Asymmetry analysis in Area 1, produces null results because of the large distances between channels where nest densities drop to zero and channel adjacency effects do not to exist.

Results

Spatial statistical analysis of the distribution of *P. rugosus* colonies in both study areas 1 and 2 indicate that there is a propensity for nests to occur more often near channel edges, and for nest density to decrease away from channel edges (Figure 5). There was a notable abundance of nests closest to the channel edges in both areas despite the change in size of the drainages. The pattern can

be interpreted as "clustered" with more distances being closer to channels in the sample area than expected if the nest-to-edge distances were randomly distributed. Notably, the distance index of dispersion (*I*) for the nest-to-edge measurements for Area 2 is considerably larger (15.04) than for Area 1 (4.78) (Table 1). A visual inspection of the mapped distributions, however, does not convey this as well for Area 2 (Figure 3) as for Area 1 (Figure 2). Area 1 has a maximum density of 80.0 nests ha⁻¹ where edge clustering was highest within the first five meters of the channel edge (Dugas 2001). Area 2's maximum density is also immediately adjacent the channels but only reached 17.78 nests ha⁻¹ (Table 1). The larger *I* value in Area 2 is due to the higher drainage density and shorter channel-to-channel distances overall. The limited area in which dispersion away from the bank *could* have occurred in Area 2 has created a somewhat artificial clustering as represented by the *I* value.

Table 1 also shows that while Area 2 has a higher nest density per hectare, Area 1 shows higher nest densities per channel edge length. When examined in terms of nest densities within 5 m of channel edges, Area 1, as noted, has by far the highest values. These values suggest that the larger-size channel at Area 1 had a greater influence on nest distribution, whereas the channels in Area 2 (while still having an edge effect despite their smaller size) had a more complex influence because of the higher drainage density. Adjacent channels are acting as opposing geomorphic spatial attractors, but are possibly concurrent with overdispersion as a behavioral spatial factor.

An examination of the asymmetry ratio reveals these effects. Area 2 has an asymmetry ratio of 0.238; indicating evenly dispersed distribution between channels and therefore effectively less edge clustering (recall that a nearcentered clustered distribution = .50; clustering toward an edge = .125; and an evenly dispersed distribution = .25). While the distance index of dispersion shows clustering along channel edges in Area 2, the asymmetry ratio suggests a dispersed pattern due to the closely spaced channel acting as opposing spatial attractors. At the same time, overdispersion is possibly having a similar influence by driving a more uniform, less clustered, distribution. Discerning the relative effects of these influences is problematic. It is notable that Schooley and Weins (2003) concluded that although spacing of *P. rugosus* colonies were either regular or random tending towards regular, they found that landscape heterogeneity (such as the channels) also influence the spacing of colonies.

Discussion

Spatial statistical analysis of the distribution of *P. rugosus* colonies in the study areas confirmed that there was a propensity for nests to occur more often nearest the channel edges, and for nest density to decrease away from edges. This was particularly evident from the results of the distance index of dispersion analysis where *I* values indicated general aggregation along channel edges. This result is similar to other studies where greater ant biomasses occurred along vegetation edge zones at the contact between different plant communities

(Levings and Traniello, 1981; Helle, 1985; Hammond, 1987; Scougall *et al.*, 1992). In the study areas, the contact zone was the narrow edge of the fan above the arroyo or gully channel. Along the larger arroyo of Area 1 this was also a transition between the sparser vegetation of the fan surface and the denser riparian vegetation in the arroyo. It is possible that there is an advantage for the colonies to be out of the flood susceptible zone of the arroyo channel, yet nearest to the forage available in the riparian corridor. In Area 2, however, there was no vegetation, or very little, in the gullies indicating that riparian vegetation is unlikely the edge attractor. It has been proposed that criteria for selection of colony sites by Western Desert harvester ant queens might include vegetation density (Nagel and Rettenmeyer, 1973), however Whitford *et al.* (1976) found no relation between *P. rugosus* nest distribution and vegetation.

Soil texture may also have had an influence. The fan surface soil in Area 1 is more clay and carbonate-rich than the younger inset terrace soils (Soil Survey Staff, 1977). Johnson (1992) observed a tendency for *P. rugosus* colonies to occur in more clay-rich soils, and Whitford *et al.* (1976) noted that *P. rugosus* nests commonly penetrated carbonate hardpan, which retained noticeable moisture levels. In Area 2, however, where the gully channels where considerably shallower (0.25 to 1.25 meters) the fan surface soil texture was the same as within the channel walls and floor.

While some of the factors discussed above may be influencing the edge clustering of the colonies, the specific reason(s) were not demonstrated by this study. A general understanding of spatial tendencies among ants, and *Pogonomyrmex* in particular, is informative however, in terms of the spatial pattern observed. As noted previously, most studies of ant colony distributions have found that overdispersion was the most commonly observed spatial characteristic, with regular nest arrays spaced so that the distances between nests were too uniform to have been random (Hölldobler and Wilson, 1990).

While overdispersion appears to be very widespread among various ant species, other less uniform, more random spatial tendencies have also been noted. Levings and Traniello (1981) found that while overdispersion is most common among *Formica* species which depend on randomly or unpredictably distributed resources, those *Formica* which nest along margins of a habitat tend to have more random or clustered distributions. Whitford *et al.* (1976) found that *P. rugosus* colonies in their Chihuahuan Desert study areas were typically randomly distributed except in one instance, on a narrow fan between two dry stream beds, where colonies of *P. rugosus* were found to be aligned along the edge of one channel and *P. barbatus* along the other. They did not provide an explanation for the observed distribution. The spatial clustering reported in the present study may describe a similar distribution, although Whitford *et al.* (1976) did not report density diffusion away from the channel edges.

In addition to the diffusion and edge effects documented in the present study areas, high nest densities for Area 1 were significant. Recall that nest densities per hectare were approximately 80, 25, 27.5, 15, 15, 7.5 for each 5-

meter nest-to-edge distance interval within the first 30 m away from the arroyo edge in Area 1. The high nest density of 80 ha⁻¹ in the first five-meter zone is particularly remarkable. Nest densities among *P. rugosus* in the Chihuahuan Desert have previously been reported at approximately 20 ha⁻¹ (Whitford and Ettershank,1975; Whitford *et al.*,1976). Area 2's density of 17.78 nests ha⁻¹ is more in agreement with their estimates.

Foraging behavior appears to be an important control on ant nest density (Levings and Traniello, 1981; Hölldobler and Wilson, 1990). Colonies dependent on persistent resources frequently use chemically and visually marked trunk trails to efficiently channel foragers to and from nests. Hölldobler (1976) and Hölldobler and Wilson (1990) noted that because of the exploitation of patchy, but relatively stable food supplies, P. rugosus tend to show a more complex partitioning structure based on well-established trunk foraging trails. Significantly, between-nest distances are shorter among populations of P. rugosus where trunk trails guarantee an efficient partitioning of foraging grounds, in contrast to individually foraging *P. maricopa* populations that lack trunk trails (Hölldobler, 1976; Davidson, 1977). The efficiency of a trunk trail type of foraging strategy may, in part, have allowed for the extremely high nest densities found nearest the arroyo edges in the present study area. Is it possible that the restriction of the channel edges, particularly in Area 2, partially limit the distribution of longer trunk trails to directions parallel to the channel edges, as foraging trails perpendicular to the edges would be too short and inefficient?

Conclusions

This study sought to determine whether or not higher-density, smaller alluvial fan channels would produce similar ant nest spatial distributions to that found adjacent lower-density, larger alluvial fan channels. Despite differences in the size of these geomorphic features, study areas 1 and 2 show similar results. The distance index of dispersion (I) for the nest-to-edge measurements clearly indicate strong edge clustering. Significantly, the reduced channel size of Area 2 does not result in reduced edge effects according to its I value. Nests in Area 2 do reveal a tendency toward aggregated channel edge-to-nest distances nearest the bank with decreasing densities away from the bank edges, similar to the Area 1 pattern. A test of distribution asymmetry in Area 2, however, shows adjacent channels act as opposing spatial attractors causing a more dispersed pattern perpendicular to the channel trend. It is possible that both overdispersion, as a colony's behavioral response, and higher density, smaller channels acting as opposing spatial attractors have a cumulative effect on edge clustering patterns of *Pogonomyrmex rugosus* ant colonies in the study area. Given the lack of definite conclusions regarding the *causes* of the edge distributions seen in this study and others, the arroyo and gully edge is clearly a geomorphic setting in which presently undetermined factors are playing an important role in nest distribution and density regardless of the associated landform size.

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