

**Soil texture as an influence on the distribution
of the desert seed-harvester ants *Pogonomyrmex rugosus*
and *Messor pergandei***

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Received February 8, 1991 / Accepted in revised form August 21, 1991

Summary. *Pogonomyrmex rugosus* and *Messor pergandei* are ecologically similar species of desert seed-harvester ants that coexist in numerous areas throughout the Sonoran and Mohave Deserts. However, these two species also commonly segregate along physical gradients, with each species predominating in areas that differ in soil texture and/or topographic relief. Along gradients that included bajada and alluvial flat habitats, *P. rugosus* occurred alone in coarse-textured soils near mountains, while *M. pergandei* occurred alone in finer-textured soils further away. Conversely, along a vegetation gradient that included creosote bush and saltbush habitats, *P. rugosus* occurred alone in finer-textured soils than those occupied by either *M. pergandei* alone or both species in coexistence. However, in both situations clay content was significantly higher in areas occupied by *P. rugosus* alone, and at the latter site clay content was correlated with relative abundance of each species. Moreover, local distribution pattern of these two species may be related to the effects of clay on water retention, with retention being highest in areas occupied by *P. rugosus* alone. Differences in reproductive ecology may also affect these patterns as *P. rugosus* reproductive flights follow summer monsoon rains, while those of *M. pergandei* occur during the milder winter and spring.

Key words: Ants – Distribution pattern – Soil texture – Sonoran desert

Many natural communities contain ecologically similar species whose coexistence has been attributed to differences in resource use; competitive interactions should preclude the existence of certain species combinations (MacArthur 1958; Diamond 1975; Cole 1983). One type of indirect evidence that has been used to infer such

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competitive interactions is the occurrence of apparently non-random assemblages comprised of species that differ in size of trophic structure or body size (Hutchinson 1959; Bowers and Brown 1982; Brown 1975; Pyke 1982). Such community patterns could facilitate species coexistence via partitioning food resources by size. Coexistence of seed-harvester ants in deserts appears to depend on both partitioning food resources by size and mode of foraging (Davidson 1977a, b, 1978). Differences in body size may facilitate coexistence through partitioning seeds by size, while individual and group foraging strategies may allow species to harvest seeds that differ in their spatial distribution (Davidson 1977b).

Pogonomyrmex rugosus and *Messor* (= *Veromessor*) *pergandei* (Bolton 1982) are two species of desert seed-harvester ants that have great potential to compete for food resources, as both species occur throughout most of the Sonoran and Mohave Deserts, often in close sympatry (Davidson 1977a; Rissing 1981, 1988a). *Pogonomyrmex rugosus* is larger than *M. pergandei* (Davidson 1977a). Yet, where both species are common and sympatric and in different parts of the species' ranges, there is high overlap in relative abundance of seed species collected (Mehlhop and Scott 1983; Rissing 1988a). Additionally, both species apparently specialize on high-density seed patches as both are group foragers (Davidson 1977b) that use foraging columns that extend ≥ 20 m from the nest (Rissing 1988a).

The very similar foraging ecologies of *P. rugosus* and *M. pergandei* leads to the question of how these two species coexist. Numerous studies have examined biotic relations and interactions of these two species (Bernstein 1974, 1975; Davidson 1977a, b, 1978; Rissing 1988a; Rissing and Pollock 1989; Rytty and Case 1984, 1986, 1988), while few have addressed the influence of abiotic factors (Lighton and Feener 1989; Rissing 1988b). This paper examines distribution of these two species along topographic and/or vegetational gradients wherein each species predominates in different areas. One abiotic habitat feature, soil texture, is then examined as a potential influence on observed distribution patterns.

Methods

Study sites

Soil texture was examined relative to occurrence of *P. rugosus* alone, *M. pergandei* alone, or both species in coexistence at five sites in central Arizona: 1) west of the McDowell Mountains (MDM) (elevation 475–600 m; site boundaries 33°38'30"–40°30'N and 111°51'–53'E), 2) east and north of the San Tan Mountains (STM) (415–550 m; 33°10'30"–12'N and 111°40'–44'E), 3) east of the White Tank Mountains (WTM) (385–515 m; 33°34'–37'N and 112°28'–32'E), 4) 0.5 km east of WTM (WTME) (375–385 m; 33°33'N, 112°27'30"E), and 5) south of the Sacaton Mountains (SM) (435–445 m; 32°56'–57'N, 111°39'30"–41'E).

These five sites represented three types of topographic and/or vegetational gradients; both *P. rugosus* and *M. pergandei* occurred along these gradients, though each species predominated in different locations. MDM, STM, and WTM were near mountain ranges and represented gradients across bajada and alluvial flat habitats. Vegetation on bajadas was a palo verde (*Cercidium* spp.) – saguaro (*Carnegiea gigantea*) association while that on alluvial flats was a creosote bush (*Larrea tridentata*) – triangle bursage (*Ambrosia deltoidea*) association (Turner and Brown 1982). WTME represented a localized topographic gradient that consisted of a juxtaposition of gravelly to cobbly-surfaced shallow ridges and level fine-textured swales; ridges typically rose 2–3 m above the swales. Creosote bush predominated throughout WTME. SM represented a vegetation gradient including areas both within and adjacent to the historic floodplain of Santa Cruz Wash. Vegetation adjacent to the floodplain was a creosote bush association while that within the floodplain was a saltbush (*Atriplex polycarpa* and *A. linearis*) association.

Distribution

Colonies of both species were mapped while walking transects across bajada and alluvial flat habitats at MDM, STM, and WTM. Such a census served to verify predominance of each species along the gradient and to identify locations at which the composition changed from one species to the other. Transects (five at MDM and three at STM and WTM) began ≤ 0.5 km of the mountains and ran perpendicular to and away from the mountains until > 10 colonies of each species had been sighted. Transects were 20–25 m wide and 1.8 to 5.3 km long. Locations on each transect in which occurrence changed from one ant species to the other, i.e., transition points, were defined as points at which a sequence of colonies of one species was followed by three successive colonies of the other species.

At WTME, colonies of both species were quantified while walking transects within ridge and swale habitats. These two habitats were easily differentiated based on surface soil texture, which shifted abruptly from large gravels and cobbles at the base of ridges to fine-textured soils in the intervening swales. Numerous transects of various lengths were walked until > 75 ant colonies were sighted in each habitat. Transects were 20–25 m wide except when this width exceeded that of the habitat.

The SM site consisted largely of areas occupied by *P. rugosus* alone and those in which both species coexisted, though *M. pergandei* occurred alone in one area of several hectares. Due to the more heterogeneous species occurrence at SM, colony abundance was quantified in six 1.0 ha plots: two plots each within areas occupied by *P. rugosus* or *M. pergandei* alone, and two plots in areas in which both species coexisted. Five of these plots were within 200 m of areas in which species abundance/composition changed except for one coexistence plot which was about 400 m from such an area.

Soil texture

Soil texture at MDM, STM, and WTM was estimated from surface and subsurface samples (surface only at STM) collected within

200 m on either side of transition points. Collecting samples only near transition points facilitated examining abiotic habitat differences correlated with changes in ant species composition. Surface texture was measured at 20 randomly chosen colonies per species along each transect at MDM, STM, and WTM and 20 random colonies of the predominant species on ridge and swale habitats at WTME. Surface texture was not measured at SM as it appeared similar among areas occupied by each ant species alone and in areas where both species coexisted. Subsurface samples were collected from the center of the first five surface texture plots for each species along transects at MDM, STM, and WTM and from the first 10 colonies at WTME. At SM, subsurface samples were collected near five randomly selected colonies per plot and five samples per species in plots where both species coexisted.

Surface texture was measured in 1.0 m² plots, centered in a random direction 2.5 m from the nest entrance. This distance facilitated measuring microhabitat typical of the nest site, but avoided soil disturbance caused by ant activity. These locations typify nest sites as *P. rugosus* is not known to move its nest entrance (Rissing 1988b), and *M. pergandei* may have multiple nest entrances within several square meters, though typically only one or two openings are used at a time (Wheeler and Rissing 1975; Rytty and Case 1984). In each plot, cover of bare soil (0.0–0.2 cm), gravel (0.2–7.6 cm), cobble (7.6–25.4 cm), and stone (> 25.4 cm) was estimated visually

Table 1. Number of *Pogonomyrmex rugosus* (Pr) and *Messor pergandei* (Mp) colonies sighted along transects or within plots (Sacaton Mountains only) at five study sites near Phoenix, Arizona. Transects near the McDowell, San Tan, and White Tank Mountains were divided into areas predominated by each species (see text). Each plot was 1.0 hectares at the Sacaton Mountain site

		Close to Mountains		Away from Mountains	
		Pr	Mp	Pr	Mp
<i>McDowell Mountains</i>					
Transect	#1	13	0	2	16
	#2	20	1	0	15
	#3	40	1	2	12
	#4	28	0	1	18
	#5	24	1	0	15
Total		125	3	5	76
<i>San Tan Mountains</i>					
Transect	#1	51	4	0	15
	#2	29	0	0	13
	#3	56	4	3	28
Total		136	8	3	56
<i>White Tank Mountains</i>					
Transect	#1	24	2	4	35
	#2	19	1	0	42
	#3	34	2	2	21
Total		77	5	6	98
<i>White Tank Mountains East</i>					
Ridge Habitat		5	76		
Swale Habitat		68	21		
<i>Sacaton Mountains</i>					
<i>M. pergandei</i>	#1	0	25		
	#2	0	32		
<i>P. rugosus</i>	#1	25	1		
	#2	31	1		
Both species	#1	19	31		
	#2	22	17		

in 10% increments, i.e., 0–10, 10–20, 20–30. Cobbles and stones were also counted. Surface texture was analyzed using intermediate values of each 10% increment, e.g., 5 for 0–10, 15 for 10–20. Percent data were arc-sin transformed, and number of cobbles and stones were square-root transformed.

Subsurface soil samples (ca. 30 cm × 15 cm × 15 cm) were collected 25 cm below surface to avoid differences in various surface phases of the same soil series (Bill Johnson, pers. comm.). This depth also approximates that inhabited by queens of both species during the days following colony founding. Coarse fragments and soil were separated by passing samples through a 2 mm sieve. Fractions were dried ≥ 24 h at 55° C and weighed. Coarse fragments were separated into five size classes (> 2.54 cm, 1.91–2.54 cm, 1.27–1.91 cm, 0.48–1.27 cm, 0.20–0.48 cm) by mechanical shaking for 5 min through a series of sieves; each fraction was then weighed. Soil fractions were analyzed for percentage composition of sand, silt, and clay using the Bouyoucos mechanical method (Day 1965). Samples at SM were also analyzed for salinity due to presence of salt in areas occupied by saltbush. Electrical conductivity (mmho/cm) was determined as a measure of total salinity using a saturated paste extract.

Interspecific differences in surface and subsurface soil texture were examined using the multivariate analysis-of-variance (MANOVA) procedure in SPSS (Hull and Nie 1981); data from transects at MDM, STM, and WTM were pooled for one analysis, while data from WTME and SM were analyzed separately. For analysis, data were divided into three sets, subsurface coarse frag-

ments, subsurface soil texture, and surface cover. The variables in each set summed to 100%; consequently colinearity was minimized by first running the MANOVA on each data set and eliminating the variable that had the lowest F value and those that were not significant ($P > 0.05$). Two MANOVA's were then performed on the remaining variables: one on surface variables and one on subsurface variables. Analyses were performed similarly for data from SM, except that soil texture was first compared between species within each coexistence plot. A second MANOVA then compared soils among *P. rugosus* plots, *M. pergandei* plots, and those in which both species coexisted. An *a posteriori* univariate F test was used to determine the nature of among-plot differences for those variables that differed significantly.

Clay largely determines the physicochemical properties of soil (Hillel 1971, Marshall and Holmes 1988). Consequently, the association of percent clay content and relative abundance of each species was examined across the six SM plots by regressing the proportion of *P. rugosus* colonies to those of both species (independent variable) against percentage clay content (dependent variable).

Results

Distribution of *P. rugosus* and *M. pergandei* differed markedly at all five sites. Along transects at MDM, STM, and WTM, *P. rugosus* occurred alone close to mountains and *M. pergandei* occurred alone further

Table 2. Probability values for comparing surface and subsurface soil texture between areas in which *P. rugosus* or *M. pergandei* occurred alone; both species also coexisted at the Sacaton Mountain site. Overall significance levels for each of two data sets, surface texture and subsurface texture, are based on Wilks' lambda values obtained from a multivariate ANOVA (MANOVA) (see text);

significance levels for each variable are based on univariate *F*-tests. NS = Not significant ($P > 0.05$). DROPPED = Variables that were significant (univariate *F* test, $P < 0.05$) in the initial MANOVA; however, these variables had the lowest *F* value in that data set and were subsequently dropped to minimize colinearity. One-way ANOVA results for the Sacaton Mountain site are in Fig. 3

	McDowell, San Tan, and White Tank Mountains	White Tank Mountains-East	Sacaton Mountains
<i>Surface</i>			
Wilks' Lambda	$P < 0.001$	$P < 0.001$	Not sampled
Percent bare ground (Soil; 0.0–0.2 cm)	$P < 0.001$	$P < 0.001$	
Percent gravel (0.2–7.6 cm)	$P < 0.001$	$P < 0.001$	
Percent cobble (7.6–25.4 cm)	$P < 0.001$	Dropped	
Percent stone (> 25.4 cm)	Dropped	None present	
Number of cobbles	$P < 0.001$	$P < 0.001$	
Number of stones	$P < 0.001$	None present	
<i>Subsurface</i>			
Wilks' Lambda	$P < 0.001$	$P > 0.21$	$P < 0.001$
Electrical Conductivity (mmhos/cm)	Not sampled	Not sampled	$P < 0.001$
Percent rocks (≥ 0.2 cm)	$P < 0.001$	NS	$P < 0.012$
Percent size class > 2.54 cm	$P < 0.001$	NS	NS
1.91–2.54 cm	$P < 0.001$	NS	NS
1.27–1.91 cm	Dropped	NS	$P < 0.014$
0.48–1.27 cm	$P < 0.001$	NS	$P < 0.011$
0.20–0.48 cm	$P < 0.001$	NS	NS
Percent sand	NS	NS	NS
Percent silt	NS	NS	$P < 0.003$
Percent clay	$P < 0.001$	NS	$P < 0.001$

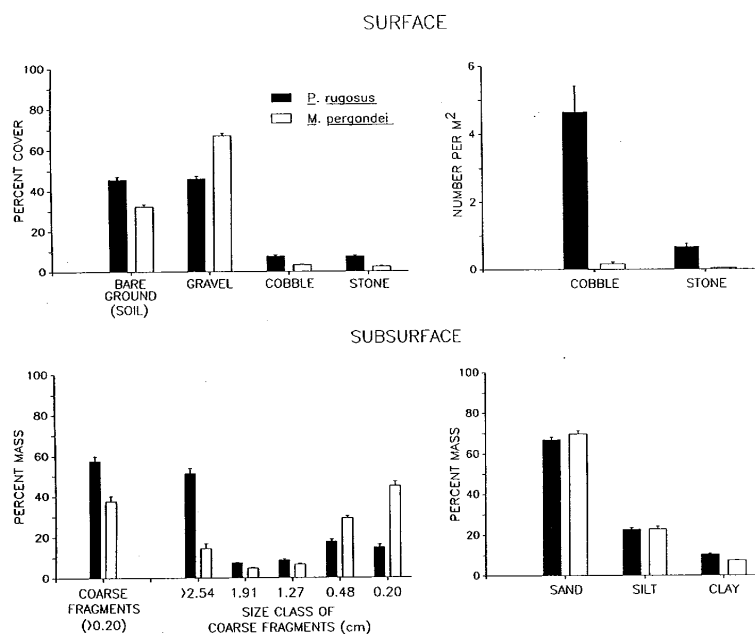


Fig. 1. Surface and subsurface soil texture near *Pogonomyrmex rugosus* and *Messor pergandei* colonies along transects near the McDowell, San Tan, and White Tank Mountains, Arizona (data pooled across sites). Percent values sum to 100 for each species within panels except for the lower left panel in which only percent coarse fragments is shown (soil omitted); percent size class of coarse fragments does sum to 100 in this panel. Significance levels are in Table 2

away (Table 1). Transition zones between areas in which each species predominated ranged up to 0.7 km wide along these transects. At WTME, *P. rugosus* predominated in swales and *M. pergandei* predominated on ridges (Table 1). At SM, *P. rugosus* occurred alone within plots in saltbush habitat, while either *M. pergandei* occurred alone or both species coexisted within plots in creosote bush habitat (Table 1).

The change in occurrence of the two ant species along transects at MDM, STM, and WTM coincided with differences in soil texture (Fig. 1, Table 2). On the surface, cover of bare ground, and cobbles, and number of cobbles and stones were significantly higher (MANOVA followed by a univariate F test, $P < 0.001$), while cover of gravel was significantly lower ($P < 0.001$) where *P. rugosus* occurred alone. Similarly, subsurface texture of areas where *P. rugosus* occurred alone was comprised of a significantly higher percentage mass of coarse fragments, i.e., those > 0.2 cm diameter ($P < 0.001$). These coarse fragments were also larger in size, as the percentage mass in the two largest size classes was significantly higher in areas where *P. rugosus* occurred alone ($P < 0.001$), while this percentage was significantly lower for the two smallest size classes ($P < 0.001$; Fig. 1, Table 2). The percentage composition of clay was significantly higher in soils where *P. rugosus* occurred alone ($P < 0.001$), while the percentage of sand and silt did not differ between areas in which each species occurred alone ($P > 0.10$; Fig. 1). Though seeming inconsistent, the higher percentage clay content in soils of bajada-like habitats is expected due to their greater age (Bill Johnson, pers. comm.).

At WTME, surface texture of ridges, on which

M. pergandei predominated, had a significantly lower cover of bare ground, a higher cover of gravel and more cobbles (MANOVA followed by a univariate F-test, $P < 0.001$) than did the swales in which *P. rugosus* predominated. None of the subsurface soil fractions differed between these two habitats (Fig. 2, Table 2; MANOVA, $P > 0.20$).

At SM, subsurface texture did not differ between species within either of the coexistence plots (Wilks' lambda, $P > 0.13$) and the data were pooled. However, subsurface texture differed significantly among plots in which *P. rugosus* occurred alone, *M. pergandei* occurred alone, and those in which both species coexisted (Wilks' lambda, $P < 0.001$; Table 2, Fig. 3). Relative to other plots, those in which *P. rugosus* occurred alone were more fine-textured (Fig. 3); the percentage mass of coarse fragments was significantly lower and these fragments were smaller in size (Fig. 3), and the percentage clay content was higher ($P < 0.001$). Soils in these plots were also significantly (one-way ANOVA, $P < 0.001$) more saline (14.79 ± 1.74 mmho/cm [$\bar{x} \pm 1$ SE]) than those occupied by *M. pergandei* alone (0.53 ± 0.12) or by both species in coexistence (0.53 ± 0.15). Plots in which *M. pergandei* occurred alone contained a significantly higher percentage silt content than plots in which *P. rugosus* occurred alone or those in which both species coexisted (Fig. 3).

The proportion of *P. rugosus* colonies in the SM plots was positively correlated with percent clay content ($R^2 = 0.63$, $Y = 0.13X - 0.46$, $N = 6$, $P < 0.05$). Comparing only the two coexistence plots, clay content was significantly higher (t -test, $P < 0.001$), by about 3%, in that in which *P. rugosus* was more common (Table 1).

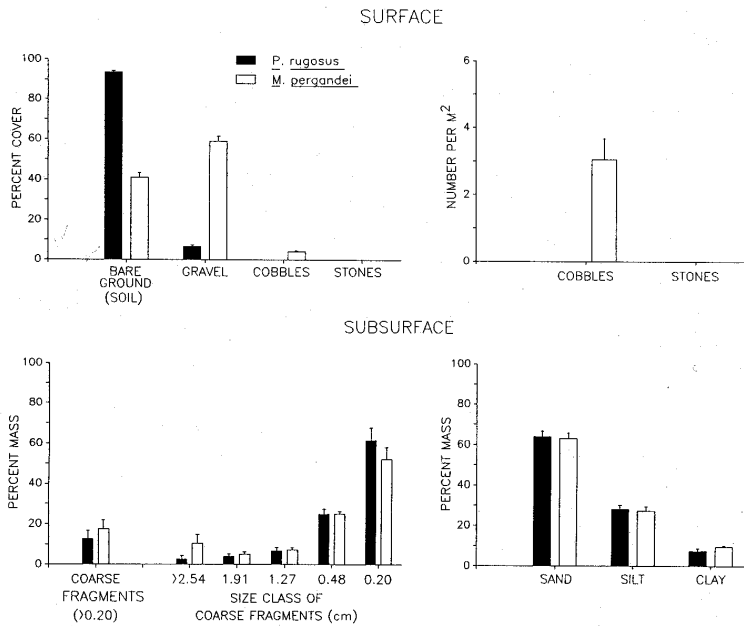


Fig. 2. Surface and subsurface soil texture near *Pogonomyrmex rugosus* and *Messor pergandei* colonies east of the White Tank Mountains, Arizona. Soil samples for *P. rugosus* were taken from swale habitats while those for *M. pergandei* were taken from adjacent ridge habitats (see text). See Fig. 1 for explanation of percent values. Significance levels are in Table 2

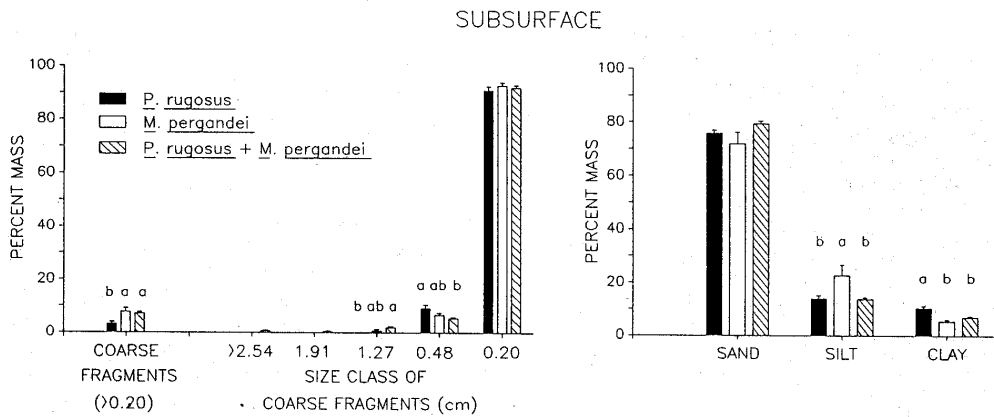


Fig. 3. Subsurface soil texture near *Pogonomyrmex rugosus* and *Messor pergandei* colonies south of the Sacaton Mountains, Arizona, in which each species occurred alone and both species also coexisted. See Fig. 1 for explanation of percent values. Significance

levels are in Table 2. Significant differences among the three plot types (*P. rugosus* alone, *M. pergandei* alone, and both species in coexistence) are indicated by the letters a and b: a > b. Values that do not differ are denoted by the same letter

Discussion

The ecologically similar ant species *P. rugosus* and *M. pergandei* often occur sympatrically, but do not partition food types (Mehlhop and Scott 1983, Rissing 1988a) or microhabitat based on soil texture (this study) when doing so. These two species also commonly segregate along physical gradients, with each species occurring alone in nearby areas that differ in soil texture and/or topographic relief. Across sites examined herein, *P. ru-*

gosus occurred alone in soils that were both more coarse- and more fine-textured than nearby areas occupied by *M. pergandei* alone; percent clay content, however, was significantly higher in both types of areas occupied by *P. rugosus* alone. These patterns of habitat segregation suggest that *P. rugosus* and *M. pergandei* are ecological equivalents that replace one another along physical gradients due to differences in competitive ability and/or physiological tolerances.

The higher clay content in areas occupied by *P. ru-*

gossus alone at MDM, STM, and WTM, and the correlation at SM between relative abundance of *P. rugosus* and *M. pergandei* colonies with percent clay suggests that clay is the soil fraction that affects habitat segregation in these two ant species; additionally, within the two SM coexistence plots clay content was significantly higher in the plot in which *P. rugosus* was more common. However, the correlative nature of these analyses leave open the possibility that clay content is correlated with some other causative factor. That *P. rugosus* occurs alone both in areas with more coarse- and more fine-textured soils suggests that local distribution is less affected by sand, silt, and coarse fragments.

How might clay content affect differences in species distribution patterns? Because of its large specific surface area, clay essentially determines physicochemical properties of soil including water retention (Hillel 1971; Marshall and Holmes 1988). Soils with higher clay content lose water more slowly and such differential water retention may affect local distribution patterns. These effects are enhanced in areas occupied by *P. rugosus* alone at MDM, STM, and WTM as the coarser fragments promote infiltration and retard evaporation (Grant and Struchtemeyer 1959; Hillel and Tadmor 1962; Alizai and Hulbert 1970; Munn et al. 1987); the higher salt content in *P. rugosus* plots at SM would also enhance water retention.

SM was the only site at which both ant species commonly coexisted, without such coexistence representing a transition zone across areas in which each species occurred alone. However, local differences in soil texture also influenced species abundance at this site as indicated by differences in clay content and relative abundance of the two species in the two coexistence plots. Such local differences are also demonstrated in that *M. pergandei* occurred alone only in an area of several hectares while areas in which both species coexisted or *P. rugosus* occurred alone approached hundreds of hectares.

WTME was the only site at which subsurface texture did not differ between areas predominated by each ant species. Consequently, the predominance of *M. pergandei* on ridges and *P. rugosus* in swales was probably not related to differences in infiltration rate or water retention. However, differences in species composition could be due to the topographic relief of ridges and/or the higher surface cover of coarse fragments on ridges; both of these factors could increase runoff to and soil moisture of adjacent swales where *P. rugosus* predominated, especially during short, intense, summer rains.

Differences in local distribution pattern based on soil texture and/or associated soil properties may be related to differences in reproductive ecology of these two species. Reproductive flights of *P. rugosus* are triggered by heavy summer rains (Hölldobler 1976), which ameliorate soil thermal and/or moisture conditions at times when soil surface temperatures otherwise exceed 70° C (Louw and Seely 1982). Such conditions should enhance survival of *P. rugosus* queens in soils with higher clay content and consequently higher water retention, while survival may be much poorer in soils with lower clay content, such as those occupied by *M. pergandei*, due to

increased thermal and/or moisture stress. Alternatively, reproductive flights of *M. pergandei* extend from late January to late March (Pollock and Rissing 1985), a season during which low temperature and moisture stress would allow colonizing dry habitats. That *M. pergandei* did not occur in all examined habitats could be due to competition and/or exclusion by *P. rugosus* or to physiological limitations imposed by soil texture or related factors.

In conclusion, these data suggest that local distribution of *P. rugosus* and *M. pergandei* is influenced by soil texture and/or associated soil properties. Consequently, these two species might only coexist in areas comprised of soils that have properties intermediate to those in which each species occurs alone. Further examination of geographic and habitat variation in these and other desert seed-harvester ants will facilitate understanding species interactions and community structure.

Acknowledgements. I thank Hilda Hatzell and Bill Johnson for early discussion and comments regarding this project, Dennis Duffy for use of sieving facilities, and especially Steven Rissing for his guidance and support. The manuscript benefited from comments by Diane Davidson, Bill Johnson, Joel Kingsolver, Thomas Martin, Joseph McAuliffe, Mark Newton, Steven Rissing, Randall Rytty, and an anonymous reviewer. Partial financial support was provided by two Sigma Xi grants and two Graduate Research grants from the Department of Zoology at Arizona State University. Parts of this paper were submitted in partial fulfillment of the requirements of the degree Doctor of Philosophy to the Zoology Department at Arizona State University.

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