

# Habitat segregation based on soil texture and body size in the seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus*

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**Abstract.** 1. The seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* are ecologically equivalent sister species that have broadly overlapping distributions in the south-western U.S.A.; however the two species are only sympatric in localised contact zones.

2. Soil regimes at 25–50 cm below the surface were quantified across contact zones to assess abiotic habitat factors related to distribution pattern. Physiological parameters related to foundress survival were also measured in order to test for a correlation between these parameters and distribution pattern.

3. The two species segregated among microhabitats based on soil texture; *P. barbatus* occurred alone in soils with a higher clay content and/or higher moisture retention. In areas of sympatry, soil texture was similar for both species but was intermediate to that in areas where the two species occurred allopatrically. The pattern of microhabitat segregation was similar across three sites that encompassed a broad range of soil regimes.

4. The only measure of foundress survival correlated with microhabitat differences was an  $\approx 8\%$  greater dry mass for alate females of *P. rugosus*. This resulted in their surviving significantly longer than did alate females of *P. barbatus* under desiccating conditions.

5. This microdistribution pattern may be caused indirectly by soil texture affecting plant species distribution and hence the seeds available to ants. A companion laboratory experiment demonstrated, however, that soils could also cause this distribution pattern of both ant species directly via effects on foundress wet mass.

**Key words.** Allopatry, ants, Chihuahuan Desert, distributions, foundress physiology, *Pogonomyrmex*, soil type, sympatry.

## Introduction

Differences in geographic distribution of ecologically similar species often result from small differences in morphology, physiology, or life-history traits. Several studies on this topic have indicated that segregation along local gradients is maintained by biotic interactions, while physiological tolerance to abiotic factors such as temperature, moisture, and salinity determines precisely where segregation occurs (for a review see Dunson & Travis, 1991). These studies have enhanced understanding of the relative importance of biotic

and abiotic factors causing zonation patterns in marine intertidal and plant communities. In contrast, physiological tolerances and abiotic controls have seldom been examined in many zoological systems (Dunson & Travis, 1991).

Physiological tolerances should be important in determining the distribution of invertebrates because their small sizes and high surface : volume ratios make them prone to desiccation (Edney, 1977; Hadley, 1994). If this is the case, species with the highest tolerances to desiccation would be predicted to inhabit the driest portions of a moisture gradient. Studies often support this prediction, with increased desiccation tolerance for the xeric species resulting from a lower water loss rate, larger body size, or both (Schultz & Hadley, 1987; Chown, 1993; Kaspari, 1993; Le Lagadec *et al.*, 1998; Worthen *et al.*, 1998).

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Desert seed-harvester ants comprise a system in which studies have emphasised biotic interactions and the partitioning of seed resources based on body size and foraging pattern (Davidson, 1977a,b, 1978, 1985; Rissing, 1988a; Rytí & Case, 1988a). In contrast, comparisons of physiological performances and distributional patterns are rare for desert ants (but see Whitford *et al.*, 1975), although this approach has proved useful for ants in other habitats (Talbot, 1934; Hood & Tschinkel, 1990). For ants, abiotic limiting factors should be most important during nest founding and establishment, when colonies are small and vulnerable (Tschinkel, 1992; Kaspari & Vargo, 1995; Johnson, 1998).

The study reported here examined abiotic habitat factors and physiological tolerances related to the microdistributions of the two ecologically equivalent sister species of seed-harvester ants, *Pogonomyrmex rugosus* Emery and *P. barbatus* (F. Smith) (Cole, 1968; Taber, 1990). The two species have similar foraging behaviours (except for small daily and seasonal differences in temporal activity schedules), nest sites, and diets (Cole, 1968; Hölldobler, 1976; Whitford *et al.*, 1976), and both species are aggressive during intra- and inter-specific encounters (Hölldobler, 1976; Gordon, 1992, 1995). Summer rains trigger mating flights, and the claustral foundresses initiate nests singly (Hölldobler, 1976). The two species have broadly overlapping geographic distributions from south-eastern Arizona to western Texas and into Mexico. Sympatry is rare, however, except in localised contact zones (Whitford *et al.*, 1976; Davidson, 1977a). Observations suggest that the two species coexist by occurring in different micro- and macro-habitats. On a local scale, *P. rugosus* appears to inhabit more xeric areas than does *P. barbatus* (MacKay, 1991), and on a regional scale *P. rugosus* replaces *P. barbatus* across the gradient of decreasing rainfall from east to west Texas (Moody & Francke, 1982). Based on these micro- and macro-habitat differences, two hypotheses were tested relative to the distribution of the two species along localised contact zones: (1) *P. rugosus* colonies occurred in coarser-textured soils (i.e. drier soils with lower clay content) than those occupied by *P. barbatus*, and (2) physiological tolerances of the foundresses (newly mated females that initiate colonies) were correlated with this distribution pattern. That is, foundresses of *P. rugosus* were predicted to survive longer than those of *P. barbatus* under desiccating conditions. Microhabitat differences were assessed by quantifying soil composition and soil water retention across contact zones where the two species occurred both allopatrically and sympatrically. Desiccation tolerance was assessed by quantifying physiological parameters that have the potential to affect survival of foundresses.

## Methods

### Study sites

Abiotic habitat factors associated with local areas in which the two ant species occurred allopatrically were examined by quantifying soil composition across three contact zones in south-western New Mexico: (1) 2–4 km north of Rodeo,

Hidalgo County, elevation 1250–1265 m (31°53'N, 109°02'W), (2) 11 km north-west of Lordsburg, Hidalgo County, 1360–1365 m (32°11'N, 108°21'W), and (3) 5 km east of Separ, Grant County, 1370–1380 m (32°36'N, 108°41'W). All sites were in extensive valleys of desert scrub/grassland habitat. Dominant plants near Rodeo were tobosa grass *Pleuraphis mutica*, burroweed *Isocoma tenuisecta*, joint-fir *Ephedra* sp., soap tree yucca *Yucca elata*, honey mesquite *Prosopis glandulosa*, and white thorn acacia *Acacia constricta*. Tobosa grass dominated the Separ site, with the few shallow washes in which the two ant species occurred sympatrically also containing soap tree yucca and joint-fir. Burroweed and several grasses dominated the Lordsburg site. Visual assessment indicated that plant species composition and relative abundance of each species were similar across each of the three contact zones. Sites were separated by 43–77 km.

### Distribution and soil composition

Soil samples were collected from six 1.0-ha plots per site, three each in areas occupied by *P. barbatus* and *P. rugosus* in allopatry; plots were 55–1500 m apart. Three plots in which the two species occurred sympatrically were also included at Separ and Lordsburg. In each plot, soil samples were collected near seven randomly selected colonies (or seven per species in plots where the two species were sympatric), with the constraint that all sections of each plot were sampled. Each soil sample was taken in a random direction 2.5 m from the colony entrance. This sampling strategy allowed measurement of microhabitats typical of colony sites but avoided soil disturbance caused by ant activity. Soil samples ( $\approx 30 \times 15 \times 15$  cm) were taken from 25–50 cm below the surface to avoid differences in surface phases of the same soil series (W. Johnson, pers. comm.). Samples were passed through a 0.2-cm sieve to separate coarse fragments and soil; each fraction was then separated further. Coarse fragments were divided into four size classes (>1.9, 1.3–1.9, 0.5–1.3, and 0.2–0.5 cm) by shaking this part of the sample through a series of sieves. Fractions were dried for >24 h at 50–55 °C and weighed. Soil fractions were analysed for soil texture, i.e. percentage composition of sand, silt, and clay, using the Bouyoucos mechanical method (Day, 1965). Composition of the soil surface was not assessed because it appeared to be similar within and among sites.

Water retention and clay composition were also analysed for soils at Separ in order to assess more subtle differences between areas in which each species occurred allopatrically. Water retention was measured for each soil sample using a pressure plate apparatus that applied –0.033 and –1.50 MPa pressure to water-saturated samples until moisture content reached equilibrium (Richards, 1965). Moisture content was then determined gravimetrically as grams of water per gram of dry soil. For clay composition, the soil samples for each species were pooled into a composite sample and mixed; one subsample per species was analysed using X-ray diffraction. Soil analyses were conducted by the Soil, Water, and Plant Analysis Laboratory at the University of Arizona.

At each site, soil composition was compared between areas occupied by the two species in sympatry and allopatry using the multivariate ANOVA (MANOVA) procedure in SPSS (SPSS, 1990). Separate MANOVAs were used for each of three data sets: mass of coarse fragments and soil, size composition of coarse fragments, and soil texture. Values were expressed as percentages so that variables in each data set summed to 100%. Collinearity was reduced by first running the MANOVA on each data set and eliminating both the variable with the lowest *F*-value and variables that were not significant ( $P > 0.05$ ). Data from areas of sympatry were analysed first to determine whether the two species occupied different soil microsites. A second MANOVA compared soils from areas in which the two species occurred in allopatry and sympatry. An *a posteriori* Duncan's multiple range test was used to determine the nature of within-site differences. Data were transformed, as necessary, to meet the assumptions of MANOVA. For both transformed and untransformed variables, the assumption of homogeneity of covariance matrices was not met for size composition of coarse fragments and soil texture (Box's *M*-test,  $P < 0.001$ ).

Soil composition was also examined across sites using MANOVA; slopes were fitted separately for species within sites because of heterogeneity in slopes. This analysis examined the same three data sets as above for areas in which two species were allopatric; collinearity was reduced by eliminating one variable in each data set haphazardly prior to analysis. For two data sets, size composition of coarse fragments and soil texture, at least one variable did not meet the assumption of homogeneity of variance after various transformations. Outlier observations were deleted from each data set (three and 10 observations respectively) in order to meet this assumption. Outliers were selected visually using plots of each variable by species and by site. The assumption of homogeneity of covariance matrices was not met for either data set (Box's *M*-test,  $P < 0.001$ ).

#### Physiological measures

Physiological parameters affecting survival of foundresses include temperature tolerance, water loss rate, critical water content, and body size. Alate females were used to examine several of these parameters because foundresses were only available for short intervals following the mating flight. Females were hydrated for several hours prior to all tests by providing access to moistened paper towels.

High temperature tolerance was assessed by comparing survival for alate females of each species at 1 °C increments from 43 to 48 °C. Trials used test tubes that were partially filled with water trapped by cotton plugs. Alate females were placed into the tubes and the openings were plugged with moist cotton, providing *ad libitum* water at both ends. Trials at each temperature used 100 individuals per species, with each tube containing 25 individuals of one species; individuals in each tube were collected in approximately the same numbers from at least four colonies. A separate set of individuals was used at each temperature. The tubes were placed in a darkened

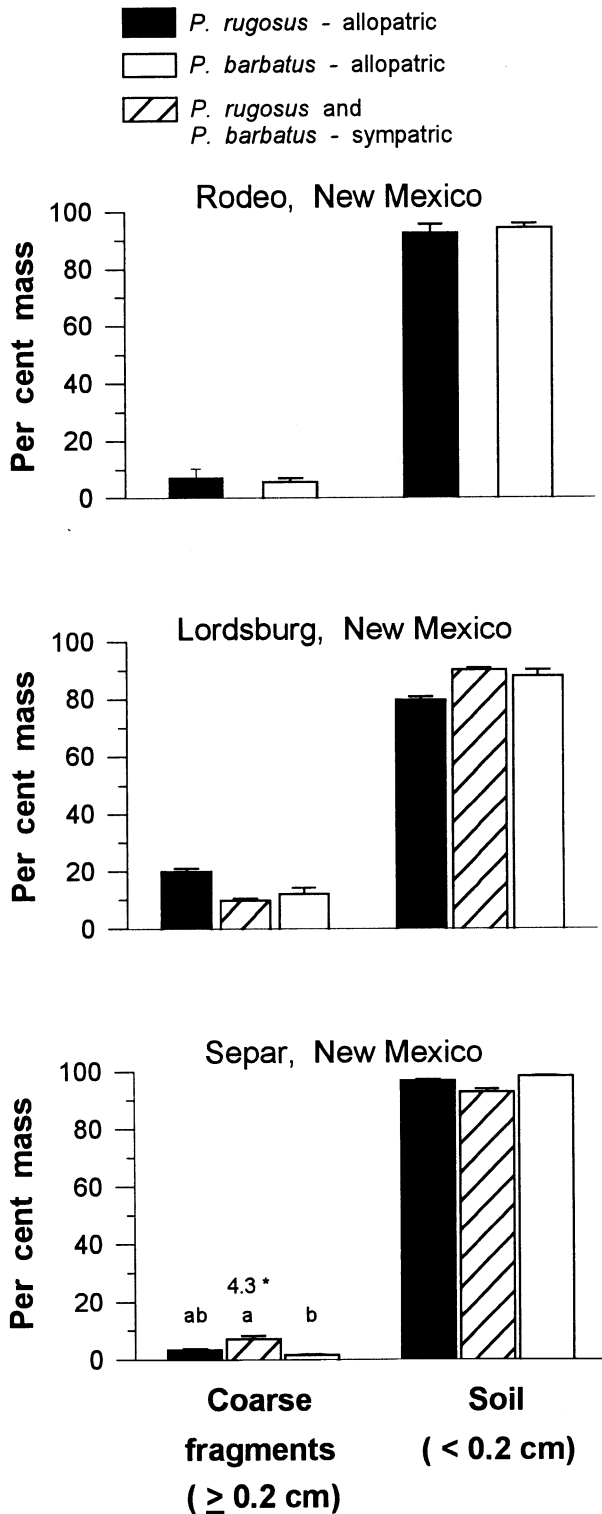
incubator for 2 h; individuals unable to right themselves after that time were considered dead.

Water loss rates in flowing air were determined for alate females and foundresses from 2-day-old nests. Ten alates from each of four colonies per species were tested at 25, 30, 35, and 40 °C; foundresses were tested at 30 °C. Ants were enclosed individually in 20 × 7 mm chambers made of rigid plastic tubes sealed at both ends with push-fit caps of stainless steel screen. In all tests, the chambers were weighed, an ant was inserted, and the chamber was reweighed. Four columns were assembled by connecting the chambers in tandem using short lengths of pliable plastic tubing; each column contained a maximum of 10 chambers with ants plus one empty control chamber. The columns were placed in a constant-temperature room, and air desiccated by Drierite (W. A. Hammond Drierite Co., Xenia, Ohio) was forced through the columns at a flow rate of 100–150 ml min<sup>-1</sup>, as controlled by a needle valve and rotameter. A Vaisala HMT 31 humidity gauge (Vaisala Inc., Boston, Massachusetts) indicated that air exiting the columns remained at <3% RH. After 8 h, the chambers and ants were weighed to 0.01 mg. The final mass for each ant was calculated then adjusted by the mean change in mass of the four control chambers. Chambers were handled using only latex gloves or forceps. Water loss rates of foundresses were also measured at 30 °C and 97.5% RH. Pre-weighed foundresses were enclosed in mesh chambers and placed on supports inside a Petri dish containing a saturated solution of K<sub>2</sub>SO<sub>4</sub>, which maintained humidity at 97.5% (Winston & Bates, 1960). After 48 h, individuals were removed from the Petri dish and reweighed. In all trials, mass loss was considered equivalent to water loss (Edney, 1977; Duncan & Lighton, 1994).

Water loss rate for each individual was calculated by dividing the water loss per unit time (µg h<sup>-1</sup>) by the estimated surface area (cm<sup>2</sup>) and the water vapour pressure saturation deficit between the inside of the cuticle and the air, yielding units of µg H<sub>2</sub>O cm<sup>-2</sup> Torr<sup>-1</sup> h<sup>-1</sup> (Torr corrects for mmHg). Surface area was estimated from an equation that relates body mass to area ( $A = 12 \times M^{0.67}$ , where *A* is surface area in cm<sup>2</sup> and *M* is initial wet mass in grams (Edney, 1977)). Vapour pressure saturation deficit varies with temperature and RH and was standardised accordingly in each test. For live ants, this calculation of water loss rate includes respiratory water loss through the spiracles. Water loss rates were compared using a two-way ANOVA with species, temperature, and species × temperature as the independent variables.

Critical water content was defined as the body water content at which an individual was unable to maintain normal locomotion and orientation, divided by its water content in a hydrated state. To determine critical water content, foundresses from 2-day-old nests were weighed and placed in the water loss chambers at 30 °C, 0% RH, and an air flow rate of 100–150 ml min<sup>-1</sup> (see above). Individuals were examined every 1–2 h until they could not right themselves, then weighed, dried for >72 h at 50–55 °C, and reweighed. Water content for hydrated and dehydrated foundresses was calculated as:  $WC = WM - DM$ , where WC is water content (mg), WM is wet mass (mg), and DM is dry mass (mg). Critical water content was calculated using the formula:  $CW = 100 \times (WCD/$

WCH), where CW is per cent critical water content, WCD is water content at the time of losing locomotor ability, and WCH is water content in a hydrated state.



Mortality curves derived from desiccating individuals integrate temperature tolerance, water loss rate, critical water content, and body size into one measure of survival. Curves were derived at 25, 30, 35, and 40 °C using 100 alate females per species taken from several locales in south-western New Mexico over 2 years. Females were collected from at least four colonies per species (<25 females per colony) for trials at each temperature then placed in the water loss chambers at 0% RH and an air flow rate of 100–150 ml min<sup>-1</sup> (see above). The two species were tested simultaneously at each temperature. In order to separate the effects of desiccation and heat stress, the 40 °C trial also included females placed in closed containers with *ad libitum* moisture supplied by moistened paper towels. Individuals that could not right themselves were counted every few hours, dried at 50–55 °C for >72 h, and weighed.

*Foundress microhabitat selection*

Microhabitat that foundresses selected to initiate nests was quantified about 4 km north of Rodeo, New Mexico, in an area where the two species were sympatric. Foundress excavations were located following a mating flight. The excavations are similar for both species, so identity of the foundress was unknown. The microhabitat for each foundress was then categorised as: (1) open area, which included bare ground away from vegetation, sites at the bases of small rocks, or small depressions, or (2) protected area, which included stands of perennial grass (*Pleuraphis mutica*) or under bushes or shrubs. The foundress was then excavated and identified. Differences in selection of these two microhabitats by foundresses of the two species were compared using a contingency table.

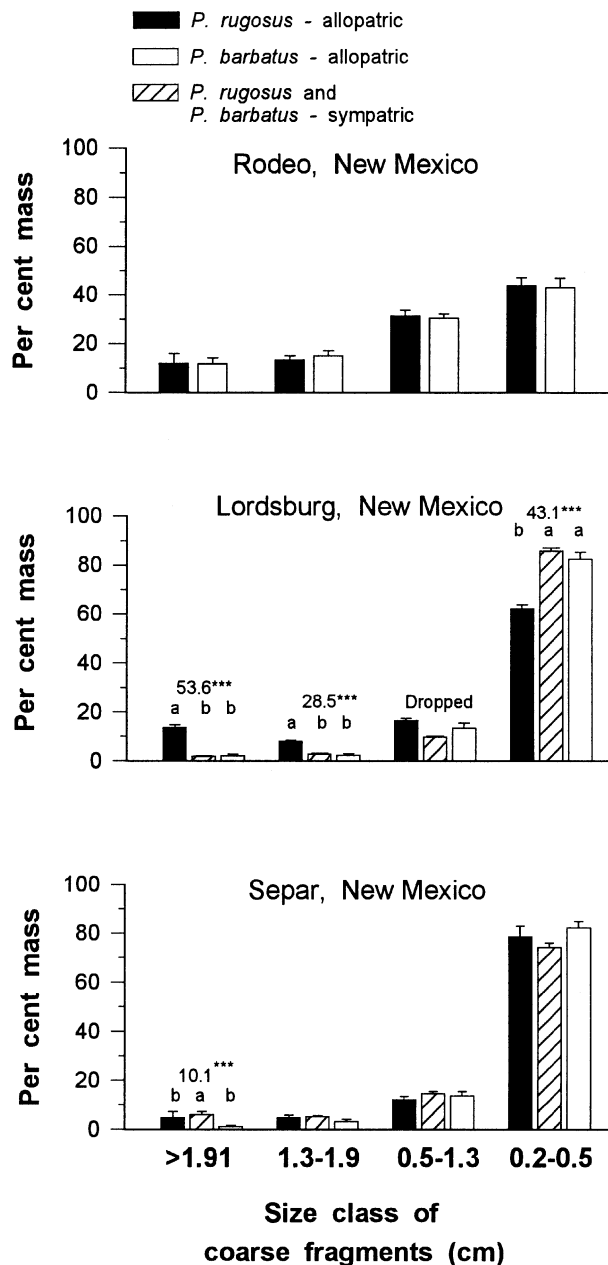
**Results**

*Distribution and soil composition*

Change in local distribution of *P. rugosus* and *P. barbatus* coincided with differences in soil composition and/or moisture retention at all three sites (Figs 1–3). At Rodeo, percentage mass of coarse fragments and the size composition of these fragments were similar in areas where the two species were allopatric (Wilks' lambda, *P* > 0.05). In contrast, soil texture

**Fig. 1.** Per cent composition of coarse fragments and soil (>0.2 and <0.2 cm diameter respectively) in samples collected from contact zones along which *Pogonomyrmex rugosus* and *P. barbatus* occurred in allopatry and sympatry (no zone of sympatry at Rodeo). *F*-values and significance levels above each soil fraction were obtained from a multivariate ANOVA: \**P* < 0.05. Within a site, significant differences among areas in which the two species occurred in allopatry and sympatry were based on an *a posteriori* Duncan's multiple range test (*P* < 0.05), and are given for each soil fraction by the letters a, b: a > b. Values that do not differ significantly have the same letter.

differed significantly between the two areas ( $F_{2,39}=8.9$ ,  $P<0.001$ ), as soils in areas occupied by *P. barbatus* contained



**Fig. 2.** Size composition of coarse fragments (>0.2 cm diameter) in samples collected from contact zones along which *Pogonomyrmex rugosus* and *P. barbatus* occurred in allopatry and sympatry (no zone of sympatry at Rodeo). *F*-values and significance levels above each soil fraction were obtained from a multivariate ANOVA: \*\*\* $P<0.001$ . Within a site, significant differences among areas in which the two species occurred in allopatry and sympatry were based on an *a posteriori* Duncan's multiple range test ( $P<0.05$ ), and are given for each soil fraction by the letters a, b, c:  $a>b>c$ . Values that do not differ significantly have the same letter. Dropped=soil fractions that were significant in an initial MANOVA but had the lowest *F*-value and were dropped to minimise collinearity.

a higher percentage mass of clay and a lower percentage mass of silt than did soils in areas occupied by *P. rugosus* ( $P<0.05$ ; Figs 1–3).

At Lordsburg and Separ, all three soil data sets were similar for the two species in areas of sympatry (Wilks' lambda,  $P>0.05$ ). Data were pooled and compared with areas in which each species was allopatric. At Lordsburg, percentage mass of coarse fragments was similar ( $P>0.05$ ; Fig. 1) but the size composition of these fragments differed across areas occupied by the two species in allopatry and sympatry ( $F_{6,158}=17.4$ ,  $P<0.001$ ); the size of these fragments was larger in areas occupied by *P. rugosus* than in areas occupied by *P. barbatus* or both species in sympatry ( $P<0.05$ ; Fig. 2). Soil texture also varied among areas occupied by the two species in allopatry and sympatry ( $F_{4,160}=47.5$ ,  $P<0.001$ ; Fig. 3), as percentage mass of sand was highest in areas occupied by *P. rugosus*, intermediate in areas of sympatry, and lowest in areas occupied by *P. barbatus* ( $P<0.05$ ). The converse pattern occurred for clay content (Fig. 3).

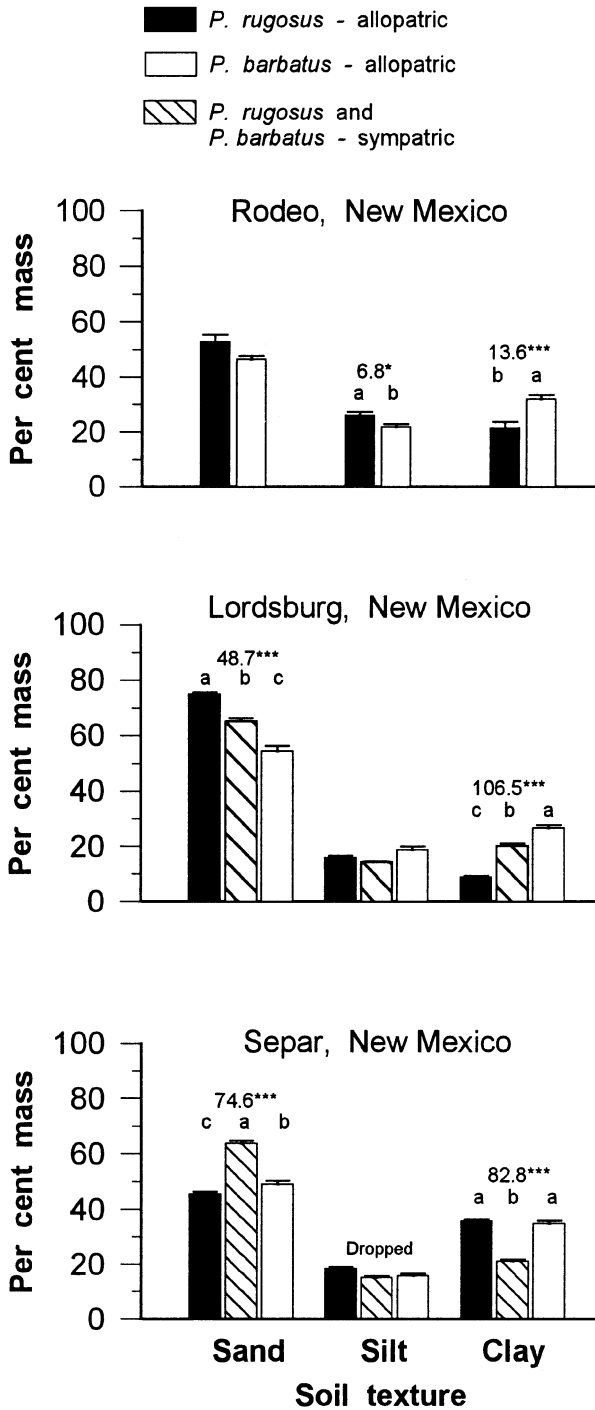
At Separ, all three soil data sets differed across areas occupied by the two species in allopatry and sympatry [ $F_{2,81}$  (percentage mass of coarse fragments)=4.3,  $P<0.05$ ;  $F_{6,158}$  (size composition of coarse fragments)=3.6,  $P<0.001$ ;  $F_{4,160}$  (soil texture)=33.3,  $P<0.001$ ; Figs 1–3]. Percentage mass of coarse fragments was higher and fragment size was larger in areas occupied by the two species in sympatry (Figs 1 and 2). For soil texture, the percentage mass of sand was higher and the percentage mass of clay lower in areas where the two species were sympatric than in areas where the species were allopatric ( $P<0.05$ ; Fig. 3). Soils in areas occupied by *P. barbatus* retained a significantly higher percentage of water than did areas occupied by *P. rugosus* at  $-0.033$  MPa (one-tailed *t*-test,  $P<0.05$ , *P. barbatus*:  $\bar{X}=28.5 \pm 1.0$ ; *P. rugosus*:  $\bar{X}=26.4 \pm 0.6$ ,  $N=42$ ) but not at  $-1.5$  MPa ( $P>0.05$ , *P. barbatus*:  $\bar{X}=16.4 \pm 0.6$ ; *P. rugosus*:  $\bar{X}=16.1 \pm 0.4$ ). X-ray diffraction indicated that soils in areas occupied by *P. barbatus* had a greater amount of the very small-particled smectite than did soils in areas occupied by *P. rugosus* (Table 1).

Analysis across sites indicated that soils varied significantly between species and among sites for all three soil data sets, except for an absence of species and species-within-site differences for percentage mass of coarse fragments (Table 2). Lower probabilities for site effects than for species effects in all three data sets indicate that site differences were greater than species differences (Table 2).

#### Physiological measures

Alate females of *P. rugosus* and *P. barbatus* had similar tolerance to high temperatures ( $5 \times 2$  contingency table analysis,  $\chi^2=2.2$ , 4 d.f.,  $P>0.05$ ; Table 3), with most individuals surviving for 2 h at temperatures up to 47 °C.

Water loss rates for alate females of *P. rugosus* and *P. barbatus* varied significantly from 25 to 40 °C [ $F_{3,312}$  (temperature)=554.4,  $P<0.001$ ; Table 4]. In contrast, water loss rates did not differ between the two species [ $F_{1,312}$  (species)=0.9,  $P>0.05$ ] or for the interaction term [ $F_{3,312}$



**Fig. 3.** Soil texture (<0.2 cm diameter) in samples collected from contact zones along which *Pogonomyrmex rugosus* and *P. barbatus* occurred in allopatry and sympatry (no zone of sympatry at Rodeo). *F*-values and significance levels above each soil fraction were obtained from a multivariate ANOVA: \**P*<0.05, \*\*\**P*<0.001. Within a site, significant differences among areas in which the two species occurred in allopatry and sympatry were based on an *a posteriori* Duncan's multiple range test (*P*<0.05), and are given for each soil fraction by the letters a, b, c: a>b>c. Values that do not differ significantly have the same letter.

**Table 1.** Relative composition of clay types in areas where *Pogonomyrmex rugosus* and *P. barbatus* occurred in allopatry near Separ, New Mexico.

	Clay type				
	Smectite	Vermiculite	Chlorite	Mica	Kaolinite
<i>P. rugosus</i>	4*	0	0	2	2
<i>P. barbatus</i>	5	0	0	2	2

\*0=not detected; 2=small amount; 3=medium amount; 4=large amount; 5=dominant.

**Table 2.** Multivariate ANOVA results for comparing soils across three contact zones along which *Pogonomyrmex rugosus* and *P. barbatus* occurred allopatrically; slopes were fitted separately for species within sites because of heterogeneity in slopes.

	d.f.	<i>F</i>	<i>P</i>
<b>Percentage mass of coarse fragments</b>			
Site	2,120	8.8	<0.001
Species	1,120	3.4	0.07
Species (Site)	2,120	0.5	0.62
<b>Size composition of coarse fragments</b>			
Site	6,230	23.8	<0.001
Species	3,115	5.9	0.001
Species (Site)	6,230	3.1	0.006
<b>Soil texture</b>			
Site	4,218	54.0	<0.001
Species	2,109	36.7	<0.001
Species (Site)	4,218	22.9	<0.001

(species × temperature) = 1.8, *P*>0.05], indicating that water loss rates for the two species were similar across a range of temperatures. Water loss rates of foundresses from 2-day-old nests were also similar for the two species at 0 and 97.5% RH (*t*-test, *P*>0.05; Table 4).

Critical water content for foundresses from 2-day-old nests was similar for both species (*t*-test, *P*>0.05; *P. rugosus*:  $\bar{X}$  = 75.0 ± 1.0%; *P. barbatus*:  $\bar{X}$  = 75.4 ± 1.0%). In both species, critical water content was correlated inversely with dry mass (mg) (*P. rugosus*:  $Y = -1.54x + 112.7$ ,  $R^2 = 0.88$ ,  $N = 12$ ,  $P < 0.001$ ; *P. barbatus*:  $Y = -1.34x + 106.0$ ,  $R^2 = 0.90$ ,  $N = 10$ ,  $P < 0.001$ ).

Alate females of *P. rugosus* survived longer than those of *P. barbatus* under desiccating conditions, although differences were not significant at 25 °C (*t*-test, *P*>0.05) (*P*<0.01 at 30 °C; *P*<0.001 at 35 and 40 °C; Fig. 4). Across the four temperatures, females of *P. rugosus* survived an average of ≈ 10% longer than females of *P. barbatus*. As expected, mean time to mortality decreased at higher temperatures in both species (Fig. 4). All females maintained at 40 °C with *ad libitum* water were alive after those exposed to desiccating conditions had died, indicating that temperature did not induce mortality. Interspecific differences in survival time were associated with dry mass, which was significantly greater, by

≈8%, for *P. rugosus* ( $\bar{X}=26.01 \pm 0.14$  mg,  $N=394$ ) than for *P. barbatus* ( $\bar{X}=24.10 \pm 0.11$ ,  $N=397$ ;  $t$ -test,  $P<0.001$ ; Fig. 5).

#### Foundress microhabitat selection

The microhabitat that foundresses selected to initiate nests did not differ between the two species ( $\chi^2=0.50$ , 1 d.f.,  $P>0.05$ ). Rather, foundresses of both species strongly preferred to start nests in barren to relatively open microhabitats and avoided sites under vegetative cover ( $P<0.001$ ; Table 5).

## Discussion

#### Local distribution pattern

The sister species *P. barbatus* and *P. rugosus* occur allopatrically along physical gradients that differ in soil texture

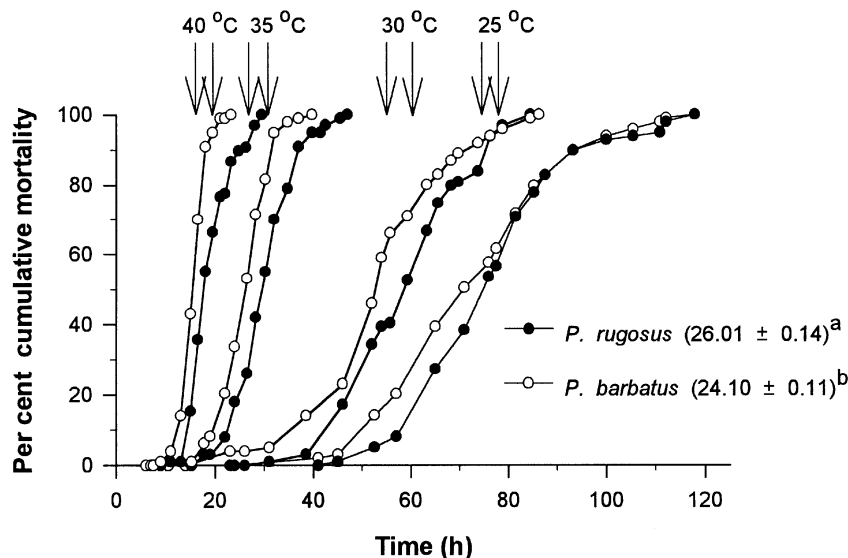
**Table 3.** High temperature tolerance for alate females of *Pogonomyrmex rugosus* and *P. barbatus*. Numbers are per cent mortality ( $n=100$  per species at each temperature) over 2 h with *ad libitum* moisture.

Temperature (°C)	<i>P. rugosus</i>	<i>P. barbatus</i>
43	0	0
44	0	0
45	2	0
46	0	0
47	49	43
48	100	100

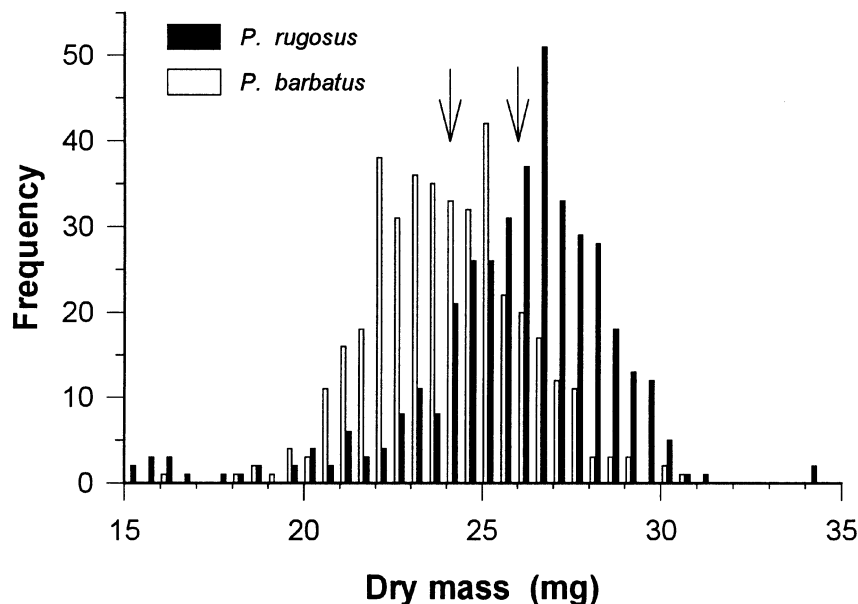
and/or moisture retention. At each of three sites, *P. barbatus* occupied areas with a higher clay content and/or soil moisture retention, as predicted by local and regional differences in geographical distribution. In contrast, soil texture did not differ between areas occupied by the two species in sympatry. The gradient of soil texture was continuous across the contact zone at Lordsburg as clay content in areas of sympatry was intermediate to that in areas of allopatry (see also Johnson, 1992). At Separ, soil texture in areas of sympatry was not intermediate to that in areas of allopatry. This difference related to the two species only occurring sympatrically in broad, shallow washes, which comprised a different habitat from that in which the species were allopatric. Across the three sites, change in ant species composition occurred along gradients in soil texture that ranged from steep to very subtle. For example, ant species composition changed from all *P.*

**Table 4.** Water loss rates in flowing air for females of *Pogonomyrmex rugosus* and *P. barbatus*. Values are means  $\pm$  1 SE;  $n=40$  per species at each temperature, except as noted in parentheses. Foundresses were collected 2 days after mating. Values are corrected for water vapour saturation deficit in Torr (see text).

Stage	Temperature		Water loss rate ( $\mu\text{g cm}^{-2} \text{h}^{-1} \text{Torr}^{-1}$ )	
	(°C)	RH	<i>P. rugosus</i>	<i>P. barbatus</i>
Alate	25	0	$4.8 \pm 0.2$	$5.2 \pm 0.4$
Alate	30	0	$7.2 \pm 0.3$	$6.7 \pm 0.3$
Alate	35	0	$8.9 \pm 0.3$	$10.0 \pm 0.3$
Alate	40	0	$11.3 \pm 0.4$	$11.3 \pm 0.4$
Foundress	30	0	$15.1 \pm 0.5$ (42)	$16.5 \pm 0.8$ (34)
Foundress	30	97.5	$76.6 \pm 8.8$ (9)	$91.3 \pm 7.8$ (9)



**Fig. 4.** Mortality curves caused by desiccation for alate females of *Pogonomyrmex rugosus* and *P. barbatus*. Each curve is derived from 100 females (maximum of 25 per colony). Pairs of curves from left to right are trials at 40, 35, 30, and 25 °C. Arrows give mean time to mortality for each curve. Numbers in parentheses are dry mass (mean  $\pm$  1 SE); significant differences are denoted by the superscripts a and b:  $a>b$ .



**Fig. 5.** Frequency distribution of dry mass for alate females of *Pogonomyrmex rugosus* and *P. barbatus* in desiccation tests (see Fig. 4). Arrows indicate species means.

**Table 5.** Microhabitat selected by foundresses of *Pogonomyrmex rugosus* and *P. barbatus* to initiate nests. See text for microhabitat descriptions.

Microhabitat	<i>P. rugosus</i>	<i>P. barbatus</i>
Open	52	81
Protected	1	3

*barbatus* to all *P. rugosus* in plots separated by 55 m at Rodeo (a steep gradient in soil texture) and across areas that differed in soil moisture retention but not soil texture at Separ (a subtle gradient in clay type). On a larger scale, segregation of the two species across sites with different soil regimes indicates that this microdistribution pattern occurs over a broad range of soil conditions. Site differences probably relate to factors that influence local soil moisture and include parent material, soil depth, rainfall, and vegetation.

Consistent differences in clay content and clay type suggest that this is the soil component that affects local distribution patterns (see also Johnson, 1992). The importance of clay in determining the physical and chemical properties of soil, including water retention, results from its large specific surface area (Marshall *et al.*, 1996). Soils with higher clay contents dry more slowly and thus provide less xeric conditions. Smaller-sized clays such as smectite have a disproportionately large influence on soil moisture. At Separ, the higher amounts of smectite in areas occupied by *P. barbatus* affect changes in water retention and ant species composition.

Soil texture might affect microdistribution patterns indirectly by influencing plant species composition and hence seeds

available to ants. This in turn may influence the ant species present. This indirect influence is unlikely given the broad range of soil regimes and associated habitats across which this distribution pattern occurred (see also Whitford *et al.*, 1976). In contrast, direct influence of soil texture is indicated by the effect of clay content on foundress mass under controlled conditions. In a companion laboratory test, foundresses of both species were placed in bottles containing either high clay or low clay soils for about 2 months. At the end of the experiment, wet mass, which was the best indicator of foundress survival and brood production, was significantly higher for foundresses in the high clay than in the low clay soils (Johnson, 1998). Over the 40–45-day interval until the first workers eclose, the 5–10% effect of clay content on foundress wet mass equates to foundresses in high clay soils surviving several days longer than those in low clay soils under desiccating conditions.

These data supplement previous studies on *P. rugosus* and indicate that soils correlate with microdistribution pattern across the geographic range of this species. In xeric western areas, *P. rugosus* is limited by sandy soils with low clay content, i.e. dry soils, where it is replaced by *Messor pergandei* (Johnson, 1992). As demonstrated here, in more mesic eastern areas *P. rugosus* is limited by soils with high clay content, i.e. wet soils, where it is replaced by *P. barbatus*.

#### *Ecological and physiological correlates of microdistribution*

Larger body size, and a correspondingly lower metabolic rate, for *P. rugosus* is the only physiological or ecological variable that has been shown to differ between foundresses of



these two species; water loss rate, critical water content, high temperature tolerance, and fat content are similar (Johnson, 1998). The estimated amount of metabolic water produced by fat metabolism is slightly greater for *P. rugosus* but the small amount of water produced by this pathway appears inconsequential for long-term water balance (Johnson, 1998). Microsite variation in success appears to result because the larger mass of *P. rugosus* provides more energy to raise brood and a greater resistance to desiccation via a decreased surface : volume ratio. The approximately 10% longer survival time for *P. rugosus* under desiccating conditions equates to  $\approx 4$  days over the interval until workers eclose. This difference, along with experimental demonstration that *P. rugosus* has a higher per cent survival of foundresses and workers, and produces more workers in dry soils, suggests that the drier soils occupied by *P. rugosus* impose an abiotic limitation on distribution of *P. barbatus* (Johnson, 1998).

The hypothesis that females of *P. barbatus* die more quickly under warm, arid conditions, which was supported, assumes that foundress mortality in natural systems is caused primarily by desiccation, and that survival patterns affect micro- and macro-distribution. Foundress mortality over the first year typically exceeds 95% in desert ants (Nagel & Rettenmeyer, 1973; Rytí & Case, 1988b; Pfennig, 1995; Wiernasz & Cole, 1995; Gordon & Kulig, 1996). During early colony stages, desiccation is probably the largest source of density-independent mortality, as the rainfall that triggers the mating flights of most desert species has short-lived effects on soil moisture (Young & Nobel, 1986; Pantastico-Caldas & Venable, 1993). Foundresses then desiccate and eventually die given insufficient subsequent rainfall (R. Johnson, unpublished). Indeed, soil and moisture conditions effect differential microhabitat survival of *P. rugosus* foundresses in other parts of this species' geographical range (Rissing, 1988b). That mature colonies of *P. rugosus* and *P. barbatus* experience water stress is indicated by their reducing or ceasing foraging activities during hot, dry periods (Whitford & Ettershank, 1975; Whitford *et al.*, 1976; Johnson, 1991), and by the tendency of young colonies to prune leaves from shrubs that compete for water (Rissing, 1988b). Such stress is more severe for foundresses and incipient colonies (Kaspari & Vargo, 1995).

In conclusion, desiccation tolerance for foundresses of these two ant species is associated with their distribution pattern along local soil moisture gradients. While desiccation stress restricts the smaller *P. barbatus* to more mesic microhabitats, the factors that restrict the larger *P. rugosus* to more xeric microhabitats are unclear. High soil moisture does not restrict either species during early colony stages and thus does not explain the absence of *P. rugosus* from more mesic microhabitats (Johnson, 1998). Other unmeasured physiological tolerances and/or biotic interactions are probably also involved in restricting *P. rugosus* to more xeric microhabitats.

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