Research article

Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae)

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Summary

A three-factor laboratory experiment (2 species × 2 soil types × 4 moisture levels) demonstrated that water is the most important factor effecting colony establishment and growth in the two ecologically equivalent sister species of desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus*. All experimental indices, percent gyne survival, gyne live wet mass, percent of gynes producing workers, and mean number of individuals (workers, larvae, and pupae), increased from low to moderate moistures and then levelled off. Soil texture also displayed a significant effect as gyne wet mass was 5–10% higher across treatments in soils that had a higher clay content. The only species effect was that *P. barbatus* gynes were smaller but produced more workers and brood than those of *P. rugosus*. That *P. rugosus* survives longer under arid conditions was demonstrated by a significantly higher number of nests with live workers in the driest treatment; number of live gynes displayed a similar pattern but differences were not significant. Additionally, *P. barbatus* produced fewer workers than *P. rugosus* in the driest treatment, while this number was higher than *P. rugosus* at all other moisture levels. Metabolic rate was higher and workers eclosed sooner in *P. barbatus* compared to the larger *P. rugosus*.

Introduction

Colony founding is the most vulnerable stage in the life of ant colonies (Hölldobler and Wilson, 1990; Tschinkel, 1992a, b; Herbers, 1993), and it is this stage that likely determines micro- and macrodistribution of adult colonies. This pattern parallels that of plants in which seed and seedling characteristics often determine adult distribution, with seed mass the most important component of success (Schall, 1980; Gross, 1984; Tripathi and Khan, 1990). The general pattern for plants is that heavier seeds (both intra- and interspecifically) have higher germination rates under similar conditions, are more successful in harsher microhabitats (Black, 1956, 1957; Stanton, 1984; Tripathi and Khan, 1990), and are advantageous where drought

stress is a major source of seedling mortality (Baker, 1972; Stanton, 1984). Similar patterns should occur in ants because foundresses are analogous to plant seeds, except that foundresses cannot remain dormant until occurrence of appropriate conditions but rather must "germinate" immediately. Such data are lacking for ants, however, as the few experimental studies that test factors effecting foundress survival and/or brood production examine one species (Waloff, 1957; Taki, 1976; Tschinkel, 1992b; Rissing and Pollock, 1987; Evans and Pierce, 1995).

This paper examines factors effecting foundress survival and brood production in the two ecologically equivalent sister species of desert seed-harvester ants *Pogonomyrmex rugosus* Emery and *P. barbatus* (F. Smith) (Cole, 1968; Taber, 1990). Though both species are sympatric across large areas of the southcentral and southwestern United States, the two rarely coexist (Whitford et al., 1976; Fig. 1) but rather segregate microhabitats based on differences in soil texture (R. Johnson,
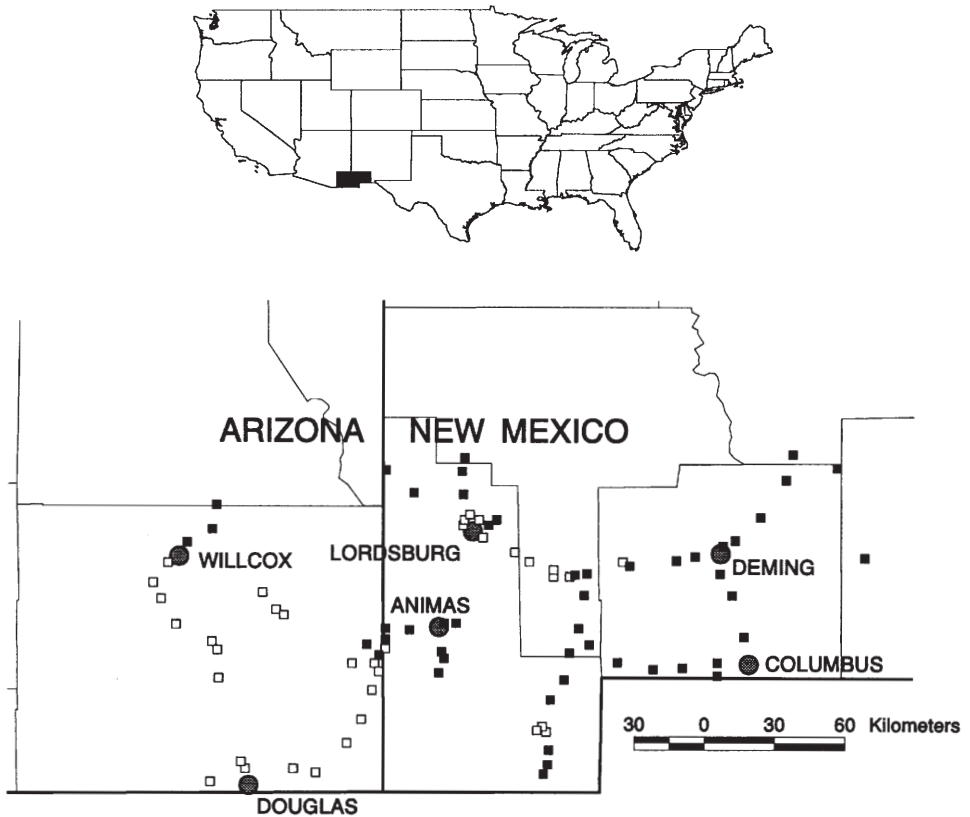

Figure 1. Distribution pattern of *Pogonomyrmex rugosus* (solid squares) and *P. barbatus* (open squares) in southeastern Arizona and southwestern New Mexico, showing allotopic distribution pattern and locations of contact zones between the species. Nest densities in the general area varied from 10–113 per hectare (R. Johnson, unpubl. data). The bold lines are state boundaries and the lighter lines are county boundaries. The map on top shows the location of the area within the United States

unpubl. data). For the several ecological and physiological variables that have been measured, only body size differs between the two species (R. Johnson, unpubl. data); dry mass of *P. rugosus* alate females averages 8% greater than that of *P. barbatus*, and the former species inhabits soils that have a significantly lower percent clay content, and thus are drier (R. Johnson, unpubl. data). Consequently, I tested experimentally the affect of moisture and soil texture on foundress survival and brood production in these two species to examine their potential for effecting microhabitat differences. Three hypotheses are tested: 1) the larger body size of *P. rugosus* confers a survival advantage under xeric conditions, 2) high moisture limits success of *P. rugosus* but not *P. barbatus*, thus explaining absence of the former species from moister soils, and 3) soils with a higher clay content, and thus higher moisture retention, effect foundress survival and brood production in a manner similar to moisture. With regard to the first hypothesis, two factors, cuticular permeability and body size, effect desiccation resistance in small arthropods like ants. Given that cuticular water loss rates for alates and foundresses are similar in both ant species (R. Johnson, unpubl. data), then survival effects related to desiccation should be influenced only by body size.

Methods

Foundress survival and brood production. Effect of soil texture and moisture on foundress survival and worker production in *P. rugosus* and *P. barbatus* were examined using a three-factor laboratory experiment (2 species × 2 soil types × 4 moisture levels); each treatment contained 26 bottles for a total of 416 bottles. The experiment used 8 ounce glass bottles, which contained 275 g of soil, 30 mls of water, and one foundress; bottles were covered with a plastic petri dish containing several holes. Soil was collected near Lordsburg, New Mexico, at two adjacent sites in which each species occurred alone; clay content differed significantly between these sites and averaged $9.02 \pm 0.40\%$ in areas occupied by *P. rugosus* alone and $26.80 \pm 0.97\%$ in areas occupied by *P. barbatus* alone (R. Johnson, unpubl. data). Soil from each area was passed through a 2 mm sieve, with that from each area mixed into a composite sample before placing into bottles. Foundresses were collected near Separ, New Mexico, as they exited the mating aggregation (*P. barbatus*) or excavated from incipient nests the following morning (*P. rugosus*). Treatments were randomly positioned in a darkened room maintained at 25–30°C. Four water levels, 0, 5, 10, and 15 mls, were added every 10 days beginning on day 20. Moreover, moisture levels mimicked wet conditions following mating, but thereafter ranged from desiccating to very wet.

Bottles were emptied after 58 days to determine foundress (hereafter gyne) condition (live or dead) and wet mass and number of live workers, pupae, and larvae. This interval allowed for assessing moisture effects on gynes and brood because it was 2–3 weeks beyond that required for worker eclosion. Gynes were dried for ≥72 h at 50–55°C and reweighed. Data were analyzed using a Kruskall-Wallis test and a three-way analysis-of-variance (ANOVA) that assessed all effects simultaneously (PROC GLM, SPSS 1990); species, soil type, and moisture level were the independent variables. The initial model included all main effects and interactions.

The final model was obtained by iterative runs that proceeded from high to low order interactions, i.e., three-way, two-way, and then main effects; the term with the highest P value was dropped after each run and the model was rerun until only significant terms remained. An *a posteriori* one-way ANOVA followed by a Duncan's multiple range test was used to determine the nature of within treatment differences for variables that differed significantly. Foundresses were not weighed at the start of the experiment. Consequently, potential treatment variation due to initial gyne wet mass (grams) was assessed by a three-way ANOVA using dry gyne head width (mm), as these two variables were positively correlated in both species (*P. rugosus*: $Y = 0.036\,X - 0.045$, $R^2 = 0.58$, $N = 40$, $P < 0.001$, *P. barbatus*: $Y = 0.025\,X - 0.022$, $R^2 = 0.35$, $N = 38$, $P < 0.001$).

Metabolic data. Foundress O_2 consumption and CO_2 production were measured by John Lighton and Barbara Joos (University of Utah, Salt Lake City) using an Ametek S-3A oxygen analyzer and LiCor infrared CO_2 analyzer. Measures were taken at 26°C and then standardized to 30°C by the transformation $Q_{10} = (k_2/k_1)^{10/T2-T1}$, where Q_{10} was assumed 2.0, k_1 and k_2 are rate measures at 26° and 30°C and T is temperature (Withers, 1992). Measures were taken intermittently for up to 84 days on 12 *P. rugosus* and 24 *P. barbatus* foundresses. During this time, foundresses were maintained in water tubes to allow normal brood development. Metabolic rate was calculated using mean wet mass of each species in water loss trials (R. Johnson, unpubl. data) because initial mass of these foundresses was not measured. Respiratory quotients were calculated as (CO_2 produced/O_2 consumed).

Fat content was measured by placing 18 dried alate females per species in individual vials of petroleum ether (boiling point 30–60°C). Females were crushed to expose fat bodies and remained in ether for ≥ 24 h. Individuals were then rinsed through filter paper, dried, and weighed to 0.01 mg.

Time to worker eclosion was quantified for each species by placing foundresses in water tubes inside a darkened incubator at 30°C. Tubes were monitored every 1–2 days until workers eclosed.

Results

That *P. rugosus* survives longer than *P. barbatus* under arid conditions is demonstrated by significantly more bottles with live workers in the 0 ml treatment (17:7; X^2 test, $P < 0.05$); number with live gynes displayed a similar pattern (5 *P. rugosus*: 2 *P. barbatus*) but differences were not significant ($P > 0.10$). For *P. barbatus*, greater stress in the 0 ml treatment was also indicated by a lower mean number of workers compared to *P. rugosus*, while this number was higher than *P. rugosus* at all other moisture levels (also see below), as predicted by emergence time and metabolic data.

Percent of bottles with live gynes varied across moisture levels for *P. rugosus* and *P. barbatus* (Kruskall – Wallis test, $P < 0.015$, $N = 16$; Fig. 2); the percentage increased from the 0 ml through 10 ml treatments and then levelled off. Live gyne wet mass varied by species and moisture level (Table 1), with *P. rugosus* being significantly heavier than *P. barbatus* (t-test, $P < 0.001$). Across moisture levels, wet
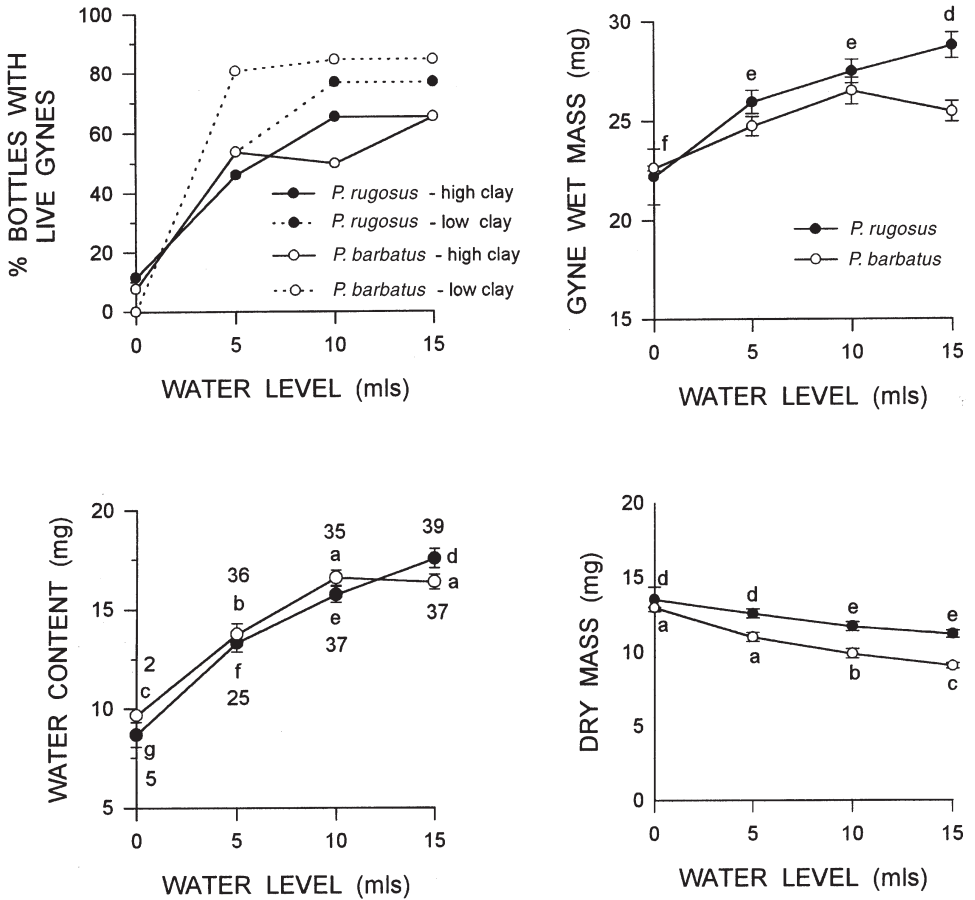
Figure 2. Percent of bottles with live gynes of *Pogonomyrmex rugosus* and *P. barbatus* and mass measures for those individuals across moisture levels in the bottle experiment. The first panel gives data by soil type for each species, while other panels pool data for live gynes across soil types. Significant differences across moisture levels are indicated by the letters a, b, c : a > b > c for *P. barbatus* and d, e, f, g : d > e > f > g for *P. rugosus*. Sample size for each species is given in the bottom left panel, *P. barbatus* above and *P. rugosus* below

mass of *P. rugosus* gynes was lowest in the 0 ml treatment, intermediate in the 5 ml and 10 ml treatments, and highest in the 15 ml treatment (Fig. 2; oneway ANOVA followed by a Duncan's multiple range test, $P < 0.05$). Wet mass of *P. barbatus* gynes did not vary significantly across moisture levels ($P > 0.12$), but displayed the same pattern as *P. rugosus* (Fig. 2). Though soil type did not effect gyne wet mass, I also examined this effect non-parametrically because of the large amount of variation. Using this analysis, mean gyne wet mass was significantly higher across all treatments, by about 0.4 mg, in soils with a higher percent clay content ($P < 0.02$, Wilcoxon rank sum test, $N = 7$).

Dry mass of gynes varied significantly between species and across moisture levels, while water content (mg) only varied across moisture levels (Fig. 2; Table 1).

Table 1. Initial and final models for a three-way analysis-of-variance for the dependent variables wet mass of live gynes, dry mass of live gynes, water content of live gynes, and number of live workers, pupae, and larvae, in the seed-harvester ants *Pogonomyrmex barbatus* and *P. rugosus* from a 3-factor bottle experiment (2 species × 2 soils × 4 moisture levels; independent variables)

	Live gyne wet mass (mg)			Live gyne dry mass (mg)			Live gyne water content (mg)			Number of workers and brood		
	df	F	P	df	F	P	df	F	P	df	F	P
Initial model	14,	2.9	(<0.001)	14,	8.7	(<0.001)	14,	8.5	(<0.001)	15,	9.3	(<0.001)
Species	1,	4.0	(0.046)	1,	23.5	(<0.001)	1,	0.1	(0.75)	1,	1.7	(0.19)
Soil	1,	0.7	(0.39)	1,	0.3	(0.58)	1,	0.7	(0.42)	1,	1.7	(0.20)
Moisture	3,	6.4	(<0.001)	3,	14.5	(<0.001)	3,	33.6	(<0.001)	3,	30.5	(<0.001)
Species × soil	1,	0.0	(0.94)	1,	1.5	(0.22)	1,	0.9	(0.36)	1,	2.9	(0.09)
Species × moisture	3,	1.7	(0.17)	3,	0.5	(0.66)	3,	2.2	(0.09)	3,	1.1	(0.37)
Species × moisture	3,	0.1	(0.95)	3,	0.2	(0.89)	3,	0.0	(0.99)	3,	0.2	(0.92)
Species × soil × moisture	2,	0.1	(0.90)	2,	1.7	(0.19)	2,	1.7	(0.18)	3,	1.4	(0.24)
Error	201			199			199			194		
Total	216			214			214			210		
R-square	0.17			0.38			0.37			0.42		
Final model	4,	8.7	(<0.001)	4,	28.9	(<0.001)	3,	35.6	(<0.001)	6,	21.3	(<0.001)
Species	1,	14.3	(<0.001)	1,	67.5	(<0.001)				1,	7.6	(0.006)
Moisture	3,	6.9	(<0.001)	3,	15.9	(<0.001)	3,	35.6	(<0.001)	3,	37.3	(<0.001)
Soil										1,	1.7	(0.19)
Species × soil										1,	6.1	(0.014)
Error	211			209			210			203		
Total	216			214			214			210		
R-square	0.14			0.36			0.34			0.39		

As expected, dry mass was significantly higher for *P. rugosus* (t-test, P<0.001). For *P. barbatus*, dry mass was highest in the 0 and 5 ml treatments, intermediate in the 10 ml treatment, and lowest in the 15 ml treatment (P<0.05), while water content was highest in the 10 ml and 15 ml treatments, intermediate in the 5 ml treatment, and lowest in the 0 ml treatment (P<0.05, Fig. 2). For *P. rugosus*, dry mass was significantly lower in the 10 ml and 15 ml treatments (P<0.05), while water content progressively increased from low to high moisture levels (P<0.05, Fig. 2). Soil type did not effect dry mass or water content (Wilcoxon rank sum test, P>0.10). Lastly, gyne head width did not vary by soil type or moisture level (P>0.45, N=212), indicating that initial wet mass did not cause any of these differences. However, as expected, average head width was significantly higher for *P. rugosus* (2.70 mm versus 2.64 mm: t-test, P<0.001).

Percent of bottles with live workers also varied across moisture levels (Kruskall-Wallis test, P<0.01, N = 16; Fig. 3), and similar to gynes increased from the 0 ml through 10 ml treatments and then levelled off (Fig. 3). I first compared number of workers and number of larvae and pupae (brood) for a similar pattern across moisture levels. The number increased from low to high moistures for both groups (Page's L statistic; workers, P<0.01; larvae and pupae, P<0.001; n = 4 soil by species treatments, k = 4 moisture levels; Fig. 3), and the data were pooled for further analysis. Total number of workers and brood varied significantly between species and across moisture levels (Table 1, Fig. 3). Number of workers and brood was significantly higher in *P. barbatus* (t-test, P<0.003). For *P. barbatus*, this number was lowest in the 0 ml treatment, intermediate in the 5 ml treatment, and highest in the 10 and 15 ml treatment (P<0.05; Fig. 3). For *P. rugosus*, number of workers and brood was lowest in the 0 and 5 ml treatments and significantly higher in the 10 and 15 ml treatments (P<0.05). Though soil type was not a significant effect, this term was retained in the final model because of the significant interaction between species and soil type (Table 1, P<0.014). This interaction resulted from *P. barbatus* producing more workers and brood than *P. rugosus* in the high clay soil, i.e., wetter soils, at the highest moisture level and fewer workers and brood in the low clay soil at the lowest moisture level (Fig. 3).

Oxygen consumption and respiratory quotients were similar for foundresses of *P. barbatus* and *P. rugosus* (t-test, P>0.15; Table 2). Respiratory quotients (RQ) near 0.71 indicate foundresses metabolize fat almost exclusively, at least while it is available. Based on oxygen consumption rates, average sized *P. barbatus* and *P. rugosus* foundresses would completely utilize fat reserves in 35.7 and 38.4 days, respectively (Table 2). Metabolism of body tissue other than fat was indicated by six RQ's that exceeded 0.9 ($\bar{X}$ = 0.98) after an average interval of 52.5 days (range = 14–84). When omitting values above 0.9, RQ's averaged 0.68 ± 0.01 (N = 57) for *P. barbatus* and 0.65 ± 0.01 (N = 35) for *P. rugosus*; 95 % confidence limits of both means were below the expected value of 0.71. Using mean alate mass, metabolic rate of *P. barbatus* was about 10 % higher than *P. rugosus* (Table 2).

As predicted by size and metabolic differences, workers eclosed significantly faster for *P. barbatus* (t-test, P<0.02, N = 26; $\bar{X}$ = 40.8 ± 0.8 days) than *P. rugosus* ($\bar{X}$ = 45.2 ± 1.6 days).

Total fat content was similar for both species at 40.80 ± 0.80 % for *P. rugosus* and 39.93 ± 0.76 % for *P. barbatus* (t-test, P>0.10, N = 18 per species).
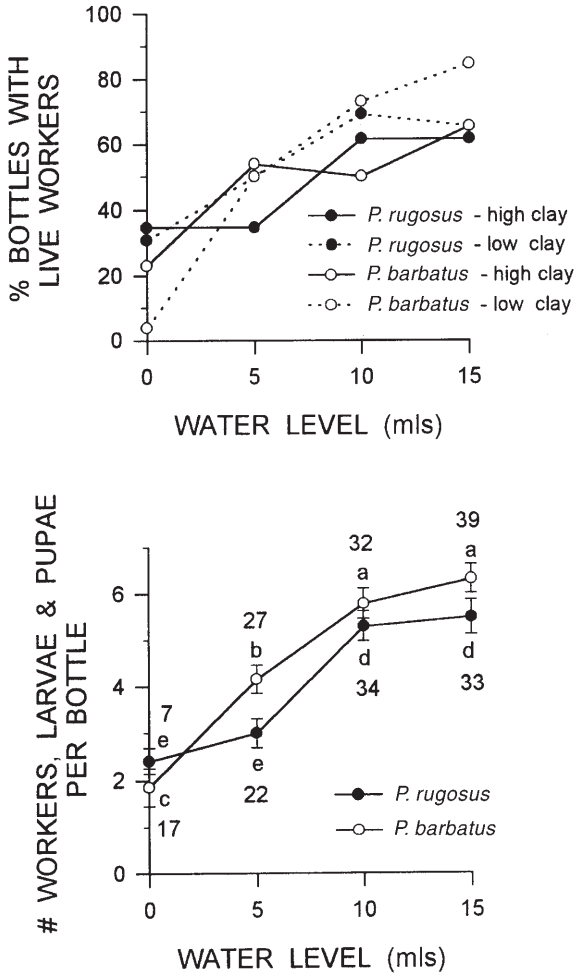
Figure 3. Worker and brood production across moisture levels for *Pogonomyrmex rugosus* and *P. barbatus* in the bottle experiment. Data are percent of bottles with live workers (top) and mean number of workers and brood (larvae and pupae) in these bottles (bottom). The top panel gives data by soil type for each species, while the bottom panel pools data for bottles with live workers and brood across soil types. In the bottom panel, significant differences in worker plus brood number across moisture levels are indicated by the letters a, b, c : a > b > c for *P. barbatus* and d, e : d > e for *P. rugosus*. Sample size for each species is given in the bottom panel, *P. barbatus* above and *P. rugosus* below

Discussion

That water is the most important factor effecting survival and establishment of *P. barbatus* and *P. rugosus* colonies is demonstrated by increases in percent gyne survival, gyne wet mass, percent of bottles with live workers, and mean number of workers and brood per bottle, from low to high moistures. Indices levelled off at moderate to high soil moistures, at which point water is no longer limiting because

Table 2. Metabolic data ($\overline{X} \pm SE$) for *P. rugosus* and *P. barbatus* foundresses at 30 °C. Values other than oxygen consumption and respiratory quotients are means as initial wet mass was not measured for tested individuals

	P. rugosus	P. barbatus
Oxygen consumption (mls/h)	0.0227 ± 0.001	0.0226 ± 0.001
Respiratory quotient	0.70 ± 0.02	0.67 ± 0.01
Mean wet mass (mg)	53.5	48.5
Mean fat content (mg)	10.404	9.640
Fat consumption (days)	38.4	35.7
Metabolic rate (mls O_2 g^{-1} h^{-1})	0.424	0.468
Metabolic water (mls)	11.13	10.31

individuals can replenish themselves by drinking (R. Johnson, unpubl. data). Field colonies typically experience conditions at the dry end of the experimental regime, while soil moistures in the 10 and 15 ml water treatments occur at best, for brief intervals following rain. Overall, moisture limitation undoubtedly occurs through at least the first year for incipient colonies, until the nest is deep enough and/or sufficient workers are present to buffer environmental harshness.

Energetic reserves must also interact with moisture to influence survival of incipient colonies. For example, gynes surviving in the 0 ml water treatment had a low mass, few workers, and no larvae or pupae, inferring a lack of body reserves to sustain themselves and brood through an additional 35–40 day cycle, even given an influx of water. Though not measured, workers in this treatment must also have experienced water stress, especially given their higher surface/volume ratio. Successful colonies such as those in the 10 and 15 ml water treatments may also succumb to extended dry periods because of decreased brood production and inability to maintain worker number until the colony is well established. Thus, quickly replenishing depleted gyne reserves should be paramount for enabling her to survive short-term decreases in moisture and/or worker number, which suggests a premium on early worker production and food collection.

Gyne wet mass was the best indicator of gyne and colony condition at the end of the experiment, as it was positively correlated with all indices of worker and brood production. This was supported by observations that gynes from low moisture treatments were docile and sluggish while those from high moistures were active and displayed typical aggressive postures. Soil type effected a consistently greater gyne wet mass in the finer-textured *P. barbatus* soils because water evaporates more slowly from soils with higher clay contents. The mean difference of 0.4 mg, though small relative to final wet mass, correlates to a 5–10 % effect given that wet mass differed by 3.8–6.6 mg across moisture treatments (Fig. 2). This approximately 10 % difference in survival time under desiccating conditions equates to about 4 days over the interval until workers eclose. Alternatively, dry mass and water content were not effected by soil type because small differences in wet mass were then partitioned between two inversely correlated variables (Fig. 3). Lower dry mass of gynes at higher moistures undoubtedly reflects the energetic cost of raising more workers and brood (see also Balas and Adams, 1996).

Larger body size for *P. rugosus* is the only physiological or ecological difference that has been measured that differs between foundresses of these two species.

Alternatively, cuticular water loss rates for alates and foundresses, fat content, high temperature tolerance, and critical water content of foundresses were similar for both species (R. Johnson, unpubl. data). Microsite variation in success then results 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. Differences in body size combined with experimental demonstration that *P. rugosus* has a higher percent survival of gynes and workers and more workers and brood in the driest soil, strongly infer that the drier soils occupied by *P. rugosus* alone impose an abiotic limitation on *P. barbatus*. Additionally, the dry soils in the 0 ml moisture treatment reflect those experienced in the field, where water potentials are regularly well below -1.5 MPa and rainfall provides only short-term increases in water potential (Young and Nobel, 1986; Moorhead et al., 1989; Pantastico-Caldos and Venable, 1993).

At the other end of the scale, high soil moisture is surprisingly not a physiological limit for either of these desert species and does not explain absence of *P. rugosus* in moister microhabitats normally occupied by *P. barbatus* alone. These results also show that gynes and developing brood do not have differential sensitivity to high moisture as both not only tolerated but did increasingly well in the near-saturated conditions present upon emptying the 10 ml and especially 15 ml water treatments. However, both species are probably limited at higher soil moistures because seeds germinate and/or rot and because of increased susceptibility to fungal attack. The only congener that occurs in very wet areas, *P. badius* in the southeastern United States, may partially escape the problem of seed rot because insects comprise a large portion of the diet (Traniello and Beshers, 1991).

Absence of high soil moisture limiting nest establishment for both species suggests that competitive interactions may restrict *P. rugosus* from areas occupied by *P. barbatus* alone, especially given that both species are highly aggressive intra- and interspecifically (Hölldobler, 1976). The mechanism may involve brood raiding, which occurs in several ants including *P. rugosus* and *P. barbatus* (Hölldobler and Markl, 1989), with winners typically having larger colonies (Bartz and Hölldobler, 1982; Rissing and Pollock, 1987; Tschinkel, 1992a, b). The advantage for *P. barbatus* then is a higher metabolic rate and faster development and emergence time, which leads to more workers than equal-aged *P. rugosus* colonies.

RQ's near 0.71 indicate foundresses of both species support themselves and brood by metabolizing fat, at least while it is available. RQ's substantially below 0.71 have also been observed in birds, and indicate that unidentified processes affect the fate of carbon dioxide, oxygen, or both (see Walsberg and Wolf, 1995). The fine-tuning of fat allocation is demonstrated by correspondence between the interval until all fat is metabolized and eclosion of the first workers (Table 2). That foundress dry mass decreased about 20% below that possible by complete metabolism of fat indicates that a substantial fraction of muscle and other body tissue can also be metabolized should outside energy sources be lacking (see Wheeler and Buck, 1996). The approximately 10 mls of water produced by fat metabolism is probably inconsequential for maintaining long-term water balance, as metabolic water only accounts for about 2% of cuticular water loss in *P. rugosus* foragers (Lighton and Feener, 1989). The only comparable metabolic rate data are for *P. rugosus* alate females calculated on a dry mass basis (MacKay, 1982). Given a

50% water content in *P. rugosus* alate females (R. Johnson, unpubl. data), oxygen consumption rates in this study, calculated on a dry mass basis, are about 37% lower than those obtained by MacKay (1982) (0.84 versus 1.35 µl O_2 mg^{-1} h^{-1}). This difference is undoubtedly caused by lower activity levels in this study as oxygen consumption was measured on single individuals and omitted data during periods of activity. Conversely, MacKay (1982) measured multiple individuals simultaneously and thus could not control for activity. Moreover, the lower rates obtained during this study likely reflect more accurate basal metabolic rates.

In conclusion, patterns of survival and brood production for foundresses of these two desert ant species are analogous to those of plant seeds in which larger size confers a survival advantage in harsher microhabitats. However, while larger seeds often germinate earlier and/or produce larger seedlings (Schall, 1980; Zimmerman and Weis, 1983; Tripathi and Khan, 1990; Zhang and Maun, 1990), the converse pattern occurs in ants because of higher metabolic rates in smaller foundresses.

Acknowledgements

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