

Biogeographical parallels between plants and ants in North American deserts (Hymenoptera: Formicidae; Spermatophyta)

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Abstract

Water is the most limiting factor in deserts, yet researchers have very different emphases on the relative importance of water, depending on the organisms that they study. For example, soil moisture is considered the most critical factor for recruitment of desert succulent plants, and numerous studies have linked plant distribution patterns with soil texture, rainfall, and soil moisture. By comparison, ant biologists have neglected the importance of water and its affect on recruitment, population dynamics, and biogeography, probably because ant communities have been viewed as stable systems that are regulated by interactions among adult colonies.

This paper argues that there are several similarities between desert plants and desert ants in regard to patterns of germination and recruitment, and that investigating and integrating these similarities will lead to better understanding population dynamics and biogeographic patterns of desert ants. Four similarities shared by these two groups of taxa include: (1) the trigger and timing of germination events, (2) early survival and establishment result from physiological tolerance, (3) propagule production and recruitment success vary across years, and (4) geographic variation in recruitment results from local and regional variation in soil moisture. Moreover, ant biologists would benefit from integrating the experiments, hypotheses, and approaches that plant biologists have used to understand population dynamics and geographic distribution patterns of desert succulent plants.

Key words: Biogeography, desert ants, population demographics, rainfall gradients, recruitment, soil moisture, soil texture, succulent plants.

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Introduction

Water is the primary factor controlling ecological processes in deserts, including demographic patterns, distribution patterns, physiological processes, response thresholds, and life history attributes of species (NOY-MEIR 1973, BEATLEY 1974, JORDAN & NOBEL 1979, 1981, GIBSON & NOBEL 1986, NOBEL 1988, ROSENTHAL & al. 2005). Dissecting these patterns and processes requires detailed information on how intraseasonal variation in timing and amount of rainfall affects response thresholds such as germination and establishment, combined with a detailed understanding of soil moisture dynamics (REYNOLDS & al. 2004). Most of this research has focused on water relations of plants, especially in regard to linking distribution patterns with soil texture, geomorphology, rainfall, and soil moisture (JORDAN & NOBEL 1979, 1981, MCAULIFFE 1994, SPERRY & HACKE 2002).

By comparison, factors affecting distribution patterns and the population dynamics of desert ants are poorly known, with most data limited to correlative studies (e.g., DAVIDSON 1977). Desert ants and desert plants have several biogeographic and life history parallels, however, and better understanding these parallels should lead to a more integrative approach to investigating population dynamics and biogeography of desert ants (for other parallels between ants and plants see ANDERSEN 1991, LÓPEZ & al. 1994). One of the most significant differences in research programs on these two groups of taxa is that plant ecolo-

gists emphasize recruitment as one of the most important mechanisms to influence demographics and distribution patterns, whereas ant ecologists emphasize food availability and intra- and interspecific competition among adult colonies. In comparison, recruitment is considered to be of minor importance for ants and has been little studied (but see ADAMS & TSCHINKEL 1995a, 1995b, WIERNASZ & COLE 1995, GORDON & KULIG 1996, COLE & WIERNASZ 2002).

Desert succulent plants and desert ants appear to share at least four similarities in regard to recruitment: (1) the trigger and timing of "germination" events, (2) early survival and establishment is the most limiting phase, with establishment resulting from physiological tolerance, (3) propagule production and recruitment success vary across years, and (4) recruitment success varies geographically, with local and regional distribution patterns correlating with soil moisture availability. Similarities between desert plants and desert ants also extend to life history traits given that many species in both taxa exhibit very high juvenile mortality combined with high adult survival. Additionally, adults in both taxa typically live for an extended number of years, and they produce large numbers of propagules during most years following maturation (iteroparity). One notable difference between the two groups, however, is that the affect of abiotic factors such as moisture should be more pronounced for ants than for plants because seeds often remain dor-

mant for several years until the occurrence of appropriate germination conditions. In contrast, ant queens "germinate" immediately, and hence cannot avoid inclement conditions in any one year. One other difference for ants is that the definition of individual shifts between recruitment (individual ant queens) and adults (colonies). Overall, these strong parallels suggest that integrating the more extensive literature on water balance and micro- and macrodistribution patterns in desert plants can greatly facilitate understanding the biogeography of desert soil-dwelling ants.

This paper takes the approach that water availability is also a primary factor affecting distribution patterns, demographics, and population dynamics for many species of desert ants. Consequently, the objectives of this paper are to examine how water affects distribution patterns of desert succulent plants and desert ants for: (1) local scale variation caused by soil texture and geomorphology (microscale distribution patterns), and (2) regional variation caused by rainfall gradients (macroscale distribution patterns).

Soil texture and soil moisture in arid systems

Rainfall has very different affects on soil moisture availability in arid and semi-arid areas compared to more mesic areas. The plentiful rainfall that occurs in mesic areas wets the soil to below the root zone, and thus becomes unavailable because of drainage. Consequently, water availability is linked to storage capacity. In contrast, rains rarely wet soils to the bottom of the root zone in arid areas, with the result that amount of available water is determined by rate of evaporation from surface layers rather than by storage capacity (ALIZAI & HULBERT 1970, NOY-MEIR 1973, REYNOLDS & al. 2004).

Soil texture is probably the most important determinant of soil water relations in arid regions because of its affect on infiltration, retention, and availability (HILLEL 1971, MARSHALL & al. 1996, MCAULIFFE 2003, REYNOLDS & al. 2004, ROSENTHAL & al. 2005). Rains rarely infiltrate to below 80 cm in desert regions of North America, and frequency of infiltration to this depth is inversely correlated with percent clay content (REYNOLDS & al. 2004). Clay content is also the largest factor to affect water retention because clays hold a larger volume of water compared to more coarse-textured soils. Clays also hold water more tightly, such that water evaporates more slowly from clays than from sands. Consequently, sandy soils have a higher (less negative) water potential than clay soils even at a lower soil water contents (HILLEL & TADMOR 1962, NILSEN & ORCUTT 1996, REYNOLDS & al. 2004, ROSENTHAL & al. 2005). However, the relationship between water content and soil water potential is also much more steep below about -1.5 MPa in sandy soils compared to loams and clay soils (JACKSON & al. 2000). Thus, relatively dry sandy soils have much lower water potentials (more negative) for plants and lower humidities for insects compared to clayey soils (NOY-MEIR 1973). Moreover, differences in soil type and soil texture effect much larger differences in water availability in xeric regions compared to mesic sites that have much wetter soil profiles (JACKSON & al. 2000).

Rocks also affect soil moisture because they can increase both infiltration of rainfall and retention of soil moisture. Rocks enhance retention of soil moisture because they block the upward movement of water to the soil sur-

face where it can evaporate; the undersurface of rocks can also act as a site of condensation. Moreover, soil beneath rocks maintains higher water potentials for longer periods of time compared to nearby soils that lack rocks (DEAN & TURNER 1991, NOBEL & al. 1992). Rocks also serve as an area for roots to get water, and this higher water availability enhances root growth under rocks (NOBEL & al. 1992). Rocks are probably also important to species of desert ants that commonly nest under them (DEAN & TURNER 1991).

Soil moisture for plants versus insects

Soil moisture influences plants and insects quite differently. Water potential is the key measure of water availability for plants, while humidity is the key measure for ants and other soil-dwelling insects. Many plant species can extract water from soils down to water potentials of about -1.5 to -2.0 MPa, with extreme values of about -6.0 to -8.0 MPa for desert plants such as creosote bush, *Larrea tridentata* (DC.) COVILLE, and triangle-leaf bursage, *Ambrosia deltoidea* (TORR.) PAYNE (HALVORSON & PATTEN 1974, SYVERTSEN & al. 1975, HAMERLYNCK & al. 2004). The lower limit at which plants can extract water from the soil is the wilting point, below which plants experience water stress.

Alternatively, humidity is the key measure related to water stress for insects such as ants because absolute amount of water loss is inversely associated with humidity (APPEL & al. 1986, HADLEY 1994). The difference between plants and insects relates to the fact that soil humidity remains very high far beyond the wilting point of most plant species. For example, soil water potentials of -1.0 MPa and -10.0 MPa correspond to humidities of about 99.3 % and 93.0 %, respectively (BRISCOE 1984). Consequently, soil-dwelling insects lose water when the soil is sub-saturated, but their absolute rate of water loss is very low under all but the most severe conditions. Ability to inhabit such stressful environments correlates with length of time that individuals can survive desiccating conditions, and this tolerance results from a combination of water loss rate, body size, and amount of body water that can be lost prior to desiccation. In arid habitats, increased body size appears to be one of the more important characters related to increasing desiccation resistance for insects (EDNEY 1977, SCHOLTZ & CAVENEY 1988, HADLEY 1994, LE LAGADEC & al. 1998, CHOWN & KLOK 2003).

Other avenues of water availability appear to be lacking in ants. Metabolic water is considered to be a minor source of body water for most insects, including ants (HADLEY 1994). Fat metabolism by ant queens appears to be inconsequential for maintaining long-term water balance, and metabolic water only accounts for about 2 % of cuticular water loss for foragers of *Pogonomyrmex rugosus* EMERY, 1895 (LIGHTON & FEENER 1989, JOHNSON 1998). Some insects can extract water from saturated vapor, but such ability requires specialized structures that are not known to occur in ants (HADLEY 1994, CHOWN & NICOLSON 2004). Moreover, ant colonies in arid or semi-arid regions will experience seasonal water stress unless the nest depth and / or nest structure provide access to water. One additional advantage that ants have over plants is that ants can take advantage of moisture and temperature gradients by moving themselves and brood throughout the soil profile.

Analogous patterns of recruitment for desert plants and desert ants

1. Germination, establishment, and physiological tolerance

Germination by desert succulent plants depends upon adequate summer rainfall (GIBSON & NOBEL 1986, JOHNSON & al. 1993). Continued survival of seedlings results from physiological tolerance because they must be able to survive the extended drought period until the next rainfall, which allows the plant to rehydrate; this rainfall thus resets the clock for drought tolerance. Seedlings are particularly susceptible to drought because their small size results in a high surface-to-volume ratio and a low water storage capacity. Consequently, length of drought tolerance is positively associated with age/size for seedling succulent plants. For example, a 4-week-old seedling of desert agave, *Agave deserti* ENGELM., can tolerate 2 weeks of drought, whereas a 15-week-old seedling can withstand 12 weeks of drought (JORDAN & NOBEL 1981, NOBEL 1988). By comparison, mature individuals can survive very extended droughts because they have low surface-to-volume ratios and can store much larger volumes of water. Moreover, two easily measured variables (plant size and water storage capacity) affect drought tolerance in desert succulent plants, making them a system that is particularly well-suited to examine how physiological tolerance influences recruitment.

Desert ants display a wide range of strategies in regard to timing and triggers for mating flights, but the vast majority of species have mating flights that are triggered by summer rains. Notable exceptions to this pattern include several species that appear to have evolved in hot desert habitats, including *Pogonomyrmex californicus* (BUCKLEY, 1867), *Pogonomyrmex magnacanthus* COLE, 1968, *Messor* spp., and *Aphaenogaster megommata* M.R. SMITH, 1963 (JOHNSON 2000b).

Desiccation tolerance of queens has been long recognized as a factor correlated with distribution patterns of ants (TALBOT 1934, KASPARI 1993), but few studies have examined physiological aspects of nest founding. Studies on three species of desert seed-harvester ants, *Pogonomyrmex barbatus* (F. SMITH, 1858), *P. rugosus*, and *Messor pergandei* (MAYR, 1886), demonstrate that moisture is positively associated with queen survival, queen condition (higher wet mass and fully hydrated), and number of first brood produced (JOHNSON 1998, 2000a, R.A. Johnson, unpubl.). Larger queens might also have a higher desiccation tolerance given that they have lower surface-to-volume ratios and proportionately higher volumes of water (R.A. Johnson, unpubl.). This pattern suggests that desiccation tolerance may underlie the finding that larger queens of *Pogonomyrmex occidentalis* (CRESSON, 1865) are significantly more likely to survive early stages of colony founding (WIERNASZ & COLE 2003).

In the manner that seedling size is correlated with length of drought tolerance in cactus, so might colony size (number of workers) be correlated with physiological tolerance for ant colonies. The few available data support this hypothesis. Desiccation tolerance was significantly longer for colonies than for solitary queens of *Solenopsis invicta* BUREN, 1972, with the workers appearing to catabolize their own tissue to maintain the queen, such that she was typi-

cally one of the last individuals to die (KASPARI & VARGO 1995). Similarly, it was estimated that founding queens of *M. pergandei* could survive 3 - 4 weeks of desiccating conditions in the field, whereas all mature colonies and numerous 8-month-old colonies survived a drought that lasted about 140 days (R.A. Johnson, unpubl.). Higher desiccation tolerance for grouped compared to solitary queens might also favor nest founding behaviors such as pleometrosis (cooperative associations of unrelated queens) (CAHAN 1999, R.A. Johnson, unpubl.) in a manner similar to that observed for grouping by other insects (YODER & SMITH 1997, KLOK & CHOWN 1999).

Some desert ants (e.g., *Myrmecocystus* spp. in the New World, *Melophorus* spp. and *Camponotus inflatus* in the Old World) have a specialized replete caste that can store water, nectar, or fluids from extrafloral nectaries. This storage behavior might be analogous to water storage by cactus if the ants can use these fluids to decrease the affects of desiccation during dry periods. Honeydew might also provide an external source of fluids for some species. Note, however, that such sources of fluids are often lacking because plant species that provide extrafloral nectaries, especially cactus, are scattered or rare in most of the extensive alluvial valley habitats in North American deserts.

2. Annual variability in reproductive effort

Desert succulent plants display high annual variability in reproductive effort that is positively correlated with rainfall. Flower production is positively correlated with rainfall for several species of cactus, suggesting that water availability limits flower production (BRUM 1973, STEENBERGH & LOWE 1977, HEINS & al. 1981, JOHNSON & al. 1993).

Few data are available on annual variation in production of reproductive sexuals by desert ants. Similar to many desert succulent plants, colonies of *M. pergandei* produce significantly fewer reproductive sexuals in dry than in wet years (RYTI & CASE 1988, CAHAN 2001b). One other study examined annual variation in production of reproductive sexuals by *P. occidentalis*, but did not examine the possible affects of abiotic factors on reproductive output (COLE & WIERNASZ 2000).

3. Population dynamics and demography

Population dynamics and demographic patterns of desert succulent plants are also correlated with annual variation in rainfall. For example, number of new seedlings and percent survival by juveniles of acuña cactus, *Echinomastus erectocentrus* var. *acunensis* (W.T. MARSHALL) L. BENSON, were both positively correlated with summer rainfall across four years. In contrast, adult mortality rate did not vary over these same four years, indicating that the affect of low rainfall on survival is disproportionately concentrated on young plants (JOHNSON & al. 1993). Other studies found distinct size classes in populations of two species of cactus, the barrel cactus, *Ferocactus acanthodes* (LEM.) BRITT. & ROSE, and saguaro, *Carnegiea gigantea* (ENGELM.) BRITT. & ROSE. Year of establishment of each size class could be back-calculated based on the relationship between stem height and plant age. Rainfall data were then used to model soil water potential, which allowed calculating length of the maximum drought in each year, i.e., days in which water could not be taken up by the plants. Number of

days in which water could be taken up by plants was then graphed against number of days that a plant can withstand desiccation, providing a predictive model for determining years in which establishment did and did not occur (see JORDAN & NOBEL 1979, 1981, 1982, YOUNG & NOBEL 1986). Annual variation in establishment also influenced population age structure because a much higher proportion of juveniles occurred at sites with increased summer rainfall compared to those located at drier sites (JORDAN & NOBEL 1982).

Population dynamics and demographics of desert ants are probably also associated with annual variation in rainfall, but few data are available. A population of *P. barbatus* displayed high annual variability in number of newly recruited colonies over six years, but possible abiotic factors influencing this variation were not assessed (GORDON & KULIG 1996). Additionally, a long-term census indicated that recruitment occurred in only 4 of 12 years for a central Arizona population of *M. pergandei*. Years in which recruitment occurred had higher amounts of rainfall in the several months following nest founding than did years in which recruitment was lacking (R.A. Johnson, unpubl.). Overall, these data suggest that desert ant populations show cohorts of recruitment, similar to the pattern exhibited by desert succulent plants. Unfortunately, colony age is difficult to obtain for ants in comparison to obtaining size/age classes for cacti. The best available method appears to be the labor intensive task of excavating colonies and collecting the queen, which could then potentially be aged by examining rates of sperm depletion (TSCHINKEL 1987).

4. Microdistribution patterns

Desert plants also show strong local distribution patterns that are driven by variation in soil texture, soil development, and geomorphology. One highly visible pattern of variation in local distribution and species composition occurs near the base of desert mountain ranges, along the gradient of gently sloping bajadas to the nearly level basin floors (YANG & LOWE 1956, KLIKOFF 1967, MCAULIFFE 1994, HAMERLYNCK & al. 2002). Density, species composition, and distribution pattern also vary across subtle and visually unrecognizable ecotones in the basin floors because of marked local heterogeneity in soil properties (BESTELMEYER & al. 2006). These variations in local soil properties influence distribution and availability of soil moisture, which can effect local variation in seedling establishment (HARRINGTON 1991, TOFT 1995, MAESTRE & al. 2003) in a manner similar to annual variation in establishment within a site (see above). Ecological and physiological attributes of plants also influence local scale distribution patterns. For example, cacti often occur in sandy, highly porous soils, probably because these soils hold water at the high water potentials that cacti often require for water uptake (NOBEL 1988).

Soil texture and soil moisture have long been associated with microdistribution patterns of ants (COLE 1934, TALBOT 1934, GREENSLADE 1976, 1987). Soil properties often exhibit significant local variation in arid regions, such that distribution, composition, and physiological properties of desert organisms can shift over very short distances. For example, ant species composition changed from all *P. rugosus* to all *P. barbatus* in 1 ha plots that were separated by only 55 m at a site in the Chihuahuan Desert

(JOHNSON 2000a). The few studies that have addressed these observations quantitatively relate to analyses of soil texture (JOHNSON 1992, 2000a) and soil moisture (HOLWAY & al. 2002, HOLWAY & SUAREZ 2006). In one case, the closely related and ecologically equivalent species *P. barbatus* and *P. rugosus* have broadly overlapping geographic distributions, but the two species occur sympatrically only in localized contact zones. Segregation between the two species occurred along a gradient of soil texture, with both species co-occurring only in areas of intermediate soil texture. *Pogonomyrmex rugosus* inhabited more coarse-textured soils (drier soils with lower clay content), which correlated with the larger body size and increased desiccation resistance by founding queens of this species (JOHNSON 2000a). The effect of soil texture was most pronounced under very dry conditions, where the smaller queens of *P. barbatus* produced fewer brood than *P. rugosus*, whereas *P. barbatus* queens produced more brood than *P. rugosus* at all higher moisture levels (JOHNSON 1998).

The second case involves the seed-harvester ants *P. rugosus* and *M. pergandei*, which also have broadly sympatric geographic distributions, and similarly, the two species rarely occur in sympatry. Segregation of these two species also occurs along a soil texture gradient, and again the two species occur sympatrically only in areas of intermediate soil texture (JOHNSON 1992). Interestingly, the mechanism causing this sharp shift in species composition might differ for these two pairs of species. Strong intra- and interspecific interactions occur between colonies of *P. rugosus* and *P. barbatus* (HÖLLDOBLER 1976, HÖLLDOBLER & MARKL 1989), suggesting that competitive interactions may be involved in producing this gradient. Alternatively, *P. rugosus* and *M. pergandei* do not display aggressive interspecific interactions (nests can be next to one another and their foraging columns can cross one another without incident) (R.A. Johnson, pers. obs.), suggesting that interspecific interactions are not involved in producing this gradient.

5. Macrodistribution patterns

Desert plants also show strong geographic distribution patterns that are driven by rainfall gradients. As amount of summer rainfall decreases, such as across the gradient from the Chihuahuan Desert in the east to the Mohave Desert in the west, so does the percentage of years in which seedling establishment occurs. At some point, increasingly low seedling establishment results in a geographic range limit due to demographic constraints. For example, saguaro cactus occur at sites where $\geq 10\%$ of the years are suitable for seedling establishment, but not in areas where $< 10\%$ of the years are suitable (JORDAN & NOBEL 1982, NOBEL 1988). Species vary in this percentage (JORDAN & NOBEL 1979, 1981), which should result in predictable patterns of species loss across rainfall gradients. That insufficient summer rainfall limits geographic distributions via seedling establishment is also supported by the fact that adults of these same species can be transplanted into and survive in areas where they do not occur naturally (GIBSON & NOBEL 1986).

A decrease in summer rainfall across the gradient from the Chihuahuan to the Mohave Deserts results in parallel patterns of geographic distribution for ants, but the factors causing these similar patterns for plants and ants were sug-

gested to be different. While distribution patterns of desert succulent plants were suggested to be directly influenced by rainfall (see above), those of harvester ants were suggested to be indirectly influenced by rainfall. The predictive basis of the pattern for harvester ants was derived from the correlation between productivity (i.e., seeds produced by annual plants) and precipitation in arid regions (ROSENZWEIG 1968), with the idea that ant species richness should be positively correlated with seed abundance (the seed limitation hypothesis). That harvester-ant species richness was positively associated with total annual rainfall across a broad geographic area provided indirect support for the seed limitation hypothesis (DAVIDSON 1977).

An alternative hypothesis, the recruitment limitation hypothesis, was later suggested to also explain this gradient in species richness. This hypothesis differed in that it emphasized the direct affect of rainfall on geographic distribution patterns and patterns of species richness. Based on this hypothesis, insufficient summer rainfall would preclude triggering mating flights and/or result in xeric conditions subsequent to flights that would limit colony establishment in drier, more western locales (or in drier years) (JOHNSON 2001). It is unclear what specific predictions can be made relative to the order of species loss under the seed limitation hypothesis, whereas the recruitment limitation hypothesis offers several testable predictions. The first prediction for the recruitment limitation hypothesis is that ant species that have mating flights triggered by summer rainfall should drop out of the fauna in drier western locales, combined with these species being replaced by congeners whose mating flights are triggered by events other than rainfall (e.g., photoperiod) (JOHNSON 2000b, 2001). This predicted pattern of species replacement occurs in western Arizona as species with mating flights triggered by summer rainfall drop out of the fauna (e.g., *Pogonomyrmex desertorum* WHEELER, 1902, *Pogonomyrmex maricopa* WHEELER, 1914, *Pogonomyrmex pima* WHEELER, 1909, *Aphaenogaster cockerelli* (ANDRÉ, 1893), while species that are added are those that have mating flights triggered by photoperiod (e.g., *P. magnacanthus*, *A. megommata*) (JOHNSON 2000b).

A second prediction of the recruitment limitation hypothesis relates to the idea that body size is a large contributor to desiccation tolerance in arid systems (see above and HADLEY 1994, KLOK & CHOWN 2003). Assuming that desiccation tolerance is positively correlated with body size, then species that have mating flights triggered by summer rainfall should drop out of the fauna in a predictable pattern as amount of summer rainfall progressively decreases further to the west, i.e., the smallest, least desiccation tolerant species should drop out first, and the largest, most desiccation tolerant species should drop out last. Geographic distribution data support this prediction as *P. pima* (1.5 mg dry mass for queens) drops out first, followed by *P. desertorum* (12.2 mg dry mass for queens), then *P. maricopa* (16.4 mg dry mass for queens), and lastly *P. rugosus* (26.5 mg dry mass for queens), which occurs throughout most of these desert areas (JOHNSON 2000b). A similar pattern occurs for *Aphaenogaster albisetosa* MAYR, 1886 (19.7 mg dry mass for queens) and *A. cockerelli* (21.2 mg dry mass for queens). These two species segregate habitat by elevation, with the larger *A. cockerelli* inhabiting lower, hotter, and drier locales (CREIGHTON 1955). As might

be predicted, only the larger, more desiccation tolerant *A. cockerelli* occurs in drier, more western areas of Arizona and southern California. In these areas, *A. cockerelli* inhabits rocky hillsides at higher elevations, and thus displays a habitat shift relative to other portions of its range (SNELLING & GEORGE 1979, JOHNSON 2000b).

A powerful approach to separating the seed limitation and the recruitment limitation hypotheses involves examining intraspecific variation across this rainfall gradient. Two such cases involve variation in mode of nest founding. In the first case, *M. pergandei* displays a shift from haplometrotic (solitary queens) to pleometrotic nest founding across a narrow transition zone in southern California (CAHAN & al. 1998, CAHAN 2001a). A survey of ecological factors across this zone found that pleometrosis was correlated with areas of decreased rainfall, lower vegetation biomass, and lower adult colony density (CAHAN 2001b). Decreased colony density associated with decreased productivity supports the seed limitation hypothesis, whereas changes in mode of nest founding and possible changes in rates of nest establishment support the recruitment limitation hypothesis. Queen body size also varies across this gradient, with haplometrotic queens being larger than pleometrotic queens (CAHAN & RISSING 2005). Moreover, variation across this zone makes it ideal for examining hypotheses related to mode of nest founding and environmental constraints on nest establishment in desert ants. Similar studies should investigate geographic variation in nest founding behaviors in other desert ants (see RISSING & al. 2000).

The second case of intraspecific variation involves *P. pima*, which displays a queen dimorphism that consists of winged (alate) and wingless (intermorph) queens. The generally accepted pattern of nest founding in such species is that alate queens initiate nests via independent colony founding (with very low survival rates) and that intermorph queens initiate nests via colony fission (with high survival rates). Such queen polymorphisms have been suggested to be common in deserts, especially in cases where success at independent colony founding is very low (TINAUT & HEINZE 1992, HEINZE & TSUJI 1995). Consequently, the frequency of each queen type is predicted to vary geographically in relation to potential survival of dealate founding queens. Summer rains trigger the mating flights of *P. pima*, leading to the prediction that successful nest founding by dealate queens should decrease at sites that have lower amounts of summer rainfall. In this case, preliminary data support the recruitment limitation hypothesis because the proportion of nests with each queen phenotype varies geographically; a central Arizona population (summer rainfall ~ 11 cm) contained 60 % intermorph versus 40 % dealate queen colonies, whereas a population in much drier areas of western Arizona (summer rainfall ~ 5 cm) contained 80 % intermorph versus 20 % dealate queen colonies (R.A. Johnson, unpubl.).

***Messor pergandei* and *Pogonomyrmex rugosus* as complementary species to understand water balance**

The different patterns of foraging consistency for these two species suggest that water availability is much lower for mature colonies of *P. rugosus* compared to those of *M. pergandei*, even in areas of sympatry. Colonies of *P. rugosus* forage for limited periods following rainfall, whereas col-

onies of *M. pergandei* forage throughout the year (RISSING 1987). That water availability limits foraging activity of *P. rugosus* is supported by observations that watering a colony induces foraging for up to several days (see JOHNSON 1991). In contrast, colonies of *M. pergandei* appear to have access to water given that they send out extensive foraging columns on a daily basis, even though foragers lose substantial amounts of water during a foraging period (FEENER & LIGHTON 1991). That *M. pergandei* have access to water is also supported by data showing that field colonies contained fully-hydrated alate queens over a two-week period in a very dry year, whereas founding queens from upper levels of the soil profile exhibited significant levels of desiccation over the same interval (R.A. Johnson, unpubl.).

Differences in water relations between the two species could result from nest structure and/or nest depth (TSCHINKEL 2003), or the two species might differ in morphology, physiology, or ability to regulate their nest microenvironment. Nests of both *M. pergandei* and *P. rugosus* extend to at least 3 - 4 meters deep (TEVIS 1958, MACKAY 1981), but no studies compare nest depth for the two species in areas of sympatry. Some species of *Pogonomyrmex*, including *P. rugosus*, also clear their nest mound of vegetation, which appears to increase soil moisture content in some portions of the nest (ROGERS & LAVIGNE 1974, LAUNDRE 1990). No information is available on how morphology, physiology, or ability to regulate nest microenvironment might differ between the two species. Overall, these two species appear to have significantly different water budgets, and determining the cause for these differences would lend to understanding the various physiological strategies used by these and other desert ants.

Measuring and modeling soil moisture

Plants provide one of the best systems to examine how limited availability of water affects population dynamics, productivity, and distribution patterns because soil texture, soil water potential, and leaf water potential can be measured directly. Consequently, physiological response by conspecific individuals can be used to measure variation in water availability across microhabitats that vary in such as soil texture. In desert habitats, such comparative studies predict that coarser-textured soils capture and store rainfall more efficiently than finer-textured soils (see above). At the extreme, coarse-textured sand dunes are considered to be the equivalent of mesic desert islands because soil water potential and plant water potential are higher in dunes than in nearby off-dune sites (SPERRY & HACKE 2002, ROSENTHAL & al. 2005). In a similar manner, plant water potential for individuals of creosote bush differed across several soils that varied in horizon development and soil hydrologies (HAMERLYNCK & al. 2000, HAMERLYNCK & al. 2002, HAMERLYNCK & al. 2004). Microhabitat variation in water limitation also influences physiological performance because water use efficiency (ratio of dry matter production to water consumption) increased as soil water availability decreased (EHLERINGER & COOPER 1988). Unfortunately, such detailed techniques are not available for ants or other soil invertebrates. However, these studies can be used to better understand microhabitat variation in water availability and how this variation might affect microdistribution patterns of desert ants. These studies can also be used to address novel questions about desert ants, such as

possible microhabitat variation in physiological performance. One simple study would be to examine variation in water-related foraging limitations for a species that occurs across several soil texture microhabitats that differ in water availability.

Soil moisture and water availability can be measured in several ways (MARSHALL & al. 1996), but all methods have limited capability as they are very time consuming and/or expensive, and all methods have a very limited ability to replicate measures within and across sites. Consequently, measurements of seasonal water dynamics are exceedingly few in number in non-agricultural soils of arid and semiarid regions (see also MCAULIFFE 2003). As a result, several models of soil moisture dynamics have been developed, and sometimes verified with field data (YOUNG & NOBEL 1986, FLERCHINGER & SAXTON 1989a, 1989b, McDONALD & al. 1996, KEMP & al. 1997). Models that estimate water availability typically include daily data on precipitation and evapotranspiration (measured as a combination of wind, radiation, and humidity), possibly in combination with variables such as soil texture, soil depth, and the relationship between soil water volume and soil water potential. The importance of intra-seasonal patterns on biological processes has also become apparent in recent years, such that these models also include variability in rainfall event size, frequency, and timing (BEATLEY 1974, REYNOLDS & al. 2004, SCHWINNING & al. 2004). Moreover, these models can become valuable tools to predict complex processes of soil water dynamics, which in turn can be used to predict biological processes and events that include developing mechanistic models for species distributions. Recruitment events and distribution patterns in desert succulent plants appear to be closely linked to the maximum length of drought (JORDAN & NOBEL 1979, 1981, 1982, YOUNG & NOBEL 1986), and it seems likely that such rainfall linked patterns of recruitment should also occur for soil invertebrates such as ants. This hypothesis is being tested by modeling soil moisture patterns in years with recruitment versus years lacking recruitment for the seed-harvester ant *M. pergandei* (R.A. Johnson, unpubl.).

Conclusions

Ant biologists are in the early stages of understanding biogeography of desert ants compared to that for species of desert plants. However, the several parallel patterns of recruitment and life history between the two groups suggest that ant biologists can greatly benefit by integrating experiments, hypotheses, and approaches to population demographics and geographic distribution limits that have been used by plant ecologists. In particular, ant biologists have neglected studies on recruitment and water balance, whereas such studies have been a focal area of research for plant ecologists. The deficit of studies on recruitment by ants probably relates to the view that ant communities are stable systems that are regulated by territorial aggression and food limitation, and that recruitment plays a minor role in producing this structure. This view needs to be adjusted, however, given that more extensive studies demonstrate temporal variability in colony density. One population of *P. barbatus* displayed a > 2-fold increase in colony density over five years (GORDON & KULIG 1996), and density of *P. occidentalis* colonies was limited by lack of recruitment (WIERNASZ & COLE 1995, BILICK & al. 2001,

COLE & WIERNASZ 2002, BILICK & al. 2004), even though space was presumed limiting in both systems. Density of *P. rugosus* colonies also decreased dramatically during a long-term study in the Chihuahuan Desert (BROWN & al. 1997). Similarly, population dynamics of *M. pergandei* can also vary dramatically through time, even though colonies appear to compete intraspecifically for food and space (RYTI & CASE 1988). Interestingly, plant ecologists have found that level of intraspecific competition and rates of mortality and growth can vary across different soils (HAMERLYNCK & al. 2002). It seems likely that similar patterns occur for desert ants, such that degree of community stability might vary across habitats.

Plant ecologists have also developed ideas and hypotheses that are likely to enhance our understanding of ant communities. One hypothesis suggests that variation in soil texture and soil moisture should result in plants having deeper root profiles in coarse-textured than in fine-textured soils (JACKSON & al. 2000, SPERRY & HACKE 2002). Such a pattern could occur in ants via intraspecific variation in nest depth or structure. Second, geographic variation in plant population demographics promotes understanding how variation in factors such as rainfall can affect population structure and dynamics. Similar patterns of population demography probably occur for both desert plants and ants, but such patterns are much more difficult to measure for ants. One alternative is to conduct long-term studies that correlate recruitment with events such as rainfall, combined with experiments that manipulate water availability to incipient colonies. Third, plant ecologists have shown that physiological performance can vary for individuals that live in different microhabitats, and these ideas might also apply to ants. Lastly, integrating studies on desert plants provide a stronger understanding of microhabitat variation as well as the potential causes and processes that lead to habitat specialization such as that exhibited by the several desert ant species that are largely restricted to sand dune habitats (JOHNSON 2001).

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Zusammenfassung

In Wüsten ist Wasser der am stärksten limitierende Faktor, aber Forscher fokussieren – abhängig von der untersuchten Organismengruppe – in ihren Studien in unterschiedlichem Ausmaß auf Wasser. Zum Beispiel gilt die Bodenfeuchte als der entscheidendste Faktor für das Überleben von Wüstensukkulanten, und zahlreiche Studien haben die Verbreitungsmuster von Pflanzen mit Bodenstruktur, Niederschlag und Bodenfeuchte in Beziehung gesetzt. Damit verglichen, haben Ameisenkundler die Bedeutung von Wasser und dessen Einfluss auf Überleben, Populationsdynamik und Biogeographie vernachlässigt. Das liegt wahrscheinlich daran, dass man Ameisengemeinschaften als stabile Systeme betrachtet, die durch Interaktionen zwischen adulten Kolonien reguliert werden.

Vorliegende Arbeit zeigt auf, dass es zwischen Wüstenpflanzen und Wüstenameisen eine Reihe von Ähnlichkeiten gibt, was Gründung und Überleben von Populationen anlangt, und dass das Untersuchen und Berücksichti-

gen dieser Ähnlichkeiten zu einem besseren Verständnis von Populationsdynamik und biogeographischen Mustern bei Wüstenameisen führen wird. Die beiden Gruppen weisen vier Ähnlichkeiten auf: (1) Auslösen und Zeitsteuerung von Gründungsereignissen, (2) Überleben und Etablieren junger Populationsstadien abhängig von physiologischer Toleranz, (3) zwischen den Jahren variierende Produktion von Ausbreitungseinheiten und deren Überlebenserfolg und (4) aus lokalen und regionalen Unterschieden in der Bodenfeuchte resultierende geographische Unterschiede im Überlebenserfolg. Ameisenkundler würden davon profitieren, jene Hypothesen und experimentellen Ansätze zu integrieren, welche Botanikern zu ihrem Verständnis von Populationsdynamik und geographischen Verbreitungsmustern von sukkulenten Wüstenpflanzen verholfen haben.

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