

# BIOGEOGRAPHY AND COMMUNITY STRUCTURE OF NORTH AMERICAN SEED-HARVESTER ANTS

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■ **Abstract** Seed-harvester ants are a dominant and conspicuous insect group throughout arid portions of the southwestern United States and northern Mexico, and they include ~75 species. Intense study in the late 1970s and early 1980s led to the paradigm that interspecific competition for limited seed resources is the primary factor that structures seed-harvester ant communities. This review attempts to adjust this paradigm, suggesting that interspecific competition for food is probably less important than previously thought, whereas intraspecific competition is common and strong. Abiotic-habitat factors also have important effects on local species composition and attributes. This review also emphasizes several aspects of seed-harvester ants that have been poorly studied, including historical factors, adaptive radiation, and biogeography, to provide a more detailed evolutionary background for understanding existing species assemblages.

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## PERSPECTIVES AND OVERVIEW

Seed-harvester ants are a dominant component of invertebrate communities in deserts and grasslands in both warm temperate and tropical regions around the world (3, 77, 96). In North America, seed-harvester ants are common throughout the drier western areas of the United States and in most of temperate and subtropical Mexico; in some areas, seed harvesters compose ~25% of the ant species (86, 107, 142). Seed-harvester ants can number from several hundred thousand to several million individuals per hectare and can have a total biomass comparable to that of small vertebrates (156). By virtue of their numbers, these ants harvest up to several million seeds per hectare per year (primarily from annual plants). Thus, these ants have a significant impact on energy flow and also affect the species composition and relative abundance of annual plants (20, 45, 147).

Competition is generally considered the predominant factor in structuring ant communities (2, 52, 77, 139), including those of seed-harvester ants (20, 40, 41, 44). Competition is manifested at the intraspecific level by territoriality and aggressive interference for space (72, 73), and at the interspecific level, by exploitative and interference competition for food (52, 78). However, it has become evident that patterns of species composition and the distribution of ant species are also influenced by biotic factors such as parasitoids (49) and predation (66), abiotic factors such as moisture or soils (84, 87, 124, 146), stochastic factors such as the order of species arrival at a locale (34), demographic factors such as birth rates and death rates (137), and historical factors that relate to phylogeny (the available species pool) and the degree of specialization in food consumption (4, 113).

Competition and resource partitioning have been studied extensively as explanations for community structure and species coexistence in North American seed-harvester ants, with a series of early studies providing the first synthesis of understanding at local and regional scales (9, 10, 12, 40–42). These studies suggested that interspecific competition for limited seed resources was the predominant factor structuring this community. Support for this hypothesis involved field experiments (often with granivorous rodents) in which density and/or ant activity increased in plots where potential competitors were removed, compared with control plots. Three types of correlative data were also invoked to suggest seed limitation. First, ant species richness and diversity were positively correlated with productivity, that is, seed abundance. Second, a correlation of ant body size and size of seeds harvested indicated that these limited seed resources were partitioned by size among the ant species. Third, at a particular locale, similarly sized species did not coexist unless they differed in foraging methods (group vs solitary foraging). These different foraging methods facilitated further partitioning of seeds because group-foraging species harvest high-density seed patches, whereas solitary foraging species harvest low-density seed patches. These early studies stimulated an abundance of research on seed-harvester ant ecology and community structure that largely focused on diets and partitioning of seed resources as explanations for species coexistence (69, 114, 123).

In this review, I summarize and synthesize information on communities of North American seed-harvester ants, and thus supplement previous reviews that have examined these ants as part of a larger system (20, 77, 107) or have emphasized aspects of their natural history (86). Seed-harvester ants are common and abundant in many parts of Mexico, but this fauna is very poorly known (86; RA Johnson & PS Ward, submitted for publication). Consequently, in this paper I focus on ants from deserts of the southwestern United States, where numerous studies have been conducted over the past 10–15 years. Most of these studies have been restricted to several group-foraging species, more specifically, those with large, easily studied colonies, while studies on species with small colonies are uncommon. In this paper, references to studies of non-seed-harvester ants are included only for topics that are poorly known for seed-harvester ants.

## SEED-HARVESTER ANTS

### Seed-Harvester Ant Genera

North American seed-harvester ants include the myrmicine genera *Pogonomyrmex*, *Messor* (formerly *Veromessor*), and *Pheidole*. *Aphaenogaster* (formerly *Novomessor*) and *Solenopsis* are also commonly included in community studies because individuals harvest seeds from baits (9, 10, 12, 40–42), although in both of the latter cases, the species are opportunists rather than true seed harvesters (148, 158, 160). However, in the broad sense, both of these genera could be considered seed harvesters because they store seeds in underground chambers. As a group, seed-harvester ants, *senso stricto*, encompass ~75 species in North America and thus represent ~5%–10% of the ant species in this region (86).

*Pogonomyrmex* is a moderate-sized New World genus that consists of ~62 species. The 29 species that occur in North America are divided into two subgenera, *Po.* (*Pogonomyrmex*) with 25 species and *Po.* (*Epehebomyrmex*) with 4 species. The subgenus *Epehebomyrmex* is considered a separate genus by several authors (13). The more primitive morphological characteristics of South American species (144, 145) suggest that *Pogonomyrmex* evolved in South America and later migrated to and radiated throughout North America (101, 145).

North American species in the subgenus *Pogonomyrmex* are highly specialized granivores, although insects and termites are taken when available. Two notable exceptions are *Pogonomyrmex montanus* (105) and *Pogonomyrmex badius* (149) because both may harvest large numbers of insects. *Po. badius* is the only species in which the workers are polymorphic (33). The subgenus *Pogonomyrmex* consists of three monophyletic complexes (144), with species in each complex generally affiliated with particular geographic regions. The *Po.* (*Pogonomyrmex*) *barbatus* complex consists of 11 species (including 2 workerless social parasites that live inside nests of a congeneric host) that occur at low latitudes in the United States and Mexico, from low to mid elevations (<1550 m). These species commonly inhabit

hot desert habitats, although the ranges of most species also extend into semiarid to more mesic locales. The *Po. (Pogonomyrmex) occidentalis* complex consists of six species, all of which are primarily restricted to higher latitudes in the United States and southern Canada, typically at mid to high elevations (>1550 m) (86). Some species, such as *Po. occidentalis*, extend south of their primary geographic range by inhabiting mid to high elevation habitats in southern mountain ranges. The *Po. (Pogonomyrmex) californicus* complex consists of eight species that occur at low latitudes of the United States and Mexico, from low to mid elevations. Although members of the *Po. (Pogonomyrmex) californicus* complex range across the southern United States and Mexico, their greatest radiation is in the western deserts. Four species (*Pogonomyrmex anzensis*, *Pogonomyrmex magnacanthus*, *Pogonomyrmex snellingi*, and *Pogonomyrmex* sp. B) are geographically restricted to these deserts, and *Po. californicus* is very common in these areas, though it also occurs farther east (86). Three species, *Po. magnacanthus*, *Po.* sp. B, and *Po. anzensis* are also habitat specialists; the first two of these species are restricted to sand dunes or other very sandy soils (33, 142), and the third is restricted to rocky hillsides of specific geologic origin (R Johnson, personal observation). Evolution of these complexes, each with distinct geographic distributions, has greatly enhanced radiation and habitat expansion of the subgenus *Pogonomyrmex* in North America.

North American species in the subgenus *Epebomyrmex* are also granivorous, but to a lesser degree than *Po. (Pogonomyrmex)* and *Messor* species, because significant numbers of insects, especially ants, are also harvested (36, 142). The subgenus occurs in Mexico and low latitudes of the southwestern and south-central United States, at low to high elevations (<2000 m) (86).

*Messor* is a large genus (~105 species) that consists of 10 granivorous species in North America. The phylogenetic relationships of the Nearctic *Messor*, however, are unclear. *Messor* is predominantly an Old World genus, suggesting that the Nearctic components invaded North America from Asia via Beringia (R Snelling, personal communication). Alternatively, some recent evidence suggests that the *Aphaenogaster* species belonging to the former *Novomessor* (including *Aphaenogaster albisetosa* and *Aphaenogaster cockerelli*) are the sister group to Nearctic *Messor* (8). Nearctic species of *Messor* are restricted to western North America, with four species reaching northern Mexico (86). Most species are crepuscular/nocturnal foragers; only *Messor andrei*, *Messor chamberlini*, and *Messor pergandei* forage diurnally (35, 86). Three species, *Messor chicoensis*, *M. pergandei* and *Messor stoddardi*, are polymorphic (8). The genus occurs throughout most of the western United States and northwestern Mexico, at low to high elevations (86).

*Pheidole* is an extremely large genus that occurs worldwide. Approximately 100 species occur in the United States (EO Wilson, manuscript in preparation); ~30–40 of these species are granivorous (86). The genus, which appears to be tropical in origin, is characterized by dimorphic workers and thus consists of large workers (majors) and small workers (minors) but no workers of intermediate

sizes. The majors of some *Pheidole* species are also polymorphic (e.g. *Pheidole rhea*). Species vary widely in foraging behavior, diet, and colony size, but most arid-zone species are granivorous. In many species, minors compose the entire foraging force, while majors remain in the nest and apparently serve as specialists to mill seeds (e.g. *Pheidole barbata*). Majors are recruited to rich food resources in some species, but otherwise do not forage. In other *Pheidole* species, majors forage on a regular basis (e.g. *Pheidole tucsonica* and *Ph. rhea*). The genus occurs throughout most of North America from low to high elevations, but species richness is highest in arid regions, where it is typically the most speciose ant genus.

*Aphaenogaster* is a large genus (~150 species) that occurs worldwide except for the Afrotropical region. Approximately 25 species occur in the United States. The few species that occur in the southwestern deserts include the partial seed harvesters *A. albisetosa* and *A. cockerelli*, both of which are nocturnal/crepuscular foragers during summer months. These two ants occur at low latitudes of the south-central and southwestern United States and Mexico and at low to moderate elevations (<1550 m).

*Solenopsis* is a large genus (~190 species) that occurs worldwide. The ~25 species that occur in the United States are divided into 2 subgenera, *Solenopsis* (*Solenopsis*) and *Solenopsis* (*Diplorhoptrum*). The subgenus *Solenopsis* consists of six species including the introduced *Solenopsis wagneri* (= *Solenopsis invicta*) and *Solenopsis richteri* (148). Species in this subgenus occur in low latitudes throughout most of the United States and Mexico, at low to moderate elevations (<1550 m). In south-central and southeastern areas, *S. wagneri* has displaced numerous invertebrates including congeners (120). The genus *Solenopsis* also includes the taxonomically unstable subgenus *Diplorhoptrum*, which consists of minute workers that are partial seed harvesters. However, these species are rarely found at baits and thus are typically excluded from community studies. Species in this subgenus also occur throughout North America, from low to high elevations (<2700 m).

In addition, several species of seed-harvester ants display intraspecific variants in behavior or genetics that may include multiple cryptic species. For example, *Po. californicus* displays geographic variation in metrosis (i.e. the number of foundresses that initiate a colony) and queen number; populations in southern California are pleometrotic (i.e. have multiple cooperating foundresses) and polygynous, whereas those in Arizona are haplometrotic (i.e. have single foundresses) and monogynous (125; R Johnson, unpublished information). *M. pergandei* also displays geographic variation in metrosis along a sharp contact zone, with correlated differences in foundress behavior and in one allozyme (27, 28). Finally, population genetic structures of *Pogonomyrmex rugosus* vary regionally. Populations in central Arizona are in Hardy-Weinberg equilibrium for several allozymes and have one male type, whereas populations in southwestern New Mexico are out of equilibrium for these same allozymes and have two male color morphs that differ in allozymes and mitochondrial DNA (S Cahan, J Parker, unpublished information). Populations of *Pogonomyrmex barbatus* from the same location in New Mexico

show a similar pattern of genetic disequilibrium, when examined by using randomly amplified polymorphic DNAs (D Deroma, G Julian, J Fewell, unpublished information). Hybridization also appears relatively common in *Pogonomyrmex* species (33, 74).

## Life History and Ecology

The few life history data available for seed-harvester ants suggest a general pattern, probably common to most ants (14), of extremely high rates of mortality for foundresses and incipient colonies and high longevity (~15 to >30 years) after colonies reach ~2 years of age (29, 56, 61, 94, 98, 163). Colonies grow rapidly and after several years produce up to several hundred alate males and females (i.e. winged reproductive castes) per year (58, 60, 61, 102, 105, 117). One shortcoming of these demographic data is the focus on species with large colonies, so that comparisons cannot be made to congeners with small colonies. However, species with small colonies may exhibit shorter longevity because of increased susceptibility to catastrophic events (97, 101). In one aspect of life history, ants differ dramatically from other organisms—ant colonies can survive without food for >1–2 months. Members of a colony apparently catabolize their own tissue to maintain the queen, and she is typically one of the last individuals to die; colony survival time is correlated with worker number (97). Relative to such potential food shortages, seed-harvester ants store seeds in underground chambers. Thus, unlike many ants, seed-harvesting species have a relatively long-term, stable food supply that provides a buffer during food shortages.

Mating flights are also an important life history attribute, because the timing and cues that trigger flights determine the conditions that foundresses experience. Mating flights take two general forms in desert ants. Summer rains trigger synchronous flights for most species, while a few species have asynchronous flights (over several weeks) that appear to be triggered by photoperiod. In the former group, mating flights occur for 2–3 days following sufficient rain, with alates leaving the nest at a predictable time each day. Subsequent rains trigger additional mating flights as long as alates are present in the nest (74). Moreover, these species have synchronous mating flights on a local scale, but on a broader scale, the flights are often asynchronous because most summer storms are highly localized. Few data are available on species whose mating flights appear to be triggered by photoperiod. That photoperiod triggers the flights of these species is based on observations that several ant species exhibit sharp daily activity peaks under controlled light cycles and that these cycles appear to be under endogenous control (112). Additionally, few other environmental cues appear to be available because the flights of these species can occur up to several weeks from any rain (R Johnson, unpublished information). The seasonal timing of the mating flight can vary regionally in these species. For example, alates of *Po. californicus* are released almost every day from mid May to early June in desert habitats, but the flights do not begin until late June or early July in cooler upland areas of southern California (R Johnson,

unpublished information). Foundresses of most species are claustral, meaning that they seal themselves inside their incipient nest and metabolize fat and other body tissue to support themselves and brood until the first workers eclose (84). However, in at least two species, *M. andrei* and *Po. californicus*, the foundresses are semiclaustral (23; R Johnson, unpublished data); that is, they must forage to obtain sufficient energy to eclose their first workers.

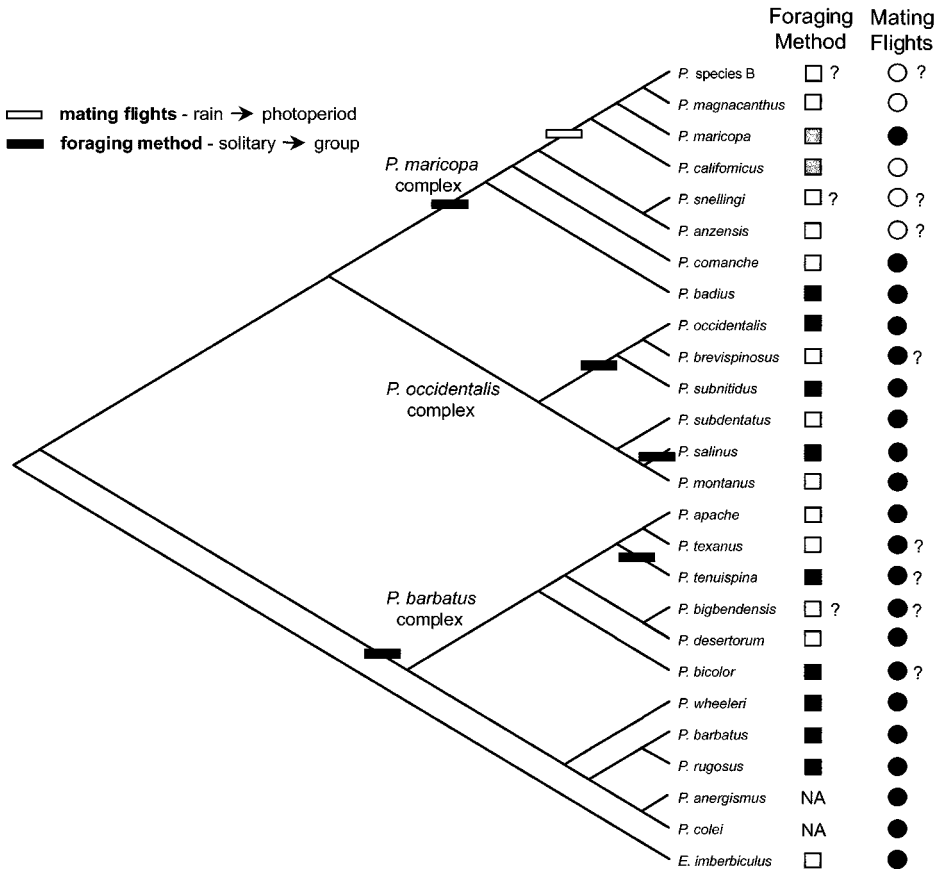
The two primary foraging methods, solitary and group foraging, tend to be species specific, but can be influenced by factors such as vegetation density (53). In group-foraging species, workers exit the nest in a column or along a trunk trail and break off to forage solitarily at the distal end of the column. The workers actively recruit nestmates to seed patches, thus facilitating rapid harvest of localized resources. In contrast, workers of solitary-foraging species radiate out from the nest in all directions, and these workers exhibit poor nestmate recruitment; seed patches are mostly harvested via repeated trips by the same individual. Several species (e.g. *Po. californicus* and *Pogonomyrmex maricopa*) also exhibit an intermediate foraging method. In this case, workers are typically solitary foragers, but recruit nestmates for high-density food patches, although at a slower rate than do group-foraging species (41, 73, 86, 101).

## PHYLOGENY, BEHAVIOR, AND RADIATION

Phylogenies based on morphological traits are available for *Messor* and *Po.* (*Pogonomyrmex*) species (8, 144). Consequently, phylogenetic relationships can be used to examine the evolution of novel traits, and these novel traits can be correlated with current geographic distribution patterns. Two traits, cues triggering mating flights and foraging method, appear to have been particularly important in the radiation and habitat expansion of both *Po.* (*Pogonomyrmex*) and *Messor* species in North America. The evolutionary scenario presented herein for *Messor* is tentative, however, because the unclear phylogenetic relationships of Nearctic *Messor* make it difficult to determine the sequence of character-state change. Further evaluation will require determining the appropriate outgroup for Nearctic *Messor*.

### Mating Flights

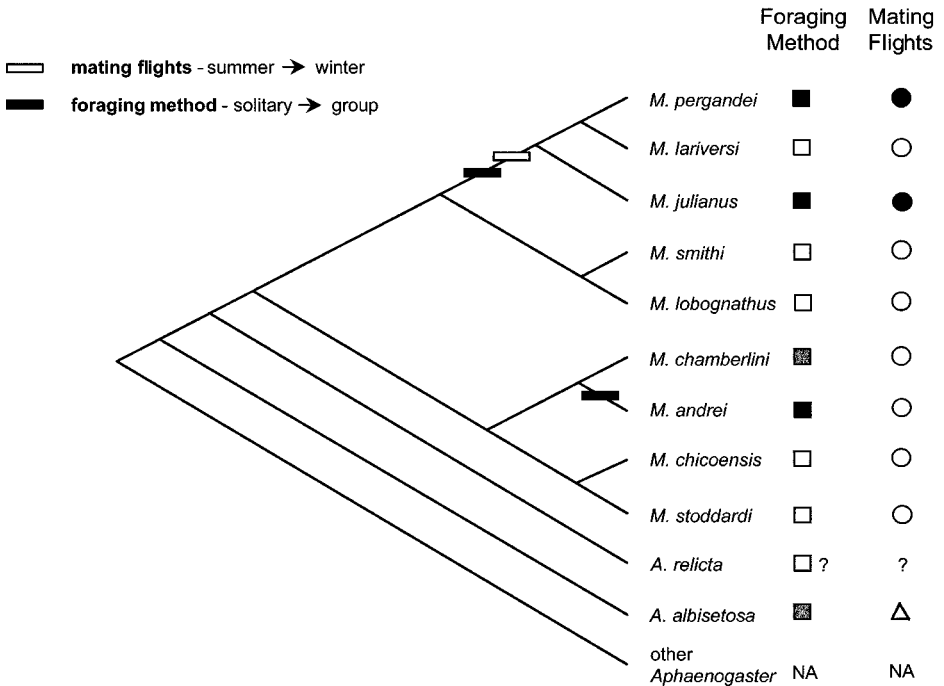
Summer rains trigger mating flights for most species in the subgenus *Pogonomyrmex* (Figure 1). However, two closely related species, *Po. californicus* and *Po. magnacanthus*, diverged from this pattern and have late-spring/early-summer flights that appear to be triggered by photoperiod. This divergence correlates with the invasions by these two species into the Colorado and Mohave Deserts, where summer rains are unpredictable and generally lacking (108). Three other species in the *Po.* (*Pogonomyrmex*) *maricopa* complex are restricted to these deserts and probably have similar mating flights by descent (86) (Figure 1).



**Figure 1** Phylogenetic tree for North American seed-harvester ants in the genus *Pogonomyrmex* based on parsimony analysis; *Po. (Epehebomyrmex) imberbiculus* is the outgroup (redrawn from 144, Figure 19). Foraging methods and cues that trigger mating flights are mapped to the right of each species. Trait values were taken from available data; *question marks* indicate that the trait is inferred from close relatives or anecdotal data (86). Foraging method: *open square*, solitary foraging with limited recruitment; *gray, shaded square*, solitary foraging with recruitment; *closed square*, group foraging; NA, not applicable because the species is workerless. Mating flights: *closed circle*, rain triggered; *open circle*, photoperiod triggered. The *rectangles* mapped on the stem of the tree denote the locations of shifts from the ancestral to the derived trait; these locations were determined using the Farrish optimization method (16). *Open rectangle*, location of shift from rain- to photoperiod-triggered mating flights; *solid rectangles*, locations of shifts from solitary to group foraging.



In the genus *Messor*, most species have summer mating flights (M Bennett, R Snelling, personal communication) that appear to be triggered by photoperiod (112). In contrast, late-winter/early-spring flights evolved in the two closely related species *Messor julianus* and *M. pergandei* (89; Figure 2). It is interesting that these are the only two species with geographic distributions restricted to hot desert habitats. This seasonal shift was probably a prerequisite to invading hot desert habitats because alate females of *Messor* species have poor heat tolerance



**Figure 2** Phylogenetic tree for North American seed-harvester ants in the genus *Messor* based on parsimony analysis; *Aphaenogaster* is the outgroup, but further evaluation is needed to determine if this is the appropriate outgroup (redrawn from reference 8, Figure 3). The phylogeny is a composite tree that summarizes the best resolved and most stable topologies across a maximal number of trees generated by partition analyses. Foraging methods and cues that trigger mating flights are mapped to the right of each species. Trait values were taken from available data; *question marks* indicate that the trait is inferred from close relatives or anecdotal data (86). Foraging method: *open square*, solitary foraging with limited recruitment; *gray, shaded square*, solitary foraging with recruitment; *closed square*, group foraging. Mating flights: *open circle*, photoperiod triggered in summer; *closed circle*, photoperiod triggered in late winter/early spring; *open triangle*, rain triggered in summer. The *rectangles* mapped on the stem of the tree denote the locations of shifts from the putative ancestral to the derived trait; these locations were determined using the Farrish optimization method (16). *Open rectangle*, locations of shift from summer to winter mating flights; *solid rectangles*, locations of shifts from solitary to group foraging.

compared with species in other genera of desert ants (89). Thus, physiological constraints probably necessitated the different paths along which mating flights diverged from the ancestral condition in *Messor* and *Po.* (*Pogonomyrmex*) species. In both cases, however, these changes facilitated the invasion of novel habitats, that is, hotter, drier deserts, and they suggest convergent evolution in these two genera. A similar pattern occurs in the genus *Aphaenogaster*. This genus has few desert species, and *Aphaenogaster megommata* is the only species in the genus that is common in the Colorado and Mohave Deserts. This occurrence of *A. megommata* also correlates with the apparent triggering of mating flights by photoperiod, such that this species may also have diverged from those with the rain-triggered mating flights that are typical of *Aphaenogaster* spp. (86).

## Foraging Methods

Solitary foraging and group foraging occur in species of *Messor* and *Pogonomyrmex*; solitary foraging appears to be the ancestral condition in both genera (Figures 1 and 2). Group foraging has evolved five times in North American *Pogonomyrmex* species and is present in all three species complexes, but is lacking in South American congeners (101). Group foraging appears to have evolved two times in *Messor* species. That group foraging has evolved multiple times in these two functionally similar genera suggests convergent adaptation for this trait (16).

Colony size is correlated with foraging method. Solitary-foraging species have relatively few workers (<500), whereas column- or trunk trail-foraging species typically have much larger colonies (>5,000–10,000 workers) (86). An apparent by-product of large colony size is a wider geographic distribution. In the subgenus *Po.* (*Pogonomyrmex*), group-foraging species as a whole have a vastly larger geographic range than solitary-foraging species, with the former group reaching colder, more northern areas of the United States and southern Canada. However, group-foraging species of the genus *Messor* have invaded southern, warm desert habitats, where small-colonied congeners are uncommon. This colony size effect relative to geographic distribution may result from the better buffering provided by larger colonies against severe environments (97).

## BIOGEOGRAPHY

### Historical Considerations

Seed-harvester ants are widespread in North America (86), but their species richness and proportional representation are highest in desert habitats. Despite their predominance in deserts, few of these species evolved in or are geographically restricted to these areas (86, 142, 157). Rather, like most species of desert plants (5), most desert ants probably originated in adjacent upland, semiarid habitats, where they are also common. Those species that were preadapted to greater drought gradually invaded more marginally to typically hot desert habitats during the recent

drying of the southwestern deserts (5). The less drought-tolerant species persist as relict populations in the numerous upland areas and mountain ranges of this region. The few true hot-desert species that apparently evolved in situ did so by acquiring novel traits that included differences in colony size, mating flights, habitat specialities, and other physiological adaptations such as decreased cuticular water loss rates.

## Distribution Patterns and Species Coexistence

Distribution patterns appear to result from a combination of historical factors related to the geographical origin of each genus and to species interactions and abiotic factors that restrict coexistence of ecologically equivalent species. Species interactions and exploitative competition for seeds have been suggested to determine the local ant species composition, while regional patterns of species richness are correlated with abiotic factors that affect seed productivity (see below). The ant species that coexist locally appear to consist of a nonrandom assemblage of species that differ in body size and foraging methods; species of similar size coexist only if they differ in foraging method. Species with the same foraging method only coexist if they differ in body size (40, 41, 140, 161). This pattern extends to the regional scale when separating species into functional groups based on genus and foraging method (Table 1). Thus, these functional groups consist of informal groups of species that share a common evolutionary history and exploit the physical environment in a similar manner (86). On a regional scale, species of *Po.* (*Pogonomyrmex*), *Po.* (*Ephebomyrmex*), *Messor*, *Aphaenogaster*, and *Pheidole* are broadly sympatric across the south-central and southwestern United States and northern Mexico, but only one species per functional group predominates at a given locale. The primary difference among species within each functional group is that each species occurs in specific micro- and macrohabitats, with species replacing one another across contact zones that are often delineated by abiotic habitat features (86, 87). Moreover, allopatric and parapatric distribution patterns are common within functional groups and sometimes also extend between functional groups such as group-foraging

**TABLE 1** Functional groups of North American seed-harvester ants (excluding the genus *Pheidole*)<sup>a</sup>

Genus (subgenus)	Functional Groups
<i>Pogonomyrmex</i> ( <i>Pogonomyrmex</i> )	Group foraging Solitary foraging with recruitment Solitary foraging with limited recruitment
<i>Pogonomyrmex</i> ( <i>Ephebomyrmex</i> )	Solitary foraging with limited recruitment
<i>Messor</i>	Group foraging Solitary foraging with recruitment Solitary foraging with limited recruitment

<sup>a</sup>Adapted from 86.

species of *Messor* and *Po.* (*Pogonomyrmex*) (83, 86). In sum, these distribution patterns suggest three levels of mechanisms that modulate species interactions and structure this community locally and regionally: (a) mechanisms that structure and maintain local contact zones between ecologically equivalent species, (b) mechanisms that permit coexistence of several species at one locale (both congeners in different functional groups and noncongeners), and (c) mechanisms that maintain widespread sympatry of species that apparently inhabit similar microhabitats (86).

## Patterns of Species Richness

Studies have correlated the species richness of seed-harvester ants along precipitation gradients with variable results. Although the correlation is positive in the Namib Desert (110) and in North American deserts (40, 137), it is absent in South America (113) and Australia (115). The predictive basis for this pattern is derived from the correlation between productivity (i.e. seeds produced by annual plants) and precipitation in arid regions (131), with the idea that ant species richness should be positively correlated with seed abundance.

All of the above studies examined gradients of species richness relative to mean annual precipitation, but did not assess the potential importance of annual variation and seasonality (5, 48). Across the North American sites surveyed by Davidson (40), amount and seasonality of precipitation covary as both the total and the percentage of precipitation that occur during summer increase from the Mohave Desert in the west to Chihuahuan Desert in the east (108). This seasonality gradient confounds the task of assessing patterns of species richness because summer precipitation triggers mating flights for most desert ants. Consequently, an alternative explanation to the seed limitation hypothesis is that summer precipitation may be insufficient to trigger mating flights and/or to ensure foundress survival and colony establishment in drier western locales (or in drier years). Support for this hypothesis comes from patterns of species loss and species replacement in seed-harvester and other ants, as one moves from the Sonoran Desert in the east to the Colorado Desert in the west. Species that drop out of the fauna have mating flights triggered by summer rains, while mating flights of their ecologically equivalent replacement species (if present) are triggered by photoperiod (86). A parallel pattern of species loss occurs in succulent plants, as those species that require summer rains for germination and establishment drop out of the fauna in western locales (25, 92, 93, 150).

## COMMUNITY STRUCTURE

### Abiotic Limitations

Soil types and soil moisture have long been associated with micro- and macrodistribution patterns of ants (32, 146). Although the idea is mostly unexplored at the species level, it is apparent that several seed-harvester ants have specific soil

requirements. For example, *Po. magnacanthus*, *Pheidole psammophila*, and *Ph. barbata* are restricted to sand dunes and other very sandy areas, and *Po. californicus* and *M. pergandei* are most common in sandy soils (83, 142). Conversely, *Po. rugosus*, *Po. barbatus*, and *M. stoddardi* appear to be restricted to soils of higher clay content (83, 87; M Bennett, personal communication). Colony density—and sometimes species composition—also vary locally in association with topography and soil texture (38, 83, 87, 100).

For soil types, clay content and clay type are particularly important to microdistribution patterns because clay determines the physical and chemical properties of soil, including moisture availability (87, 111). For a given moisture level, availability of water is maintained at a higher level and for a longer time in soils with a higher clay content, thus causing moisture availability to vary across local gradients of soil texture. Wet mass is the best indicator of foundress and colony conditions during the founding stage, and wet mass remains higher for foundresses placed in high-clay compared with low-clay soils (84). Consequently, ecologically equivalent species that differ in aspects such as body size commonly replace one another across local gradients that vary in soil texture and especially clay content (67, 68, 83, 87).

Moisture is probably the most limiting abiotic factor for desert organisms. In ants, moisture can affect all stages of the colony cycle including alate production, mating flights, survival of foundresses and incipient colonies, microdistribution pattern, and foraging behavior. In many species, precipitation initiates the colony cycle by triggering the mating flight. As such, reproductive events in these species become increasingly sporadic as the amount and predictability of precipitation decrease. Moisture level is also positively associated with parameters that enhance colony success after the mating flight, including foundress survival, foundress wet mass, and brood production (27, 84). That desiccation may cause death for a significant fraction of incipient colonies is supported by field data demonstrating that the water content of *M. pergandei* foundresses decreases in dry soils (R Johnson, unpublished information). Group founding mitigates this effect because survival is significantly higher for grouped compared with single foundresses under dry, but not wet, conditions (27). In contrast, water does not appear to limit foraging in mature colonies of *M. pergandei* (51), but colonies may produce a lower number of alate sexuals in dry years (27, 135).

The high surface-to-volume ratio of small arthropods such as ants makes them prone to desiccation. Cuticular water loss rate and body size are the primary determinants of desiccation tolerance. Studies on non-seed-harvester ants and other arthropods demonstrate abiotic constraints related to desiccation tolerance (31, 103). The general pattern is that species with a higher desiccation tolerance (79, 146, 162) or larger body size (95) occur in more xeric microhabitats. A similar pattern occurs in two sister species of *Pogonomyrmex*. Alate females of *Po. rugosus* are larger than those of *Po. barbatus*, and this difference effects a higher desiccation tolerance for *Po. rugosus* and facilitates their habitation of drier soils (84). Larger body size confers an advantage for rearing brood under desiccating

conditions, but under mesic conditions, foundresses of smaller species have the advantage because time to eclosion of the first workers is inversely correlated with foundress size (84, 87; R Johnson, unpublished information). Earlier eclosion of workers in smaller foundresses presumably correlates with faster colony growth, thus giving these species an advantage over those with larger foundresses under more mesic conditions.

A more extensive study indicates that the correlation between desiccation tolerance and differences in local distribution is geographically and taxonomically widespread in seed-harvester ants (e.g. species of *Aphaenogaster*, *Messor*, and *Pogonomyrmex*). For several pairs of ecologically equivalent congeners, the dry mass of alate females is consistently greater for the species inhabiting the hotter, drier microhabitat across a local contact zone. Water loss rates of alate females sometimes differ among species, but these species differences disappear in foundresses because digging a nest abrades the cuticle and greatly increases water loss rates (85, 88). Group-foraging species of *Pogonomyrmex* also exhibit a latitudinal pattern in that the dry mass of alate females increases both intra- and interspecifically along a north-to-south gradient of increasing desiccation stress (85).

## Biotic Interactions

### Competition

Competition has been examined by two approaches that differ in time frame and response variables. Long-term experiments remove potentially competing species and compare subsequent density changes in experimental and control plots. Because these ants have a yearly reproductive cycle, this type of experiment involves measuring colony density during an annual census when activity is highest. The other method compares short-term response variables such as number of foragers, diet breadth, foraging behavior, foraging success, and reproductive output between manipulated and control colonies; manipulations typically involve removing neighboring colonies and adding seeds. These studies have led to the conclusion that interspecific competition for seeds is the primary factor in structuring seed-harvester ant communities. In this report, interspecific competition is viewed as less important than previously thought in structuring these communities. Consequently, studies that led to the paradigm of interspecific competition are discussed below in detail.

### Interspecific Competition—Direct Data

Early experiments assessed interspecific competition between granivorous rodents and ants in the Sonoran Desert by using reciprocal removal plots (17, 19). For ants, competition was indicated by a 71% increase in number of active nest entrances on rodent-removed compared with control plots. However, the response was limited to three species of *Pheidole* [*Ph. tucsonica* (= *Pheidole xerophila*), *Pheidole gilvescens*, and *Pheidole rugulosa* (= *Pheidole sitarches*)], and data were pooled across these three species because of problems with identification (17, 18, 55). Nests of all three *Pheidole* species are polydomous (i.e. multiple nest entrances

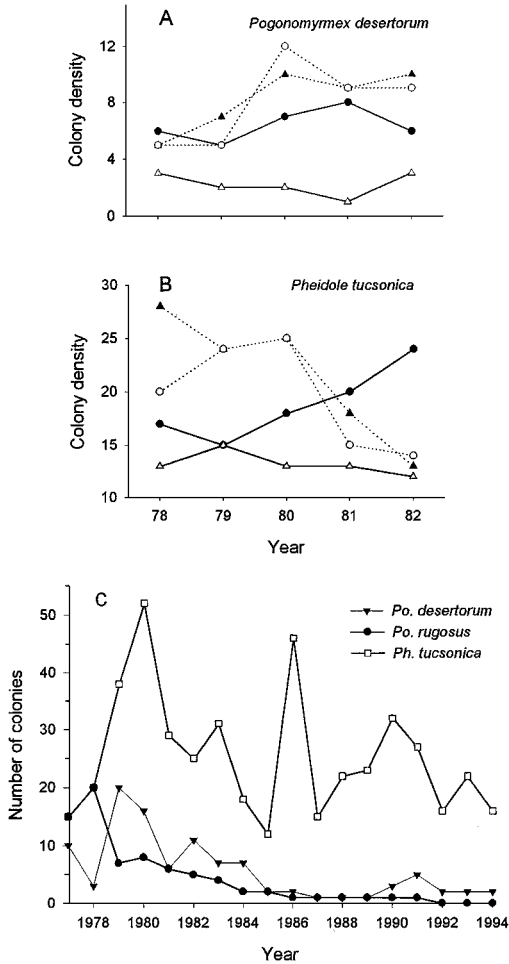
per colony), so their response to rodent removal was measured as change in foraging activity, not colony density as has sometimes been suggested (7).

These same plots were maintained over the longer term for continued study of these competitive interactions. A census of the plots was carried out again the following year, by which time the numbers of ant nest entrances had decreased significantly in treatment plots and were similar in treatment and control plots (45). Thus, to that point, the number of nest entrances exhibited a time effect in treatment compared with control plots because the number of *Pheidole* nest entrances significantly increased and then decreased (45). It was suggested that interspecific competition caused the initial increase in number of nest entrances and indirect interactions caused the later decreases. Absence of rodents in these plots resulted in increased numbers of large-seeded annuals. This, in turn, decreased the density of the small-seeded annuals that composed the primary food for the ants, thus causing their decline even in the absence of rodents.

These results, although they suggest competition between rodents and ants, have been considered equivocal. The most significant increase in ant activity occurred after 1 year, when seed densities did not differ between control and treatment plots (19, 80). In addition, the hypothesis that ants and rodents compete for seeds was based on broad overlap in size and species of seeds eaten, but later analysis indicated that the taxa differed significantly in both respects (141). Finally, Brown et al (19) estimated seed abundance by sampling seeds that weighed  $>0.4$  mg, but in similar habitat,  $>90\%$  of the seeds harvested by *Ph. tucsonica* and a high percentage of those harvested by the largest seed-harvester ants (*M. pergandei* and *Po. rugosus*) weighed  $<0.2$  mg (114, 123).

Similar experiments in the Chihuahuan Desert found little evidence of direct competition between ants and rodents because numbers of colonies and numbers of nest entrances did not change over 15 years on rodent-free compared with control plots (46, 138, 151). For individual ant species, the only significant response was a decrease in number of *Pogonomyrmex desertorum* colonies in rodent-free plots, which might be attributed to initial differences in abundance of these ants that existed before rodents were removed (46, 151). Foraging activity by *Ph. tucsonica* initially increased on rodent-free plots but not on plots in which seeds were added (46). Differences in activity level were absent later in the study and on plots initiated at a later date (151). Moreover, the only treatment effect over 15 years was a positive correlation between density of *Ph. rugulosa* colonies and percentage of grass cover (151). Thus, the interactions between ants and rodents appear to be mediated indirectly through vegetation rather than directly through competition for seeds.

Two studies have experimentally tested for interspecific competition among seed-harvester ants (44, 135). Davidson (43) predicted and then tested the outcome of diffuse competition from a species matrix of dietary overlap and interference interactions. A several-year field experiment supported the matrix predictions (44), but these results may also be equivocal because nearby plots from other experiments conducted at the same time displayed a contrasting pattern (21) (Figure 3). In the latter study, natural declines in *Po. rugosus* were accompanied by density



**Figure 3** Data from two concurrent long-term studies on seed-harvester ants near Portal, AZ, that show contrasting patterns of population dynamics for *Po. desertorum* and *Ph. tucsonica*. Top two panels (redrawn from reference 44, Figure 2), colony densities of two target species in an experiment on diffuse competition. Densities are for  $\sim 452\text{-m}^2$  circular plots, each of which was centered on a *Po. rugosus* colony; the *Po. rugosus* colony was untreated (control plots, solid lines in both panels) or removed in July 1978 (treatment plots, dotted lines in both panels) (44). (A) Densities of *Po. desertorum* (predicted to increase on treatment plots); (B) densities of *Ph. tucsonica* (predicted to decrease on treatment plots). The second study (C) (redrawn from reference 20, Figure 4) shows number of colonies for *Po. desertorum* and *Ph. tucsonica* (per 0.25-hectare plot for both species) and *Po. rugosus* (total colonies on the study site). The plots were untreated during this study, and thus show the response of *Po. desertorum* and *Ph. tucsonica* to natural declines of *Po. rugosus*. Note that density of both species increases after initial declines for *Po. rugosus*, in contrast to their opposing patterns in the top two panels.



increases for *Po. desertorum* and *Ph. tucsonica*, rather than the pattern predicted by Davidson (43) of an increase in the former species and decline in the latter species. Over a longer interval, while the number of *Po. rugosus* colonies continued to decline under unmanipulated conditions, the number of *Po. desertorum* and *Ph. tucsonica* colonies fluctuated markedly, but were positively rather than negatively correlated (21) (Figure 3).

An experiment on *M. pergandei* and *Po. californicus* also suggested the absence of interspecific competition, by explicitly testing the hypothesis that forager activity is affected by short-term changes in seed abundance [as presumed by Brown & Davidson (17) and Brown et al (19)]. For both species, forager number and diet breadth of control colonies were similar to those with neighbors removed (in both intra- and interspecific comparisons) or seeds added (135). Finally, a natural experiment compared diets of *Po. rugosus* and *M. pergandei* during periods of high and low seed abundance. When seed abundance declined after a drought, diets of these two potential competitors converged, suggesting the prevalence of intra- rather than interspecific competition (123).

### Interspecific Competition—Correlative Data

Three types of correlative data have been used to support the hypothesis that seed-harvester ant communities are structured by interspecific competition for seeds: (a) patterns of species richness and species diversity (see above), (b) positive correlations between ant body size and seed size, and (c) resource partitioning via differences in foraging methods.

The positive correlation between ant body size and the size of the harvested seeds is a common pattern that occurs among seed-harvester ant species in Australia (15, 115), North America (11, 30, 40, 69, 114), the Middle East (109), and the Neotropics (96). Although this pattern is common, it has also become evident that it is highly variable among species, among colonies within a species, and among workers within a colony (96). Additionally, although small ants harvest small seeds, large ants harvest both large and small seeds and maintain a large percentage of small seeds in their diet (37, 96). This pattern is paralleled in two of the largest southwestern seed harvesters, *M. pergandei* and *Po. rugosus*, for which very minute seeds constitute a large fraction of their diets (114, 123). Overall, these studies indicate that small ants are morphologically constrained to harvest small seeds while large ants harvest both small and large seeds. The high variation in this correlation, especially at the colony and individual level, raises doubts as to the importance of partitioning seeds based on size in community structure (96).

The correlation between body size and seed size sometimes extends to the intraspecific level in polymorphic species (42, 64, 126, 149). This correlation is best studied in the size-variable *M. pergandei*, in which the amount of size variation among workers was inversely correlated with the number of potentially competing seed-harvester ant species along a longitudinal cline (20, 42). This geographic pattern of size variation was suggested to be an adaptive response to

the local competitive environment because colonies could exploit a broader range of seed resources (sizes) in locales with fewer competitors, while diets narrowed in areas with more competitors (42). Two lines of evidence, however, suggest that this interpretation is questionable. First, the correlation of body size and seed size is highly variable among colonies of *M. pergandei*, and even when size correlations are significant, they often account for <5% of the variance (42, 64, 126, 154). Second, worker size and the amount of size variation in *M. pergandei* workers changed seasonally at two widespread locales (64, 122), and at both sites, the amount of intracolony variation in a year was similar to the total amount of geographic variation found by Davidson (42). Moreover, seasonal variation in worker size appears to be a species trait for *M. pergandei*, which suggests that the site differences noted by Davidson (42) were related to variation in timing of the cycle rather than the local competitive environment. Consequently, size variation in *M. pergandei* workers does not constitute an example of character displacement, as has been previously suggested (7).

Differences in foraging methods appear to facilitate coexistence of related species via partitioning of seed resources, based on their density distribution, in a manner similar to that observed in tropical bees (81). Group foragers recruit nest-mates to seed patches at a higher rate than do solitary foragers, inferring that the former species should be more efficient at exploiting higher-density seed patches (73). The few data that compare these foraging methods support this hypothesis, because solitary foraging species harvest more seeds from low-density dispersed baits (41), spend more time searching for a seed (41, 155), and have lower foraging success (i.e. percentage of individuals returning with food) (41). Using a two-tailed percentage test (143), reanalysis of data from Weier & Feener (155) indicated that foraging success was also significantly lower in the solitary-foraging *Po. maricopa* (76%,  $N = 58$ ) compared with the group-foraging *Po. rugosus* (96%,  $N = 62$ ) ( $t_s = 3.40$ ,  $P = 0.0006$ ).

Differences in search time between the two foraging methods become especially significant given that time costs are a much more important component of foraging than are direct energy costs (54, 155). Moreover, available ecological data support the hypothesis that different foraging methods facilitate partitioning of seeds based on their density and dispersion, but additional studies are needed to compare the costs and benefits of these foraging methods. Evolutionary data indicating that group foraging has evolved numerous times in North American species of *Messor* and *Pogonomyrmex* probably provide the strongest evidence that it is an adaptive trait (Figures 1 and 2). Moreover, both ecological and evolutionary data suggest that group foraging is a novel method for exploiting the physical environment in a manner different from that of sympatric solitary-foraging congeners.

### **Intraspecific Competition**

***Colony Establishment and Survival*** Intraspecific aggression is common and strong throughout the life of most seed-harvester ants, although its effect varies

with colony age. Foundresses of several species of desert ants select particular microsites in which to start their nests, and thus the nests often have an initially clumped distribution (87, 118, 128, 136, 163). However, the few foundresses that survive to establish new colonies are concentrated in “gaps” away from conspecific colonies (61, 163). This spatial pattern of success results because workers of established conspecific and sometimes congeneric colonies interfere with juvenile establishment, initially by removing foundresses from their territory or later by aggressive interactions with incipient colonies (6, 73, 136, 163). Levels of aggression generally increase with proximity to and size of conspecific nests (61, 163). Workers continue to be aggressive toward incipient colonies and cause mortality until colonies reach ~2 years of age. Thereafter, intraspecific encounters are unimportant in colony survival (62, 163). Incipient colonies also compete by engaging in brood raids that sometimes result in high levels of mortality (1, 127, 129).

***Foraging Behavior and Colony Interactions*** The foraging area of a colony expands over the first several years as the colony grows (58, 60). Intraspecific interactions and fighting are especially common as young colonies grow and extend their territory between established neighbors (58, 60, 72). In column-foraging species, distance and direction of foraging columns are adjusted such that they are channeled away from hostile neighbors (61, 70, 72, 94, 134, 135). Nevertheless, foragers from neighboring colonies sometimes meet, which results in fighting in some species (22, 24, 61, 72) but not others (70, 94). Aggressive interactions and fighting typically involve confrontations between two foragers at the distal end of the foraging column (61, 72, 75). Fighting is also common at territory boundaries in solitary-foraging species (47, 72, 73). Colony interactions vary seasonally and are highest after summer rains, when ant activity peaks (61, 161). Overall, fighting results in low levels of worker mortality and a decrease in foraging efficiency, thus reducing seed input to the colony (47, 61). Congeners sometimes display levels of aggression similar to that shown between conspecific colonies, but such interactions appear uncommon between noncongeners (43, 72, 73, 76). Nest relocation occurs in several species and appears to sometimes represent a method to escape local intraspecific competition (47), but factors such as nest site suitability may also be involved (22, 59).

***Alate Production*** The few studies of alate production in seed-harvester ants examine intraspecific effects by manipulating colony resources via worker removal (artificial predation) (116), food supplementation (116, 135), or treatments that include neighbor removal (135) or the effect of neighborhood density (63, 152). Artificial predation generally decreases the size and number of alates (116; P Ode, unpublished information), but food supplementation has had variable effects, increasing alate production or body mass or changing sex ratios in some studies (135; P Ode, unpublished information) but not others (116). Neighbor removal also increases alate production (135). However, the effect of neighborhood density may vary between years (63, 152).

**Dispersion Pattern** The regular patterns of nest spacing that occur both intra- and sometimes interspecifically in seed-harvester (12, 26, 47, 133–135, 153, 163) and other ants (104) are often taken as evidence of competition. However, both theoretical (119) and empirical studies (1, 57, 137) demonstrate that competitive interactions can cause any of a broad range of dispersion patterns. Additionally, intraspecific dispersion patterns can vary with age, even if intense competition occurs throughout the life of a colony. For example, incipient colonies of *S. wagneri* planted in a clumped distribution pattern experienced intense competition with >90% mortality as a result of brood raiding, yet the dispersion pattern did not increase in regularity (1). However, adult colonies of *S. wagneri* are highly overdispersed, presumably due to territorial competition (1). Consequently, dispersion cannot be used to infer competition without data indicating the causal mechanism, especially given that birth rate, death rate, colony density, and nest relocation also affect dispersion patterns (1, 22, 39, 47, 59, 70, 132, 137).

**Demographic Considerations** Simulations suggest that the general life history pattern of ants, that is, low birth rates and low death rates for established colonies, affects density, dispersion, species persistence, and level of intra- and interspecific competition (137). Most commonly, conspecific adults interfere with juvenile establishment, and adult nests compete with one another. Under this scenario, simulations indicate that, for a given birth rate, the dispersion pattern changes from random to regular as adult death rate and hence colony turnover decrease; the dispersion pattern is highly regular when death rates are similar to those observed under natural conditions. Species persistence and thus the ability to coexist are also highest under these conditions. These predictions could be tested across geographic clines where it is likely that birth rates increase but death rates remain nearly the same, such as across the rainfall gradient from the Sonoran to Mohave Deserts. Given the importance of moisture to foundress success (see above), birth rates should be more episodic at the drier western sites, resulting in lower nest densities, less regular dispersion patterns, and lower species persistence times. This provides an alternative to the seed limitation hypothesis that has been used to explain decreased colony densities in arid habitats (12, 40).

## PREDATORS, PARASITIDS, AND PARASITES

Both predators and parasitoids have been documented to influence ant community structure, but little is known about parasites. All three factors are poorly studied among seed-harvester ants. Spiders (mostly family Theridiidae), ant lions (family Myrmeleontidae), and horned lizards (*Phrynosoma* spp.) are the three primary taxa that consume seed-harvester ants. The spiders capture ants by ambush or by constructing a web over the nest entrance. Although few ants are killed by spiders, the colony often temporarily decreases or stops foraging and closes the nest entrance when under attack by spiders (71, 106). One study found that spider

predation did not affect colony-spacing patterns (134). Additional information such as the degree of species specificity is needed to assess the potential impact of spiders on ant community structure.

Ants also compose the bulk of the diet for ant lions, which are sit-and-wait-predators. Ant lions often occur in high-density aggregations and can influence ant behavior, abundance, and distribution (66). These influences may be strongest on small ants because capture success is inversely related to ant body size (66). Overall, however, the affect of ant lions on seed-harvester ants would seem to be spatially limited because abiotic factors such as high temperatures often prevent ant lions from occurring in open habitats in hot climates (65).

Horned lizards are probably the most significant predator of harvester ants because they can capture large numbers of individuals (159). Horned lizards largely specialize on *Pogonomyrmex* and, even within this genus, prefer some species over others (121). The ants respond to horned lizard predation by temporarily decreasing or stopping foraging activity and sometimes by closing the nest entrance (56, 121).

Phorid flies appear to be the most significant parasitoid of ants and are often species or caste specific in their selection of ant hosts. The presence of phorids decreases ant foraging behavior and interferes with the alarm-recruitment response; thus, phorids can influence the outcome of competitive interactions (49). Interestingly, phorids lay eggs on few ants (<5%), and thus it is their mere presence that causes changes in behavior (49, 50). Phorids attack several seed-harvesting species of *Pheidole* and have species-specific associations with these species, but little is known about their interactions. In contrast, no phorids are known to attack species of *Pogonomyrmex* or *Messor* (B Brown, personal communication).

Various microorganisms and fungi attack ants, but little is known about any aspect of this interaction. Although ants would seem to be favorable hosts for microscopic parasites and fungus, these microorganisms appear to be relatively scarce in ants, probably due to a combination of allogrooming and secretion of numerous antimicrobial agents (77, 99). How these microorganisms affect ants is unknown, but it has been suggested that even small changes in colony efficiency or productivity may have dramatic effects on intra- and interspecific competitive interactions (99).

## CONCLUSIONS AND FUTURE RESEARCH

Since the late 1970s, interspecific competition has been viewed as the primary factor structuring southwestern seed-harvester ant communities. However, close analysis of these studies indicates that interspecific competition was poorly documented or based on correlative data that can be explained by alternative hypotheses. Later studies failed to find interspecific competition, whereas numerous studies throughout this period indicate that intraspecific competition is common and strong. Likewise, historical factors and abiotic habitat features, although largely

ignored in this system, appear important relative to structuring species assemblages at both local and regional scales.

These seed-harvester ant communities provide a rich system for future research at three levels: (a) single-species studies, (b) studies on patterns of species replacement, and (c) studies on species coexistence and the role of intra- and interspecific competition. At the intraspecific level, studies document patterns of spatial dynamics, but we know little about factors that influence density or temporal dynamics, or how such factors affect micro- and macrodistribution patterns. These questions could be addressed by transplanting foundresses or incipient colonies to various microhabitats and then adding an external treatment such as moisture to determine its effect on survival and growth. At the second level, a better understanding of contact zones, species replacement patterns, and the abiotic and biotic mechanisms that cause these patterns will facilitate understanding of the processes that determine local species composition. These contact zones often include closely related species, so the factors contributing to species divergence can also be assessed. At the third level, additional studies are needed to examine intra- and interspecific competition. These studies should include removal experiments along with measurement of several response variables such as foraging behavior, foraging success, diet breadth, and worker and alate production (135). In combination, data on seed storage and worker production are needed to assess the dynamics of seed stores and their potential longevity (90). Abiotic conditions need also be considered relative to potential energy constraints. For example, foraging time is the most important component of foraging, but dry conditions limit foraging time for many species. Consequently, environmental conditions can limit seed input to the colony even if seeds are plentiful. Natural history must be better documented for a wider variety of species, especially those with small colonies and for species of *Pheidole*. Such data will provide the baseline upon which to predict the response of a species to various experimental treatments; in its absence, interpreting experimental results is problematic given that responses can be species specific. For example, *M. pergandei* and *Po. rugosus* respond in very different ways to changes in seed density; at low seed densities, colonies of *M. pergandei* increase the rotation rate of the foraging column (but not the length) and handle fewer seeds prior to harvest (82, 130). In contrast, colonies of *Po. rugosus* increase the length of the foraging column (123).

Overall, North American seed-harvester ants provide a rich assemblage of species for studies of community structure. Future studies will likely identify additional processes that are involved in structuring this community and will lead to a better understanding of the relative importance of these processes.

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