Seed-Harvester Ants (Hymenoptera: Formicidae) of North America: An Overview of Ecology and Biogeography

by

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ABSTRACT

Competition and resource partitioning have been studied extensively as explanations for community structure and species coexistence in North American seed-harvester ants, but the biogeographical and historical context within which these communities have formed are poorly known. This paper examines biogeography of North American seed-harvester ants by constructing functional groups that serve to identify ecologically equivalent ant species that share a common evolutionary ancestry. Species were thus separated into functional groups based on genus and foraging method (solitary and group/trunk trail foraging species). Ecology, behavior, and micro- and macro-distribution patterns are then discussed and synthesized for species in each functional group. Overall, this discussion includes 42 ant species in the myrmicine genera *Aphaenogaster*, *Messor*, *Pheidole*, *Ephebomyrmex*, and *Pogonomyrmex*, about 5% of the total ant species in the United States.

The general pattern is that each functional group consists of a highly structured assemblage of ecologically equivalent ant species that are similar with respect to morphology, ecology, and behavior. The primary difference among species in each functional group is that each species occurs in specific micro- and macro-habitats, with the species replacing one another across contact zones that are delineated by abiotic habitat features. On a regional scale, species in these five ant genera are broadly sympatric, but only one species per functional group predominates at a locale. Re-examination of previously noted longitudinal clines of ant species richness and diversity suggest that rainfall is indeed correlated with these community attributes. However, patterns of species loss and species replacement across this rainfall gradient suggest that fewer ant species in drier locales is effected through limitations on mating flights and foundress survival rather than by seed abundance, as previously suggested.

Key words: allopatry, biogeography, contact zone, distribution pattern, North America, parapatry, seed-harvester ants, species replacement patterns.

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INTRODUCTION

The goal of studies that examine community structure is to understand patterns of species composition and mechanisms that allow species coexistence. A critical shortfall in many such studies is that species coexistence and interactions are studied as purely local phenomena, and the larger biogeographic context, and all that it may indicate about abiotic constraints upon the examined species, are ignored.

An especially vivid example of this problem is found in studies of community structure of North American seed-harvester ants, which constitute a dominant insect group in western North America and temperate and subtropical Mexico. This system has been extensively studied, beginning with a series of papers (Bernstein 1974, 1975, Davidson 1977a, 1977b, 1978, Bernstein & Gobbel 1979) that provided the first synthetic understanding at local and regional scales. These studies stimulated additional research (e.g., Hansen 1978, Mehlhop & Scott 1983, Rissing 1988a) that has largely focused on competition as the driving force in shaping diets and the partitioning of seed resources as explanations for species coexistence. However, the biogeographic context in which these communities are formed has never been examined in depth, despite its potential to provide a foundation for understanding community composition in a historical context.

This paper attempts to readjust our understanding of harvester ant community structure by presenting the first comprehensive synthesis of harvester ant ecology, behavior, and geographic distributions. This information reveals the common occurrence of ecologically equivalent ant species replacing one another across contact zones that are often delimited by abiotic habitat features. The general result is to emphasize the vital importance of abiotic habitat factors in determining what harvester ant species occur where, and thus what species are available to interact in the local settings that have been the focus of previous studies. Information is presented in four sections. The first section places species into functional groups using taxonomic and ecological characters. The second section discusses four morphological and ecological parameters selected for comparative overview because of their potential to affect resource partitioning and/or infer patterns of colony survival and distribution. The third section summarizes data on these characters and discusses ecology, microhabitat, and biogeography for species in each functional group. The last section examines distribution patterns within and across functional groups and synthesizes this information, especially relative to contact zones, to present a framework to examine levels of interactions and mechanisms that may structure seed-harvester ant communities. Patterns of species richness and species diversity in North American deserts (see Davidson 1977a) are also reassessed by examining moisture as an abiotic limitation for these ants.

The seed-harvester ants of North America include the myrmicine genera *Messor*, *Aphaenogaster* (formerly *Novomessor*), *Pheidole*, *Ephebomyrmex* (sometimes treated as a subgenus of *Pogonomyrmex*), and *Pogonomyrmex*. This paper treats 42 species in these genera, about 5% of the total ant species in the United States; *M. julianus*, *E. laevinodis*, and *Po. wheeleri* are the only species treated herein that do not occur in the United States. The treatment of *Pheidole* is restricted to four better known species to demonstrate that the geographical patterns discussed extend to this genus. Other *Pheidole* were excluded because of the size and complexity of the genus, and ongoing revision that includes description of numerous new species (Wilson 2001).

Ecological and behavioral data are lacking for some of the species because research has mostly focused on a few species that have large, conspicuous, and easily studied colonies. In contrast, congeners with small, less obvious colonies are poorly known, even though such information is necessary for comparative studies of harvester ant ecology and evolutionary history.

FUNCTIONAL GROUPS OF SEED-HARVESTER ANTS

Morphology, ecology, and evolutionary history act in concert to determine species interactions and distribution patterns within and among ant genera. I assess these potential affects by dividing species into functional groups. As defined here, functional groups are an informal classification that serve to identify ant species that share a common evolutionary history and foraging method. Species were first separated by genus, which facilitates examining affects of evolutionary history that include morphology, ecology, physiology, biogeographic origins, and phylogenetic constraints. For example, the genera *Messor* and *Pogonomyrmex* have different evolutionary origins and apparently invaded North America from different areas, *Messor* from Asia via the Bering Strait (Snelling & Cole, unpublished data) and *Pogonomyrmex* from South America (Kusnezov 1951, Taber 1990). There are several pairs of ecologically equivalent *Messor-Pogonomyrmex* species, but their different evolutionary histories may have affected their use of micro- and macro-habitats (see Johnson 1992).

One taxonomic problem involves the status of *Ephebomyrmex*, which some authors treat as a subgenus of *Pogonomyrmex*. In revising

Pogonomyrmex, Cole (1968) treated *Ephebomyrmex* as a subgenus, but Kempf (1972) revived generic status, which was maintained by several others (Brown 1973, Snelling & George 1979, Wheeler & Wheeler 1986). Snelling & George (1979) indicate that *Ephebomyrmex* is best regarded as a separate genus because "the psammophore is not well developed and the species are matinal/crepuscular, less strictly granivorous than species of *Pogonomyrmex* s. str.". This paper treats *Ephebomyrmex* as a genus, though Bolton (1995) recently reinstated subgenus status without discussion.

Foraging method was used to further divide species into functional groups that exploit their physical environment in a similar manner. While all of these ant species harvest a common resource, differences in foraging method appear to result in these species exploiting this resource in different ways. Moreover, species that use different foraging methods can coexist at a locale because they partition seeds based on the density and distribution of seeds that are harvested. In contrast, species that use the same foraging method compete for seed resources and thus do not coexist (Davidson 1977b). Consequently, species of *Messor* and *Pogonomyrmex* were divided by foraging method, i.e., into solitary and group/trunk trail foraging species; these are the only two genera treated herein that vary in this character. In some species, foraging method varies intraspecifically depending on factors such as vegetation density (Fewell 1988a); in these cases, species were categorized into their most typical foraging method. For consistency with literature, I use "group forager" for *Messor* and "trunk trail forager" for *Pogonomyrmex*, although they result in similar patterns. In trunk trail foragers, the workers exit the nest in a column and break off near the distal end to forage individually (Kusnezov 1951, Hölldobler 1974, Davidson 1977b). Rapid and efficient nestmate recruitment by group and trunk trail foragers facilitates rapid harvest of clumped seed patches. In solitary foragers, the workers radiate out in all directions from the nest to search for and collect seeds largely independent of nestmates. Solitary foraging species have poor nestmate recruitment, spend more time searching for seeds, and often harvest seeds from scattered low-density patches (Davidson 1977b, Weier & Feener 1995). Three species, *M. chamberlini*, *Po. californicus*, and *Po. maricopa*, use an intermediate foraging method, and were thus placed in a third foraging group within their respective genera. All three species are typically solitary foragers, but each forms recruitment trails to high-density seed patches, though at a slower rate than trunk trail foragers (Hölldobler 1976a, R.R. Snelling pers. comm.).

CHARACTERS FOR COMPARING MORPHOLOGY, ECOLOGY, AND DISTRIBUTION WITHIN GROUPS

The four morphological and ecological parameters selected for comparative overview of species in each functional group are: (1) head width, (2) colony size, (3) habitat affiliation, and (4) timing of mating flights. Other available ecological data are also discussed.

Head width is a standard morphological character (Wilson 1978) that provides information on the size of food items harvested. In seed-harvester ants, head width is often used as an interspecific index of seed size harvested (Davidson 1978, Bernstein 1979, Morton & Davidson 1988). Here, I report range of head widths so as to include intra- and inter-nidal variation, which better reflects congeneric differences in potential mechanical limitations. Head width of *M. andrei*, *M. julianus*, *A. albisetosa*, *A. cockerelli*, *Ph. gilvescens*, *Ph. tucsonica*, and *Ph. vistana* were obtained by measuring specimens from several locales because literature values were lacking. I also made additional measures on *E. laevinodis*, *E. pima*, *Po. anzensis*, and *Po. tenuispinus* as literature values used few individuals. Measures were made with an ocular micrometer at 50X using a binocular microscope.

Colony size is an ecological trait associated with evolution of insect societies. Larger colonies require higher levels of social integration and communication (Michener 1964, Beckers *et al.* 1989) as manifested by an increased use of chemical communication. The general pattern in ants is that species with small colonies forage solitarily with little or no nestmate recruitment, while species with large colonies forage in groups and use chemicals to recruit nestmates (Beckers *et al.* 1989). Large colony size may also convey ability to better survive environmental vagaries (Kaspari & Vargo 1995). Colony size estimates for each species use nest excavation data, or estimates of forager number when excavation data are lacking.

Comparative data on habitat affiliation facilitates predicting patterns of colony survival relative to temperature and precipitation. For example, species restricted to hot desert habitats are predicted to be more heat and/or desiccation tolerant than mesic or high elevation congeners (for a review see Edney 1977, Hadley 1994). Habitat affiliation was used to classify species into four broad environmental regimes: (1) occurring in only hot deserts (Mojave, Sonoran, and Chihuahuan), (2) occurring in, but not restricted to, hot deserts, (3) largely restricted to cool deserts and absent from hot deserts, and (4) occurring exclusively outside of deserts. Hot desert species were taken from Appendix A of Wheeler & Wheeler (1973). Changes to their classifications involve deleting *E. huachucanus* as restricted to hot desert habitats; this is an error as *E. huachucanus* is a mid- to high-elevation species. Wheeler & Wheeler (1973) also classified *Ph. vistana* as a hot desert species, but recent data indicate this species also inhabits cool desert habitats (Snelling & George 1979, R.R. Snelling, pers. comm.).

Colony founding is the most vulnerable stage in the colony life cycle because foundresses must survive stressful ambient conditions for the extended claustral phase (Nagel & Rettenmeyer 1973, Tschinkel 1992, Herbers 1993, Johnson 1998a). Cues that trigger mating flights determine the environmental conditions experienced by foundresses and thus, influence their probability of surviving in various micro- or macro-habitats. Differences in soil temperature and soil texture and/or soil moisture affect intraspecific variation in foundress survival and hence microdistribution pattern of several desert ants (Rissing *et al.* 1986, Rissing 1988b, Johnson 1992, 2000). These affects are likely even more pronounced for ecologically equivalent species that have different mating flight regimes. Flights of desert ants take two general forms, synchronous flights that are triggered by summer rains, and asynchronous flights that occur over an extended period of time and appear triggered by photoperiod (McCluskey 1963). Mating flights for species in which we lack data are extrapolated from close congeners.

Distribution maps are based on locale data that were obtained from specimens at the Los Angeles County Museum of Natural History, Museum of Comparative Zoology (Harvard), California Academy of Sciences, American Museum of Natural History, National Museum of Natural History, the collections of Robert A. Johnson and William P. MacKay, and literature (Gregg 1963, Allred 1982, Moody & Francke 1982, Wheeler & Wheeler 1986, Snelling & Cole, unpublished data). Throughout this paper I refer to the Baja California peninsula of Mexico as Baja California and the two states as BC (Baja California) and BCS (Baja California Sur).

MORPHOLOGY, ECOLOGY, AND BIOGEOGRAPHY OF FUNCTIONAL GROUPS

***Messor*-Group Foragers**

These three similar-sized species are strict granivores that forage in columns which typically extend >20m from the nest (Table 1). As might be expected from these extensive foraging columns, colonies of all three species contain at least several thousand workers. However, worker number is highest for *M. pergandei* where colonies can have over 30,000 foragers and probably more than 50,000 total workers. Mating flights of all three species occur from early to mid-morning over a several week period. Although photoperiod appears to trigger the mating flights for all three species (see McCluskey 1963), their season of flight differs. Mating flights of the two hot desert species, *M. pergandei* and *M. julianus*, occur from late January to mid March, while those of *M. andrei*, which is not a hot desert species, occur from late June to early August (Table 1). Additionally, foundresses of *M. andrei* are semi-claustral, and thus must forage to obtain sufficient energy to eclose their first workers (Brown 1999).

These three species of *Messor* have parapatric distribution patterns with their ranges showing little to no overlap across the narrow contact zones that separate the species (Fig. 1, p. 83). *Messor julianus* is mostly restricted to central and southern portions of Baja California, while *M. pergandei* occurs in eastern portions of the peninsula to as far south as northern BCS. In northern and central BC, *M. julianus* inhabits a narrow band along the cool Pacific Coast, while *M. pergandei* is restricted to the more xeric desert and lowland areas to the east. Where these two species come in contact, *M. pergandei* occupies more xeric microhabitats, i.e., either in drier soils or at lower elevations (R. Johnson, pers. obs.). Ranges of *M. julianus* and *M. andrei* are separated by about 75km along the Pacific Coast in BC (Creighton 1953). *Messor pergandei* and *M. andrei* rarely coexist as the latter species inhabits the cool foothills of the Coastal Range and inland valleys from northern BC to southern Oregon. In contrast, *M. pergandei* inhabits hot desert areas to the east and only occasionally penetrates to the adjacent coastal valleys, but rarely above elevations of 915m (Snelling & Cole, unpublished data).

Messor-Solitary Foragers with Recruitment

Messor chamberlini is the only species in this group as the diurnal, solitary foragers recruit nestmates and forage in columns to high-density food patches. Colonies consist of up to several hundred workers, and thus colony size is similar to that of congeners with limited recruitment (see below). Mating flights of this cool desert species occur during summer and appear triggered by photoperiod.

The only congener with an ecology and biogeography similar to that of *M. chamberlini* is *M. stoddardi* (see below). These two species have broadly overlapping geographic ranges in coastal areas of southern California, though there is no evidence that the two species coexist in the same vicinity (Snelling & Cole, unpublished data) (Fig. 2, p. 84).

Messor-Solitary Foragers with Limited Recruitment

These five poorly known species are similar in size except for the smaller *M. lariversi* (Table 1). All five species are strict granivores with colonies that consist of up to several hundred workers. The workers of

Table 1. Morphological and ecological data for North American seed-harvester ants in the genera *Aphaenogaster, Messor, Pheidole, Ephebomymrex* and *Pogonomyrmex*. Species within each genus are grouped by primary foraging method (see text).

Genus / Species	Range in Head Width (mm)	Colony Size	Habitat Affiliation	Mating Flights^6 (Synchronicity/Cues)	References^7
Messor-Group Foragers					
andrei (Mayr)	1.15-1.98	several thousand^2	Hot & Cool	A/PP/Jun-Aug	(10,11,13,14,20,50,100)
julianus (Pergande)	1.23-1.86	several thousand^2	Hot	A/PP/Jan-Mar	(10,13,50,99)
pergandei (Mayr)	0.80-2.20	>35,000^2	Hot	A/PP/Jan-Mar	(1,8,10,13,17,19,20,23,31,50,51,52, 68,91,92)
Messor-Solitary Foragers with Recruitment					
chamberlini Wheeler	1.34-1.46	627	Cool	A/PP/Jun-Aug	(78)
Messor-Solitary Foragers with Limited Recruitment					
chicoensis (Smith)	1.30-2.03	<500^3	Cool	A/PP/Jun-Aug	(78)
smithi (Cole)	1.32-1.53	275	Hot & Cool	A/PP/Jun-Aug	(10,75,77,78)
lariversi (Smith)	1.00-1.43	671	Hot & Cool	A/PP/Jun-Aug	(75,77,78,79)
lobognathus Andrews	1.60-1.82	580	Cool	A/PP/Jun-Aug	(76,77,78)
stoddardi (Emery)	0.97-1.78	<500^3	Hot & Cool	A/PP/Jun-Aug	(10,78)
Aphaenogaster-Solitary Foragers					
albisetosa Mayr	1.43-1.92	1590^2	Hot	S/SR	(3,5,10,12,13,20,34,84)
cockerelli André	1.29-1.75	1115^2	Hot	S/SR	(1,2,3,5,10,12,13,18,20,34,53,84)
Pheidole-Solitary Foragers					
desertorum Wheeler	1.33-1.65^1 0.56-0.74	9881	Hot & Cool	S/SR & WR	(1,10,18,20,81)
vistana Forel	1.29-1.68 0.52-0.75	several thousand^2	Hot & Cool	S/WR^3	(10,18,20,44,82)

Table 1(cont.). Morphological and ecological data for North American seed-harvester ants in the genera *Aphaenogaster*, *Messor*, *Pheidole*, *Ephebomyrmex* and *Pogonomyrmex*. Species within each genus are grouped by primary foraging method (see text).

Genus / Species	Range in Head Width (mm)	Colony Size	Habitat Affiliation	Mating Flights[6] (Synchronicity/Cues)	References[7]
Pheidole-Groups Foragers					
gilvescens Creighton & Gregg	1.20-1.43 0.49-0.57	500	Hot & Cool	S/SR & WR[3]	(1,10,18,20)
tucsonica Wheeler	1.34-1.54 0.49-0.61	300-400	Hot & Cool	S/SR	(1,10,18,20,68,83)
Ephebomyrmex					
huachucanus Wheeler	1.38-1.60	<200	Hot & Cool	S/SR	(6,20,49)
imberbiculus Wheeler	0.97-1.21	50-75	Hot & Cool	S/SR	(1,6,10,15,18,39,45,93,94)
laevinodis Snelling	0.90-1.13	50-75[3]	Hot	S/SR[3]	(7,20)
pima Wheeler	0.93-1.17	50-75	Hot	S/SR	(1,6,10,15,20)
Pogonomyrmex-Trunk Trail Foragers					
badius (Latreille)	1.62-2.50[4]	>5000	Non-Desert	S/SR	(6,32,35,43,57,58,59,60,80,85,88,97)
barbatus (Smith)	2.05-2.70	12,000	Hot & Cool	S/SR	(2,6,10,16,20,24,28,65,66,67,68,72)
bicolor Cole	1.82-2.28	several thousand[2]	Hot	S/SR[3]	(6,10,20,44)
occidentalis (Cresson)	1.44-2.13	3190	Hot & Cool	S/SR	(6,10,21,33,41,54,55,56,73,86,87)
rugosus Emery	1.75-2.70	8598	Hot & Cool	S/SR	(1,2,4,6,10,16,24,62,63,64,65)
salinus Olsen	1.37-1.68	>3000	Hot & Cool	S/SR	(6,10,22,29,61,70,98)
subnitidus Emery	1.29-1.94	5934	Hot & Cool	S/SR	(4,6,10,42,44)
tenuispinus Forel	1.98-2.38	several thousand[2]	Hot	S/SR[3]	(6,7,10,20,44)
wheeleri Olsen	2.72-2.89	very populous[2]	Hot	S/SR	(6,10,47)

Table 1(cont.). Morphological and ecological data for North American seed-harvester ants in the genera *Aphaenogaster, Messor, Pheidole, Ephebomymrex* and *Pogonomyrmex*. Species within each genus are grouped by primary foraging method (see text).

Genus / Species	Range in Head Width (mm)	Colony Size	Habitat Affiliation	Mating Flights[6] (Synchronicity/Cues)	References[7]
Pogonomyrmex-Solitary Foragers with Recruitment					
californicus (Buckley)	1.39-1.99	2000-4500[5]	Hot & Cool	A/PP/May-Jul	(1,6,10,20,25,38,40,91,95,96)
maricopa Wheeler	1.52-2.05	500-1000[2]	Hot & Cool	S/SR	(1,6,10,16,20,24)
Pogonomyrmex-Solitary Foragers with Limited Recruitment					
anzensis Cole	1.52-1.72	several hundred[2]	Hot	A/PP/May-Jun[3]	(6,18,20,89)
apache Wheeler	1.79-2.28	<200	Hot & Cool	S/SR	(6,20,48)
bigbendensis Francke & Merickel	1.61-1.87	several hundred[3]	Hot & Cool	S/SR[3]	(37)
brevispinosus Cole	1.56-1.79	<200	Cool	S/WR[3]	(6,44,69)
comanche Wheeler	1.18-1.87	<1500	Non-Desert	S/SR	(6,27,42,46)
desertorum Wheeler	1.38-2.16	<500	Hot & Cool	S/SR	(1,6,10,15,16)
magnacanthus Cole	1.18-1.41	100-225	Hot	A/PP/May-Jun	(1,6,18)
montanus MacKay	1.22-1.72	1665	Cool	S/SR	(4,36,42)
snellingi Taber	1.64-1.77	several hundred[3]	Hot	A/PP/May-Jun[3]	(46)
subdentatus Mayr	1.48-1.90	several hundred	Cool	S/WR	(6,15,44,69,74,90)
texanus Francke & Merickel	2.15-2.56	<100	Hot	S/SR[3]	(37)
n. sp. B	No Data	several hundred[3]	Hot	A/PP/May-Jun[3]	(44)
NONCONGENERS					
Pogonomyrmex rugosus Emery	1.75-2.70	8598	Hot & Cool	S/SR	(1,2,4,6,10,16,24,62,63,64,65,66)
Messor pergandei (Mayr)	0.80-2.20	>35,000[2]	Hot	A/PP/Jan-Mar	(1,8,10,13,17,19,20,23,31,50,51,52)

Table 1(cont.). Morphological and ecological data for North American seed-harvester ants in the genera *Aphaenogaster, Messor, Pheidole, Ephebomyrmex* and *Pogonomyrmex*. Species within each genus are grouped by primary foraging method (see text).

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[1] *Pheidole* workers are dimorphic; head widths of majors and minors are listed in the first and second rows, respectively.

[2] Colony size is based on estimates of forager number and/or partial excavations.

[3] No data are available; thus, predictions are derived from related congeners.

[4] Head width data for this polymorphic species include only size classes that forage.

[5] Colony size varies geographically, and probably ranges from 500-1000 workers in eastern portions of the geographic range.

[6] Mating flights are categorized in regard to synchronicity; A=Asynchronous, S=Synchronous, and cues that trigger mating flights; PP=Photoperiod, SR=Summer Rains, WR=Winter Rains.

[7] References (for complete citation, refer to Literature Cited section). (1) Davidson (1977a); (2) Whitford *et al.* (1976); (3) Whitford *et al.* (1980); (4) MacKay (1981); (5) Hölldobler *et al.* (1978); (6) Cole (1968); (7) Snelling (1982a); (8) Pollock & Rissing (1985); (9) Hölldobler (1971); (10) Wheeler & Wheeler (1973); (11) McCluskey (1963); (12) Hölldobler *et al.* (1995); (13) Wheeler & Creighton (1934); (14) Hobbs (1985); (15) Creighton (1956); (16) Hölldobler (1976a); (17) Rissing & Wheeler (1976); (18) Snelling & George (1979); (19) Rissing (1987); (20) R.A. Johnson, unpublished data; (21) Nagel & Rettenmeyer (1973); (22) Rust (1988); (23) Wheeler & Rissing (1975); (24) Hölldobler (1976b); (25) Michener (1942); (26) Bohart & Knowlton (1953); (27) Strandtmann (1942); (28) Gordon (1983); (29) Shattuck (1987); (30) Snelling & Cole, unpublished data; (31) Johnson (1991); (32) Turner (1909); (33) Fewell (1990); (34) Whitford *et al.* (1976); (35) McCoy & Kaiser (1990); (36) MacKay (1980); (37) Francke & Merickel (1981); (38) De Vita (1979); (39) MacKay *et al.* (1985); (40) S.W. Rissing, pers. comm.; (41) Crist & MacMahon (1991); (42) W. P. MacKay, pers. comm.; (43) Traniello & Beshers (1991); (44) R.R. Snelling, pers. comm.; (45) Heinze *et al.* (1992); (46) S. Taber, unpublished data; (47) J. Schmidt, pers. comm.; (48) Cole (1954); (49) Creighton (1952); (50) Creighton (1953); (51) Went *et al.* (1972); (52) Bernstein (1974); (53) Hölldobler & Carlin (1989); (54) Chew (1960); (55) Lavigne (1969); (56) Rogers (1972); (57) Gentry & Stiritz (1972); (58) Gentry (1974); (59) Golley & Gentry (1964); (60) Harrison & Gentry (1981); (61) Jorgensen & Porter (1982); (62) Peck (1976); (63*) Wildermuth & Davis (1931); (64) Johnson *et al.* (1994); (65) Hölldobler (1974); (66) Gordon & Kulig (1996); (67) Gordon (1992); (68) Davidson (1977b); (69) Wheeler & Wheeler (1986); (70) Porter & Jorgensen (1980); (71) Costello (1972); (72) Garcia-Perez *et al.* (1994); (73) Fewell (1988b); (74) Mallis (1941); (75) Cole (1963); (76) Wheeler & Wheeler (1959); (77) Cole (1966); (78) M. R. Bennett, unpubl. data: (79) Cole (1955); (80) M. Dehyrup, pers. comm.; (81) Helms (1996); (82) Pullen (1961); (83) Mehlhop & Scott (1983); (84) Creighton (1950); (85) Tschinkel (1998); (86) Clark & Hainline (1975); (87) Mull & Crist (1993); (88) Harmon (1993); (89) S. P. Cover, pers. comm.; (90) P.S. Ward, pers. comm.; (91) Ryti & Case (1988); (92) Gordon (1978); (93) Wheeler (1917); (94) MacKay & MacKay (1984); (95) Rissing *et al.* (2000); (96) Erickson (1972); (97) Ferster & Traniello (1995); (98) Gaglio *et al.* (1998); (99) Johnson (in press); (100) Brown (1999).

[(63*)] At this time *P. barbatus* and *P. rugosus* were subspecies of *P. barbatus*. This reference lists the species as *P. barbatus* but it is *P. rugosus*, as the former species does not occur near Tempe, Arizona, where the study was conducted.

all five species are primarily solitary twilight/nocturnal foragers. Mating flights occur during summer and appear to be triggered by photoperiod for all five of these cool desert species. One additional undescribed species that is only known from one locale in southwestern Arizona probably falls into this group.

Various distribution patterns occur in this group of species (Fig. 2, p. 84). *Messor chicoensis* is geographically separated from all other species in the group as its range is restricted to the upper Sacramento Valley and the northern Coastal Range of California. Two other species, *M. lariversi* and *M. smithi*, have broadly overlapping geographic distributions in the Great Basin area across eastern California and western and southern Nevada, with the latter species also extending into pinyon-juniper habitat in central Arizona. However, these two species rarely coexist as *M. lariversi* typically inhabits low elevation desert basins while *M. smithi* occurs in mid-elevation to montane habitats (M. Bennett, pers. comm., Snelling & Cole, unpublished data). The geographic distribution of the other high-elevation species, *M. lobognathus*, ranges from the Dakotas to western Nevada. *Messor smithi* and *M. lobognathus* contact one another in central and western Nevada but the two species are rarely sympatric (Snelling & Cole, unpublished data). The last species, *M. stoddardi*, is the only species in the group that occurs along coastal southern California, with the only similar congener in this area being *M. chamberlini* (see above).

Aphaenogaster

The two largest desert species of *Aphaenogaster* (formerly *Novomessor*), *A. cockerelli* and *A. albisetosa*, are similar in size, and both species are better categorized as omnivores/scavengers because they harvest substantial numbers of insects and other debris in addition to seeds. The two species are solitary foragers that recruit nestmates to food, the workers retrieve prey items cooperatively, and the nests have multiple entrances. Colonies of both species probably consist of about 1000-3000 workers. The two species are restricted to hot desert habitats, and both species have crepuscular/nocturnal mating flights that are triggered by summer rains (Table 1).

These two species of *Aphaenogaster* have broadly overlapping geographic distributions from Texas to Arizona and south into Mexico (Fig. 3). Sympatry is rare, however, as each species occurs in distinct habitats: *A. cockerelli* inhabits open intermountain plains and level areas near streams while *A. albisetosa* occurs at higher elevations and inhabits sloping hills and foothills (Wheeler & Creighton 1934). Creighton (1955) suggested elevation was the primary factor separating these two species. In terms of overall distribution, *A. cockerelli* ranges farther west

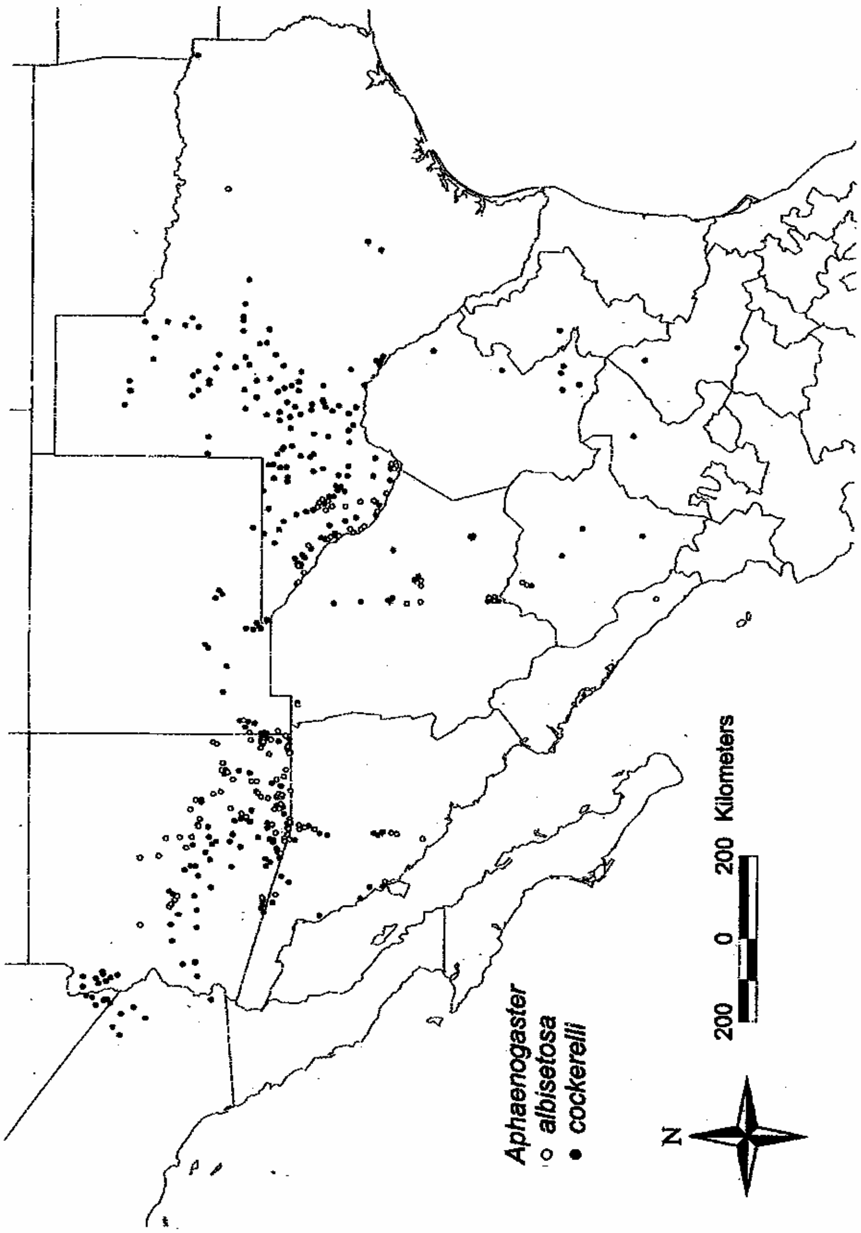

Fig. 3. Distribution of *Aphaenogaster albisetosa* (open circle); *A. cockerelli* (solid circle).

than does *A. albisetosa* as only the former species reaches western Arizona and southeastern California. In these latter more xeric areas, *A. cockerelli* inhabits rocky hillsides at higher elevations (900-1500m) (Snelling & George 1979), and thus displays a habitat shift in these areas relative to other portions of its range.

Pheidole

The four species of *Pheidole* treated here consist of two groups that differ in foraging pattern and diet. All four species are among the most common and well known *Pheidole* in deserts of the southwestern United States, and all but *Ph. vistana* were discussed by Davidson (1977a, 1977b). I include *Ph. desertorum* because it was mistakenly considered to be a seed-harvester by Davidson (1977a, 1977b) (see below), while *Ph. vistana* is included because it is an ecological equivalent of *Ph. desertorum.* Seed-harvester species of *Pheidole* in the United States are listed in Table 2.

Pheidole desertorum and *Ph. vistana*

The majors and minors of these two species are similar in size, and diets of both species primarily consist of arthropods and termites. The two species are nocturnal, solitary foragers, but actively recruit nestmates and form diffuse foraging columns to larger food sources. Colonies of *Ph. desertorum* average about 10,000 workers; although excavations are lacking, colonies of *Ph. vistana* appear similar in size. The two species occur in both hot and cool desert habitats. Summer rains trigger the pre-dawn mating flights of *Ph. desertorum* in eastern portions of its geographic range, while in more western locales (California desert areas), the mating flights appear to be triggered by winter rains as dealate females have been observed on the ground in May. The mating flights of *Ph. vistana,* though unknown, are probably also triggered by winter rains. Both species are sometimes polygynous.

These two closely related species have a parapatric distribution pattern with their ranges overlapping across a broad contact zone in the Colorado Desert. *Pheidole desertorum* is an eastern species that ranges from Texas and Oklahoma to southern Nevada and southeastern California and into Mexico. In contrast, *Ph. vistana* is restricted to the Mojave Desert and western portions of the Sonoran Desert. The two species co-occur in western Arizona and southeastern California, but each species predominates in different habitats throughout this area; *Ph. desertorum* generally occurs at lower elevations in more xeric locales and is replaced by *Ph. vistana* at higher elevations in desert transition and chaparral habitats (Snelling & George 1979).

Pheidole gilvescens and *Ph. tucsonica*

The majors and minors of these two seed-harvesters are similar in size, and both species forage in columns that may extend several meters from the nest. The two species have polydomous nests that consist of several hundred workers, and colonies of the two species have been noted to interact aggressively. The two species occur in both hot and cool desert habitats. In central Arizona, the mating flights of both species are triggered by summer rains.

Geographic distribution of these two closely related species broadly overlaps from southern Nevada to southeastern California, Arizona, and south into Mexico. However the range of *Ph. tucsonica* is more expansive as it also extends into New Mexico and much of Baja California. The two species sometimes occur sympatrically and in such cases both species can be common. However, the two species often occur allopatrically in different microhabitats, with *Ph. tucsonica* typically predominating in soils that consist of coarser sands, i.e., drier soils (Cole 1956, R.R. Snelling, pers. comm.). Consequently, *Ph. gilvescens* is the somewhat less xeric of the two species, and as might be expected it is replaced by *Ph. tucsonica* in many parts of the Colorado Desert (Snelling & George 1979).

Ephebomyrmex

These four species are similar in size with the exception of the larger *E. huachucanus* (Table 1). All four species are granivorous, though dead insects are harvested to the extent that their diets are more generalized than are those for species of *Messor* and *Pogonomyrmex*. Ants comprise the bulk of harvested insects. All four species forage solitarily and colonies consist of 50-200 workers, and sometimes up to 400-500 workers for *E. huachucanus*. *Ephebomyrmex pima* and *E. laevinodis* are the only species restricted to hot desert habitats (Table 1). Mating flights of *E. imberbiculus* and *E. pima* occur from early to mid-morning following summer rains. Both species form numerous, small mating aggregations in and near bushes and shrubs. Other observations of reproductive ecology include polymorphic gynes (winged and wingless ergatoids) in *E. imberbiculus* (Heinze *et al.* 1992) and the presence of brachypterous and dealate queens in nests of *E. huachucanus* (Creighton 1952). Recent data indicate that *E. huachucanus* queens are brachypterous at eclosion and shed their wings within several days, thus explaining Creighton's observation of both winged and wingless queen forms in the same nest. The dealate queens are uninseminated and can remain in the natal nest for several months (R. Johnson, unpublished data).

Three of these species (*E. imberbiculus*, *E. pima*, and *E. laevinodis*) have parapatric distribution patterns with little or no overlap across the narrow contact zones that separate the species (Fig. 4, p. 85). *Ephebomyrmex pima* is restricted to low desert habitats (< 915m) in Arizona and Sonora, Mexico. *Ephebomyrmex imberbiculus* typically occurs above 915m and its broad geographic range completely encircles that of *E. pima* (Creighton 1952, 1956, MacKay *et al.* 1985). *Ephebomyrmex laevinodis* is restricted to central and southern areas of Baja California, where it replaces *E. imberbiculus* (Snelling 1982) (Fig. 4, p. 85). *Ephebomyrmex huachucanus* is a mid- to high-elevation species (1200-2000m) that ranges from northern Arizona and New Mexico to northern Mexico. Throughout much of its range, *E. huachucanus* occurs in discrete populations within the numerous desert mountain ranges but is absent from intevening desert habitats. *Ephebomyrmex huachucanus* and *E. imberbiculus* are distributed allopatrically across a narrow elevation zone with the former species replacing *E. imberbiculus* at higher elevations (Creighton 1956, MacKay *et al.* 1985).

***Pogonomyrmex*-Trunk Trail Foragers**

Head width varies considerably among these species and is lowest for *Po. occidentalis*, *Po. salinus*, and *Po. subnitidus*, which are the only high elevation and/or cool habitat species in the group (also the only *Po. occidentalis* complex species) (Table 1). In contrast, head width of *Po. wheeleri* eclipses that of all species, while all other species have head widths that are intermediate to these two groups. Note, however, that majors of the polymorphic *Po. badius* are larger than other congeners, but only the smaller individuals leave the nest to forage.

All of the species in this group are strict granivores, with the exception that insects may comprise up to 50% of the diet for *Po. badius*. Colonies of all nine species average >5,000-10,000 workers. Recruitment pheromones probably occur in all of these species but are only known in *Po. badius*, *Po. barbatus*, *Po. occidentalis* and *Po. rugosus*. Three species, *Po. bicolor*, *Po. tenuispinus*, and *Po. wheeleri*, are restricted to hot desert habitats, while all others also occur in, or are restricted to, cooler, less arid areas. *Pogonomyrmex badius* is the only species that occurs outside of desert habitats. Summer rains trigger the mating flights for seven of these species, and those of *Po. bicolor* and *Po. tenuispinus*, while unknown, are probably similar (Table 1).

Most of these trunk trail foraging species have parapatric distribution patterns across broad contact zones relative to those exhibited in *Messor* and *Ephebomyrmex* (Figs. 5-6). These broad contact zones are caused by extensive topography and the resulting cool habitats afforded by numerous mountains, which permit isolated populations of species such as *Po. occidentalis* to occur considerably south of their primary range. Several species also follow watercourses outside their primary range (Cole 1968).

Pogonomyrmex badius is only species in the genus that occurs east of the Mississippi River. The species occurs in the Coastal Plains states from North Carolina to Florida and west to Louisiana, where its range is contiguous with that of *Po. barbatus* (Cole 1968) (Fig. 6, p. 87).

Pogonomyrmex rugosus is a geographically widespread species that contacts several group members. The geographic range of *Po. rugosus* and its sister species, *Po. barbatus*, overlap broadly from southeastern Arizona to western Texas and into Mexico. However, the two species have an allopatric distribution pattern as they segregate among microhabitats based on soil texture, with *Po. barbatus* occurring alone in soils that have a higher clay content and/or higher moisture retention. The two species are only sympatric in localized contact zones, where percentage clay content is intermediate to that of adjacent areas in which the two species occur allopatrically (Johnson 2000). The ranges of *Po. rugosus* and *Po. barbatus* are contiguous with the geographic range of *Po. wheeleri*, which occurs in southwestern Mexico at elevations below 150m (Cole 1968, MacKay *et al.* 1985). *Pogonomyrmex rugosus* contacts *Po. bicolor* from southern Arizona to central Sonora, Mexico. These two species have an allopatric distribution pattern with *Po. bicolor* occurring on bajadas and rocky foothill habitats while *Po. rugosus* predominates in alluvial valleys (R. Johnson, pers. obs.).

Scattered populations of *Po. rugosus* reach central portions of Baja California, but the species is most common in and largely confined to the Pacific Coast and central montane areas in northwestern portions of the peninsula. *Pogonomyrmex rugosus* contacts *Po. tenuispinus* in southern portions of the San Felipe Desert of BC. *Pogonomyrmex tenuispinus* becomes increasingly common to the south and replaces *Po. rugosus* in central and southern BC. Further north, *Po. rugosus* contacts *Po. subnitidus*, which is a coastal to upland species that is distributed along a north-south band from northwestern BC to western Nevada. These two species segregate along an elevation gradient with *P. subnitidus* occurring at higher elevations (Snelling & George 1979, MacKay 1981, Wheeler & Wheeler 1986).

Pogonomyrmex rugosus contacts *Po. occidentalis* in southern Utah and Nevada, and in several mountain ranges from southern Arizona to Chihuahua, Mexico. In these southern mountain ranges the two species have an allopatric distribution pattern as they segregate across an elevation gradient, with *Po. occidentalis* occurring at mid- to high-elevations, while *Po. rugosus* predominates at lower elevations (MacKay *et al.* 1985, Wheeler & Wheeler 1986). *Pogonomyrmex rugosus* contacts *Po. salinus* in southern Nevada, where each species occupies distinct microhabitats (S.W. Rissing, pers. comm.).

Pogonomyrmex occidentalis and *Po. salinus* also have contiguous ranges with the latter species replacing *Po. occidentalis* north of a broad contact zone that occurs across central Nevada (Fig. 5, p. 86). Within this contact zone, each species occupies the microhabitat that correlates with their different geographic distributions: *Po. salinus* inhabits higher elevation pinyon-juniper forest habitats while *Po. occidentalis* predominates at lower elevations (Cole 1968, R. Johnson, pers. obs.). *Pogonomyrmex subnitidus* contacts *Po. salinus* and *Po. occidentalis* in western Nevada, but data to assess microhabitat segregation between *Po. subnitidus* and the latter two species are lacking. However, the more southern geographic range of *Po. subnitidus* would suggest that this species occurs at lower elevations along contact zones with *Po. salinus.*

***Pogonomyrmex*-Solitary Foragers with Recruitment**

This group includes the two similar-sized species *Po. californicus* and *Po. maricopa.* The two species are solitary foragers that recruit nestmates to localized seed patches, though at a slow rate compared to trunk trail foragers. For *Po. californicus*, colonies contain 2000-4500 workers in some western locales, but this number appears to be lower in central and eastern portions of their geographic range. Variation in colony size appears related to queen number as the larger colonies at western sites are polygynous while those in other areas are monogynous (Rissing *et al.* 2000, R. Johnson, unpublished data). Data are lacking on size of *Po. maricopa* colonies, though Cole (1968) comments that "nest type, habitat, colony strength, and foraging behavior are often nearly identical" for these two species. The two species occur in both hot and cool desert habitats. Overall, ecology of these two species appears to only differ with respect to mating flights. Whereas flights of *Po. maricopa* typify the genus in being synchronous and triggered by summer rains, those of *Po. californicus* are asynchronous and appear triggered by photoperiod. Additionally, foundresses of *Po. californicus* are semiclaustral (R. Johnson, unpublished data).

These two closely related species often occur sympatrically throughout their ranges from Texas to southern Nevada and southeastern California and into Mexico, although *Po. californicus* occurs farther to the west (Fig. 7). Relative colony abundance, however, changes across a geographic cline as *Po. maricopa* becomes increasingly common and replaces *Po. californicus* in eastern portions of its geographic range (see also MacKay *et al.* 1985) (Fig. 7). The increased relative abundance of

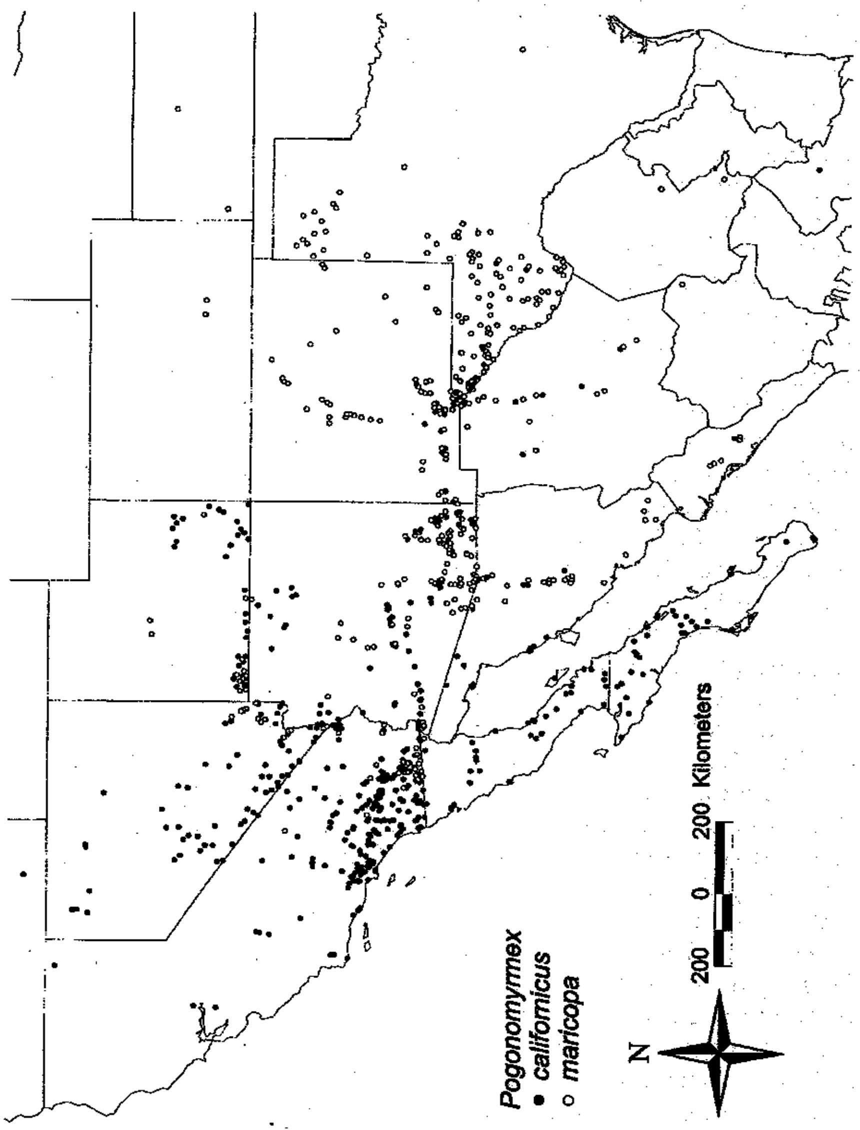

Fig. 7. Distribution of *Pogonomyrmex*-solitary foragers with recruitment; *P. californicus* (solid circle); *P. maricopa* (open circle).

Po. maricopa colonies in eastern areas correlates with the occurrence of predictable summer rains which trigger the mating flights of this species. In contrast, summer rains are rare and unpredictable in the Mojave Desert (see MacMahon & Wagner 1985), where *Po. californicus* is most common. As might be expected, *Po. maricopa* largely replaces *Po. californicus* in irrigated areas of the Coachella-Imperial Valleys, California (Snelling & George 1979).

Pogonomyrmex-Solitary Foragers with Limited Recruitment

Few data are available on ecology and microhabitat of these 12 species because colonies are small, difficult to locate, and rarely studied (Table 1). Four species (*Po. bigbendensis*, *Po. snellingi*, *Po. texanus* and *Po.* sp. B) were placed in this group using anecdotal data because information on ecology and foraging behavior are lacking. I classified *Po. snellingi* as a solitary forager because individuals were collected under the assumption that they were solitary foragers of *Po. californicus* (R.R. Snelling, pers. comm.). Solitary foraging is also probable for *Po. texanus* because colonies only consist of about 100 workers.

Head width is similar for most species in this group with the exception of the smaller *Po. magnacanthus* and the larger *Po. apache* and *Po. texanus* (Table 1). All species are granivorous, though harvested items may also include vertebrate fecal material and dead insects. Only *Po. montanus* includes a large proportion of non-seed items in its diet. Recruitment pheromones occur in *Po. desertorum* (B. Hölldobler, pers. comm.) and probably other species, but their efficiency is low relative to that of congeners. Colonies in this functional group typically consist of up to several hundred workers except in *Po. montanus* and *Po. comanche*, where colonies may reach 1500 workers. Rain (summer or winter, depending on the species) triggers the mating flights for several species, while photoperiod triggers the asynchronous late spring flights of the hot desert species *Po. magnacanthus*. Asynchronous photoperiod-triggered flights are also probable for the three other hot desert species (*Po. anzensis*, *Po. snellingi*, *Po.* sp. B) that are related to *Po. magnacanthus* (Table 1).

The geographic distribution is restricted to western North America for seven of the 12 species in this group (Fig. 8, p. 88). The geographic ranges of two species, *Po. brevispinosus* and *Po. subdentatus*, include central to northern California and western Nevada. Their distributions are mostly non-overlapping, however, as *Po. brevispinosus* occurs in western Nevada, southern Oregon, and northern California, while *Po. subdentatus* is largely restricted to the central valley of California (Fig. 8, p. 88). The five other species in this group occur to the south. Two species, *Po. magnacanthus* and *Po.* sp. B, nest in loose, sandy soils (Cole

text is reversed
for these 2 species

1968, R.R. Snelling, pers. comm.) and appear to have parapatric distribution patterns; *Po. magnacanthus* is restricted to the Colorado Desert, while *Po.* sp. B occurs to the northwest in Inyo County, California, and southwestern Nevada. *Pogonomyrmex anzensis*, which is only known from the Anza Borrego Desert, is the only other low elevation species in this region. Microhabitats occupied by *Po. anzensis* are restricted to rocky hillsides underlain by relatively coarse-textured soils (S.P. Cover, pers. comm., R. Johnson pers. obs.), and thus are distinctly different from areas occupied by *Po. magnacanthus*. *Pogonomyrmex montanus* is the only mid- to high-elevation species in this group and is restricted to isolated mountain ranges in southern California and northern BC, usually at elevations above 1500m (MacKay 1980). Lastly, *Po. snellingi* is only known from central Baja California, well disjunct from other species in this group (Fig. 8, p. 88).

The geographic ranges of the other five species in this group occur to the east and largely consist of allopatric distribution patterns. Among these species, *Po. comanche* is mostly restricted to sandy soils near open post-oak woods of the southcentral United States (Fig. 8, p. 88). *Pogonomyrmex comanche* has a parapatric distribution pattern with *Po. texanus* and *Po. apache* along narrow contact zones; *Po. comanche* contacts *Po. texanus* in northern Texas and *Po. apache* along a north-south band through central Texas. *Pogonomyrmex bigbendensis* has a limited distribution in southwestern Texas and Chihuahua, Mexico (Francke & Merickel 1981, MacKay *et al.* 1985). *Pogonomyrmex desertorum* is the most widely distributed species in this group, occurring from western Texas to western Arizona and south into Mexico. The western range of *Po. desertorum* extends into the Colorado Desert, where it is replaced by *Po. magnacanthus*. *Pogonomyrmex desertorum* and *Po. apache* exhibit an allopatric distribution pattern as the two species segregate across a narrow elevation zone where they contact one another in southeastern Arizona and southern New Mexico; *Po. apache* occurs at higher elevations (R. Johnson, pers. obs.).

Distribution Patterns Between Complexes of *Pogonomyrmex*

The most significant phylogenetic pattern within *Pogonomyrmex* involves the distinct geographic distribution of species in the *Po. barbatus* and *Po. occidentalis* complexes (Figs. 5-6, in part). All six species in the *Po. occidentalis* complex inhabit higher latitudes and are restricted to cool habitats and/or mid- to high-elevations. *Pogonomyrmex occidentalis* is the only species in the complex that occurs south of its primary range as it extends into montane habitats in southern Arizona and northern Mexico. In contrast, all ten species in the *Po. barbatus* complex are restricted to lower latitudes in hot desert to mid-elevation habitats.

Patterns Between Group Foraging Species of *Messor* and *Pogonomyrmex*

Messor pergandei and *Po. rugosus* are two of the largest, most conspicuous, and best studied seed-harvester ants in the southwestern United States. Where both species are common and sympatric and in different parts of their ranges, there is high overlap in relative abundance of seed species collected (Mehlhop & Scott 1983, Rissing 1988a). Moreover, these two species have high potential to compete for food resources throughout their overlapping ranges (Davidson 1977a, Rissing 1988a, Johnson 1992). Most frequently, however, these two species segregate microhabitat along steep physical gradients. *Pogonomyrmex rugosus* typically occupies microhabitats that receive more runoff, have a higher clay content, or are at slightly higher elevations than adjacent areas predominated by *M. pergandei* (Bernstein 1974, Johnson 1992). Other group-foraging congeners have a similar distribution. For example, *M. julianus* and *M. pergandei* predominate in alluvial valleys and other sandy areas in Baja California while *Po. tenuispinus* inhabits bajadas and other sites in which the soils have a higher percentage clay content (R. Johnson, pers. obs.).

BIOGEOGRAPHY AND COMMUNITY STRUCTURE

Distribution Patterns

Each functional group of seed-harvester ants consists of a highly structured assemblage. Morphology, diet, colony size, recruitment ability, and mating flights are typically similar for species within each group with the primary difference being that each species occurs in specific micro- and macro-habitats. Within each functional group, these ecologically equivalent species replace one another across contact zones that are delineated by abiotic habitat factors such as soil texture, moisture, temperature, and elevation (Johnson 1992, 2000). This general pattern of species replacement provides a system to examine both the patterns and processes organizing each assemblage at local and regional scales and to assess possible mechanisms related to species divergence.

A biogeographic approach that integrates distribution patterns and microhabitat variables such as soil texture provides potential for a general framework to examine processes structuring North American seed-harvester ant communities, and possibly those elsewhere. This approach partly resolves the inability of Davidson (1977a, 1977b) to explain sympatry of small group-foraging *Pheidole* such as *Ph. tucsonica* (= *Ph. xerophila* in Davidson) and *Ph. gilvescens*. While these two species sometimes occur sympatrically, as noted by Davidson, analysis at a larger scale indicates that these two species often occur in different micro- and macro-habitats (see above). This approach may also explain lack of support for the food limitation/interspecific competition hypothesis in Australia, where rainfall, i.e., seed production, was not correlated with species diversity or species richness even within habitats (Morton & Davidson 1988). The authors invoked edaphic variability as a potential explanation for the lack of correlation, and suggested that extreme local and regional diversity of Australian soils may have confounded productivity estimates. Given that small changes in soil texture affect species shifts across visually imperceptible gradients in North America (Johnson 1992, 2000), it seems likely that similar shifts also occur in the heterogenous soils of Australia. Indeed, related species of Australian harvester ants display parapatric distribution patterns across soil ecotones (Greenslade 1976, 1987), suggesting that soils also commonly affect microdistribution and species composition shifts in Australia. Species segregation based on abiotic habitat factors also supports the hypothesis that the phenomenal ant species richness in Australia is at least partly related to the extreme edaphic variability (see also Morton & Davidson 1988, Andersen 1997). Similar patterns of species replacement also occur across localized microhabitats in European ants. For example, *Lasius alienus* occupies higher and drier areas of English heath than *L. niger* (Brian 1964), and *Myrmica scabrinodis* occupies drier, more exposed areas than *M. rubra* (Brian 1956). Furthermore, two subspecies of *M. rubra* segregate microhabitats (Brian & Brian 1955).

Examination of regional geographic distribution patterns indicates that these five genera of seed-harvester ants are broadly sympatric across the southwestern and southcentral United States and Mexico. However, because of the common occurrence of contact zones and patterns of species replacement only one species per functional group predominates at a locale. These patterns suggest that at least three levels of mechanisms modulate species interactions and structure this community locally and regionally: (1) mechanisms that structure and maintain local contact zones between ecologically equivalent species, (2) mechanisms that permit coexistence of several species at one locale (both congeners in different species groups and noncongeners), and (3) mechanisms that maintain widespread sympatry of species that apparently inhabit similar microhabitats, e.g., *Po. californicus* and *Po. maricopa*.

Abiotic Limits to Distribution

Moisture is probably the major factor constraining micro- and macro-distribution of many southwestern desert ants as most species require summer rains to trigger mating flights. In terms of micro-distribution, local gradients in physical factors such as soil texture can impose an abiotic limit through their affect on soil moisture availability. In the case of *Po. barbatus* and *Po. rugosus*, the restriction of the former species to wetter soils is correlated with its lower resistance to desiccation. Of several physiological parameters that were measured, alate females of these two species only differed in body size, which resulted in the smaller *Po. barbatus* dying significantly faster under desiccating conditions (Johnson 2000). Patterns of worker production also suggested that moisture restricts *Po. barbatus* to wetter soils. As predicted by differences in metabolic rate, *Po. barbatus* foundresses produced significantly more workers than did those of *Po. rugosus* at moderate to high moisture levels. In contrast, *Po. rugosus* foundresses produced significantly more workers in the driest treatment because they lived longer and could provide more energy to developing brood under drier conditions (Johnson 1998a).

The common occurrence of contact zones in several desert ant genera (see above) provides an opportunity to test for widespread correlation, both taxonomic and geographic, between desiccation resistance and local distribution patterns. If desiccation is a primary source of foundress mortality, then species with the highest tolerances to desiccation would be predicted to inhabit the driest portions of a moisture gradient (see also Talbot 1934). Thus, for ecologically equivalent pairs of ants, the species with the higher resistance to desiccation is predicted to occur in the lower, hotter, and/or drier portion of a contact zone (Table 3). Patterns of body size support this prediction as dry mass of alate females in the genera *Aphaenogaster*, *Messor*, and other *Pogonomyrmex* was greater for the species inhabiting the more xeric portion of several contact zones (Johnson 1998b). Trunk trail foraging species of *Pogonomyrmex* also displayed a latitudinal pattern in body size as dry mass of alate females increased 3-4-fold along a north to south gradient of increasing desiccation stress, from central Nevada to central Sonora, Mexico (Johnson 1998b).

Macroscale effects are also manifested as a decrease in ant species richness and species diversity that coincides with the longitudinal cline of decreasing annual rainfall from the Chihuahuan Desert in the east to the Colorado and Mojave Deserts in the west (Davidson 1977a, this study). Given the strong correlation between productivity (i.e., seeds produced by annual plants) and precipitation in arid regions (Rosenzweig

Table 3. Predicted patterns of survival under desiccating conditions for foundresses of ecologically equivalent species. Species inhabiting lower, hotter, and/or drier habitats are predicted to have a higher tolerance to desiccating conditions.

Genus	Species
Messor	*pergandei > julianus*
Aphaenogaster	*cockerelli > albisetosa*
Pheidole	*desertorum > vistana* *tucsonica > gilvescens*
Ephebomyrmex	*pima > imberbiculus* *laevinodis > imberbiculus*
Pogonomyrmex	*barbatus > badius* *barbatus > occidentalis* *rugosus > barbatus* *rugosus > bicolor* *rugosus > salinus* *rugosus > subnitidus* *occidentalis > salinus* *subnitidus > salinus* *californicus > maricopa* *magnacanthus > desertorum* *desertorum > apache*

1968), Davidson (1977a) attributed both patterns to food limitation in drier locales, and suggested that interspecific competition for seeds structured seed-harvester ant communities. One potential weakness of this argument is that Davidson (1977a) examined patterns of species richness relative to mean annual precipitation, even though annual variation and seasonality may be equally important (Axelrod 1979, Ezcurra & Rodrigues 1986). Like annual rainfall, the seasonality of rainfall follows a gradient across these deserts as the percentage of annual rainfall occurring during summer months decreases from >65% in the Chihuahuan Desert to becoming a minor portion of the annual total in the Colorado and Mojave Deserts (MacMahon & Wagner 1985).

Examining patterns of species loss across this gradient provides insight into the potential causal mechanisms. Across this regional gradient, *Aphaenogaster cockerelli*, *Ephebomyrmex pima*, *Pogonomyrmex desertorum*, *Po. maricopa*, and other common Sonoran Desert ants (e.g., *Tetramorium hispidum*) progressively drop out of the fauna as one moves from central Arizona to western Arizona and southeastern California (see also Snelling & George 1979). Replacement species are lacking for *Ephebomyrmex*, and the two replacement species of *Pogonomyrmex*, *Po. californicus* and *Po. magnacanthus*, are the only *Pogonomyrmex* known to have mating flights that are not triggered by rain. In *Aphaenogaster*, *A. megommatus* replaces *A. cockerelli* in the Colorado and Mojave Deserts. These two species are probably not ecologically equivalent as *A. megommatus* is a smaller nocturnal species. Nevertheless, the replacement pattern of *A. cockerelli* by *A. megommatus* in drier locales coincides with late spring/early summer mating flights that are triggered by photoperiod in the latter species (Snelling & George 1979, R.R. Snelling pers. comm.). Moreover, species that drop out of the fauna across this gradient are those that have mating flights triggered by summer rains, while the species that are added are those that have mating flights triggered by photoperiod.

In summary, rainfall seems to be the causal mechanism for the observed longitudinal cline in ant species richness and diversity. However, patterns of species loss and species replacement suggest that fewer ant species in western locales is effected through mating flights rather than by seed production. Moreover, lack of summer rainfall precludes flights and/or successful foundress establishment for species with rain-triggered flights in western locales and thus limits their western distribution. Fewer species in the Colorado and Mojave Deserts then result because photoperiod triggered mating flights have evolved in relatively few species. Two other lines of evidence also suggest that the lack of summer rainfall imposes an abiotic limit to the western distribution of these ants. First, *Aphaenogaster cockerelli* displays a habitat shift, from valley floors over most of its geographic range, to upland and foothill habitats in western Arizona and southeastern California (Snelling & George 1979). Second, the pattern of species loss in ants coincides with the pattern found in several species of succulent plants; in western locales, summer precipitation is too low to effect germination and/or establishment and the species drop out of the flora (Brum 1973, Jordan & Nobel 1981, 1982, Turner *et al.* 1995).

CONCLUSIONS

Comparing morphology, ecology, and distribution patterns within and among functional species groups of seed-harvester ants facilitates understanding patterns of community structure and potential mechanisms that segregate some species but allow others to coexist. The prevalence of allopatric and parapatric distributions within each functional group suggests studies should address species interactions and coexistence/segregation patterns within functional groups by focusing on mechanisms that maintain or structure contact zones between congeners. Additional studies should also further address the coexistence of species that differ in recruitment ability. Overall, this group of ants seems to be a rich system for examining several aspects of evolutionary ecology including the evolution of body size, species divergence, and the role of biotic and abiotic factors in structuring contact zones.

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LITERATURE CITED

Allred, D.M. 1982. Ants of Utah. Great Basin Naturalist 42:415-511.

Andersen, A.N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. Journal of Biogeography 24:433-460.

Axelrod, D.I. 1979. Age and origin of Sonoran Desert vegetation. Occasional Papers of the California Academy of Sciences 132:1-74.

Beckers, R., S. Goss, J.L. Deneubourg & J.M. Pasteels. 1989. Colony size, communication and ant foraging strategy. Psyche 96:239-256.

Bernstein, R.A. 1974. Seasonal food abundance and foraging activity in some desert ants. American Naturalist 108:490-498.

Bernstein, R.A. 1975. Foraging strategies of ants in response to variable food density. Ecology 56:213-219.

Bernstein, R.A. 1979. Evolution of niche breadth in populations of ants. American Naturalist 114:533-544.

Bernstein, R.A. & M. Gobbel. 1979. Partitioning of space in communties of ants. Journal of Animal Ecology 48:931-942.

Bohart, G.E. & G.F. Knowlton. 1953. Notes on food habits of the western harvester ant. Proceedings of the Entomological Society of Washington 55:151-153.

Bolton, B. 1995. A New General Catalogue of the Ants of the World. Harvard University Press, Cambridge, Massachusetts.

Brian, M.V. 1956. Segregation of species of the ant genus *Myrmica.* Journal of Animal Ecology 25:319-337.

Brian, M.V. 1964. Ant distribution in a southern English health. Journal of Animal Ecology 33:451-461.

Brian, M.V. & A.D. Brian. 1955. On the two forms macrogyna and microgyna of the ant *Myrmica rubra* L. Evolution 9:280-290.

Brown, M.J.F. 1999. Semi-claustral founding and worker behaviour in gynes of *Messor andrei.* Insectes Sociaux 46:194-195.

Brown, W.L. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas, pp. 161-185. In B.J. Meggers, E.S. Ayensu & W.D. Duckworth (eds.), Tropical Forest Ecosystems in Africa and South America: a Comparative Review. Smithsonian Institute Press, Washington, D.C.

Brum, G.D. 1973. Ecology of the saguaro (*Carnegiea gigantea*): phenology and establishment in marginal populations. Madroño 22:195-204.

Chew, R.M. 1960. Note on colony size and activity in *Pogonomyrmex occidentalis* (Cresson). Journal of the New York Entomological Society 68:81-82.

Clark, W.H. & J.L. Hainline. 1975. Observations on nuptial flights of the western harvester ant *Pogonomyrmex occidentalis* (Cresson), in Nevada (Hymenoptera: Formicidae). Journal of the Idaho Academy of Science 11:5-10.

Cole, A.C. 1954. Studies of New Mexico ants. IX. *Pogonomyrmex apache* Wheeler a synonym of *Pogonomyrmex sancti-hyacinthi* Wheeler (Hymenoptera: Formicidae). Journal of the Tennessee Academy of Science 29:266-272.

Cole, A.C. 1955. Studies of Nevada ants. I. Notes on *Veromessor lariversi* M.R. Smith and a description of the queen (Hymenoptera: Formicidae). Journal of the Tennessee Academy of Science 30:51-52.

Cole, A.C. 1956. Observations of some members of the genus *Pheidole* in the southwestern United States with synonymy (Hymenoptera: Formicidae). Journal of the Tennessee Academy of Science 31:112-118.

Cole, A.C. 1963. A new species of *Veromessor* from the Nevada test site and notes on related species (Hymenoptera: Formicidae). Annals of the Entomological Society of America 56:678-682.

Cole, A.C. 1966. Ants of the Nevada Test Site. University Publications, Brigham Young University, Provo, Utah.

Cole, A.C. 1968. *Pogonomyrmex* Harvester Ants: a Study of the Genus in North America. University of Tennessee Press, Knoxville, Tennessee.

Costello, D.F. 1972. The Desert World. Crowell Publishers, New York.

Creighton, W.S. 1950. The ants of North America. Bulletin of the Museum of Comparative Zoology 104:1-585.

Creighton, W.S. 1952. Studies on Arizona ants (3). The habits of *Pogonomyrmex huachucanus* Wheeler and a description of the sexual castes. Psyche 59:71-81.

Creighton, W.S. 1953. New data on the habits of the ants of the genus *Veromessor*. American Museum Novitates 1612:1-18.

Creighton, W.S. 1955. Studies on the distribution of the genus *Novomessor* (Hymenoptera: Formicidae). Psyche 62:89-97.

Creighton, W.S. 1956. Studies on the North American representatives of *Ephebomyrmex* (Hymenoptera: Formicidae). Psyche 63:54-66.

Creighton, W.S & R.E. Gregg. 1955. New and little-known species of *Pheidole* (Hymenoptera: Formicidae) from the southwestern United States and northern Mexico, University of Colorado Studies Series in Biology 3:1-46.

Crist, T.O. & J.A. MacMahon. 1991. Foraging patterns of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae) in a shrub-steppe ecosystem: the role of temperature, trunk trails, and seed resources. Environmental Entomology 20:265-275.

Davidson, D.W. 1977a. Species diversity and community organization in desert seed-eating ants. Ecology 58:711-724.

Davidson, D.W. 1977b. Foraging ecology and community organization in desert seed-eating ants. Ecology 58:725-737.

Davidson, D.W. 1978. Size variability in the worker caste of a social insect (*Veromessor pergandei* Mayr) as a function of the competitive environment. American Naturalist 112:523-532.

De Vita, J. 1979. Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave Desert. Ecology 60:729-737.

Edney, E.B. 1977. Water Balance in Land Arthropods. Springer-Verlag, New York.

Erickson, J.M. 1972. Mark-recapture techniques for population estimates of *Pogonomyrmex* ant colonies: an evaluation of the ^{32}P technique. Annals of the Entomological Society of America 65:57-61.

Ezcurra, E. & V. Rodrigues. 1986. Rainfall patterns in the Gran Desierto, Sonora, Mexico. Journal of Arid Environments 10:13-28.

Ferster, B. & J.F.A. Traniello. 1995. Polymorphism and foraging behavior in *Pogonomyrmex badius* (Hymenoptera: Formicidae): worker size, foraging distance, and load size associations. Environmental Entomology 24:673-678.

Fewell, J.H. 1988a. Variation in foraging patterns of the western harvester ant, *Pogonomyrmex occidentalis*, in relation to variation in habitat structure, pp. 257-282. In R.L. Jeanne (ed.), Inter-individual Variation in Social Insect Behavior. Westview Press, Boulder, Colorado.

Fewell, J.H. 1988b. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. Behavioral Ecology and Sociobiology 22:401-408.

Fewell, J.H. 1990. Directional fidelity as a foraging constraint in the western harvester ant, *Pogonomyrmex occidentalis*. Oecologia 82:45-51.

Francke, O.F. & F.W. Merickel. 1981. Two new species of *Pogonomyrmex* harvester ants from Texas (Hymenoptera: Formicidae). Pan-Pacific Entomologist 57:371-379.

Gaglio, M.D., W.P. MacKay, E.A. Osorio & I. Iniguez. 1998. Nest populations of *Pogonomyrmex salinus* harvester ants (Hymenoptera: Formicidae). Sociobiology 32:459-463.

Garcia-Perez, J.A., A. Rebeles-Manriqez & R. Pena-Sanchez. 1994. Seasonal changes in trails and the influence of temperature in foraging activity in a nest of the ant, *Pogonomyrmex barbatus*. Southwestern Entomologist 19:181-187.

Gentry, J.B. 1974. Response to predation by colonies of the Florida harvester ant, *Pogonomyrmex badius*. Ecology 55:1328-1338.

Gentry, J.B. & K.L. Stiritz. 1972. The role of the Florida harvester ant, *Pogonomyrmex badius*, in old field mineral nutrient relationships. Environmental Entomology 1:39-41.

Golley, F.B. & J.B. Gentry. 1964. Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. Ecology 45:217-225.

Gordon, D.M. 1983. The relation of recruitment rate to activity rhythms in the harvester ant, *Pogonomyrmex barbatus* (F. Smith) (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 56:277-285.

Gordon, D.M. 1992. How colony growth affects forager intrusion between neighboring harvester ant colonies. Behavioral Ecology and Sociobiology 31:417-427.

Gordon, D.M. & A.W. Kulig. 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. Ecology 77:2393-2409.

Gordon, S.H. 1978. Food and foraging ecology of a desert harvester ant, *Veromessor pergandei* (Mayr). Ph.D. Dissertation, University of California, Berkeley, California.

Greenslade, P.J.M. 1976. Distribution of two forms of the meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) on Kangaroo Island and in the Yorke Peninsula. Australian Journal of Zoology 24:557-564.

Greenslade, P.J.M. 1987. Environment and competition as determinants of local geographical distribution of five meat ants, *Iridomyrmex purpureus* and allied species (Hymenoptera: Formicidae). Australian Journal of Zoology 35:259-273.

Gregg, R.E. 1963. The Ants of Colorado. University of Colorado Press, Boulder, Colorado.

Hadley, N.F. 1994. Water Relations of Terrestrial Arthropods. Academic Press, New York.

Hansen, S.R. 1978. Resource utilization and coexistence of three species of *Pogonomyrmex* ants in an upper Sonoran grassland community. Oecologia 35:109-117.

Harmon, G. 1993. Mating in *Pogonomyrmex badius* (Hymenoptera: Formicidae). Florida Entomologist 76:524-526.

Harrison, J.S. & J.B. Gentry. 1981. Foraging pattern, colony distribution, and foraging range of the Florida harvester ant, *Pogonomyrmex badius*. Ecology 62:1467-1483.

Heinze, J., B. Hölldobler & S.P. Cover. 1992. Queen polymorphism in the North American harvester ant, *Ephebomyrmex imberbiculus*. Insectes Sociaux 39:267-273.

Helms, K.R. 1996. Natural history of the ant *Pheidole desertorum* Wheeler in a desert grassland habitat. Psyche 102:35-47.

Herbers, J.M. 1993. Ecological determinants of queen number in ants, pp. 262-293. In L. Keller (ed.), Queen Number and Sociality in Insects. Oxford University Press, New York.

Hobbs, R.J. 1985. Harvester ant foraging and plant species distribution. Oecologia 67:519-523.

Hölldobler, B. 1971. Homing in the harvester ant *Pogonomyrmex badius*. Science 171:1149-1151.

Hölldobler, B. 1974. Home range orientation and territoriality in harvesting ants. Proceedings of the National Academy of Science 71:3274-3277.

Hölldobler, B. 1976a. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behavioral Ecology and Sociobiology 1:3-44.

Hölldobler, B. 1976b. The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). Behavioral Ecology and Sociobiology 1:405-423.

Hölldobler, B. & N.F. Carlin. 1989. Colony founding, queen control, and worker reproduction in the ant *Aphaenogaster* (=*Novomessor*) *cockerelli* (Hymenoptera: Formicidae). Psyche 96:131-151.

Hölldobler, B., N.J. Oldham, E.D. Morgan & W.A. König. 1995. Recruitment pheromones in the ants *Aphaenogaster albisetosus* and *A. cockerelli* (Hymenoptera: Formicidae). Journal of Insect Physiology 41:739-744.

Hölldobler, B., R.C. Stanton & H. Markl. 1978. Recruitment and food-retrieving in *Novomessor* (Formicidae, Hymenoptera). I. Chemical signals. Behavioral Ecology and Sociobiology 4:163-181.

Johnson, R.A. 1991. Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. Ecology 72:1408-1419.

Johnson, R.A. 1992. Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. Oecologia 89:118-124.

Johnson, R.A. 1998a. Foundress survival and brood production in the desert seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus* (Hymenoptera, Formicidae). Insectes Sociaux 45:255-266.

Johnson, R.A. 1998b. Desiccation resistance in North American seed-harvester ants: local and latitudinal patterns in body size and habitat. Social Insects at the turn of the Millenium: Proceedings of the XIII International Congress of IUSSI, Adelaide, Australia, XIII Congress of IUSSI.

Johnson, R.A. 2000. Habitat segregation based on soil texture and body size in the seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus*. Ecological Entomology, in press.

Johnson, R.A. in press. Reproductive biology of the seed-harvester ant *Messor julianus* (Pergande). Journal of Hymenoptera Research in press.

Johnson, R.A., S.W. Rissing & P.R. Killeen. 1994. Differential learning and memory by co-occurring ant species. Insectes Sociaux 41:165-177.

Jordan, P.W. & P.S. Nobel. 1981. Seedling establishment of *Ferocactus acanthodes* in relation to drought. Ecology 62:901-906.

Jordan, P.W. & P.S. Nobel. 1982. Height distribution of two species of cacti in relation to rainfall, seedling establishment, and growth. Botanical Gazette 143:511-517.

Jorgensen, C.D. & S.D. Porter. 1982. Foraging behavior of *Pogonomyrmex owyheei* in southeast Idaho. Annals of the Entomological Society of America 11:381-384.

Kaspari, M. & E.L. Vargo. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. American Naturalist 145:610-632.

Kempf, W.W. 1972. Catálogo abreviado das formigas da Regiao Neotropical (Hymenoptera: Formicidae). Studia Entomologica 15:3-344.

Kusnezov, N. 1951. El genero *Pogonomyrmex*. Acta Zoologica Lilloana 11:227-333.

Lavigne, R.J. 1969. Bionomics and nest structure of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 62:1166-1175.

MacKay, E.E. & W.P. MacKay. 1984. Apoyo a la actual division generica de hormigas usando etologia comparativa (Hymenoptera, Formicidae). Folia

Entomologica Mexicana 61:179-188.

MacKay, W.P. 1980. A new harvester ant from the mountains of southern California (Hymenoptera: Formicidae). Southwestern Naturalist 25:151-156.

MacKay, W.P. 1981. A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Psyche 88:25-74.

MacKay, W.P., E.E. MacKay, J.F. Perez Dominguez, L.I.V. Sanchez & P. Vielma Orozco. 1985. Las hormigas del estado de Chihuahua Mexico: el genero *Pogonomyrmex* (Hymenoptera: Formicidae). Sociobiology 11:39-54.

MacMahon, J.A. & F.H. Wagner 1985. The Mojave, Sonoran and Chihuahuan Deserts of North America, pp. 105-202. In M. Evanari, I. Noy-Meir & D.W. Goodall (eds.), Hot Deserts and Arid Shrublands. Elsevier Science Publisher, Amsterdam.

Mallis, A. 1941. A list of the ants of California with notes on their habits and distribution. Bulletin of the Southern California Academy of Sciences 40:61-100

McCluskey, E.S. 1963. Rhythms and clocks in harvester and Argentine ants. Physiological Zoology 36:273-292.

McCoy, E.D. & B.W. Kaiser. 1990. Changes in foraging activity of the southern harvester ant *Pogonomyrmex badius* (Latreille) in response to fire. American Midland Naturalist 123:112-123.

Mehlhop, P. & J. Scott, N.J. 1983. Temporal patterns of seed use and availability in a guild of desert ants. Ecological Entomology 8:69-85.

Michener, C.D. 1942. The history and behavior of a colony of harvester ants. Scientific Monthly 55:248-258.

Michener, C.D. 1964. Reproductive efficiency in relation to colony size in Hymenopterous societies. Insectes Sociaux 4:317-342.

Moody, J.V. & O.F. Francke. 1982. The Ants (Hymenoptera, Formicidae) of Western Texas. Part I, Subfamily Myrmicinae. Texas Tech Press, Lubbock, Texas.

Morton, S.R. & D.W. Davidson. 1988. Comparative structure of harvester ant communities in arid Australia and North America. Ecological Monographs 58:19-38.

Mull, J.F. & T.O. Crist. 1993. Timing of mating flights in the western harvester ant, *Pogonomyrmex occidentalis* Cresson (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 66: 372-375.

Nagel, H.G. & C.W. Rettenmeyer. 1973. Nuptial flights, reproductive behavior and colony founding of the western harvester ant, *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 46:82-101.

Peck, S.B. 1976. The myrmecophilous beetle genus *Echinocoleus* in the southwestern United States (Leiodidae, Catopinae). Psyche 83:51-62.

Pollock, G.B. & S.W. Rissing. 1985. Mating season and colony foundation of the seed-harvester ant, *Veromessor pergandei*. Psyche 92:125-134.

Porter, S.D. & C.D. Jorgensen. 1980. Recapture studies of the harvester ant, *Pogonomyrmex owyheei* Cole, using a fluorescent marking technique.

Ecological Entomology 5:263-269.

Pullen, B.E. 1961. Non-granivorous food habits of *Pheidole grallipes* Wheeler and its possible phyletic significance. Pan-Pacific Entomologist 27:93-96.

Rissing, S.W. 1987. Annual cycles in worker size of the seed-harvester ant *Veromessor pergandei* (Hymenoptera: Formicidae). Behavioral Ecology and Sociobiology 20:117-124.

Rissing, S.W. 1988a. Dietary similarity and foraging range of two seed-harvester ants during resource fluctuation. Oecologia 75:362-366.

Rissing, S.W. 1988b. Seed-harvester ant association with shrubs: competition for water in the Mojave Desert? Ecology 69:809-813.

Rissing, S.W., R.A. Johnson & J.W. Martin. 2000. Colony founding behavior of some desert ants: geographic variation in metrosis. Psyche. in press.

Rissing, S.W., R.A. Johnson & G.B. Pollock. 1986. Natal nest distribution and pleometrosis in the desert leaf-cutter ant *Acromyrmex versicolor* (Hymenoptera: Formicidae). Psyche 93:177-186.

Rissing, S.W. & J. Wheeler. 1976. Foraging response of *Veromessor pergandei* to changes in seed production. Pan-Pacific Entomologist 52:63-72.

Rogers, L., R. Lavigne, & J.L. Miller. 1972. Bioenergetics of the western harvester ant in the shortgrass plains ecosystem. Environmental Entomology 1:763-768.

Rust, R.W. 1988. Nuptial flights and mating behavior in the harvester ant, *Pogonomyrmex salinus* Olsen (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 61:492-494.

Ryti, R.T. & T.J. Case. 1988. Field experiments on desert ants: testing for competition between colonies. Ecology 69:1993-2003.

Shattuck, S.O. 1987. An analysis of geographic variation in the *Pogonomyrmex occidentalis* complex (Hymenoptera: Formicidae). Psyche 94:159-179.

Snelling, R.R. 1982. The taxonomy and distribution of some North American *Pogonomyrmex* and descriptions of two new species (Hymenoptera: Formicidae). Bulletin of the Southern California Academy of Sciences 80:97-112.

Snelling, R.R. & C.D. George. 1979. The Taxonomy, Distribution and Ecology of California Desert Ants (Hymenoptera: Formicidae). Report to Bureau of Land Management, United States Department of Interior, Riverside, California.

Strandtmann, R.W. 1942. On the marriage flight of *Pogonomyrmex comanche* Wheeler. Annals of the Entomological Society of America 35:142.

Taber, S.W. 1990. Cladistic phylogeny of the North American species complexes of *Pogonomyrmex* (Hymenoptera: Formicidae). Annals of the Entomological Society of America 83:307-316.

Traniello, J.F.A. & S.N. Beshers. 1991. Polymorphism and size-pairing in the harvester ant *Pogonomyrmex badius*: a test of the ecological release hypothesis. Insectes Sociaux 38:121-127.

Tschinkel, W.R. 1992. Brood raiding in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae): laboratory and field observations. Annals of the Entomological Society of America 85:638-646.

Tschinkel, W.R. 1998. Sociometry and sociogenesis of colonies of the harvester ant, *Pogonomyrmex badius*: worker characteristics in relation to colony size and season. Insectes Sociaux 45:385-410.

Turner, C.H. 1909. The mound of *Pogonomyrmex badius* Latrl. and its relation to the breeding habits of the species. Biological Bulletin 17:161-170.

Turner, R.M., J.E. Bowers & T.L. Burgess. 1995. Sonoran Desert Plants: An Ecological Atlas. University of Arizona Press, Tucson, Arizona.

Weier, J.A. & D.H. Feener. 1995. Foraging in the seed-harvester ant genus *Pogonomyrmex*: are energy costs important? Behavioral Ecology and Sociobiology 36:291-300.

Went, F.W., J. Wheeler & G.C. Wheeler. 1972. Feeding and digestion in some ants (*Veromessor* and *Manica*). Bioscience 22:82-88.

Wheeler, G.C. & J. Wheeler. 1959. *Veromessor lobognathus*: second note (Hymenoptera: Formicidae). Annals of the Entomological Society of America 52:176-179.

Wheeler, G.C. & J. Wheeler. 1973. Ants of Deep Canyon. University of California Press, Berkeley, California.

Wheeler, G.C. & J.N. Wheeler. 1986. The Ants of Nevada. Natural History Museum of Los Angeles County, Los Angeles, California.

Wheeler, J. & S.W. Rissing. 1975. Natural history of *Veromessor pergandei*. II. Behavior. Pan-Pacific Entomologist 51:303-314.

Wheeler, W.M. 1917. Notes on the marriage flights of some Sonoran ants. Psyche 24:177-180.

Wheeler, W.M. & W.S. Creighton. 1934. A study of the ant genera *Novomessor* and *Veromessor*. Proceedings of the American Academy of Arts and Sciences 69:341-387.

Whitford, W.G., E. Depree & P. Johnson. 1980. Foraging ecology of two Chihuahuan Desert ant species: *Novomessor cockerelli* and *Novomessor albisetosus*. Insectes Sociaux 27:148-156.

Whitford, W.G., P. Johnson & J. Ramirez. 1976. Comparative ecology of the harvester ants *Pogonomyrmex barbatus* (F. Smith) and *Pogonomyrmex rugosus* (Emery). Insectes Sociaux 23:117-132.

Whitford, W.G., C.A. Kay & A.M. Schumacher. 1976. Water loss in Chihuahuan Desert ants. Physiological Zoology 48:390-397.

Wildermuth, V.L. & E.G. Davis. 1931. The red harvester ant and how to subdue it. Farmer's Bulletin 1668:1-21.

Wilson, E.O. 1978. Division of labor in fire ants based on physical castes (Hymenoptera: Formicidae: *Solenopsis*). Journal of the Kansas Entomological Society 51:615-636.

Wilson, E.O. 2000. *Pheidole* in the New World: A Dominant, Hyperdiverse Ant Genus. Harvard University Press, Cambridge, Massachusetts, (in prep.).

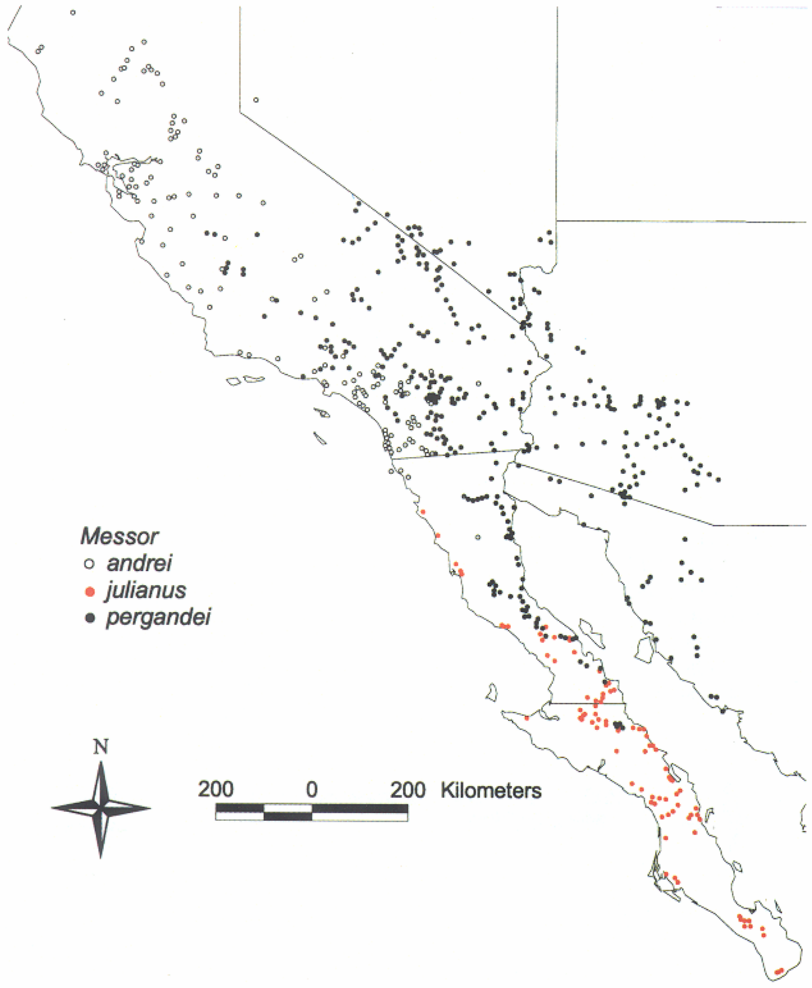


Fig. 1. Distribution of *Messor*-group foragers; *M. andrei* (open circle); *M. julianus* (solid red circle); *M. pergandei* (solid black circle). Text reference p. 95.

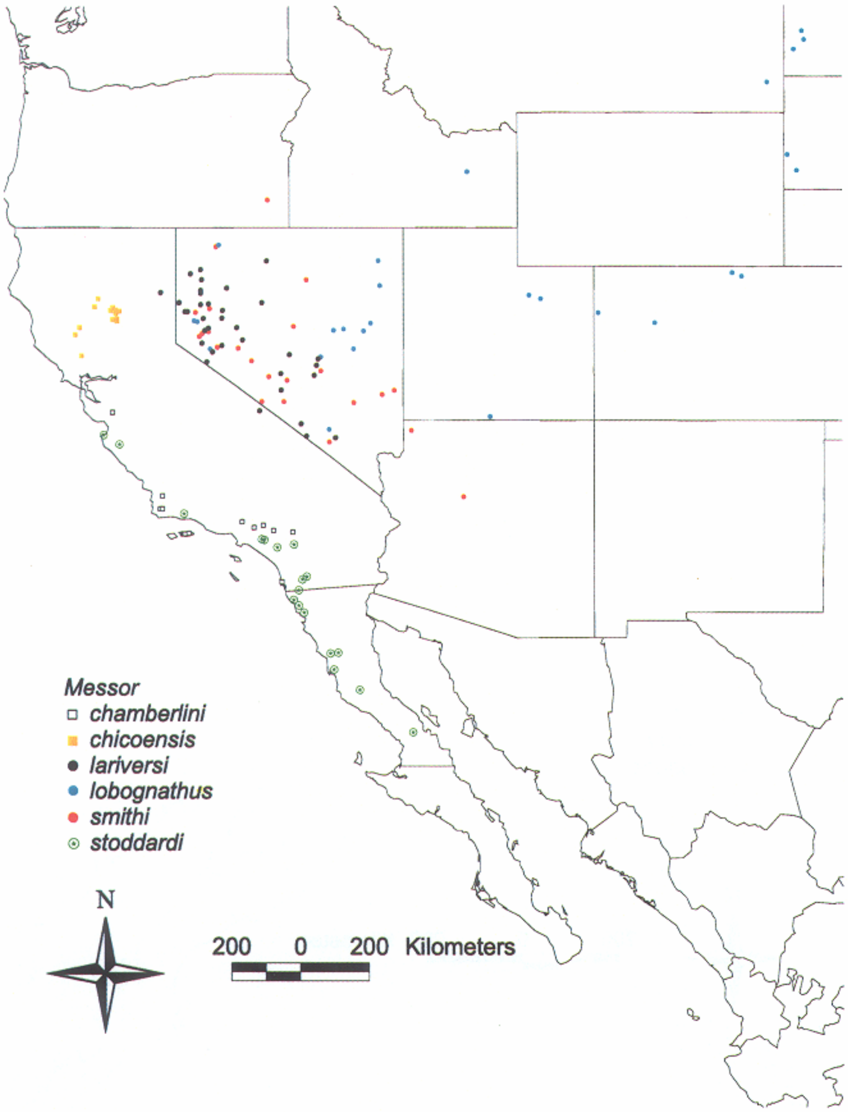


Fig. 2. Distribution of *Messor*-solitary foragers with recruitment; *M. chamberlini* (open square), and solitary foragers with limited recruitment; *M. chicoensis* (yellow square); *M. lariversi* (solid black circle); *M. lobognathus* (solid green circle); *M. smithi* (solid red circle); *M. stoddardi* (green circle with green dot). Text reference p. 95.

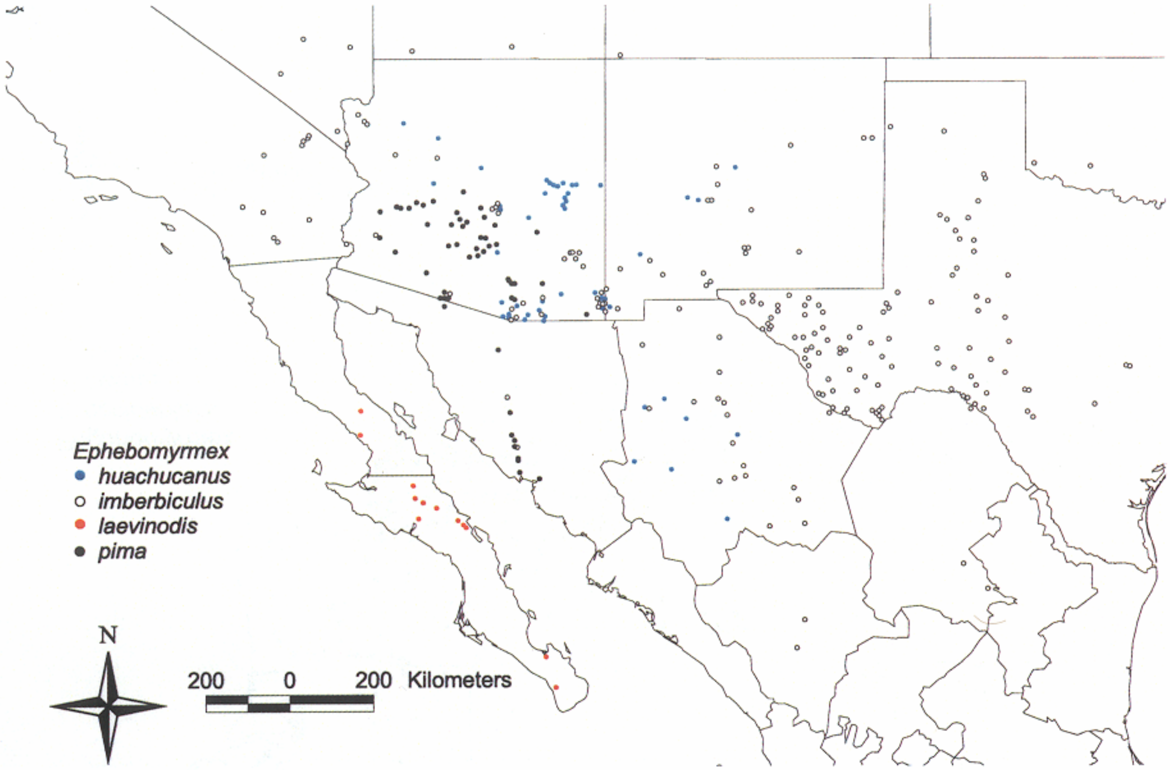


Fig. 4. Distribution of *Ephebomyrmex huachucanus* (solid geen dot), *E. imberbiculus* (open circle); *E. laevinodis* (solid red circle); *E. pima* (solid black circle). Text reference p. 104.

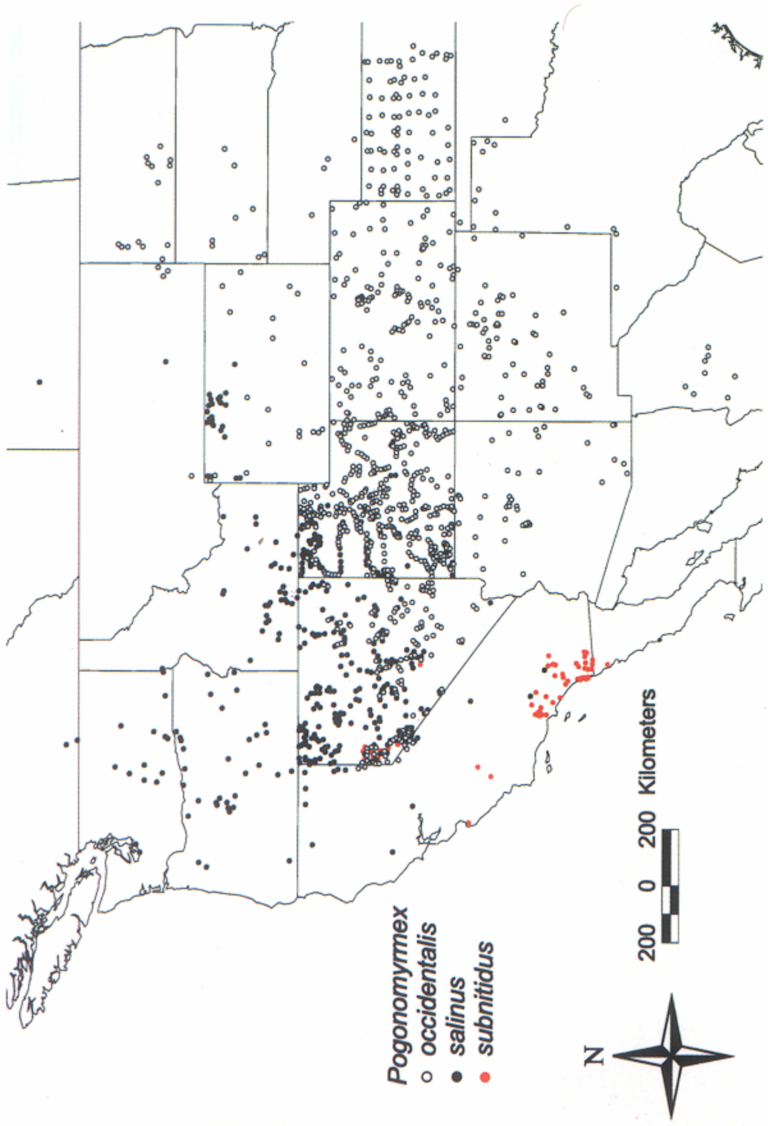


Fig. 5. Distribution of *Pogonomyrmex*-trunk trail foragers in the *P. occidentalis* complex: *P. occidentalis* (open circle); *P. salinus* (solid black circle); *P. subnitidus* (solid red circle). Text reference pages 104 & 106.

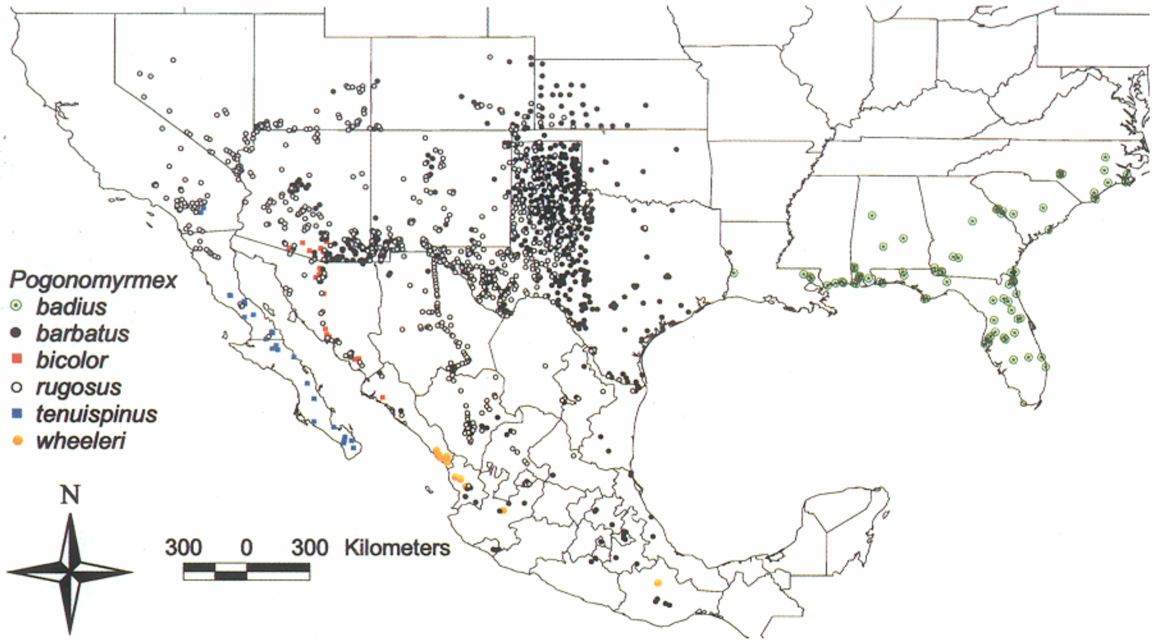
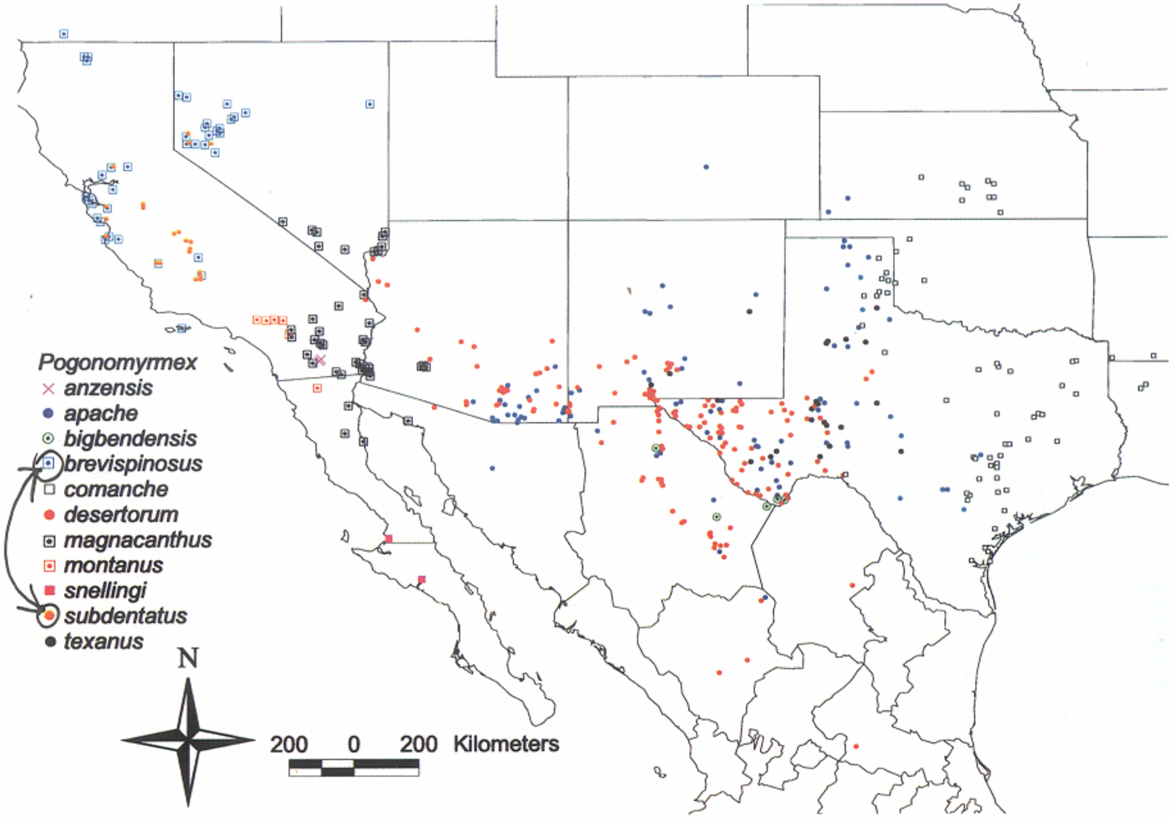


Fig. 6. Distribution of *Pogonomyrmex*-trunk trail foragers in the *P. barbatus* complex: *P. barbatus* (silid black circle); *P. bicolor* (red solid square); *P. rugosus* (open circle); *P. tenuispina* (solid green square); *P. wheeleri* (solid yellow circle), and the *P. californicus* complex; *P. badius* (green circle with green dot in center). Text reference p. 104 & 105.



caption are reversed (see also text)

Fig. 8. Distribution of *Pogonomyrmex*-solitary foragers with limited recruitment; *P. anzensis* (yellow x); *P. apache* (solid blue circle); *P. bigbendensis* (green circle with green dot in center); *P. brevispinosus* (blue square with dot in center); *P. comanche* (open square); *P. desertorum* (solid red circle); *P. magnacanthus* (open black square with black center dot); *P. montanus* (orange open square with center dot); *P. snellingi* (solid red square); *P. subdentatus* (solid yellow circle); *P. texanus* (solid black circle). Text reference p. 108.

Seed Harvesting Species of *Pheidole* (Hymenoptera: Formicidae)

by

Robert A. Johnson[1]

The following table was inadvertently omitted by the editor from my recent paper (Johnson 2000). It is presented here.

Table 2. Seed-harvesting species of *Pheidole* in the United States. The list was compiled from literature (Creighton and Gregg 1955; Snelling and George 1979) and the observations of S.P. Cover and R.A. Johnson. The list includes only taxa for which good data exist to substantiate their classification. Consequently, the number of seed-harvesters will undoubtedly expand as natural history data become available for additional species. Taxonomy follows Bolton (1995). However, the names of some taxa may change in a forthcoming revision of the genus (Wilson 2001).

Genus *Pheidole*

absurda Forel
adrianoi Naves
artemisia Cole
barbata Wheeler
bicarinata Mayr
campestris Creighton
carrolli Naves
cavigenis Wheeler
cerebrosior Wheeler
clementensis Gregg
coloradensis Emery
davisi Wheeler
gilvescens Creighton & Gregg
littoralis Cole
micula Wheeler
militicida Wheeler
pacifica Wheeler
paiute Gregg
pilifera (Roger)
pinealis Wheeler
psammophila Creighton & Gregg
rhea Wheeler
rugulosa Gregg
senex Gregg
sitarches Wheeler
soritis Wheeler
spadonia Wheeler
tucsonia Wheeler
tysoni Forel
xerophila Wheeler
yaqui Creighton & Gregg
n. sp. 1 nr. micula
n. sp. 9 nr. cavigenis

REFERENCES

Johnson, Robert A. 2000. Seed-harvestor ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. Sociobiology 36(1): 89-122 plus color supplement.

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