

Reproductive Biology of the Seed-harvester Ants *Messor julianus* (Pergande) and *Messor pergandei* (Mayr) (Hymenoptera: Formicidae) in Baja California, Mexico

ROBERT A. JOHNSON

Department of Biology, Arizona State University, Tempe, Arizona 85287-1501, USA

Abstract.—The seed-harvester ant *Messor julianus* (Pergande) exhibits a parapatric distribution pattern with the ecologically equivalent congener *M. pergandei* (Mayr) in the Baja California peninsula of Mexico; *M. pergandei* replaces *M. julianus* in drier soil microhabitats within the contact zone between these two species. This paper describes the reproductive biology of *M. julianus* and *M. pergandei* to provide a first step in understanding factors involved in causing this replacement pattern. Mating flights of *M. julianus* were observed over a several week period from early February to early March, and thus appear similar to those of *M. pergandei*. Likewise, starting nests of both species contained one foundress. Moreover, the similar ecology and mating flights of *M. julianus* and *M. pergandei* suggest that the replacement pattern exhibited by these two species is associated with patterns of foundress survival. In regard to mating flights, both *M. julianus* and *M. pergandei* are postulated to have diverged from the putative ancestral condition of summer mating flights that occur in other Nearctic congeners. This seasonal difference in timing of the mating flight for these two species correlates with their being the only Nearctic species of *Messor* that are restricted to hot desert habitats. Alate females for both *M. julianus* and *M. pergandei* have poor tolerance to high temperature relative to desert ants in the genera *Aphaenogaster* and *Pogonomyrmex*.

The seed-harvesting ant genus *Messor* (Hymenoptera: Myrmicinae) is common throughout the southwestern deserts of the United States and northwestern Mexico. Four species of *Messor*, *M. andrei* (Mayr), *M. julianus* (Pergande), *M. pergandei* (Mayr), and *M. stoddardi* (Emery), occur in the Baja California peninsula of Mexico; *M. julianus* is endemic to the peninsula (Johnson 2000a; R. Johnson and P. Ward, unpubl. data) (Fig. 1). Two of these species, *M. julianus* and *M. pergandei*, are common in most low elevation habitats (< ≈1000 m) with their combined geographic distributions encompassing all but the northwest portion of the peninsula. The other two species, *M. andrei* and *M. stoddardi*, are largely restricted to coastal and adjacent inland areas along the Pacific Coast. In the Baja California peninsula, *M. andrei* is restricted to the relatively mesic

California Floristic province in the northwest portion of the peninsula (R. Johnson and P. Ward, unpubl. data). The range of *M. stoddardi* extends to central portions of the peninsula, but this species rarely coexists with *M. julianus* or *M. pergandei* (R. Snelling, unpubl. data; R. Johnson, pers. obs.) (Fig. 1).

Messor julianus and *M. pergandei* are ecologically similar species. Colonies of both species consist of many thousands of workers that forage in long columns (Johnson 2000a), and these two species are the only Nearctic *Messor* that are restricted to occurring in hot desert habitats (Wheeler and Wheeler 1973). Geographically, *M. julianus* is mostly restricted to central and southern portions of the peninsula, while *M. pergandei* occurs in eastern portions of the peninsula to as far south as northeastern BCS (the state of Baja California Sur)

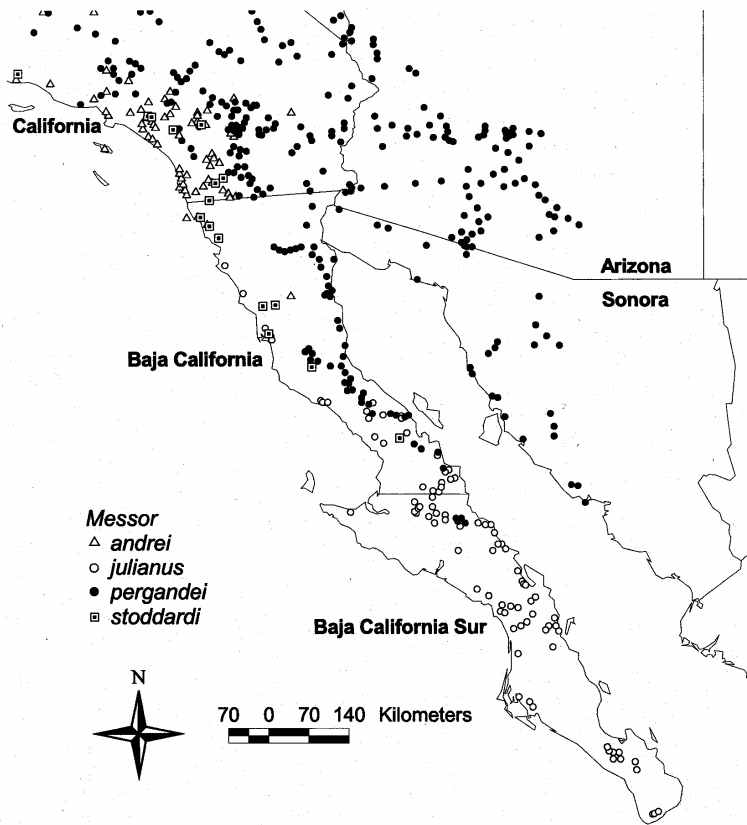


Fig. 1. Geographic distribution of species of *Messor* that occur in the Baja California peninsula, Mexico. The full geographic distribution of each species is given in Johnson (2000a).

(Fig. 1). In northern and central BC (the state of Baja California), *M. julianus* inhabits a narrow range along the cool Pacific Coast, while *M. pergandei* is restricted to xeric desert areas along the eastern coast. Moreover, these two species exhibit a parapatric distribution pattern (herein defined as species that occupy separate but adjoining areas, such that only a small

fraction of individuals in each encounters the other [Futuyma and Mayer 1980]) with ranges of the two species overlapping across a contact zone in the central peninsula (Fig. 1). While the two species are often sympatric within the contact zone, the pattern across the contact zone is one in which the two species replace one another along local gradients that correlate

with abiotic habitat features (Johnson 2000a). Across the contact zone, *M. pergandei* inhabits the drier microhabitats, i.e., those that are lower in elevation or in which the soils have a higher percentage composition of sand (drier soils) (R. Johnson, pers. obs.).

Colony founding is the most vulnerable stage in the life history of ants (Tschinkel 1992, Herbers 1993, Johnson 1998), and it is this stage that likely determines micro- and macro-distribution of adult colonies. Thus, comparative data on reproductive biology of *M. julianus* and *M. pergandei* provide a first step in understanding factors involved in causing the replacement pattern exhibited by these two species. Mating flights of *M. pergandei* are well known and typically occur between late January and mid-March (Pollock and Rissing 1985, Rytí 1988, Cahan *et al.* 1998), and thus deviate seasonally from the summer mating flights of other Nearctic *Messor* (Creighton 1953, Cole 1963, McCluskey 1963, Wheeler and Wheeler 1973, Snelling and George 1979, Brown 1999, R. Snelling, unpubl. data, M. Bennett, pers. comm.). In contrast, the mating flights and the female sexuals of *M. julianus* are undescribed in the literature. Based on the fact that *M. julianus* and *M. pergandei* are the only Nearctic *Messor* that are restricted to hot desert habitats, I hypothesized that the seasonal timing of mating flights was similar for these two species. I assessed potential physiological constraints on mating flight season by comparing high temperature tolerance for alate females of *Messor*, *Aphaenogaster*, and *Pogonomyrmex*.

METHODS

I observed ten colonies of *M. julianus* over nine days in mid-February 1993, near Highway 1 at 26 km northwest of Santa Rosalía, BCS (27°23'N, 112°28'W). All ten colonies had large nests and an active foraging column. The site was a sandy plain dominated by *Larrea tridentata*, *Opuntia cholla*, and *Pachycereus pringlei*. Through-

out the flight period each day, alates flying from nests were counted during sequential 2 minute visits to each nest. Ambient temperature was measured periodically about 5 cm above ground using a thermocouple thermometer.

The number of foundresses per starting colony was determined by excavating founding nests of *M. julianus* and *M. pergandei*. Data for *M. julianus* were collected 17–18 km west of La Purísima, BCS, (26°09'N, 112°13'W) in March 1992, and near Punta San Hipolito, BCS, (27°00'N, 114°00'W) in February 1998. These same data were collected for *M. pergandei* near Highway 1 at 17.5 km west of Bahía de los Angeles, BC, (28°59'N, 113°44'W) and along Highway 1 at 6 km south of the paved turnoff to Bahía de los Angeles, BC, (29°00'N, 114°10'W) in February 1995.

I assessed relative tolerance to high temperature by comparing survival for alate females of *M. julianus* and *M. pergandei* with that of two species of *Aphaenogaster* (*A. albisetosa* and *A. cockerelli*) and four species of *Pogonomyrmex* (*P. barbatus*, *P. occidentalis*, *P. rugosus*, and *P. salinus*) (see Table 1 for collection data); mating flights of both species of *Aphaenogaster* and all four species of *Pogonomyrmex* are triggered by summer rains (Johnson 2000a). Trials used test tubes that were partially filled with water trapped by cotton plugs. Alate females were placed into the tubes and the openings were plugged with moist cotton, thus providing *ad libitum* water at both ends. Trials at each temperature used one tube containing 25 individuals of one species that had been collected from at least four colonies. A separate set of individuals was used at each temperature. Each species was tested over 1° C increments that resulted in mortality ranging from 0–100%. The tubes were placed in a darkened incubator for 2 hours at the appropriate temperature; individuals unable to right themselves after that time were considered dead. Mortality data were compared among congeners and

Table 1. Collection data for alate females used in temperature tolerance tests. Localities are in the United States except as noted.

Species	Collection Locale	Latitude	Longitude	Elevation (m)	Collection Date
<i>Aphaenogaster</i>					
<i>A. albisetosa</i> Mayr	AZ: Pinal Co., 8 km NE Casa Grande	32°56'N	111°42'W	430	26 JUL 1995
<i>A. cockerelli</i> André	NM: Hildago Co., Jct. Hwys 9 & 80	31°56'N	109°02'W	1260	16 JUL 1994
<i>Messor</i>					
<i>M. julianus</i> (Pergande)	MEXICO: Baja California, 47.5 km S Bahía de los Angeles	28°38'N	113°20'W	80	3 FEB 1995
<i>M. pergandei</i> (Mayr)	MEXICO: Baja California, 29 km S Bahía de los Angeles	28°41'N	113°26'W	105	4 FEB 1995
<i>Pogonomyrmex</i>					
<i>P. barbatus</i> (Smith)	NM: Hildago Co., 3 km N Rodeo	31°52'N	109°02'W	1225	5 JUL 1993
<i>P. occidentalis</i> (Cresson)	AZ: Yavapai Co., Chino Valley	34°46'N	112°27'W	1450	30 JUL 1995
<i>P. rugosus</i> Emery	NM: Hildago Co., Jct. Hwys 9 & 80	31°56'N	109°02'W	1260	5 JUL 1993
<i>P. salinus</i> Olsen	NV: Clark Co., Dry Lake	35°54'N	114°56'W	520	30 AUG 1993

across genera using a contingency table analysis. For across genera comparisons, data sometimes were not available for temperatures below or above those causing 0 and 100% mortality. To make these comparisons, I assumed that the upper and lower bounds were threshold temperatures.

Voucher specimens are deposited at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, the Los Angeles County Museum of Natural History, Los Angeles, California, and the Robert A. Johnson collection, Tempe, Arizona.

RESULTS

I observed mating flights of *M. julianus* from early February to early March. At the site northwest of Santa Rosalía, BCS, alates flew from 6 of the 10 observation colonies, with few alates released each day. Flights occurred on 4 of 9 days and were relatively synchronous among colonies, i.e., on a given day, alates either flew from several colonies or none of the colo-

nies (Figure 2). Mating flights typically occurred from 0830–1000 h (MST) at temperatures of 16–23° C. Flights occurred irrespective of mild breezes or overcast skies, but were precluded by light rain or moderate breezes. Alates temporarily retreated into nests following gusts of wind. After the last day, I excavated the ten observation colonies and several adjacent colonies. In all colonies, alates were present in very low numbers or absent.

Mating flights of *M. julianus* were also observed on 5 March, 1992, at 17 km west of La Purísima, BCS, (26°09'N, 112°13'W) and on 5 February, 1995, at 48.7 km south of Bahía de los Angeles, BC (28°38'N, 113°20'W). At the latter site, ten marked colonies of *M. julianus* were observed on 31 January and 5 February. On 31 January, no alates were observed outside any of the ten colonies and no foundresses were located at the site. On 5 February, alates were observed outside 6 of the 10 colonies and individuals flew from one of these nests and from several unmarked nests. Mating flights of *M. pergandei* were ob-

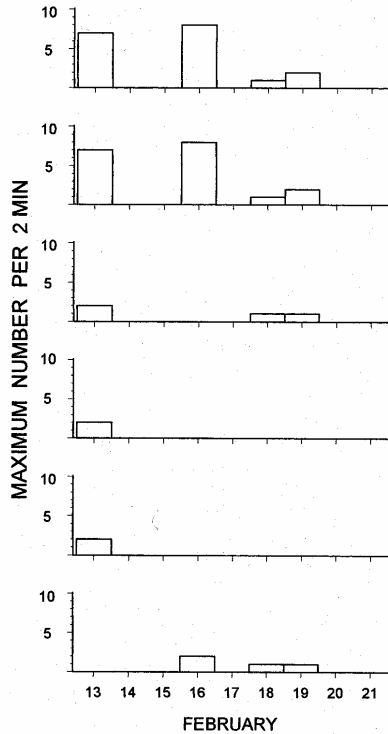


Fig. 2. Flight activity for six colonies of *Messor julianus* northwest of Santa Rosalía, Baja California Sur, Mexico, during February 1993. For each day, data are from the two minute observation period in which the highest number of alates were released from the nest.

served on 26 February, 1991, at Punta Estrella, BC, (30°55'N, 114°43'W) on 29 February, 1992, along Highway 1 at 16.0 km east of San Ignacio, BCS, (27°20'N, 112°46'W) and on 1-2 February, 1995, along Highway 1 at 17.5 km west of Bahía de los Angeles, BC (28°59'N, 113°44'W). The latter site had been visited several days earlier, but no foundresses of *M. pergandei* were located. All of 44 and 127 starting nests for *M. julianus* and *M. pergandei*, respectively, contained one foundress (Table 2).

Tolerance to high temperature was first compared between congeners. Species within all three genera had similar tolerance to high temperature (Chi-square, $P > 0.10$), so data for species within each genus were pooled. In contrast, tolerance to high temperature varied significantly across genera (Chi-square = 231.9, 14 df, $P < 0.001$). Subsequent between-genus tests demonstrated that temperature tolerance differed between *Messor* and both *Aphaenogaster* (Chi-square = 34.9, 5 df, $P < 0.001$) and *Pogonomyrmex* (Chi-square = 181.3, 7 df, $P < 0.001$). The primary contributors to Chi-square values were at low temperatures, where mortality was higher than expected for *Messor* and lower than expected for *Aphaenogaster* and *Pogonomyrmex* (Table 3). Overall, most individuals survived to 42–43° C in *Messor*, 44–45° C in *Aphaenogaster*, and 46–47° C in *Pogonomyrmex*.

DISCUSSION

Reproductive biology of *M. julianus* appears similar to that of *M. pergandei*. The asynchronous late winter to early spring mating flights of both species appear cued by photoperiod (McCluskey 1963) and extend for several weeks both within and among nests (Pollock and Rissing 1985). Mating flights of *M. julianus* were observed from early February through early March, and anecdotal observations suggest that most alates were released during this several week period. For example, at one site alates were observed outside of nests in early February but not several days earlier, which suggests that this was near the beginning of the mating flight season. Similarly, few if any alates could be excavated from nests after late February, suggesting the end of the mating flight season.

Mating flights of *M. pergandei* occur from early to mid-morning under clear skies as air temperatures reach about 22° C. The lower temperatures at which *M. julianus* initiates mating flights are associat-

Table 2. Number of foundresses in starting nests of *Messor julianus* and *M. pergandei* in the Baja California peninsula, Mexico. For location, BC = Baja California; BCS = Baja California Sur.

Species	Foundress Association Size		Location	Latitude	Longitude	Elevation (m)	Date
	1	>1					
<i>M. julianus</i>	40	0	17–18 km W La Purísima, BCS	26°09'N	112°13'W	100	4–5 MAR 1992
	4	0	Punta San Hipolito, BCS	26°58'N	113°59'W	5	10 FEB 1998
Total	44	0					
<i>M. pergandei</i>	23	0	Punta Estrella, BC	30°55'N	114°43'W	5	25–27 FEB 1991
	51	0	Highway 1 at 17.5 km W of Bahía de los Angeles, BC	28°59'N	113°44'W	80	3 FEB 1995
	53	0	Highway 1 at 6 km S of turnoff to Bahía de los Angeles, BC	29°00'N	114°10'W	365	3 FEB 1995
Total	127	0					

ed with this species also foraging at much lower temperatures. During winter and spring, foraging columns of *M. julianus* form prior to dusk and foraging continues into the night until ground temperatures decrease to < 11° C (R. Johnson, unpubl. data). Conversely, *M. pergandei* forages diurnally during this season, beginning after ground temperatures reach about 18° C (Bernstein 1974). While flights of *M. pergandei* are often precluded by overcast weather or slight breezes (Pollock and Rissing 1985), those of *M. julianus* often

proceeded, at least at low levels, under these conditions.

Both *M. pergandei* and *M. julianus* are haplometrotic (one foundress per starting nest) in the Baja California peninsula. In *M. pergandei*, the number of foundresses varies geographically from haplometrosis in southern California to pleometrosis (multiple foundresses per starting nest) in southeastern California and Arizona (Pollock and Rissing 1985; Rytty 1988; Cahan *et al.* 1998; Rissing *et al.* 2000). However, mature colonies of *M. pergandei* have a single

Table 3. High temperature tolerance (°C) for alate females in the ant genera *Aphaenogaster*, *Messor*, and *Pogonomyrmex*. Values are per cent mortality for 25 individuals over 2 h with *ad libitum* moisture.

Species	Temperature (°C)									
	40	41	42	43	44	45	46	47	48	
<i>A. albisetosa</i>			0.0	0.0	48.0	80.0	100.0			
<i>A. cockerelli</i>		0.0	0.0	4.0	44.0	100.0	100.0			
<i>M. julianus</i>			0.0	72.0	100.0	100.0				
<i>M. pergandei</i>	0.0	4.0	4.0	88.0	100.0	100.0	100.0			
<i>P. barbatus</i>					0.0	0.0	0.0	44.0	100.0	
<i>P. occidentalis</i>						0.0	12.0	100.0	100.0	
<i>P. rugosus</i>					0.0	2.0	0.0	48.0	100.0	
<i>P. salinus</i>						0.0	0.0	80.0	100.0	

queen regardless of the initial founding strategy (Rissing and Pollock 1987; S. Rissing and J. Parker, unpubl. data). These data extend the distribution of haplometrosis for *M. pergandei* from southeastern California to its southern range limit in the Baja California peninsula such that both *M. pergandei* and *M. julianus* are haplometrotic where the two species are sympatric. Mating occurs in the air for *M. pergandei* (S. Rissing, pers. comm.) and *M. andrei* (R. Johnson, pers. obs.), with *in copulo* pairs of both species sometimes falling to the ground; mating in *M. julianus* is probably similar.

The replacement pattern exhibited by *M. julianus* and *M. pergandei* is common among seed-harvester ants in western North America (Johnson 2000a). For example, the ecologically equivalent species *Pogonomyrmex barbatus* and *P. rugosus* segregate microhabitats along gradients of soil texture. Foundresses of *P. rugosus* have a higher tolerance to desiccating conditions, which correlates with this species occurring in drier soil microhabitats (Johnson 2000b). The similar ecology and mating flights of *M. julianus* and *M. pergandei* suggest that the micro- and macro-habitat differences exhibited by these two species are also associated with patterns of foundress survival. Given that *M. pergandei* inhabits the more xeric micro- and macrohabitats, it is predicted that foundresses of this species are more desiccation tolerant than are foundresses of *M. julianus* (Johnson 2000a).

The late winter to early spring mating flights of *M. julianus* and *M. pergandei* are correlated with these being the only two Nearctic *Messor* that are restricted to hot desert habitats (Wheeler and Wheeler 1973). However, it is difficult to determine the sequence of character-state change in timing of the mating flight within Nearctic *Messor* because the phylogenetic relationships of this species group are unclear. *Messor* is a predominantly Old World genus, with the Nearctic components pre-

sumably having invaded North America from Asia via Beringia (R. Snelling, pers. comm.). Alternatively, some recent evidence suggests that the *Aphaenogaster* species belonging to the former *Novomessor* (including *A. albisetosa* and *A. cockerelli*) are the sister group to Nearctic *Messor* (Bennett 2000). Moreover, evaluating the ancestral mating flight condition depends upon determining the appropriate outgroup. The relationship between *M. julianus* and *M. pergandei* is also poorly resolved (Bennett 2000) because the clade containing these two species also contains *M. lariversi*, which is a Great Basin species that has summer mating flights.

One possible evolutionary scenario is the late winter to early spring flights evolved one time and are common by descent in *M. pergandei* and *M. julianus*. If this is the case, the shift from a summer to a late winter to early spring flight season may have been necessitated by physiological constraints related to temperature tolerance, and prerequisite to these two species invading hot desert habitats. Moreover, alate females of both species have poor heat tolerance compared to species of *Aphaenogaster* and *Pogonomyrmex*, suggesting *Messor* foundresses could not survive soil temperatures present during summer. A similar temperature constraint occurs in the desert leaf-cutter ant *Acromyrmex versicolor*, whose mating flights are triggered by late summer rains. Females of *A. versicolor* also have poor tolerance to high temperature, and the foundresses survive by selectively initiating nests in shaded, cooler microhabitats (Rissing *et al.* 1986).

ACKNOWLEDGMENTS

This manuscript benefited from comments and discussions with S.W. Rissing and R.R. Snelling, and by comments from two anonymous reviewers.

LITERATURE CITED

- Bennett, M. 2000. Systematics of the Nearctic granivore ant genus *Veromessor*. PhD thesis, Univ. Calif.

- Bernstein, R.A. 1974. Seasonal food abundance and foraging activity in some desert ants. *American Naturalist* 108:490-498.
- Brown, M.J.F. 1999. Semi-claustral founding and worker behaviour in gynes of *Messor andrei*. *Insectes Sociaux* 46:194-195.
- Cahan, S., Helms, K.R., Rissing, S.W. 1998. An abrupt transition in colony founding behaviour in the ant *Messor pergandei*. *Animal Behaviour* 55:1583-1594.
- 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.
- Creighton, W.S. 1953. New data on the habits of the ants of the genus *Veromessor*. *American Museum Novitates* 1612:1-18.
- Futuyma, D.J., Mayer, G.C. 1980. Non-allopatric speciation in animals. *Systematic Zoology* 29:254-271.
- 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.
- Johnson, R.A. 1998. 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. 2000a. Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. *Sociobiology* 36:83-122.
- Johnson, R.A. 2000b. Habitat segregation based on soil texture and body size in the seed-harvester ants *Pogonomyrmex rugosus* and *P. barbatus*. *Ecological Entomology*, in press.
- McCluskey, E.S. 1963. Rhythms and clocks in harvester and Argentine ants. *Physiological Zoology* 36:273-292.
- Pollock, G.B., Rissing, S.W. 1985. Mating season and colony foundation of the seed-harvester ant, *Veromessor pergandei*. *Psyche* 92:125-134.
- Rissing, S.W., Pollock, G.B. 1987. Queen aggression, pleometrotic advantage and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). *Animal Behaviour* 35:975-981.
- Rissing, S.W., Johnson, R.A., Martin, J.W. 2000. Colony founding behavior of some desert ants: geographic variation in metrosis. *Psyche* 103:95-101.
- Rissing, S.W., Johnson, R.A., Pollock, G.B. 1986. Natal nest distribution and pleometrosis in the desert leaf-cutter ant *Acromyrmex versicolor* (Hymenoptera: Formicidae). *Psyche* 93:177-186.
- Ryti, R.T. 1988. Geographic variation in cooperative colony foundation in *Veromessor pergandei* (Hymenoptera: Formicidae). *Pan-Pacific Entomologist* 64:255-257.
- Snelling, R.R., George, C.D. 1979. *The Taxonomy, Distribution and Ecology of California Desert Ants (Hymenoptera: Formicidae)*. Report to Bur. Land Manage., US Dept. Int., Riverside, Calif.
- Tschinkel, W.R. 1992. Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. *Ecological Entomology* 17:179-188.
- Wheeler, G.C., Wheeler, J. 1973. *Ants of Deep Canyon*. Univ. Calif. Press, Berkeley.