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# Divergence in mating-flight patterns of the seed-harvester ant *Pogonomyrmex rugosus* (Hymenoptera: Formicidae) in the western Mojave Desert

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**Abstract**

In the Chihuahuan, Mojave, and Sonoran deserts of the United States, mating flights of the seed-harvesting ant *Pogonomyrmex rugosus* EMERY, 1895 are only known to occur in summer in response to seasonal rains. In parts of the Sonoran and Mojave deserts, however, summer rain is largely absent and most precipitation occurs during the winter and early spring. We observed a mating flight of *P. rugosus* at a western Mojave Desert location in late winter, four to six months earlier than reported for other areas. In this portion of their range, *P. rugosus* must either produce alates for summer flights and then over-winter them for late-winter to early-spring flights when summer precipitation is insufficient, or else they have fully converged on the mating-flight patterns of other desert species dependent upon winter and early spring rains.

**Key words:** Ants, geographic variation, mating flights, *Pogonomyrmex rugosus.*

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## Introduction

Many ants exhibit mating flights, where winged (alate) males and females fly from colonies in order to mate. Newly mated queens then attempt to establish a new colony or they are adopted into colonies already established. Mating flights are synchronized within populations, occurring during a particular time interval during the day and under specific climatic conditions, often at a particular time of year. Synchronization prevents significant mating among close relatives and ensures that males and females find a mate of the correct species. In most ants, when mating flights occur, these appear to be determined by external environmental cues that indicate suitable conditions for flight and new colony establishment (WHEELER 1910, HÖLLDOBLER & WILSON 1990).

In the warm deserts lying within the United States, the Mojave, Sonoran, and Chihuahuan, a major condition for successful colony establishment is adequate soil moisture, and mating flights generally coincide with seasonal rainfall (JOHNSON 2000, 2001). In the northern Chihuahuan Desert, winters are relatively cold and dry, and most mating flights are triggered by summer rains, while in portions of the Sonoran and Mojave deserts, winters are relatively warm and annual precipitation comes in two primary pulses, in the summer and in winter. Here, some species exhibit summer mating flights, while others have flights in late winter or early spring (JOHNSON 2001). Other parts of the Mojave and Sonoran deserts, however, receive on average very little summer rain, with the great majority of precipitation occurring in the winter into early spring. Ants in these regions often have mating flights in late winter or early spring (JOHNSON 2001).

*Pogonomyrmex rugosus* EMERY, 1895 is a well-studied, common, and conspicuous seed-harvester ant in the three major deserts of the southwestern United States. Mating flights have been noted for sites in all three deserts, and like the great majority of *Pogonomyrmex* spp., flights have only been observed during the summer following significant rainfall (HÖLLDOBLER 1976, RISSING 1983, JOHNSON 2000, ANDERSON & al. 2006). Observations of summer flight activities have been made in regions where substantial summer precipitation is on average predictable; however, *P. rugosus* can also be common in some western regions of the Mojave and Sonoran deserts where summer rains are largely absent (Fig. 1).

## Methods and Results

On 18 March 2009, in the Mojave Desert near Mojave, Kern County, California, we walked randomly located transects and observed 48 *P. rugosus* colonies over a four hour period (11:00 - 15:00, local times). Most had recently emerged from over-wintering and had begun to remove vegetation from the nest perimeter. Based on observations during previous visits to the site, open nests begin to appear around 1 March. At three of the 48 transect colonies, alates were emerging from the nest entrances, climbing onto stalks of vegetation and flying away. The first colony was observed flying at 12:30, the second at 13:00, and the third at 14:00. We collected a majority of alates present on the surface (21, 28, and 32 individuals, respectively) as well as workers for identification; males were not present in the collections. The behavior of *P. rugosus* workers during mating flights was variable among colonies; at the first colony

only a small number of workers were outside the nest during flight activity. At the second, no workers were visible outside the nest, while at the third, substantial numbers of workers were outside and milling about, as is common at sites where summer flights occur (e.g., RISSING 1983).

Consistent with our observations near Mojave, a single dealate *P. rugosus* female was observed walking on the ground the following day, on 19 March, at a second Mojave Desert site 33 km south of Mojave, near Lancaster, Los Angeles County, California. On 20 March, we also excavated a *P. rugosus* foundress queen in a starting nest close to the original transects near Mojave. This nest was in close proximity to starting nests of the seed-harvesting ant *Messor pergandei* (MAYR, 1886) which were known to have had their first substantial mating flight of the year at the site on 17 March.

To verify that the samples were *P. rugosus* and not a cryptic species and also to exclude the possibility that the alates were an unknown social parasite, the species identities of workers were first determined using the taxonomic keys of WHEELER & WHEELER (1973). We then sequenced a 433 bp portion of the *cytochrome-c-oxidase-subunit-I* mitochondrial gene of a single alate female and worker from each of the three colonies following the methods of HELMS CAHAN & KELLER (2003). These sequences were compared to those of four species in the *P. barbatus* complex (TABER 1990), using a combination of previously published sequences and sequencing of additional samples (HELMS CAHAN & KELLER 2003): *P. rugosus*, *P. barbatus* (SMITH, 1858), *P. desertorum* WHEELER, 1902, and *P. apache* WHEELER, 1902, with *Pogonomyrmex californicus* (BUCKLEY, 1867) as an outgroup. The sequences from the Mojave samples all clustered within *P. rugosus*, and alates and workers from the same colonies possessed identical haplotypes. Voucher specimens of the Mojave *P. rugosus* have been deposited in the Zadock Thompson Natural History Collection at the University of Vermont, and their genetic sequence data have been deposited in GenBank (accession numbers GQ503633 - GQ503639).

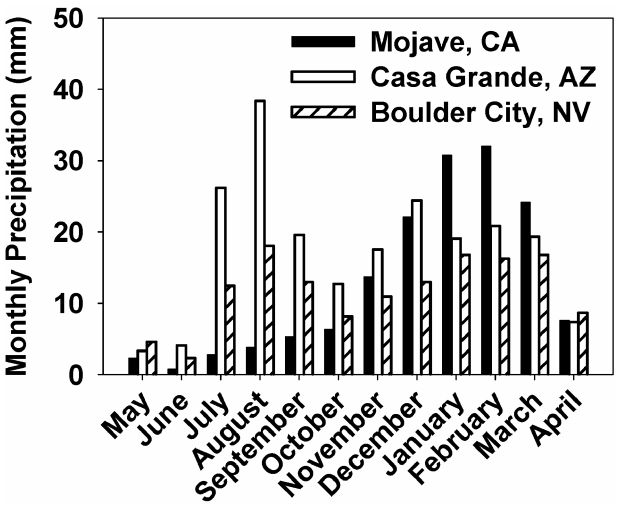


Fig. 1: Long-term monthly precipitation averages at three sites where *Pogonomyrmex rugosus* mating flights have been reported in the literature. Casa Grande, Arizona, is in the Sonoran Desert, while Boulder City, Nevada, is in the Mojave Desert. On average, both sites exhibit significant summer precipitation and mating flights are reported to occur in summer at both sites (RISSING 1983, ANDERSON & al. 2006). Mojave, California, is in the far western Mojave Desert and summer precipitation is, on average, largely absent. Most precipitation occurs there in winter, and mating flights occurred in late winter (this study). All data are from WESTERN REGIONAL CLIMATE CENTER (2006). Mojave data are averages from 1904 - 2008, Casa-Grande data are averages from 1898 - 2008, and Boulder-City data are averages from 1931 - 2004.

## Discussion

Although *Pogonomyrmex rugosus* in most of its range reproduces solely during summer mating flights, in the western Mojave Desert flights occurred four to six months earlier in the year, typical of co-occurring species whose flight season corresponds to winter rains. There are two possible explanations for our observations. First, *P. rugosus* in the western Mojave may have converged fully on the mating-flight patterns of other desert species dependent upon winter and early spring rains. Alternatively, alates could be produced for summer flights, and then maintained in the nest for late winter or early spring flights following summers when precipitation is insufficient. Either route would suggest a mating-flight strategy different than any reported for other *P. rugosus* populations. The late winter flight we observed appeared fully functional; although we did not observe males leaving nests, the presence of dealate founding queens in the days following the flight suggest that they lead to successful mating and colony foundation.

Substantial divergence in when mating flights occur across the range of *P. rugosus* could evolve via a number of possible routes. There may be a gradual shift across the species' range in the relative magnitude of precipitation in summer versus winter and early spring, progressively shifting the timing of reproduction later in the season, with eventual maintenance of alates during winter dormancy for flights that occur after nests are reopened in late winter to early spring. Alternatively, a major difference might have arisen from a polymorphism with split alternative mating seasons. Further comparative study of flight activity across the range of *P. rugosus*, particularly in regions of transitions in precipitation patterns, may help to shed light on how divergence in reproductive timing evolved. Differences in mating patterns across a species' range present important opportunities to study the process by which local adaptations to different ecological conditions arise across broad geographic scales.

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## Zusammenfassung

Für die Ernteameise *Pogonomyrmex rugosus* EMERY, 1895 in der Chihuahua-, der Mojave- und der Sonora-Wüste der Vereinigten Staaten waren Hochzeitsflüge bisher ausschließlich aus dem Sommer bekannt – als Reaktion auf saisonale Regenfälle. In Teilen der Sonora- und der Mojave-Wüste fehlt Sommerregen allerdings beinahe völlig, und der

meiste Niederschlag findet im Winter und im zeitigen Frühjahr statt. Wir beobachteten einen Hochzeitsflug von *P. rugosus* in der westlichen Mojave-Wüste im späten Winter, vier bis sechs Monate früher als für andere Gebiete berichtet. Wir diskutieren zwei Szenarien für diesen Teil des Verbreitungsgebiets von *P. rugosus*: Die Art könnte für Sommerflüge bestimmte Alate produzieren, welche bei unzureichenden Sommerniederschlägen im Nest überwintern und dann im späten Winter oder zeitigen Frühjahr fliegen. Alternativ könnte sich die Art in diesem Teil ihres Verbreitungsgebiets völlig auf den Hochzeitsflugsrhythmus anderer Wüstenarten umgestellt haben, die von Regenfällen im Winter und zeitigen Frühjahr abhängen.

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