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COLONY FOUNDING BEHAVIOR OF SOME DESERT ANTS:
GEOGRAPHIC VARIATION IN METROSIS

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ABSTRACT

The ants *Pogonomyrmex californicus* and *Pheidole tucsonica* display cooperative colony foundation with co-foundresses forming associations without respect to relatedness. Geographic variation in method of colony foundation [cooperative (pleometrosis) versus non-cooperative (haplometrosis)] occurs in *P. californicus*, *Acromyrmex versicolor*, *Myrmecocystus minutus* and *Messor pergandei*. Such variation in colony founding behavior strongly suggests that comparative studies of the adaptive value of cooperative colony founding will be extremely rewarding.

INTRODUCTION

W. M. Wheeler (1910) believed firmly that, in the vast majority of ant species, new colonies are founded by solitary queens (haplometrosis) and retain a single queen throughout the colony lifetime (monogyne). This conception was assumed to be generally true until publication of a seminal paper by Hölldobler and Wilson (1977). These authors drew attention to the frequent occurrence of multiple fertile queens in mature colonies (polygyne) and identified several species in which multiple founding queens cooperate to start new colonies (pleometrosis). While the number of ant

species displaying cooperative colony foundation has grown steadily (Rissing and Pollock 1988), the discovery and documentation of intraspecific geographical variation in pleometrosis is new and little explored (see Rytí 1988). In this paper we summarize recent observations on geographic variation in colony founding behavior for several species common in the deserts of the southwestern United States.

METHODS

Occurrence of haplometrosis and pleometrosis in the field

Nests of newly mated foundresses were excavated and censused in the field following mating flights, which are triggered by summer/fall rains for species discussed here except for *Messor pergandei* and *Pogonomyrmex californicus* which have asynchronous flights apparently triggered by photoperiod. In the field, starting colonies are identifiable by the characteristic coarse grain of soil excavated by foundresses.

Relatedness as a criterion for association formation

Queens were brought into the laboratory to determine whether foundress associations formed with respect to kinship, using the assay developed by Rissing and Pollock (1986). Associations (haplometrotic and pleometrotic) from a given locale were collected, the queens marked uniquely with paint and then permitted to form new associations in a plastic shoe box half-filled with moistened soil followed by excavation and identification of all queens in all associations 24 hours later. Similar manipulations revealed a major role for kinship in the formation of foundress associations in the wasp *Polistes fuscatus* (Noonan 1981) but not the ants *M. pergandei* (Rissing and Pollock 1986) and *Acromyrmex versicolor* (Rissing et al. 1986). The lack of close relatedness within foundress associations of these ants was later verified by allozyme electrophoresis (Hagen et al. 1988).

Geographic variation in colony founding behavior

The above assay demonstrated that *M. pergandei* queens collected after mating flights from locales that had pleometrotic and haplometrotic foundresses would start colonies pleometrotically when given the chance, even if they were originally collected as a

haplometrotic foundress (Rissing and Pollock 1986). In fact, they prefer to join associations (Krebs and Rissing 1991). Rytí (1988), however, demonstrated that foundresses collected from a completely haplometrotic population at Deep Canyon, CA, would not form pleometrotic associations when given the chance and would often fight. We used Rytí's (1988) assay on foundresses collected from newly discovered all-haplometrotic populations of species previously known to display pleometrosis in other locales [*Myrmecocystus mimicus* (Bartz and Hölldobler 1982), *A. versicolor* (Rissing et al. 1986) and *P. californicus* (see Table 1 for pleometrosis)].

RESULTS

Haplometrosis and pleometrosis in the field

Our field surveys have revealed the first known populations of *Pogonomyrmex californicus* and *Pheidole tucsonica* where pleometrosis occurs regularly (Table 1). We have also found populations of *Myrmecocystus mimicus* and *Acromyrmex versicolor*, species previously shown to be pleometrotic, where haplometrosis predominates, often exclusively (Table 1). In addition to the species in Table 1, RAJ has documented solitary colony foundation (haplometrosis) in *Pogonomyrmex apache* Wheeler (N = 22, Cochise Co., AZ), *Pogonomyrmex salinus* Olsen [N = 60 (Note: 3 additional colonies contained 2 foundresses), Clark Co., NV], *Dorymyrmex insanus* (Buckley) (N = 35, Pinal Co., AZ), and *Myrmecocystus flaviceps* Wheeler (N = 25, Pinal Co., AZ).

Foundress assortment

Pogonomyrmex californicus, *Pheidole tucsonica*, *Myrmecocystus mimicus*, and *Acromyrmex versicolor* all displayed the same patterns in our laboratory tests. Field-caught foundress associations do not retain their original composition when permitted to reform in the presence of other queens from the same population in the laboratory. New, usually larger associations develop in which queens from field-caught foundress associations mix freely. Likewise, haplometrotic (i.e. solitary) foundresses taken from populations in which pleometrosis occurs readily join pleometrotic groups in the laboratory without conflict. This does not occur in the populations where haplometrosis is the ruler: queens fight rather than join groups.

Table 1. Foundress association size of some desert ants; numbers are percent of total. Voucher specimens with detailed locality information are deposited in the insect collection at Arizona State University.

Species	County, State	Foundress Association Size										N	Reference
		1	2	3	4	5	6	7	8	9	≥10		
<i>Acromyrmex versicolor</i> (Pergande)	Maricopa, AZ	44	25	9	11	5		3		2	2	64	Rissing et al. (1986)
	Mohave, AZ	100										70	This study
<i>Messor pergandei</i> (Mayr)	Maricopa, AZ	32	28	17	8	5	2	4	5		2	132	Pollock and Rissing (1985)
	Riverside, CA	100										181	Ryti (1988)
<i>Myrmecocystus mimicus</i> Wheeler	Cochise, AZ	10	18	29	17	13	7	2	2	1		164	Bartz and Hölldobler (1982: Fig. 1a)
	Pinal, AZ	100										20	This study
<i>Pogonomyrmex californicus</i> (Buckley)	San Diego, CA	26	23	9	4	9	6	4			19	47	This study
	Maricopa, AZ	97	3									29	This study
<i>Pheidole tucsonica</i> Wheeler	Maricopa, AZ	36	19	17	11	6	6	3		3		36	This study

DISCUSSION

We add two new species (*Pogonomyrmex californicus* and *Pheidole tucsonica*) to the growing list of ants in which cooperative colony founding is known (see Rissing and Pollock 1988: Table 7.1). Further, while Wheeler (1910:190) thought that such behavior occurred only "under very exceptional circumstances [when] a couple of females from the same maternal nest may meet after their marriage flight and together start a colony," we have also shown that relatedness appears unimportant in a foundress' decision to join an association in these same species as well as the others listed in Table 1 (see references cited there).

Hymenoptera that display kin-specific foundress associations (e.g. the wasp *Polistes fuscatus*) normally form associations over several weeks (Noonan 1981). With most ant species, however, including all those displaying cooperative colony founding in Table 1, associations are formed and nest excavation usually begins immediately. This is especially true of ants (e.g. *Myrmecocystus mimicus*, *Acromyrmex versicolor*, and *Pheidole tucsonica*) attempting to establish colonies after summer rains in desert environments as death from heat and desiccation will ensue immediately unless shelter, generally in the form of a newly started nest, is found. Predation threats are similar to desiccation in the desert where even normally granivorous organisms (birds, ants) readily consume reproductive females. In short, under such forboding abiotic and biotic conditions, a female attempting to form a foundress association simply cannot afford the luxury of limiting the range of potential co-foundresses to only close relatives.

Our data also suggest that not all haplometrotic foundresses are the same: those collected from locales that also have pleometrotic associations of the same species will readily form pleometrotic associations in the laboratory while those collected from locales that have no pleometrotic associations will not, and, in fact, will fight.

Hypotheses to explain possible advantages of cooperative colony founding in ants range from crowding due to lack of available nest sites (Tschinkel and Howard 1983), intra-specific brood-raiding and territoriality following clumping of available nest sites by abiotic conditions (Rissing and Pollock 1987), and a need to

avoid desiccation/predation (Pfennig 1995). Degree of geo-graphical variation in cooperative colony founding species (Table 1) and the associated variation in mutual tolerance of foundresses in these same species may permit an evaluation of these and related hypotheses.

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