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Research article

Genetic relatedness and population structure in the social wasp, *Mischocyttarus mexicanus* (Hymenoptera: Vespidae)

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Summary

In primitively eusocial wasps workers often retain the ability to become queens, so their continued performance in the worker role is partly dependent on elevated genetic relatedness between workers and the brood they rear. In colonies of the social wasp, *Mischocyttarus mexicanus*, workers were related to female pupae by 0.29 ± 0.12, a value that is significantly below the full sister value of 0.75, but not significantly below 0.50, worker relatedness to daughters. Though individuals often build new nests within meters of their natal nest, there was no genetic population structure discernable among four nest clusters, or inbreeding of any kind.

Introduction

Colonies of *Polistes* and *Mischocyttarus* have been much studied because workers in these primitively eusocial genera retain the ability to reproduce themselves, making it particularly interesting when they choose instead to help rear young in a colony where another individual is queen. In subtropical and tropical regions queens typically are outlived by the colony as a whole (Litte, 1977; Strassmann, 1981). Queen replacement processes include supercedure by a related nestmate and usurpation by an unrelated female from another nest. The new queen often kills the eggs and young larvae while leaving the older pupae alone. Queen replacement clearly has a great effect on genetic relatedness of workers to brood, but quantifying that effect can be difficult without molecular studies of relatedness because queen replacement is a rare event in time (even when it affects most colonies), and the extent of brood abortions after queen turnover is hard to assess. Other factors that would reduce genetic relatedness between workers and brood include multiple simultaneous egg layers and multiple mating by queens.

The current study was designed to investigate genetic relatedness in *Mischocyttarus mexicanus*. We chose this species because it is a subtropical species that was the subject of a very thorough behavioral and demographic study (Litte, 1976, 1977). Litte (1977) found that this species nests all year round at her study site, Archbold Biological Station, Florida. She expected genetic relatedness among colony members to be quite high for several reasons. (1) Colonies were initiated by females that emerged from the same natal nest. (2) They did not go more than a few meters from the natal nest. (3) Nests were not joined (except for three times out of 176 colonies observed) when they were more than 10 days old. (4) Group membership was stable; female did not move among nests. (5) There was only one egg-layer at a time in spring colonies. (6) She did not report usurpation and found cofoundresses surviving past the original queen in only 5% of colonies. We were also interested in this species because of the remarkable level of small scale population subdivision we discovered in another species of the same genus, *Mischocyttarus immarginatus* (Queller et al. 1992). In that species a significant inbreeding coefficient of 0.49 ± 0.09 was largely due to substructure in a population where nest clusters were separated by less than 400 m. Our study uses allozymes to estimate population structure and genetic relatedness among colony members in the same population of *M. mexicanus* that Litte (1977) studied.

Materials and methods

We collected 27 colonies of *M. mexicanus* 25 to 28 May 1989 at Archbold Biological Station in southern Florida. The colonies were found on leaves of the saw palmetto, *Serenoa repens*. Since the colonies were collected during the day we probably missed some foragers, but this probably amounted to fewer than 3 individuals. Distance between the colonies was determined by pacing out locations. This was facilitated since many colonies were either clumped along a slash in the vegetation for a power line, or perpendicular to it. Colonies were grouped into 4 clusters, two along the power slash, and two perpendicular to it. Each cluster contained three to nine colonies and was isolated by 90 to 400 meters from other clusters. Ten colonies were each isolated from other colonies and were not included in any cluster.

Collected colonies were transported live on ice to our laboratory. We counted nest contents and removed pupae that were old enough for sex determination. Pupae whose sex was identified and adults were stored in an ultracold freezer at –70 °C until they were analyzed.

We dissected all females and distinguished egg-layers from workers by the presence of mature eggs in the ovaries. We could not distinguish between workers and possible cofoundresses with undeveloped ovaries. We ground up each wasp in buffer and conducted horizontal starch gel protein electrophoresis following standard protocols (Strassmann et al., 1991). We screened for 9 enzymes that are often found to be polymorphic in vespid wasps. Of these, 7 were polymorphic in *M. mexicanus*. However one of them, glycerol-3-phosphate dehydrogenase, had an allele that was differentially expressed in pupae, and so this locus was not used, leaving us with 6 polmorphic loci (Table 1). Genetic relatedness and *F* statistics were estimated using *Relatedness 4.2 b* (Goodnight and Queller, 1994) which applies relatedness estimators developed by Queller and Goodnight (1989). Colonies were weighted equally and standard errors were obtained by jackknifing over colonies. Ninety-five percent confidence intervals of relatednesses were determined from the *t* distribution with number of colonies – 1 degrees of freedom.

Table 1. Allele frequencies for polymorphic loci in *M. mexicanus* in 101 individuals from 25 colonies

Locus	Allele		
	a	b	c
Phosphoglucomutase (PGM)	0.569	0.403	0.29
Isocitrate dehydrogenase (IDH)	0.652	0.348	
Malate dehydrogenase (MDH)	0.724	0.276	
Aconitase Hydratase (ACON)	0.824	0.176	
Leucylproline peptidase (PEPLP)	0.985	0.015	
Glyceraldehyde-3-phosphate dehydrogenase (GA3PD)	0.985	0.015	

Results

None of the 27 colonies had more than seven adults (Table 2). Four of the larger colonies had from two to three egg-layers; the remainder had only one or no egg layers. Half of the colonies had fewer than 25 cells and were probably quite young. However the older nests were not obviously very different as colonies since they had few adults and most of their cells were empty. For example, the largest three nests had from 122 to 179 cells, but over 77% of them were empty and these colonies had only 2, 3 and 7 adults each.

All colonies were within a 500 meter square. At this scale there was no discernable population structure among the four nest clusters: $F_{st} = 0.003 \pm 0.04$, $F_{it} = 0.05 \pm 0.10$, $F_{is} = 0.06 \pm 0.12$ (4 demes, 25 colonies, 88 females). Therefore, for genetic relatedness we treated the colonies as belonging to one unsubdivided population.

Genetic relatedness among most categories of individuals averaged slightly below 0.50 (Table 3). All cases had relatednesses among females that were significantly below 0.75 but not significantly below 0.50. Males were too uncommon in our sample for any relatedness estimation except a general relatedness of females to males.

Table 2. Colony characteristics of 27 collected colonies of *M. mexicanus*

Variable	Mean ± S.E.	Range
Adults	2.9 ± 0.4	1– 7
Egg-layers	0.9 ± 0.1	0– 3
Cells	36.6 ± 8.4	1–179
Eggs	8.3 ± 1.6	0– 34
Larvae	7.8 ± 1.5	0– 26
Pupae	2.0 ± 0.5	0– 8
Empty cells	18.3 ± 7.2	0–138

Table 3. Genetic relatedness between classes of individuals

Class	r ± S. E.	# of colonies	# of individuals
Females (adults and pupae)	0.49 ± 0.06	18	81
Adult females	0.46 ± 0.07	17	54
Egg-layers	0.33 ± 0.18	4	9
Workers	0.40 ± 0.13	11	28
Female pupae	0.44 ± 0.26	8	22
Between egg-layers and workers	0.51 ± 0.10	12	33
Between egg-layers and female pupae	0.33 ± 0.11	11	40
Between egg-layers and workers plus female pupae	0.48 ± 0.07	15	69
Between workers and female pupae	0.29 ± 0.12	13	47
Females to males	0.45 ± 0.11	9	45 females, 13 males

Discussion

Relatedness among females is lower than would have been predicted from Litte's (1977) behavioral and demographic study. However the current study does not allow us to distinguish between the relatedness-lowering effects of factors Litte might have observed such as supercedure, usurpation, and multiple egg-layers, and that of multiple mating which cannot be resolved with either study. It is most probable that this species is mostly singly mated as are other polistine species (Peters et al. 1995, Strassmann et al. in prep.). Certainly Litte's (1977) study points to the factors that are likely to maintain sociality even in the face of relatively low relatedness among colon members. According to her study, colonies with multiple foundresses had slightly shorter development times, lower adult and colony mortality, and grew to larger sizes.

Genetic relatedness among females in *M. mexicanus* is similar to that reported for *M. basimacula*, and lower than that reported for *M. immarginatus* (Queller et al., 1992). Overall genetic relatedness among female colonymates in the middle of the range for primitively eusocial wasps (Strassmann et al., 1989). The lack of any deme structure such as that found for *M. immarginatus* is consistent with the lack of transfer among colonies in *M. mexicanus* (Litte, 1977). *M. immarginatus*, on the other hand had females that moved between closely-spaced nests (Queller et al., 1992).

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