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MULTIPLE MATERNITY AND MULTIPLE PATERNITY IN FIRST GENERATION BROOD FROM SINGLE FOUNDRESS COLONIES OF THE SWEAT BEE *DIALICTUS ZEPHYRUS* (HYMENOPTERA : HALICTIDAE)

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SUMMARY

Genotypes for 31 apparent, single foundresses and their first generation brood in the primitively eusocial sweat bee *Dialictus zephyrus* were inferred from starch-gel electrophoresis of 8 enzyme coding loci. Thirteen percent of the colonies contained the progeny of more than one female, and an additional twenty-three percent contained the progeny of either more than one female or a single, twice-mated female. Thus a total of thirty-six percent of colonies apparently founded by a single female contained first generation brood which were not the progeny of one, singly-mated female.

RESUME

Maternité multiple et parternité multiple dans le couvain de colonies fondées à partir d'abeilles apparemment solitaires Dialictus zephyrus **(Hymenoptera : Halictidae)**

L'électrophorèse en gel d'amidon de 8 enzymes codées par différents loci a permis de déduire, chez l'Abeille primitivement eusociale *Dialictus zephyrus*, les génotypes de 31 fondatrices, apparemment solitaires, et de leur couvain de première génération. 13 % des sociétés renfermaient une descendance provenant de plus d'une femelle et 23 % la descendance soit de plus d'une femelle, soit d'une seule femelle fécondée à deux reprises. Ainsi, un total de 36 % des sociétés apparemment fondées par une femelle unique contenaient des descendants de première génération qui ne pouvaient provenir d'une femelle, fécondée une fois pour toutes.

Evolution of eusocial behavior through kin selection involves altruist individuals who aid their relatives and in this way increase their inclusive fitness enough to compensate for the loss in fitness resulting from foregoing direct reproduction (HAMILTON, 1967a, 1967b, 1972). It is important to know the genetic composition of colonies that comprise social units in order to assess the relatedness of altruists to the beneficiaries of their altruistic behavior. Considerable progress has been made in the study of the evolution of sociality in the Hymenoptera by elucidating relatedness using electrophoretically inferred genotypes in many species of ants (e.g., CRAIG and CROZIER 1979 ; CROZIER *et al.*, 1984 ; PAMILO and VARVIO-AHO, 1979 ; WARD, 1980) and some polistine wasps (METCALF and WHITT, 1977 ; LESTER and SELANDER, 1981). On the other hand, very little is known concerning the genetic structure within colonies of primitively eusocial bees.

Dialictus zephyrus (= *Lasioglossum zephyrum*) is a primitively eusocial halictine bee. Females overwinter as mated adults and initiate annual nests in the spring singly or, less often, in multiple foundress associations (BATRA, 1966 ; MICHENER, 1974). Since multiple mating of foundresses reduces the relatedness among her brood, some of which will be altruists (workers) and some of which will be beneficiaries (the males and gynes reared by the workers), it is of interest to know if foundresses are singly or multiply inseminated. Electrophoretic studies of single foundresses and their first generation brood were conducted to investigate this question.

The study was conducted at alarge nest aggregation along Salmon Creek in Ludloville, Thompkins County, NY, in May of 1983. Each nest of *D. zephyrus* was marked ot the time of initiation, observed for up to 15 minutes on every sunny day (n = 11) to detect the presenc of more than one female during active provisioning in the first generation. Nests were excavated (as described in ABRAMS and EICKWORT, 1981) just prior to eclosion of the first generation of brood. Thirty one colonies met the following criteria and were used in this study ; 1) a single foundress was present at the time of excavation, and 2) all the female pupae were reared to adulthood in the laboratory. Thus we obtained complete, first-generation colonies. Only two males were reared in this sample and were note included in the analysis.

Genotypes of each foundress and all the brood in her nest were inferred from starch gel electrophoresis (as described by KUKUK and MAY, 1985) performed for 8 enzyme encoding loci : *Adh*, alchohol dehydrogenase ; *Gda*, guanine deaminase ; *Hbdh*, hydroxybutyric dehydrogenase ; *Idh*, isocitric dehydrogenase ; *Ldh*, lactic dehydrogenase ; *Mdh-2*, malic dehydrogenase ; *Pep-La-2*, peptidase with leucy-alanine ; and *Pgm*, phosphoglucomutase.

Nests contained up to 5 female brood ($\overline{X} = 3.2$). Thirty-six percent of the 31 colonies showed evidence of either multiple insemination of the apparent foundress or the occurrence of a second egg-laying female. A sample of data from 10 colonies is presented in *Table I*. In four cases (13 %), the apparent foundress could not have produced all the brood in her nest (e.g., colony 10, *table I*). The remaining seven cases (23 %) could be due to either multiple maternity or multiple mating (e.g., colonies 2, 6, 7 & 8 in *table I*).

Table I. — Ten examples (out of 31) of electrophoretically inferred genotypes for apparent-single foundresses (F) and their first generation female brood (B) ; *Dialictus zephyrus*, Tompkins County, N.Y., 1983 ; (* = multiple paternity or > 1 foundress ; ** = > 1 foundress) ; relative mobilities and allele designations below locus names.

Tableau I. — Sur un total de 31 sociétés, dix exemples de génotypes, déduits à partir de données électrophorétiques, de fondatrices apparemment solitaires (F) et de leur descendance femelle de première génération (B) ; *Dialictus zephyrus*, dans Tompkins County, N.Y., 1983 ; (* = paternité multiple ou > 1 fondatrice ; ** = > 1 fondatrice) ; les mobilités relatives et les désignations des allèles se trouvent sous le nom du locus.

		Locus							
Colony	Female	PEP-LA-2 100 (1) 84 (2)	MDH-2 — 27 (3) —100 (1) —146 (2)	ADH —100 (1) —132 (2)	IDH 100 (1) 89 (2)	GDA 100 (1) 87 (2) 69 (3)	LDH 100 (1) 67 (2)	HBDH 100 (1) 61 (2) 24 (3)	PGM 100 (1) 93 (2)
1	F	1/2	1/1*	1/2*	—	—	1/1	1/1	—
	B	1/2	1/1	2/2	—	—	1/1	1/1	—
	B	1/2	1/3	1/2	—	—	1/1	1/1	—
	B	1/2	1/1	1/1	—	—	1/1	—	—
2	F	2/2*	1/1	1/2	1/1	—	1/1	1/3	1/1
	B	2/2	1/1	2/2	—	—	1/1	1/1	1/1
	B	1/2	1/1	2/2	—	—	1/1	1/1	1/1
3	F	1/2	1/2	—	—	1/1	—	1/1	1/1
	B	2/2	2/2	—	—	1/1	—	1/1	1/1
	B	2/2	2/2	—	—	1/1	—	1/1	1/1
	B	2/2	2/2	—	—	1/1	—	1/1	1/1
	B	1/2	2/2	—	—	1/1	—	1/1	1/1
4	F	1/1	1/1	—	—	1/1	—	1/1	1/1
	B	1/2	1/1	—	—	1/1	—	1/1	1/1
	B	1/2	1/1	—	—	1/1	—	1/1	1/1
	B	1/2	1/1	—	—	1/1	—	1/1	1/1
	B	1/2	1/1	—	—	1/1	—	1/1	1/1
5	F	2/2	1/1	—	—	1/1	—	2/3	1/1
	B	2/2	1/1	—	—	1/1	—	—	1/1
	B	2/2	1/1	—	—	1/1	—	1/3	1/1
	B	2/2	1/1	—	—	1/1	—	1/3	1/1
6	F	1/2	—	2/2*	—	1/1	—	1/1*	1/1
	B	2/2	—	2/2	—	1/1	—	1/1	1/1
	B	1/2	—	2/2	—	1/1	—	1/1	1/1
	B	2/2	—	1/2	—	1/1	—	1/2	1/1
7	F	2/2	—	1/2	—	—	—	1/2*	1/1
	B	2/2	—	1/2	—	—	—	1/2	1/1
	B	2/2	—	2/2	—	—	—	1/3	1/1
	B	2/2	—	1/2	—	—	—	1/2	1/1
8	F	1/2	1/1	2/2	1/2	—	1/1*	1/1*	1/1
	B	1/2	1/1	1/2	1/2	—	1/2	1/1	1/1
	B	1/2	1/1	1/2	1/2	—	1/1	1/3	1/1
	B	2/2	1/1	1/2	1/1	—	1/2	1/1	1/1
	B	1/2	1/1	1/2	1/2	—	1/2	1/1	1/1
9	F	1/2	—	1/2	1/1	—	—	2/2	1/1
	B	1/2	—	2/2	1/1	—	—	1/2	1/1
	B	2/2	—	2/2	1/1	—	—	1/2	—
	B	2/2	—	1/2	1/1	—	—	1/2	1/1
	B	1/2	—	2/2	1/1	—	—	1/2	1/1
10	F	1/1**	—	1/2*	—	1/1	—	1/1*	1/1
	B	2/2	—	2/2	—	1/1	—	1/2	1/1
	B	1/2	—	1/1	—	1/1	—	1/2	1/1
	B	1/1	—	2/2	—	1/1	—	1/1	1/1
	B	1/1	—	1/2	—	1/1	—	1/1	1/1
	B	1/1	—	2/2	—	1/1	—	1/1	1/1

These results show the presence of two laying females in at least 13 % of apparently singly founded *D. zephyrus* colonies. This could be the result of nest takeover or cryptic multic multiple foundresses. Nest usurpation occurs in primitively eusocial wasps of the genus *Polistes* (KLAHN and GAMBOA, 1983 ; GAMBOA, 1978 ; MAKINO, 1985 ; STRASSMAN, 1981) and, on 7 occasions during this study, one of us (PFK) observed a returning pollen-laden forager grappling with another bee that had apparently entered her nest in her absence. Thse contests lasted from a few seconds to up to 20 minutes and ended with the returning forager (presumed foundress) pulling her adversary out of the nest entrance (n = 5) or departing after a considerable struggle (n = 2). This suggests that nest usurpation is not a rare occurrence in *D. zephyrus*. In addition, since many single foundresses die before the maturation of the first generation of brood (KUKUK, in prep) it is possible that colonies could be taken over by a second foundress after the death of the first.

The possibility also exists that these nests were established by cryptic multiple foundresses. This possibility seems unlikely since in multiply founded colonies the female remaining in the nest guards the entrance while the other female(s) forage. Guard bees are easily visible at the nest entrance and none of the colonies included in this study had females guarding the colony entrances when a pollen laden female returned to the nest.

The additional 23 % of the colonies in which the genotypes of the daughters indicate that they cannot be the progeny of one, singly mated female could be interpreted as instances of multiple maternity but may, alternatively, be cases of multiple paternity. In *Formica sanguinea* multiple mating and multiple maternity have been reported, also based on genotype frequencies (PAMILO and VARVIO-AHO, 1979). Unfortunately the technique used to estimate more precisely the number of females and the number of times they mated in *F. sanguinea* was not applicable to the data on *D. zephyrus* due to the small colony size.

However these data do indicate that, for *D. zephyrus*, first generation brood in nests apparently founded by a single female is not the of the progeny of one, singly mated female. The percentage reported here, 36 %, is an underestimate of the phenomenon since it reports only the instances of this occurrence that are detectable using the electrophoretic techniques described.

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