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Short communication

Behavioural data on the production of males by workers in the stingless bee *Melipona favosa* (Apidae, Meliponinae)

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Summary. Male production was studied in four queenright *M. favosa* colonies by permanent and long duration observation of egg-laying and subsequent bee emergence. Workers produced males in all colonies; they produced 94.5% of all males.

Key words: *Melipona*, laying workers, male production, sexuals.

Introduction

The relative role played by the laying-workers and the queen in the production of males in the eusocial stingless bees is of theoretical significance for our understanding of the social evolution of the Hymenoptera. The impact of worker reproduction in *Apis* was recently studied by Moritz et al. (1998). In the stingless bees, the laying workers occur widely among the various groups. The behaviour of *Melipona* males has been studied by Van Veen et al. (1997). In most of the species in which the queen frequently eats worker eggs, these eggs differ from reproductive worker eggs. Such distinctly larger and “specialised” trophic worker eggs typically occur in the group of the Trigonini, in which workers are also able to lay reproductive eggs. In *Scaptotrigona postica* the reproductive worker eggs are released after the queen has oviposited in the cell and in that species workers are important producers of males (Beig, 1972; Bego et al., 1983).

We established that *Melipona* workers also lay different types of eggs. In orphan colonies workers can lay eggs that give rise to males (Sommeijer and Velthuis, 1977) and we confirmed that in queenright colonies it is common for workers to lay trophic eggs. At microscopic level these worker eggs are distinct from the worker eggs that are sometimes released in colonies that have been queenless for some time (Sommeijer et al., 1984a). Reproductive worker eggs can also be released in queenright *Melipona* colonies (Van Buren

and Sommeijer, 1988; Sommeijer and Van Buren, 1992). The external morphological differences between trophic worker eggs and reproductive worker eggs are gradual and not discrete (Sommeijer, 1984). Bego also reported the occurrence of various forms of worker eggs in *S. postica*.

Our earlier hypothesis that in *Melipona*, males are produced by workers and that this is influenced by seasonal factors (Sommeijer et al., 1984), was based on our observation of these gradual differences between worker egg types as well as on our assumption that the queen controls oogenesis and even oviposition by workers. This hypothesis implied that seasonal growth of colonies would cause fluctuations in the efficiency of this control, and thereby in the production of males. Queen control was assumed to be lower in larger colonies.

In this paper we present the data of a detailed and long-term behavioural study of ovipositions by queens and by workers which resulted in the emergence of males.

Methods

We housed four colonies of *M. favosa*, originating from Trinidad and Tobago (W.I.) in our lab so that we could use video to observe continuously and simultaneously ovipositions and complete comb development from April to July 1997 (Sommeijer et al., 1984b). All ovipositions were recorded and analysed in order to identify whether it was a queen or a worker that finally oviposited in the cell. The development in each cell was followed until emergence to relate the sex of the individual bees to their paternity.

Results

The oviposition in and the emergence of 1778 cells were recorded; of these 604 (34%) were male. By identifying the sex of the emerging bees we were able to confirm that both the queen and the laying workers had laid eggs that developed into males.

Reproductive laying workers produce males regularly and in large numbers

All four nests contained reproductive laying workers. Of all the cells, 571 (32.1%) were oviposited by reproductive laying workers. Males emerged from all the eggs laid by reproductive workers. The laying workers produced 94.5% of all males.

The queen produces only a minor part of the total number of males

It is clear that the queens participated regularly in the laying of haploid eggs. It was also evident however that they were not the major producers of males. We also established that the queens released haploid male eggs while continuing to release diploid eggs. During this observation series 2.7% of the total number of 1207 eggs released by the queens developed into males. The queens oviposited only 5.5% of the total number of 604 observed cells from which males emerged.

Discussion

The results show clearly that most of the males (94.5%) were produced by workers. Our observations in colonies in the natural environment (Sommeijer et al., in prep.) have confirmed that workers are the most important producers of males. On the basis of our earlier studies of laying worker behaviour and from our data on differences between the types of worker eggs in this and in other *Melipona* species, we hypothesise that workers are the major producers of males in all species of *Melipona*. However, the queen also plays a role in the production of males. After the queen has produced some male offspring for some time, she reverts to produce female offspring.

There are three factors that can explain why this important reproductive role of workers in *Melipona* has not been reported earlier: (1) In most species it is fairly difficult to distinguish between males and workers with the naked eye (Sommeijer and Van Buren, 1994); so the presence of males in the nest is not obvious. (2) Reproductive laying workers do not produce males continuously (Sommeijer et al. in prep.). (3) No long-term behavioural studies have been carried out on the oviposition behaviour and the subsequent emergence of castes and sexuals and this has certainly not been studied simultaneously in a number of colonies. Studies using genetic techniques can obviously also shed light on this matter.

Our observations confirmed that the behaviour of laying workers that release trophic eggs differs markedly from that of workers that release reproductive eggs. A detailed description of these different forms of worker oviposition behaviour is presented in Sommeijer and Van Buren (1994). Trophic worker eggs were also laid commonly during the present observations but they were all eaten by the queen, prior to queen oviposition.

The occurrence of reproductive laying workers in queenright colonies has been reported earlier (Sommeijer and Van Buren, 1994), but we now have proof of the regular occurrence and of the substantial quantitative importance of this phenomenon of stingless bee sociality.

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