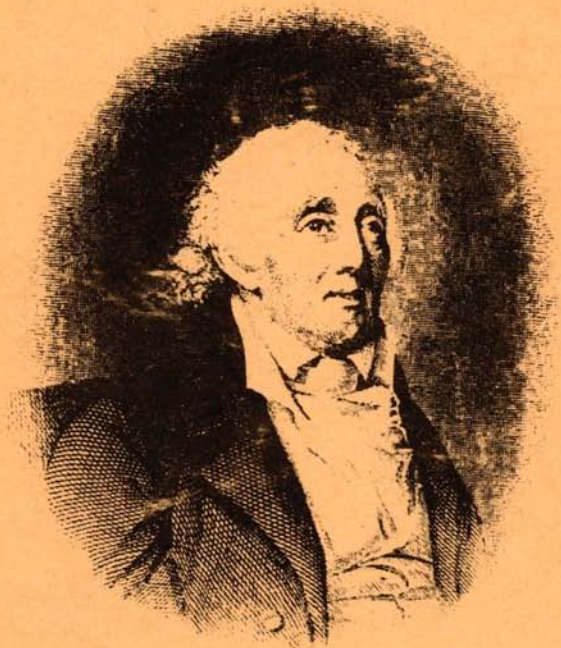


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THE INTRANIDAL ACTIVITY OF MALES OF MELIPONA WITH SOME REMARKS ABOUT MALE PRODUCTION IN STINGLESS BEES

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SUMMARY

The intranidal behaviour of males of stingless bees was studied in *Melipona favosa* and *M. rufiventris*. Males were produced both by laying workers and by unmated queens. Various observational methods were used to study the behaviour of the males in the nest. The males clearly demonstrated a very restricted behavioural pattern. We investigated experimentally the uptake of food by males. Males in absence of workers are able to take up food directly from the storage pots. In the presence of workers however, males feed themselves mainly through trophallaxis with workers.

Key words: stingless bees, *Melipona*, reproduction, male production, male behaviour.

RESUME

Comportement des mâles dans des colonies de *Melipona* avec quelques remarques sur la production de mâles chez les abeilles sans dard.

Il est très important de savoir comment sont produits les mâles du fait de leurs relations de parenté en haplo-diploïdie. Les mâles sont nés d'ovules non fécondés; ceux-ci peuvent en principe être pondus par la reine et par les ouvrières. Nous avons trouvé que les ouvrières du genre *Melipona* pouvaient pondre deux types d'ovules qui devenaient soit des oeufs trophiques, soit des oeufs reproducteurs. Chez les ouvrières qui pondent des oeufs trophiques en présence de la reine, il apparaît une recrudescence de cellules folliculaires. Les différences survenant dans ces aberrations des ovules d'ouvrières sont graduelles. En outre, les ouvrières peuvent aussi produire des oeufs reproducteurs en présence de reine. Ceci indique la possibilité d'une production saisonnière de mâles par les ouvrières pondeuses.

Il est possible d'amener aussi bien les ouvrières pondeuses que les jeunes reines non fécondées à produire des mâles. Nous pouvons admettre pour le moment que la reine, comme les ouvrières, peuvent y participer. Mais nous ne pouvons, jusqu' à présent, évaluer l'importance de la part prise par les ouvrières à la production des mâles dans les colonies naturelles.

L'étude directe du répertoire comportemental des mâles dans les colonies de *M. favosa* et de *M. rufiventris* nous montre qu' il est fort limité. Les mâles de *rufiventris* et de *favosa* ne présentent pas de différences quant à leur comportement. Le comportement des mâles a été étudié de deux autres manières en utilisant le SCAN SAMPLING et le LOCATION SAMPLING. On n'a pas observé une seule fois la participation d'un mâle à l'un des comportements d'ouvrière.

Pour répondre à la question concernant la capacité des mâles à prendre de la nourriture par eux-mêmes dans des pots, on a placé des petits groupes de mâles de *rufiventris* dans des petites ruches en les faisant jeûner pendant 24 heures en l'absence et en présence d'ouvrières. Les mâles savent se nourrir par eux-mêmes. Cependant, dans la plupart des cas, ils sont nourris par les ouvrières comme c'est le cas chez les abeilles domestiques.

Mots clés: abeilles sans dard, *Melipona*, production de mâles, comportement des mâles.

INTRODUCTION

The importance of laying workers for the production of males in stingless bees (Apidae, Meliponinae) has been indicated, especially for *Scaptotrigona postica*, in various Brazilian publications (e.g. Bego, 1982; Beig, 1972, reviewed by Sakagami in 1982). In our study of egg production by laying workers in *Melipona* (Sommeijer et al. 1984-b), we found that laying workers are able to produce two types of eggs: 1. In colonies with a laying queen, workers were found to be laying trophic eggs. 2. Workers in colonies without a queen, released reproductive eggs. Studying the differentiation of oocytes in *Melipona* workers, Koedam (Koedam et al. 1987) found that laying workers in queenright condition demonstrate two major differences in ovariole activation in comparison with workers in queenless condition: 1. lower number of follicle cells forming the micropyle, resulting in a very small or absent micropyle. 2. No deposit of exochorion-2 material, resulting in a complete or partial absence of polygonal network pattern on the egg surface.

For the hypothesized seasonal production of males by workers (cf. Sommeijer et al., 1984-a) it is first very important that these morphological aberrations in worker eggs are gradual and second that reproductive worker eggs also can be laid by workers in queenright condition (Van Buren et al., 1987).

Little is known about the behaviour of males of stingless bees within the nest. In some papers it is mentioned that these males are able to carry out duties that are, in social bees, normally performed by workers (Kerr et al. 1962; Sakagami, 1982). This appears in sharp contrast to the restricted intranidal behavioural repertoire of males of *Apis mellifera*. The behaviour of males of the Brazilian species *S. postica* outside of the nest, especially in relation to mating, has been studied by Engels and Engels (1984 and 1988). The major objective of our present study was to investigate some aspects of the intranidal behaviour of males of *Melipona*.

MATERIAL AND METHODS

For this study we used colonies of *M. favosa* and *M. rufiventris*. The colonies were kept at 28 degrees Celsius and fed with syrup and pollen according to Camargo 1976 and Sommeijer et al. 1984. The recordings of the behaviour of the males and the workers were made through direct observation under red light. In addition to "focal animal" methods we used "scan sampling" and "location sampling" (Lehner, 1979). Males of a *M. rufiventris* colony were

used to investigate experimentally the differential uptake of food by males from a feeder and trophallactically from workers. Queenright colonies of M. favosa were used to establish colonies without queens and colonies with unmated queens, in order to investigate the production of males by workers and queens. The intranidal behaviour of the various groups of males was analyzed ethologically.

RESULTS

It was confirmed that both laying workers as well as young uninseminated queens are able to produce males. The development of males of M. favosa, both for sons of workers and sons of queens is 44 days. The detailed description of the behaviour of males within the nest resulted in an ethogram with behavioural elements grouped under the following terms: locomotion, resting, grooming, antennal contact, trophallaxis, dehydrating, waste-dump acts, "hiding".

The intranidal behavioural repertoire is obviously very limited in comparison with that of workers. Typical "worker activities" were not performed by males. The repertoire was similar for males of M. favosa and M. rufiventris as well as for sons of queens and sons of workers. However, certain individual differences were found between a number of individually marked males. Evidently these differences were based on the age differences of the individuals: there was especially a significant negative correlation between the rate of "resting" and the age of the male (Spearman Rank, $\rho = -0.831$; $p < 0.05$).

The behaviour of males was recorded in two other ways in a colony of M. rufiventris to investigate further the possible participation of males in "worker activities". SCAN SAMPLING: ten individually marked males were studied in one nest and all males were scanned every five minutes for the behaviour they performed. LOCATION SAMPLING: 50 males (25 "young" males from the comb, 25 "old" males from the exterior part of the nest) were marked individually. Subsequently, the behaviour executed at specific locations, where workers perform typical worker activities, was recorded. The following locations were taken: - the young comb where broodcells are under construction, - the area where workers deposit wax secreted in their dorsal wax glands on the substrate, - the storage compartment where workers dehydrate the food that is brought into the nest and where food storage pots are constructed, - the waste dumps where workers intensively manipulate waste material transforming this into pellets that are being brought to the exterior.

Each of these locations was twice without interruption observed for a period of 30 minutes, searching especially for males participating in the observed behaviors at this location. The result of these studies was that not a single time the participation of a male could be recorded in one of the frequently recorded worker acts.

FOOD UPTAKE BY MALES

The question if and how males are able to take up food directly from the storage pots, was investigated in an experiment with males of M. rufiventris. Six groups, of five males each, were placed in small cages and treated as follows. During the first period of 48 hours, five workers were introduced

together with the five males in all cages. In this period there was plenty of food in the feeders of all six cages. The next step was that the workers were removed from three of the six cages. At the same time the feeders were removed from two cages with workers and from two cages without workers. This phase of the experiment had a duration of 24 hours. After this period, the feeders were re-introduced and immediately, during the first period of 30 minutes, the behaviour of the males was recorded precisely concerning: a. the uptake of food from the feeder, b. the uptake of food through trophallaxis. This experiment was repeated once.

The results are illustrated in fig. 1. From the total number of 60 food uptakes in cages with workers, 39 were taken from a worker, two from a male, and 19 directly from the feeder. In the cages without workers there were in total 57 food uptakes; 14 from a male, and 43 directly from the feeder.

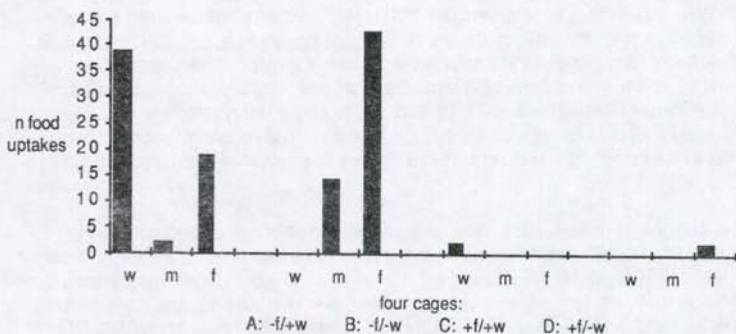


Fig. 1. Food uptakes by males from: workers (w), males (m) and directly from feeder (f) in the four cages.

Fig. 1. Prises de nourriture par des mâles à partir: d'ouvrières (w), de mâles (m) et directement à partir d'un nourrisseur (f) dans les quatre cages (A: -f/+w, B: -f/-w, C: +f/+w, D: +f/-w).

DISCUSSION

It is clear from the last results that *Melipona* males in absence from workers are capable to feed themselves in the nest directly with stored food. However also in presence of workers males did take up food from the feeder. The production of males by workers could be confirmed for a condition where the queen is not present. It is clear from these results that males hardly participate in the many diverse activities in the nest. In undisturbed colonies of *Melipona* it is difficult to discriminate well between males and workers because of minor morphological differences. It is necessary to study this aspect of stingless bee behaviour in more detail, and it is strictly necessary that males are properly marked for this.

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