

THE ADAPTIVE SIGNIFICANCE OF THE RHYTHMIC OVIPOSITION
PROCESS OF STINGLESS BEES

(LA SIGNIFICATION ADAPTATIVE DE LA RYTHMIQUE DU PROCESSUS
DE PONTE CHEZ LES ABEILLES SANS DARD)

M.J. SOMMEIJER

Laboratory of Comparative Physiology

State University of Utrecht

Jan van Galenstraat 40

3572 LA UTRECHT

THE NETHERLANDS

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Résumé

La rythmique du comportement ovipositionnel typique des abeilles sans dard est interprétée comme un trait de comportement adaptatif par rapport au "fitness" de la reine. La reine montre une domination reproductive malgré l'occurrence des ouvrières pondeuses en sa présence. Cette domination est effectuée en principe à travers le contrôle du comportement au moment où les ouvrières ovipositionnent. La chaîne de comportement intégré d'approvisionnement de la cellule et d'oviposition ne peut débiter que lorsque la reine est présente près de la cellule. Il est supposé que le groupement des ovipositions dans le temps, particulièrement dans les espèces avec de nombreuses ovipositions journalières, a évolué pour contribuer au maintien de la domination de la reine.

SUMMARY

The rhythmicity of the typical oviposition behavior of stingless bees is interpreted as an adaptive behavioral trait in relation to the fitness of the queen. The queen demonstrates reproductive dominance despite of the occurrence of laying workers in her presence. This dominance is in principle effectuated through behavioral control over the moment at which workers oviposit. The integrated behavioral sequence of cell provisioning and oviposition can only be started when the queen is present at the cell. It is suggested that the batching of ovipositions in the time, in species with numerous daily ovipositions, has evolved to contribute to the maintenance of queen dominance.

In this contribution we wish to relate our results on division of labor and the communicative significance of queen-worker coactions to other available data about stingless bees. It should be considered as an attempt to interpret both the causal and the ultimate function of typical aspects of this social organization.

The basical data are published elsewhere and are also for a major part contained in the work of Sh. SAKAGAMI. Other references of importance in this respect are : MICHENER (1974); ZUCCHI (1977); KERR (1969); IMPERATRIZ-FONSECA (1976); DARCHEN (1977); VELTHUIS (1976).

I. THE SOCIAL ORGANIZATION OF STINGLESS BEES

The species contained in the tribe of the stingless bees vary considerably in size as well in the architecture of the nest and their housing requirements (SAKAGAMI, 1982). Despite this vari-

ability within the group, the intra-nidal reproductive behavior pattern of all species is characterized by a striking similarity. This pertains specifically to the regulation of the activity of queen and workers, in which the social organization of stingless bee colonies is distinct from that of the honeybee (*Apis mellifera*). Major differences relate to the following behavioral systems:

a. Mass provisioning

The larvae are not fed progressively as in honeybees, but instead by a mechanism of mass provisioning. All larval food is deposited into the cell at once and there is no direct contact between developing larvae and nurse bees. The cells for the rearing of young bees are used only once and remains of brood-cells are removed as soon as bees have emerged from these. So, new combs are to be built continuously for the production of new brood.

b. Rhythmicity of oviposition behavior

The typical temporal pattern of the behavior related to the provisioning of new brood cells by the workers and the oviposition by the queen, which takes place immediately following the food discharges by the workers, has been described in detail for several species by SAKAGAMI and co-workers. Cells to be used for brood rearing are being constructed during the "extra-oviposition period". In the succeeding "oviposition period" the provisioning, the oviposition, and the cell operculation form an obligatorily linked behavioral sequence. This latter sequence has been denominated the "Provisioning and Oviposition Process, POP". The temporal occurrence of this behavior is in-

deed quite remarkable. It appears that in all species so far described, the POP activities are effectuated in a relative short time. This concentration of provisioning and oviposition activity within this short time is facilitated by the synchronously raised activity of a certain group of workers and the queen. Their "cooperation" in this behavioral sequence consists of specific queen-worker co-actions and mutual worker interactions. The execution of POP behavior is generally characterized by its "excited" nature. So, it is from this typical nature of the behavioral POP sequences, that the unique basic cyclic pattern results: great activity during POP sequences, alternated with less excited behavior in the much longer extra-oviposition periods.

Even in species with a daily production of numerous broodcells, this rhythmicity is generally just as pronounced. In such cases new cells are not provisioned and oviposited one by one, as in species with relative low productivity (e.g. *Melipona* spp.). Instead, in these highly productive species, this rhythmicity is maintained through the more or less simultaneous construction of a number of broodcells (a "batch", cf. SAKAGAMI and ZUCCHI, 1974). When all cells of such a batch are ready built, they are together, in a very short moment, provisioned and oviposited. After the termination of such an "integrated oviposition process" (IOP), again the typical extra-oviposition period occurs, until the next "IOP" can take place.

c. Laying workers

The third peculiarity of the social organization of stingless bees to be dealt with involves the egg laying of workers in the

presence of the queen. This is a very common feature in queen-right colonies. However, it is not as obvious in all species studied so far. From very few species it is known that workers only develop their ovaries when orphaned. TERADA (1974) reported that workers of *Frieseomelitta varia* never developed their ovaries (SAKAGAMI, 1982). Oviposition by workers occurs at two different moments of regular POP sequences:

1. Prior to the oviposition of the queen. This is followed by oophagy by the queen before she lays. In certain species an anucleate type of trophic worker egg has evolved in this respect.
2. Immediately following the oviposition of the queen. Before operculating a worker may deposit an egg into the cell, next to the queens' egg, just prior to the moment of operculation. Haploid eggs laid in such manner give rise to male larvae, which after hatching feed upon the diploid egg. As a result, a male will emerge from such a cell.

II. COMMUNICATION BETWEEN WORKERS AND QUEEN

a. Communication away from the comb

In our study of the behavior of individual workers of *M. favosa* we concluded that certain ritualized worker-queen co-actions in the royal court around the queen at her resting place can be interpreted as evolved communicative "bee-dances" (SOMMEIJER, 1982b; SOMMEIJER and DE BRUIJN, in prep.). Through this court activity, specifically performed by the building and provisioning workers, the queen departs from her resting place and moves toward the edge of the new comb. As a result the new oviposition period may be started when she arrives at the ready cell.

b. Communication on the comb

From our observations we may conclude that the queen on her way to the respective cell is further guided by other specific worker behavior. This form of worker behavior ("prefixation excitement", SAKAGAMI et al., 1965) is performed by the workers that are concentrated around the cell before the queen arrives. Their behavior consists mainly of a rapid alternation of body insertions into the cell. The communicative function of this behavior is to indicate which cell is to be serviced. The same communicative function has already been attributed to this behavior by Kerr (1969). Our interpretation is based on the fact that this typical worker behavior at the structurally ready cell is always performed prior to the arrival of the queen on the comb. Secondly, we observed that queens of *M. favosa* and *M. scutellaris trinitatis*, upon arrival on the comb, only fixated to cells that were subjected to prefixation excitement by workers. The same has been found for *M. quadrifasciata anthidioides* (SAKAGAMI et al., 1965).

We became more convinced of the important communicative significance of these behavioral elements during prefixation excitement, after we studied the oviposition behavior in *Tetragona nigra* var. *paupera* (SOMMEIJER and HOUTEKAMER, in prep.). This species is a cluster builder (cf. MICHENER, 1974) and brood-cells are built semisynchronously and are exclusively oviposited in batches (type SmBe, cf. SAKAGAMI and ZUCCHI, 1974). The queen arrives here also at the advancing front after the prefixation excitement has begun. The queen fixates to one cell. After the filling of this first cell has been started, the pro-

visioning of the other cells of the batch follow more or less immediately. After ovipositing in the first cell the queen, in an exaggerated manner, goes from cell to cell to oviposit. Very remarkably, as soon as the cells are filled by a very small number of dischargers, the workers proceed to carry out again the typical rapidly alternating body insertions; now in the cell that is provisioned. To these body insertions and to the excited worker behavior in this stage we would attribute precisely the same communicative function as to this behavior in the prefixation stage; it directs the queen to these cells that are now already filled. Such signalling is most important at this stage, because of the irregular position of the cells of the batch in the advancing front of this species; also because of the fact that not all cells are filled at the same time. The queen has to search in the advancing front for the cells ready to be oviposited. In order to find them she has to cruise several times through this area.

III. THE ULTIMATE FUNCTION OF THE TYPICAL RHYTHMICITY OF THE OVIPOSITION PROCESS AND CERTAIN RELATED COMMUNICATIVE WORKER ACTIVITIES.

We suggest that the typical rhythmicity of the oviposition behavior in stingless bees should be interpreted as an adaptive behavioral trait in relation to the fitness of the queen. This consideration will be explained as follows.

a. Reproductive dominance by means of oophagy

For all species described (except for *Meliponula bocandei*, SAKAGAMI et al., 1977) it has been reported that the provisioning of the broodcells under queenright conditions can only

take place after the arrival of the queen at the ready cell. Her arrival at the cell is usually followed by specific queen-worker interactions at this cell (e.g. tappings by the queen on bodies of inserting workers). The very fact that only after these interactions and/or after the "cell-inspection" by the queen the actual discharging can take place assures the control of the queen over worker ovipositions. Queen oophagy immediately after worker oviposition, exemplified by many *Melipona* spp. indicates how this control basically is effectuated.

b. The evolution of batched ovipositions

It is of great importance to note that the colonies of *Melipona* spp. where cells are successively built and predominantly singularly oviposited (cf. SAKAGAMI and ZUCCHI, 1974), are composed of relative small numbers of bees. In the species with more populous colonies and consequently higher oviposition rates the ovipositions are always grouped in time by the formation of batches. In my opinion, this batched type of oviposition implies drastic advantages to the queen in relation to her control over worker ovipositions, compared to a situation where a similar large number of cells would have to be serviced singularly. The very fact that those workers who construct and subsequently provision the brood cells are those with developed ovaries, implies a severe menace to the queen (SOMMEIJER et al, 1982). The only way of exercising a firm control over the reproductive activity of these workers is to present a rigid regulatory effect on some stage of the behavioral cycle of cell building, provisioning, laying, operculation. It is our opinion that the start of cell provisioning has evolved to be a regula-

tory target in this respect.

However, if large numbers of cells are being built successively, and if these have to be serviced singularly as in e.g. *Melipona favosa*, this control mechanism will not suffice anymore; or at least it will prove very inefficient.

The following observations have been important for the further development of our view. Very often we noticed that it took a relative long time before the queen came upon the comb after pre-fixation excitement had started. In most cases of such prolonged absence of the queen, the workers continued the body insertions for some time, but finally stopped this activity if the queen did not appear. In a recently arrived colony of *Melipona scutellaris trinitatis* we observed once that after prolonged absence of the queen during pre-fixation excitement, the workers did finally start the provisioning before she was on the comb. The provisioning was performed normally and subsequently a worker oviposited. The same worker also started immediately the operculation. However, the queen did arrive at the comb just prior to the final closure of the cell. Most interesting was the fact that she herself then opened the cell with her mandibles. Subsequently, she ate the workers' egg and mounted the cell for her own oviposition. Her oviposition, however, failed, she dismounted to turn around the cell. In the meantime another worker mounted the cell and oviposited. The worker succeeded in the complete operculation of the cell. This time the queen demonstrated much less interference with the operculating bee than the first time. These observations support our view that queen control over worker ovipositions is

based on a delicate communication and dominance system. This system must be less reliable when ovipositions follow each other at high frequency. The problems then involved for the queen can clearly be appreciated when the broodnest of a strong thriving colony of *M. scutellaris trinitatis* is observed. In such a colony a large number of cells under construction may be found on the edges of different combs.

I assume that the evolution of batched ovipositions in species with populous colonies promotes the control by the queen. The convenient positional arrangement of the cells as well as the servicing concentrated in the time, enhance the surveyability and control over occurring worker ovipositions for the queen. From the sociobiological point of view it is conceivable, or even imperative, that the workers have, however, tried to escape again this way of control. Indeed we may observe in certain species the probably secondarily evolved specific trophic worker eggs, next to fertile worker eggs who are now laid just after the queen has oviposited.

IV. A SUGGESTION CONCERNING THE REGULATION OF MALE PRODUCTION

In addition, as a mere hypothesis resulting from the above considerations, an interesting assumption can be made concerning the regulation of the production of males. Very little is known about this matter. BEIG (1972) was the first who found that in *Scaptotrigona postica* workers may play an important role in male production. Further observations on male production in this species were made by BEGO (1982). We have observed that queenless colonies of various *Melipona* spp. can produce large numbers of males (see also: SOMMEIJER et al., 1976). The limi-

tations of the suggested behavioral queen control over worker ovipositions described above, may in fact represent the regulatory mechanism itself. The control by the queen is weakened specifically at increasing oviposition rates in strongly expanding colonies. The then partly uncontrolled worker ovipositions may now result in the production of males. This proposed mechanism could at least be true for *Melipona* spp., whereas to date only one type of worker egg is known to be laid. Further research will be necessary to verify these assumptions.

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