

Research article

Does the queen of *Plebeia remota* (Hymenoptera, Apidae, Meliponini) stimulate her workers to start brood cell construction after winter?

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Summary. In stingless bees the Provisioning and Oviposition Process (POP) is quite complicated, involving several interactions between queen and workers. *Plebeia remota* nests typically stop cell construction and oviposition in fall and winter. However, little is known about the phenomenon. In order to investigate the role of queen and workers in the starting of cell construction after this interruption of activity, 9 pairs of *P. remota* colonies were used. Queens of active colonies were placed into inactive colonies and vice versa. The results showed that workers control brood cell construction in this colony phase. The queen seems to have little or no influence on this decision.

Key words: Brood cell construction, winter inactivity, *Plebeia remota*, stingless bees.

Introduction

Stingless bees have mass brood cell provisioning. Workers build cells and provision them with larval food, the queen oviposits, and workers seal the cells immediately after (Sakagami, 1982). This process was called the Provisioning and Oviposition Process (POP), being studied for many Meliponini species (for a review see Zucchi et al., 1999). During the POP, several complex interactions occur between both queen and workers (Zucchi, 1993; 1994). It has been suggested that ritualised dominance signals by the queen are important in transmitting information, and the participation of workers on the court of the queen was correlated to their activity in cell construction (Sommeijer and de Bruijn, 1984; Sommeijer et al., 1984; Sommeijer, 1985). However, Zucchi (1993) proposes that these signals are not mediators of information, nor responsible for the POP sequence. Instead, they evidence queen dominance.

In most species of *Plebeia* queen dominance is quite aggressive and complex (Zucchi, 1993). Particularly in *P.*

remota (Holmberg), the POP has been previously studied (van Benthem et al., 1995; Drumond et al., 1996; Drumond et al., 2000). Workers involved in cell construction are quite indifferent to the queen (van Benthem et al., 1995).

Brood cell construction and oviposition are continuous all year round in tropical stingless bee nests. However, in subtropical regions these activities cease during fall and winter. This typically occurs in some species of *Plebeia*, including *P. remota* (Imperatriz-Fonseca and Kleinert, 1992; van Benthem et al., 1995). The causes of this phenomenon seem to be related to a decrease of temperature, though details of the mechanism are lacking in the literature.

The aim of this work was to study the role of queen and workers at the moment of starting cell construction after the inactive period.

Material and methods

Colonies of *P. remota* ($n = 18$) kept in wooden boxes at the Bee Laboratory in São Paulo were used in pairs. Half of the colonies were active concerning cell construction and oviposition, the other half inactive. These pairs of colonies were chosen in order to match colony conditions (measured by the amount of stored food and approximate number of bees), and queens' age (measured by the degree of wing damage). These values were not precisely quantified, but qualitatively and subjectively estimated, in such a way that the colonies of each pair were similar in these aspects.

The queens were weighed and marked individually. Then those from inactive colonies were introduced to colonies where there was normal cell construction. Simultaneously, queens from active colonies were put into colonies with no cell construction. Although queen exchange is often successful in other species, we did not know whether the introduced queen of *P. remota* would be immediately accepted by the workers in the alien colony. Therefore, we placed her in a small cage containing a piece of porous material with diluted honey. After 4 h in the cage, the queen was released.

The cell construction of all colonies was monitored three or four times a day, with a digital camera (Sony) or through drawings of the comb. The exact number of cells built and oviposited by the queen was not relevant for this experiment, and therefore it was not counted pre-

cisely. The experiment finished after 6–7 days. The queens were weighed once more and put back into their own colonies.

The treatment groups were small, and for this reason a Binomial test was applied instead of the Chi-square test (Zar, 1999). The hypotheses were: H_0 : $p \leq 0.5$ and H_A : $p > 0.5$. In this way, H_0 predicted there would be equal chances of active colonies remaining active or becoming inactive, whereas H_A predicted unequal chances of active colonies remaining active or becoming inactive. The same analysis was carried out for colonies that were inactive, in terms of whether they remained inactive or became active.

Results and discussion

The majority of the colonies (16 colonies = 89%) remained in the same conditions as before queen introduction (Table 1). Most queens from inactive colonies started laying eggs when placed in active colonies. Contrarily, almost all queens from active colonies stopped oviposition in inactive colonies. The Binomial test with $P(X)$ calculations, rejected H_0 in both cases [$P(X \geq 8) = 0.99803$; and $P(X \geq 1) = 0.01953$]. Therefore, expectations of colonies remaining in the same situation after queen introduction were significantly different from those for the distribution of active and inactive conditions.

This means that the queen does not stimulate cell construction, at least in this colony phase. Without available cells (i.e., cells ready to be oviposited) she is obviously unable to lay eggs. The workers seem to retain overall control of cell construction and decide the exact moment to restart this activity. They probably have some way of evaluating changes in climate (temperature, photoperiod) and internal conditions (food storage), thus deciding the exact moment to restart brood cell construction. For the same reasons, workers are probably also responsible for the initial interruption of cell construction.

In two cases, however, a different result was observed (Table 1). In the first colony, which was active, cell construction stopped because the introduced queen, for some unknown reason, did not start to lay eggs. In the second colony, which was inactive, the workers started to build cells soon after the queen was introduced. Maybe the latter colony was close to the moment of starting cell construction again, just before queen exchange, so it was not necessarily the introduced queen that stimulated this worker behaviour. Nevertheless, no clear answer can be provided for this.

Figure 1 shows the variation in queen mass. Queens that started to lay eggs increased in mass, while those that ceased

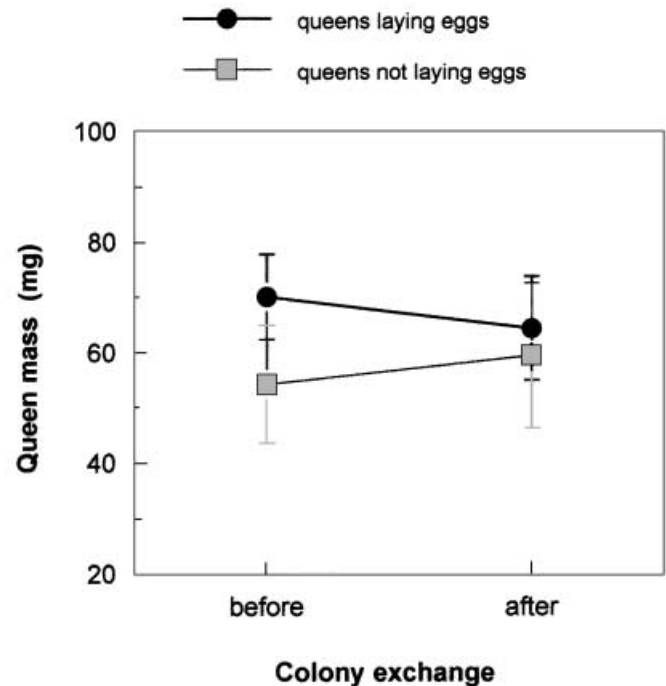


Figure 1. Mass (mg) variation for *P. remota* queens that were laying eggs or not, before and after their introduction into active or inactive colonies

laying decreased. This is certainly related to ready eggs in their ovaries. Indeed, queens reduce physogastry (and therefore, mass) during the interruption of oviposition (Ribeiro, 1998).

In the active colonies the process of cell construction by the workers was irregular while the introduced queen was caged. Even after the queen was released cells were built and frequently destroyed. However, after a few days cell construction became regular and normal. This might be caused by the inactive condition of the queens that probably take some time to recover their egg laying capability. In fact, reactivation of the queens' ovaries occurred 1 to 3 days after introduction into the active alien colony. This is quite fast, since the interruption of cell construction and oviposition may last up to 6 months (Ribeiro and Imperatriz-Fonseca, 2000). Moreover, the queen may be stimulated by the workers and/or by the presence of ready cells.

This experiment reinforces the suggestion that the queen has almost no influence on brood cell construction (van Benthen et al., 1995). The decision of starting cell construction after the inactive period is mainly taken by the workers. The queen seems not to be involved in it.

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Table 1. Number of colonies of *P. remota* that remained active, inactive or changed their situation after alien queen introduction

Before queen introduction	After queen introduction	Number of colonies
active	active	8
active	inactive	1
inactive	inactive	8
inactive	active	1

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