

# Patterns of male production in the stingless bee *Melipona favosa* (Apidae, Meliponini)

Tong X. CHINH<sup>a,b\*</sup>, Gijs B.J. GROB<sup>c</sup>, Francis J.A.J. MEEUWSEN<sup>a</sup>,  
Marinus J. SOMMEIJER<sup>a</sup>

<sup>a</sup> Department of Social Insects, Utrecht University, PO Box 80.086, 3508 TB Utrecht, The Netherlands

<sup>b</sup> National Bee Research and Development Centre, Langha, Dongda, Hanoi, Vietnam

<sup>c</sup> Nationaal Herbarium Nederland, Leiden University, PO Box 9514, 2300 RA Leiden, The Netherlands

(Received 4 April 2002; revised 3 August 2002; accepted 17 September 2002)

**Abstract** – In many stingless bee species, laying workers oviposit trophic eggs that serve as a component of the queen's diet. Workers of some species also lay reproductive worker eggs that give rise to males. Male-producing workers can occur in queenright colonies. We studied male production by workers of *Melipona favosa*. In six colonies monitored under field conditions, we observed that males emerged during distinct "Male Emerging Periods". Subsequently, we studied the laying of male eggs in laboratory observation hives with the use of video. We found that laying workers oviposited reproductive eggs in distinct "Reproductive Laying Worker Periods" and that this was followed by the clumped emergence of males afterwards. Behaviours of laying workers and of the ovipositing queen are preliminarily described.

*Melipona* / laying worker / male production / reproductive eggs / trophic eggs

## 1. INTRODUCTION

The haplo-diploid system in social Hymenoptera influences the relatedness of queens and workers to males and can contribute to conflict over male production. In the light of the kin selection theory (Hamilton, 1972), when a colony is headed by a single monandrous queen, workers are expected to favour their sons (relatedness,  $r = 0.5$ ) or other worker's sons (nephews) ( $r = 0.375$ ) above sons of the queen (brothers) ( $r = 0.25$ ) (Hamilton, 1964; Ratnieks, 1988, Peters et al., 1999). In contrast, in colonies headed by polyandrous queens, worker-queen conflict over male production may be reduced because workers are then more related to the queen's

sons than to other worker's sons (Ratnieks, 1988, Peters et al., 1999).

In colonies of the honey bee, *Apis mellifera*, which are headed by a highly polyandrous queen, males are normally produced only by the queen (Seeley, 1985; Peters et al., 1999). In queenless colonies, honeybee workers can activate their ovaries and lay unfertilised eggs. Workers in queenright colonies generally do not activate their ovaries as a result of pheromonal control by the queen (Velthuis, 1970). However, it has recently been demonstrated that queen-right *Apis mellifera* workers sometimes do lay eggs but that their contribution to male production is low because of worker policing (Barron et al., 2001; Ratnieks, 1993; Visscher, 1989).

\* Correspondence and reprints  
E-mail: T.X.Chinh@bio.uu.nl

In contrast to *Apis*, stingless bee (Meliponini) workers with active ovaries are common in queenright colonies (Sakagami, 1982). Moreover, worker oviposition in queenright colonies occurs widely among the various groups of stingless bees (Sakagami, 1982; Sommeijer and van Buren, 1992; Imperatriz-Fonseca and Kleinert, 1998; Koedam et al., 1999). However, in queenright colonies, *Melipona* workers may lay mostly trophic, not reproductive eggs (Sakagami, 1982; Sommeijer et al., 1984a). Trophic eggs are eaten by the queen prior to her oviposition, while reproductive eggs can give rise to offspring.

In some species of non-*Melipona* stingless bees, e.g., in *Scaptotrigona*, reproductive workers commonly oviposit after queen oviposition (Beig, 1972; Bego, 1982; Sakagami, 1982), which leads to cells containing both a worker egg and a queen egg. In contrast, in *Melipona*, oviposition by reproductive laying workers generally precludes oviposition by the queen in the same cell (Sommeijer et al., 1984b; Sommeijer and van Buren, 1992). Reproductive workers of *M. favosa* may also oviposit after queen oviposition, however this phenomenon is very rare.

*Melipona* trophic and reproductive worker eggs differ in their external morphology. Reproductive eggs in queenright colonies resemble reproductive worker eggs laid in queenless colonies (van Buren and Sommeijer, 1988), and have a well-developed chorion. In contrast, the chorion of trophic eggs is poorly developed. However, these differences are graded and not discrete (Sommeijer et al., 1984a). Besides a difference in trophic and reproductive egg morphology, there is a difference in the behaviour of workers that lay trophic and reproductive eggs, so the two categories of laying workers can be easily distinguished (Sommeijer and van Buren, 1992).

We have studied the production of males in *M. favosa*. In a previous paper we showed that in *M. favosa* the workers are the main producers of males (Sommeijer et al., 1999). In this paper we describe the production of males in more detail and show that it occurs periodically both under field and laboratory conditions. In the discussion we link this clumped male production to oviposition behaviour of

both the queen and the workers, and try to explain the observed patterns in light of existing theories.

## 2. MATERIALS AND METHODS

All colonies of *M. favosa* were kept in wooden box hives (W × L × H: 20.5 × 35.5 × 15 cm), which were covered by glass lids facilitating behavioural observation. The mature brood combs were partially separated from the major brood-nest by placing them in small annex boxes that were connected to the major nest box with plastic tubes. The annex served as a place where newly emerged bees could remain for about the first 24 hours after their emergence on the comb. Recently eclosed workers and males of *M. favosa* do not disperse from the comb of emergence. Upon the recording of daily-emerged adults, these were reintroduced into the main brood-nest compartment. Colony development parameters such as daily cell production, numbers of new cells and storage pots, etc., were measured weekly.

The field studies were carried out from October 1994 to February 1995 on the island of Tobago (Trinidad and Tobago, West Indies). Six queenright colonies of *Melipona favosa* that earlier had been installed in a room in a wooden building were used to study the temporal patterns of male production. These colonies had free flight to the outside in their natural habitat through plastic tubes leading through the wall. The colonies received no additional feeding. The colonies had been in this position for more than two years. The population of these colonies ranged from 129 to 204 bees, which is normal for this species.

In 1997, four queenright colonies (referred to as 7, 8, 9 and 10) of *M. favosa* were housed in the room of our laboratory at the Faculty of Biology, Utrecht University, The Netherlands. These colonies originated from Trinidad and Tobago and their populations ranged from 109 to 270 bees<sup>1</sup>. Temperature was kept constantly at 24 degrees Celsius and RH was constantly around 75%. In these lab colonies, all ovipositions were analysed to identify whether the queen or a worker oviposited in a cell. Red light and video were used to observe the ovipositions, comb development and adult emergence continuously and simultaneously from April to November. To identify the maternity of the emerged bees, the location of each oviposited cell

<sup>1</sup> The colonies studied in the Utrecht lab had an average population of 194 and were larger than the colonies studied in the field (average population 161), but this difference was not significant ( $P > 0.05$ ).

**Table I.** Some parameters of all the fifteen observed Male Emerging Periods in the field and in the lab.

MEP	Colony	Start	End	Duration (day)	Males	% Males	Intervals (day)	Abs. max	Rel. max
1	1	11 Nov	3 Jan	53	153	14.6	9	1 Dec	10 Dec
2	1	24 Jan	23 Feb	30	92	13.4	2	4 Feb	8 Feb
3	2	24 Nov	8 Dec	14	8	11.0	1	1 Feb	1 Dec
4	2	17 Jan	23 Feb	37	62	15.3	1	27 Jan	26 Jan
5	3	19 Dec	15 Feb	74	88	18.1	6	17 Jan	17 Jan
6	4	15 Nov	19 Dec	35	19	9.7	5	26 Dec	18 Dec
7	4	24 Jan	23 Feb	30	79	16.0	2	14 Feb	1 Feb
8	5	31 Oct	17 Nov	17	43	23.2	1	11 Dec	14 Nov
9	5	29 Dec	22 Jan	24	12	3.6	4	13 Jan	4 Jan
10	5	11 Feb	21 Feb	10	14	14.9	1	17 Feb	11 Feb
11	6	16 Dec	22 Jan	37	69	37.3	2	3 Jan	2 Jan
12	7*	12 May	27 Jun	46	422	70.7	0	25 May	17, 19, 24 May
13	8*	8 Sep	17 Oct	38	163	38.0	1	21 Sep	29, 23 Sep
14	9*	10 Apr	16 Jun	67	940	10.0	3	21 Apr	23, 24 Apr; 3 Jun
15	10*	9 Sep	7 Dec	60	192	33.8	5	10 Oct	10, 16, 17 Oct
Average				<b>38.1</b>	<b>157.1</b>	<b>22.0</b>	<b>2.9</b>		
St.dev.				<b>19.0</b>	<b>240.9</b>	<b>17.0</b>	<b>2.5</b>		

\* Colonies in the lab.

MEP: index number given to the Male Emerging Period. Start: the date on which the MEP starts, End: the date on which the MEP ends, Duration: The duration of the MEP in days, Males: the total number of males emerging during the MEP, % Males: the number of males emerging during the MEP as a percentage of the total number of emerging bees during the MEP. Intervals: the number of periods of no male production within MEPs of 1 day or more. Abs.max.: the date on which the absolute number of emerging males reaches its peak, Rel.max.: the day on which the % of emerging males reaches its peak.

was mapped and its development followed until emergence.

### Classification of oviposition types

The following classification of provisioning and oviposition processes (POPs) was made during this study:

1. Exclusive queen oviposition.
2. Worker oviposition followed by queen oviposition. In this case the worker laid a trophic worker egg (TWE), which was followed by subsequent laying worker withdrawal, queen oophagy, and queen oviposition.
3. Reproductive worker oviposition. This is oviposition by a laying worker that does not withdraw after oviposition but operculates the cell immediately. This excludes queen oophagy and queen oviposition, and there is no obvious response of the queen to this.
4. Oviposition competition. In this case various laying workers are competing for oviposition

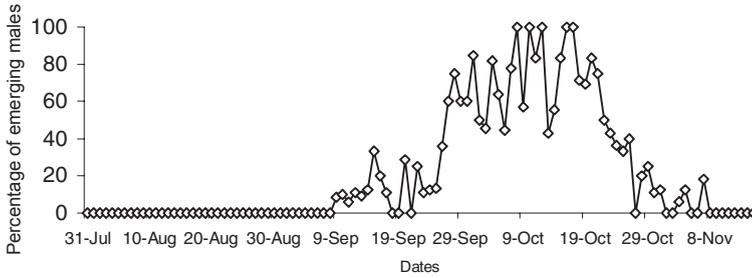
and worker oophagy as they try to operculate after their own oviposition.

5. Worker oviposition after queen oviposition, followed by immediate operculation by this laying worker.

## 3. RESULTS

### 3.1. Male emerging periods in the colonies under field condition

The analysis of emerging bees of the different sexes and castes in the field revealed that males emerged regularly in repeated periods that we define as "Male Emerging Periods" (MEPs) (Fig. 2). In the six field-observed colonies, 11 MEPs were recorded, which occurred nonsynchronously in different colonies (Tab. I). A typical MEP (Fig. 1) is



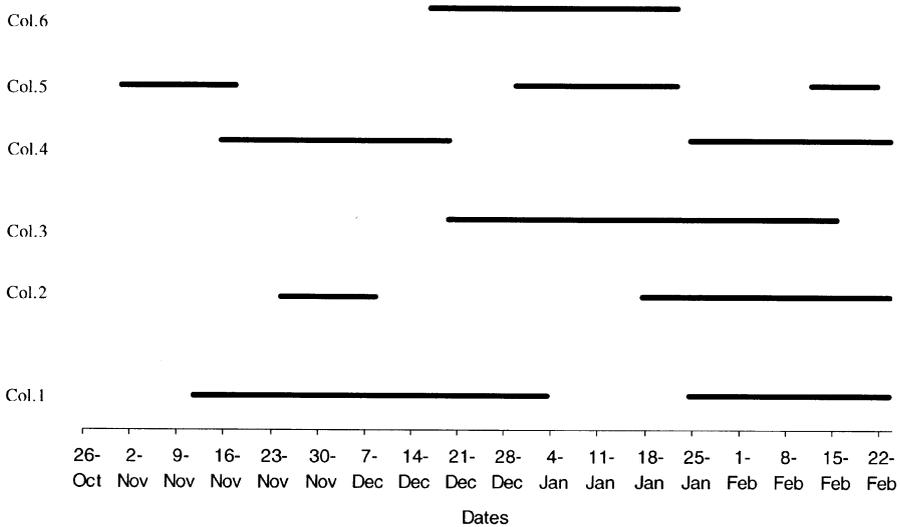
**Figure 1.** The typical pattern of an occurring MEP is presented for colony 10 as an example. The emerging males are given by percentages of daily emerging bees.

characterised by a gradual increase of the daily number of emerging males. After reaching peak values (sometimes with 100% males emerging daily) the percentage of daily emerging males declines to zero. However, some MEPs were interrupted with short intervals from 1 to 9 days in which no males emerged. The occurrence of the MEPs differed in the colonies. The length of the MEPs varied from 10 to 74 days with an average of 32.8 days (SD = 18.3, n = 11) (Tab. I, Fig. 2). Absolute and relative MEP numbers of males emerging in a single MEP varied from day to day. The number of emerging males found on one day ranged from 1 to 12 with an average of 2.1 (SD = 2.6, n = 265) over all MEPs. The number of emerging males as a percentage of the total number of emerging bees per MEP

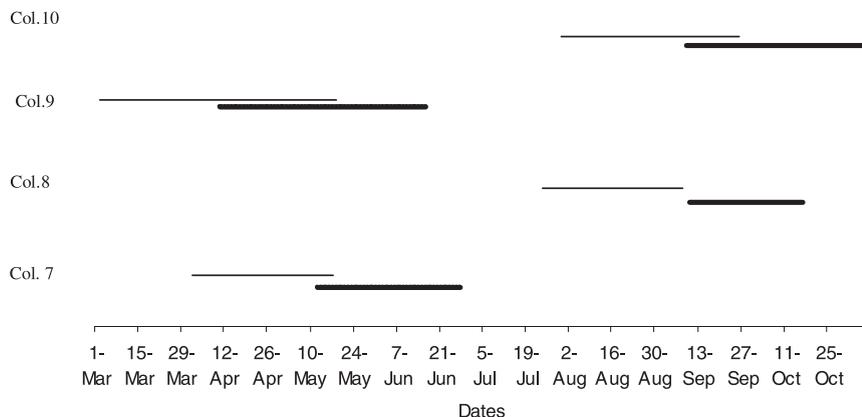
ranged from 3.6% to 37.3%, with an average of 16.1% (SD = 8.6, n = 11). The average percentage of emerging males over all MEPs was 15.6% (SD = 19.2, n = 265). The total number of males emerging during one MEP ranged from 8 to 153, with an average of 58.1 (SD = 44.7, n = 11). The values for the individual colonies are presented in Table I. The periods between the recorded MEPs in which exclusively females emerged ranged from 20 to 40 days with an average of 31.8 days (SD = 10.6, n = 5).

### 3.2. Distinct reproductive laying worker periods

The comprehensive observation of ovipositions in the colonies at the Utrecht laboratory



**Figure 2.** Male emerging periods as they occurred in the different colonies observed in the field (black bars: MEPs).



**Figure 3.** Reproductive laying worker periods and male emerging periods occurred in the different colonies observed in the lab (thin bars: RLWPs, thick bars: MEPs).

revealed that laying workers oviposited reproductive worker eggs (RWEs) in clearly distinct periods. We define such a period, which has a duration of about several weeks, as a “Reproductive Laying Worker Period” (RLWP). These RLWPs occurred in all observed lab colonies; during the observation time, a total number of four RLWPs occurred in the four colonies (Fig. 3). By definition, outside the RLWPs the workers laid no reproductive eggs at all; only trophic eggs were laid. In one complete period of 44 days outside the RLWP that we could observe in colony 8 the queen did not produce any males. In the other colonies we could not analyse the complete periods outside the RLWPs, but from the observed parts of these periods it appears that from the queen eggs operculated in these periods exclusively female bees emerged.

Unfortunately, because of the limitation of our detailed observation time, we could not measure the whole length of all these non-RLWPs.

In the RLWPs the daily number of RWEs varied and ranged from 0 to 35, with an average of 6.8 (SD = 6.7,  $n = 185$  days). The daily number of oviposited cells by both the mated queen and the laying workers during RLWPs ranged from 2 to 40, with an average of 14.7 (SD = 6.9,  $n = 185$  days). The RLWPs of Col. 7, Col. 8, Col. 9 and Col. 10 had

a duration of 46, 47, 102 and 59 days respectively.

### 3.3. Oviposition rates fluctuate with RLWPs

The average number of new cells per day was significantly higher in the RLWP (average = 14.7, SD = 6.9,  $n = 185$ , range: 0–40) than in the periods where only queen eggs were operculated (average = 10.1, SD = 6.0,  $n = 67$ , range: 1–32) (Anova,  $P < 0.0001$ ). Furthermore, the average egg production by the queen in the RLWP (average = 7.9, SD = 5.5,  $n = 185$  days, range: 0–28) was also significantly less (Anova,  $P < 0.01$ ) than outside the RLWPs. In both these periods, trophic worker eggs (TWEs) were laid and the queen always ate such eggs. However, the daily percentage of TWEs per new cell in the RLWPs (average = 16.1, SD = 20.9%,  $n = 185$ , range: 0–80%) was significantly lower than outside the RLWPs (average = 19.1, SD = 28.3%, range: 0–200%) (Anova,  $P < 0.05$ ). The daily number of TWEs (average = 1.6, SD = 2.5, range: 0–10,  $n = 185$ ) positively correlated with the number of queen eggs (average = 7.9, SD = 5.5, range: 0–28), (Spearman- $r = 0.68$ ,  $P < 0.0001$ ,  $n = 185$  days,) whereas the daily number of RWEs was obviously negatively correlated with the daily TWE number (Spearman- $r = -0.21$ ,  $P < 0.01$ ,  $n = 185$  days) in the RLWPs.

### 3.4. Number of observations of the five classes of POPs

Laying workers and the mated queen had a different oviposition time for releasing their various types of eggs. Laying workers took longer for the release of RWEs (average = 8.9 s, SD = 2.6, n = 571, range: 4–31 s) than for ovipositing TWEs (average = 4.2s, SD = 1.4, n = 295, range: 4–31 s), ( $P < 0.001$ ). Correlating the duration of the oviposition of the queen with the sex of her offspring it appeared that her oviposition act took a shorter amount of time for the release of a fertilised egg (average = 26.9 s, SD = 6.9, n = 1174, range: 12–69 s) than for that of an unfertilised egg (average = 46.1 s, SD = 35.8, n = 33, range: 21–181), ( $P < 0.01$ ).

In general, the number of observed instances of the five oviposition classes were:

1. Exclusive queen oviposition (n = 1698).
2. Worker oviposition followed by queen oviposition (n = 446).
3. Reproductive worker oviposition (n = 1248).
4. Oviposition competition (n = 26).
5. Worker oviposition after queen oviposition (n = 2). This was only observed twice and only in the RLWP of Col. 9 in which the old queen died. In this colony, at the end of the recorded RLWP, a number of workers competed to various degrees for oviposition, for feeding on eggs of other workers, and for operculation in some cells. Shortly after this, the old queen of this colony died and a new queen became accepted, developed physogastry and took over the ovipositions. This queen had exclusively male offspring, since she was unmated. In this colony, the old and the young queen were observed together in the brood nest for almost two weeks.

### 3.5. Reproductive laying worker periods (RLWPs) observed to be followed by male emergence periods (MEPs)

In the colonies at our Utrecht laboratory we could confirm that RWEs were released in distinct RLWPs and that these were followed by the emergence of males during typical MEPs after the incubation time (see Fig. 3). In these MEPs, both the absolute and the relative

number of emerging males varied from day to day. The absolute number of emerging males per day ranged from 0 to 45, with an average of 8.1 (SD = 9.3, n = 213) over all MEPs. In the MEPs of colonies Col. 7 and Col. 9, most of the emerging bees were males. On some days only males emerged. In contrast, in the MEPs of Col. 8 and Col. 10 most of the emerging bees were females. The total number of males produced during a single MEP ranged from 163 to 940 males, with an average of 429.3 (st.dev. = 359.7, n = 4). The total number of males emerging in the four recorded MEPs was 1712. The relative number of emerging males as a percentage of the total number of emerging bees per MEP ranged from 33.8 to 70.7%, with an average of 53.1% (SD = 20.0, n = 4). The length of the MEP ranged from 38 to 67 days (average = 52.8, SD = 13.0, n = 4). In Col. 8, two MEPs were observed but the first MEP was in process upon the arrival of this colony at our lab, so its actual length was unknown (MEP recorded from May 12 to July 4). The values for the individual colonies are presented in Table I.

## 4. DISCUSSION

Our results indicate that in *M. favosa* males are produced in distinct periods, the Reproductive Laying Worker Periods (or RLWPs), which lead to the clumped emergence of males in distinct Male Emerging Periods (or MEPs). This periodic pattern of male production occurs both in the field and in the laboratory, and thus occurs even in the absence of extrinsic cues, like fluctuations in temperature, sunlight, food availability and the like. Lab conditions consisted of constant photoperiods for day and night and did not mimic field conditions.

Another important observation is that under both laboratory and field conditions different colonies appear not to be synchronous in their male production. When certain colonies are producing males, others that are under the same condition are not, even when they are located in the vicinity of each other. Colonies appear to have their own rhythm for male production periods and a single colony may have a number of MEPs over the year.

In addition, our results show that the brood cell production in the RLWP is higher than that outside these periods. This is because in the RLWP both the queen and laying workers lay reproductive eggs. Since bees were not individually marked, we could not determine the individual participation in cell construction, provisioning and worker oviposition. But, besides this increase in brood production, we were not able to find any correlation between the occurrence of RLWPs and other intranidal factors such as the number of storage pots or production of queens.

Finally, we observed that in *M. favosa* workers are the main producers of males (Sommeijer et al., 1999) and that, in agreement with Kerr, 1969, the queen-worker conflict is not expressed in overt aggression, with exception of queenless and nearly queenless colonies. What causes the 'internal rhythm' of colonies in their male production? In the discussion below we will propose and evaluate a few hypotheses, in the light of circumstantial evidence and the worker-queen conflict over male parentage.

#### **4.1. Male production in *M. favosa* is not seasonal**

In Tobago we recorded MEPs occurring from the beginning of the observation period in October to the end of the observation period in February. The recorded MEPs in colonies studied in the Netherlands were from March (immediately from the arrival of the colonies) through the end of October. From these results and from unpublished observations in long established colonies in the natural habitat (Sommeijer and de Bruijn, personal observation), it appears that in *M. favosa* males are produced in batches throughout the year. *M. favosa* is not unique for not having a strict seasonal male production. *M. beecheii* (van Veen et al., 1999), *Plebeia remota* (van Benthem et al., 1995) and some *Trigona* species (Beig, 1972; Bego, 1982, 1990; Engels and Engels, 1984) are reported to produce males throughout the year as well, yet in different numbers, depending on the season. Van Veen et al. (1999) found a significant correlation between drone production and pollen storage in *M. beecheii* and male production decreased at the end of the

rainy season due to floral scarcity in this period.

We have no information about the age of the queens in the colonies studied in the natural condition and in the colonies transported to The Netherlands. The age of queens was also unknown in other, long established, colonies where similar periodicity of male production by workers was observed in 1998 (Sommeijer and de Bruijn, personal observation). This suggests that this periodicity may occur over the life of the queen.

#### **4.2. The 'switch-point' hypothesis**

In the bumble-bee, *Bombus terrestris* L., queen-worker conflict over male parentage usually follows a 'switch point', which occurs when the queen starts laying haploid eggs (Duchateau and Velthuis, 1988; Bourke and Ratnieks, 2001). This could explain the observed patterns in *M. favosa*: the queen lays a haploid egg and becomes a competitor with the workers, who start laying reproductive eggs (the beginning of a RLWP). The RLWP may stop when the mass male production is at the expense of worker production. Worker production declines during a RLWP since the queen lays fewer diploid eggs.

#### **4.3. Incomplete queen control hypothesis**

Foster et al. (2001) discuss how queen control in *Dolichovespula* colonies, headed by a monandrous queen, could result in fewer males being produced by workers than by the queen. However, the pheromonal queen control could be evolutionarily unstable, if workers were selected to ignore the pheromone (Keller and Nonacs, 1993; Foster et al., 2001). Sommeijer et al. (1984) hypothesized queen control in *M. favosa*. Diminishing queen control in colonies that are seasonally becoming larger would lead to the development of reproductive workers. However, in this study, reproductive workers were clearly observed in all colonies. Moreover, RWE laying did not occur in absence of the queen. Neither was there overt aggression between reproductive workers and the queen. The queen was present at most occurrences of RWE laying but she was far less involved in

such POPs than during her own egg-laying or the laying of TWEs. From the observations it appears that in the RLWPs the queen is much less motivated to play an active role in POPs than as she is outside these periods. The temporary occurrence of RLWs could result from incomplete “queen control” over reproductive development in workers. Perhaps the temporary “worker-dominance” in *M. favosa* is the arbitrary outcome of an arms race in favour of the workers (Foster et al., 2001). In this case it may very well be that closely related species do not show the same patterns (Foster et al., 2001). Indeed, *M. beecheii* seems to have a more seasonal male production (Moo-Valle et al., 2001; van Veen, 1999). In any case, it remains unclear why and how queen control would diminish frequently and during relatively short periods.

#### 4.4. Queen-like worker hypothesis

It has been established (Sommeijer and Velthuis, 1977) that in queenless colonies of *M. favosa*, some workers behave in a queen-like manner: they can start a POP and are responsible for many ovipositions. Through the genetic-trophic caste determination system in *Melipona* (Velthuis and Sommeijer, 1991) it may be that, also in queenright colonies, some workers are genetically more fit to become reproductive than others. According to this hypothesis, only the limited number of workers with a genetic predisposition to develop into queens, could be responsible for all RWEs. Probably the individual oviposition performance of these reproductive workers can exceed the oviposition rate of workers that release TWEs (Sommeijer and van Buren, 1992). Most likely, the number of reproductive laying workers is limited per colony. It may be assumed that these queen-like workers are able to escape from queen pheromonal control. These workers cannot start a POP in queenright situations, but they can take one over. Pheromonal control may occur in these queen-like workers and prevent overt aggression by the queen and perhaps also by their fellow-workers. According to this hypothesis, the end of a RLWP is results from the cessation of activity by these specific laying workers and after some time, some new

workers may be able to develop such queen-like reproductive behaviour.

In contrast to many Hymenoptera, workers are the main producers of males in *M. favosa*. Apparently queen control of male production is less pronounced in this species, or worker reproduction is much less costly for colony reproduction in *M. favosa* than in other Hymenoptera. The general occurrence of reproductive workers is consistent with the hypothesis that *M. favosa* colonies are headed by monandrous queens. It remains to be tested how general this phenomenon is in *Melipona* and other stingless bees. It is important to study the proximate and ultimate function of this periodical male production by workers in these stingless bees.

#### ACKNOWLEDGMENTS

The observations in Tobago (G.B.J. Grob, 1994-1995) were carried out with the co-operation of the Tobago House of Assembly and Mr. Gladstone Solomon, Tobago Apicultural Society. The subsequent Utrecht laboratory studies (October 1996 to March 1998) which comprised the MSc study of the first author, were supported by a fellowship from NUFFIC (Netherlands Universities Foundation for International Cooperation).

**Résumé – Production périodique de mâles chez l’abeille sans aiguillon *Melipona favosa* (Apidae, Meliponini).** Chez de nombreuses espèces d’abeilles sans aiguillon les ouvrières pondueuses pondent des œufs trophiques qui sont utilisés comme élément du régime alimentaire des reines. Les ouvrières de certaines espèces pondent aussi des œufs d’ouvrières reproducteurs qui donnent naissance à des mâles. Les ouvrières qui produisent des mâles se rencontrent même dans des colonies avec reine. Après avoir trouvé que les ouvrières pondueuses sont les principales productrices de mâles dans les colonies de *Melipona favosa*, nous cherchons à connaître la façon dont sont produits les mâles dans le temps. Pour cela nous avons mené des observations comportementales sur des colonies sur le terrain pour enregistrer l’émergence des mâles des rayons de couvain. Par la suite, nous avons étudié en grand détail la ponte dans un grand nombre de cellules individuelles dans des colonies maintenues dans notre laboratoire aux Pays-Bas pour analyser la maternité des mâles susceptibles d’émerger de ces cellules. Pour cela nous avons utilisé des enregistrements vidéo et un éclairage en lumière rouge. Dans une série de six colonies en

conditions naturelles nous avons trouvé que l'émergence des mâles avait lieu à différentes « périodes d'émergence des mâles » (PEM) (Figs. 1 et 2). En étudiant la ponte des œufs de mâles dans des ruches d'observation au laboratoire à l'aide de la vidéo, nous avons trouvé que les ouvrières pondieuses poussaient leurs œufs au cours de différentes « périodes d'ouvrières pondieuses reproductrices » et que ces périodes étaient suivies par l'émergence en bloc des mâles (Fig. 3). Le tableau I donne les caractéristiques des PEM. Il n'y a pas eu de synchronisation des PEM dans les colonies, bien qu'elles soient toutes sur le même emplacement. Nous discutons différentes hypothèses susceptibles d'expliquer ce mode typique de production des mâles par les ouvrières pondieuses.

***Melipona favosa* / ouvrière pondieuse / production de mâles / œuf reproducteur / œuf trophique**

**Zusammenfassung – Periodische Erzeugung von Männchen bei der Stachellosen Biene *Melipona favosa* (Apidae, Meliponini).** Bei vielen Arten der Stachellosen Bienen gibt es legende Arbeiterinnen, die trophische Eier erzeugen, die zur Ernährung der Königin beitragen. Bei einigen Arten legen die Arbeiterinnen reproduktive Eier, die sich zu Männchen entwickeln. Solche Männchen erzeugende Arbeiterinnen können in Völkern mit Königinnen vorkommen. Nach der Feststellung, dass in Völkern von *Melipona favosa* die meisten Männchen von legenden Arbeiterinnen erzeugt werden, untersuchten wir, ob ein zeitliches Muster bei der Erzeugung von Männchen besteht. Dazu führten wir zunächst Verhaltensbeobachtungen bei Völkern im Freiland durch und protokollierten das Schlüpfen der Männchen aus den Brutwaben. Anschließend untersuchten wir genau die Eiablage bei einer großen Anzahl einzelner Zellen in Völkern, die in den Niederlanden im Labor gehalten wurden, um die Mütter der aus diesen Zellen schlüpfenden Männchen zu bestimmen. Die Beobachtungen wurden mit Video und bei roter Beleuchtung durchgeführt. Bei sechs Völkern im Freiland stellten wir fest, dass die Männchen in distinkten Zeitabschnitten schlüpften, den "Schlupfperioden der Männchen" (Abb. 1 und Abb. 2). Bei den späteren Beobachtungen mit der Video Kamera im Labor über das Legen der Männcheneier fanden wir, dass legende Arbeiterinnen reproduktive Eier während einer distinkten "Reproduktiven Periode der legenden Arbeiterinnen" erzeugten und dass später die Männchen in Gruppen schlüpften (Abb. 3). Die Merkmale der "Schlupfperioden der Männchen" (MEP) werden beschrieben (Tab. I). Im Freiland gibt es keine Synchronisation innerhalb der Völker in Bezug auf die MEPs, obwohl sie im selben Gebiet nisten. Verschiedene Hypothesen für eine

Erklärung dieses typischen Ablaufs der Erzeugung von Männchen durch Arbeiterinnen werden diskutiert.

***Melipona* / legende Arbeiterinnen / Erzeugung der Männchen / reproduktive Eier / trophische Eier**

**REFERENCES**

- Barron A.B., Oldroyd B.P., Ratnieks F.L.W. (2001) Worker reproduction in honey-bees (*Apis*) and the anarchic syndrome: a review, *Behav. Ecol. Sociobiol.* 50, 199–208.
- Bego L.R. (1982) On social regulation in *Nannotrigona* (*Scaptotrigona*) *postica* Latreille, with special reference to male production cycles (Hym, Apidae, and Meliponinae), *Bolm. Zool. Univ. S. Paulo.* 7, 181–196.
- Beig D. (1972) The reproduction of males in queenright colonies of *Trigona* (*Scaptotrigona postica*), *J. Apic. Res.* 11, 33–39.
- Benthem F.D.J. van, Imperatriz-Fonseca V.L., Velthuis H.H.W. (1995) Biology of the stingless bee *Plebeia remota* (Holmberg): Observations and evolutionary implications, *Insectes Soc.* 42, 71–87.
- Bourke A.F.G., Ratnieks F.L.W. (2001) Kin-selection conflict in the bumble-bee *Bombus terrestris* (Hymenoptera: Apidae), *Proc. R. Soc. London B* 268, 347–355.
- Buren N.W.M. van, Sommeijer M.J. (1988) Étude des facteurs déterminants pour la domination reproductive de la reine de *Melipona trinitatis*, *Actes Coll. Insectes Soc.* 4, 285–290.
- Duchateau M.J., Velthuis H.H.W. (1988) Development and reproductive strategies in *Bombus terrestris* colonies, *Behaviour* 107, 186–207.
- Engels E., Engels W. (1984) Drone congregation near the nest of the stingless bee *Scaptotrigona postica*, *Apidologie* 15, 315–328.
- Foster K.R., Ratnieks F.L., Gyllenstrand N., Thoren P.A. (2001) Colony kin structure and male production in *Dolichovespula* wasps, *Mol. Ecol.* 10, 1003–1010.
- Hamilton W.D. (1964) The genetical evolution of social behaviour. I, *J. Theor. Biol.* 7, 1–16.
- Hamilton W.D. (1972) Altruism and related phenomena in social insects, *Annu. Rev. Ecol. Syst.* 3, 192–232.
- Imperatriz-Fonseca V.L., Kleinert A.M.P. (1998) Worker reproduction in the stingless bee species *Friesella schrottkyi* (Hymenoptera: Apidae: Meliponinae), *Entomol. Gen.* 23, 169–175.
- Keller L., Nonacs P. (1993) The role of queen pheromones in social insects: queen control or queen signal?, *Anim. Behav.* 45, 787–794.
- Kerr W.E. (1969) Some aspects of the evolution of social bees (Apidae), *Evol. Biol.* 3, 119–175.
- Koedam D. (1999) Production of queens, workers and males in the stingless bee *Melipona favosa*

- (Apidae: Meliponinae): Pattern in time and space, *Neth. J. Zool.* 49, 289–302.
- Koedam D., Contrera F.A.L., Imperatriz-Fonseca V.L. (1999) Clustered male production by workers in the stingless bee *Melipona subnitida* Ducke (Apidae, Meliponinae), *Insectes Soc.* 46, 387–391.
- Moo-Valle H., Quezada-Euán J.J.G., Wenseleers T. (2001) The effect of food reserves on the production of sexual offspring in the stingless bee *Melipona beecheii* (Apidae, Meliponini), *Insectes Soc.* 48, 398–403.
- Peters J.M., Queller D.C., Imperatriz-Fonseca V.L., Roubik D.W., Strassman J.E. (1999) Mate number, kin selection and social conflicts in stingless bees and honey bees, *Proc. R. Soc. London B* 266, 379–384.
- Ratnieks F.L.W. (1988) Reproductive harmony via mutual policing by workers in eusocial Hymenoptera, *Am. Nat.* 132, 217–236.
- Ratnieks F.L.W. (1993) Egg laying, egg-removal, and ovary development by workers in queenright honey bee colonies, *Behav. Ecol. Sociobiol.* 32, 191–198.
- Sakagami S.F. (1982) Stingless bees, in: Herman H.R. (Ed.), *Social Insects*, Vol. III, Academic Press, New York, pp. 361–432.
- Seeley T.D. (1985) *Honeybee ecology*, Princeton University Press, Princeton, New Jersey.
- Sommeijer M.J., Chinh T.X., Meeuwsen F. (1999) Behavioural data on the production of males by workers in the stingless bee *Melipona favosa* (Apidae, Meliponinae), *Insectes Soc.* 46, 92–93.
- Sommeijer M.J., Dohmen M.R., van Zeijl M. (1984a) Morphological differences between worker-laid eggs from a queenright colony and a queenless colony of *Melipona rufiventris paraensis* (Hymenoptera, Apidae), *Entomol. Ber.* 44, 91–95.
- Sommeijer M.J., Houtekamer L.J., Bos W. (1984b) Cell construction and egg-laying in *Trigona nigra paupera*, with a note on the adaptive significance of the typical oviposition behaviour of stingless bees, *Insectes Soc.* 31, 199–217.
- Sommeijer M.J., van Buren N.W.M. (1992) Male production by laying workers in queenright colonies of *Melipona favosa* (Apidae, Meliponinae), in: Billen J. (Ed.), *Biology and Evolution of Social insects*, Leuven University Press, Leuven, pp. 89–97.
- Sommeijer M.J., Velthuis H.H.W. (1977) Worker oviposition in orphan colonies of *Melipona favosa*, *Proc. VIIIth Int. Congr. I.U.S.S.I. Wageningen*, pp. 315–316.
- Veen J.W. van, Sommeijer M.J., Arce H.G. (1999) The role of colony development and resource availability in the regulation of queen production in *Melipona beecheii* (Apidae, Meliponini), in: Veen J.W. van (Ed.), *Colony reproduction in stingless bees*, Ph.D.-thesis, Utrecht Univ. Litografia Imprenta Lil, S.A. San José, pp. 80–87.
- Velthuis H.H.W. (1970) Ovarian development in *Apis mellifera* worker bees, *Entomol. Exp. Appl.* 13, 377–394.
- Velthuis H.H.W., Sommeijer M.J. (1991) Roles of morphogenetic hormones in caste polymorphism in stingless bees, in: Gupta A.P. (Ed.), *Morphogenetic hormones of arthropods*, Rutgers University Press, pp. 346–383.
- Visscher P.K. (1989) A quantitative study of worker reproduction in honey bee colonies, *Behav. Ecol. Sociobiol.* 25, 247–254.