Apidologie 36 (2005) 169–185

DOI: 10.1051/apido:2005014

Review article

The males of *Melipona* and other stingless bees, and their mothers[1]

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Received 4 November 2004 – Revised 7 January 2005 – Accepted 17 January 2005

Abstract – Female behaviour in social Hymenoptera and the queen-worker conflict with respect to male production have been the focus of many studies. Although male production is an investment that is in conflict with investment in colony size, males play a vital role in colony reproduction. This paper reviews the production patterns of male stingless bees, their activities once they have reached adulthood and their origin (i.e., are they sons of workers or of queens). The existence of a broad spectrum of species-specific patterns of male production, sex ratios, and male parentage offers ample opportunities to discuss the influence of ecology on the dynamics of stingless bee colony life. The paper also argues that selfishness causes the queen and the workers to compete and each to adopt certain strategies in their effort to produce male progeny. It is this competition, expressed in various forms during the characteristic and socially complex process of cell provisioning and oviposition, that could help explain the variable outcomes of male parentage at the species level as we currently know them.

stingless bee male / sex ratio / life history / male aggregation / queen-worker conflict / provisioning and oviposition process

1. INTRODUCTION

Stingless bees form an ancient (Michener and Grimaldi, 1988) and rather diversified (Michener, 1974, 2000) group of mass-provisioning eusocial bees. They vary considerably in several of the characters for which sociobiological theory would predict a basic uniformity. Trivers and Hare (1976) made clear that workers of hymenopteran colonies, headed by a single monandrous queen, have reproductive interests that are different from their mother. This discord has its expression in the origin of the males, some of which are sons of the queen whereas others are sons of some of the workers. The workers of such colonies find their genes better represented in sons and nephews than in brothers and should, accordingly, attempt to monopolize male production. This characteristic differs greatly between *Melipona* species. This genus, therefore, offers ample opportunities for studies on the factors that have had an impact on the evolutionary rules governing the dynamics of colony life. This interaction between our concepts of primary evolutionary rules and the ecology of bees will be reviewed in this paper.

Colonies of stingless bees are made up of males and females, and the latter are divided into workers and queens. Differences between males and females start with the fertilization of the egg: the unfertilized egg becomes a male, while the fertilized egg is female. Sex determination, therefore, is genetic and is related to haplodiploidy. In contrast, the main decisive factor in the development of a fertilized egg

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[1] Manuscript editor: Gudrun Koeniger

into a queen or a worker is the quality/quantity of food in the brood cell.

Queens can be reared in different ways. Most genera of the tribe Meliponini construct occasionally a larger brood cell that contains more food than the common brood cells. This quantitative factor modifies the differentiation of the female larva in the cell: she will become a queen. The smaller and more common cells harbour workers and males. Thus, like in the honeybees, queens of these genera emerge from specific queen cells. Different mechanisms are seen in the remaining genera. In *Frieseomelitta,* for example, large queen cocoons occur, but are the result of larvae perforating the wall of an adjacent cell. These larvae then gain a second portion of food, enabling the modification of their development into a queen (Terada, 1974; Faustino et al., 2002). All brood cells in the genus *Melipona* are approximately the same size. In this genus it is the minute variation in the quantity and, perhaps, also in the quality of the food that contributes to the developmental differentiation between workers and queens. A two-locus genetic mechanism may also prevent 75% of the *Melipona* females from becoming queens (Kerr, 1950; Velthuis and Sommeijer, 1991). Because the differences in the food for worker or queen development are so small, young *Melipona* queens emerge quite regularly even though hardly any are actually needed. These superfluous queens are then killed by the workers.

This peculiar and seemingly overproduction of queens and their fascinating mechanism for caste differentiation have stimulated many studies on *Melipona* (Kerr, 1950; Velthuis and Sommeijer, 1991; Koedam et al., 1995; Wenseleers and Ratnieks, 2004; Wenseleers et al., 2004). As a result and because a number of *Melipona* species have been domesticated, the genus *Melipona* is better known compared to most of the other stingless bee genera.

Males are the prime subject of this study. We will discuss the patterns of their production, their activities once they reach adulthood, and their origin (i.e., are they the sons of workers or of queens?). Alhough this paper concentrates on the genus *Melipona*, when appropriate other genera will be mentioned. *Melipona* is a neotropical genus comprising about 40 species, which, to a large extent, are uniform in their colony characteristics. However, major differences exist in the way in which males are produced.

2. THE PATTERNS OF MALE PRODUCTION

In general, male production in a social insect colony is influenced by outside factors related to climatic periodicity, and factors inside the colony such as colony strength and demographic composition. Under temperate conditions, climate has a preponderant impact. The seasonal factors force colonies to produce their sexuals during a brief period, thereby synchronizing the colonies of a population. In contrast, bees in tropical regions may be largely independent of such climatic influences, although the alternation of dry and wet seasons may cause males to be more frequent in one period of the year than in the other. Synchronous production at the population level, therefore, may become less pronounced and the role of within-colony factors more evident.

Male production is an investment that is in conflict with investment in colony size: instead of a worker a male emerges that does not participate in regular colony activities like cell building, cell provisioning, colony defense, and foraging. He does, however, represent the colony in the reproductive arena. Investments in reproduction may occur once the existence and future of the colony is assured.

How would male production be regulated at the colony level? For a perennial colony with a long life expectancy, which characterizes *Melipona* species, there may be two ways: (1) constantly as a proportion of the cells produced, in a ratio that increases both with colony size and with the rate of cell production or (2) as an outburst of limited duration once the proper colony size and conditions have been reached. In the first instance, male production is a constant but light impediment. In the second case, male production may lead to distinct fluctuations in the worker force, which forces the colony to recover after a male producing period. Long-term ecological factors, such as the probability of the presence of suitable but unoccupied nesting sites in the habitat, may also be involved. Such habitat characteristics determine the incidence of swarming. If swarming is frequent, we might expect colony growth rate to be important and thus male production to be absent or limited in smaller colonies. One possible example of this is *M. mandacaia*, a species that lives in the caatingas of the state of Bahia, Brazil. These areas are exposed to extremely long periods of drought, during which bee colonies may undergo considerable size reduction. Populations, therefore, are characterized by high colony-mortality rates. Once a rainy period has caused the vegetation to bloom, the colonies increase rapidly in size and then swarm to occupy the nesting sites that became vacant (Castro, pers. com.). We might expect male production in such a species to be concentrated in time at both the population level and the colony level, because the impact of the environment is so great that the within-colony factors have little influence. In contrast, there might not be a vacant nest cavity for long periods of time for species living in areas where the environment is more stable. Since most *Melipona* species live in more stable environments and build their nests inside living trees, unoccupied cavities of the proper size might be rare. These colonies may, therefore, have to delay reproduction through swarming. As a result, they may only reproduce through their males, one of which may find a young queen that supersedes an old one in another colony. In such a case, small colonies may also produce males as their continuous existence is not at stake. For the genus as a whole, swarming is characteristically infrequent (Roubik, 1989). We consider this ecological factor of great importance for *Melipona* biology.

2.1. Temporal patterns of male production

It has been documented at colony level of a number of species, that most of the males are produced in periods with a restricted duration. We have termed this the Male-Producing Periods or MPP (this term is preferred over the almost equivalent term Male Emerging Period or MEP proposed by Chinh et al., 2003). In recent studies, this phenomenon has been documented to occur in *M. asilvai*, *M. bicolor, M. favosa,* and *M. subnitida* as well as in *Plebeia remota, Scaptotrigona postica, Schwarziana quadripunctata* and *Trigona (Lepidotrigona) ventralis* (Bego, 1982; Koedam et al., 1999; Velthuis et al., 2002; Sommeijer et al., 2003; Alves, 2004; Alves et al., 2004; Chinh, 2004; Alves, unpubl.). It is, therefore, a wide-spread event. MPPs may be the result of a synchronous, albeit differential, production of reproductive eggs by a number of workers, sometimes with the production of haploid eggs by the queen, over a short period of time (days or weeks) (Koedam and Imperatriz-Fonseca, 2004a; Koedam et al., 2005).

Even though individual colonies may produce their males in MPPs, these periods may not be synchronous among colonies and thus, at the population level, male production is usually not restricted to certain periods of the year. This was shown in studies on *M. favosa* (Chinh et al., 2003) (Fig. 1) and *M. bicolor* (Alves, 2004). MPPs within individual colonies, therefore, have no impact on male presence at the population level and do not affect queens that are on mating flights. It also appears that MPPs

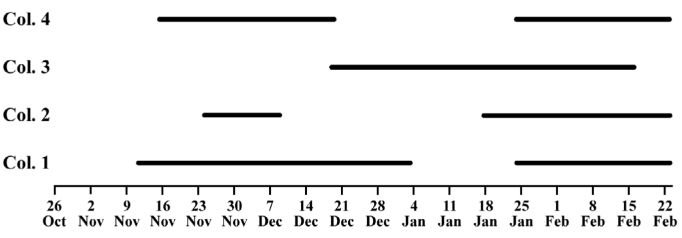

Figure 1. Male production periods in six colonies of *Melipona favosa* in Tobago. Solid bars represent the periods of male emergence in these colonies. Reproduced from Chinh et al., 2003.

Table I. The investment in sexuals as the proportion of the total brood of some well-studied species.

species	percentage	authors
Melipona asilvai	26	Alves, unpublished
M. beecheii	37.5	Moo-Valle et al., 2001
M. bicolor	12.5	Alves, 2004
M. favosa	22.5	Sommeijer et al., 2003
M. subnitida	15	Alves, unpublished
M. trinitatis	13	Sommeijer et al., 2003
Plebeia remota	29	Alves, unpublished
Schwarziana quadripunctata	20.5	Alves, unpublished

of different species have different intensities, in number as well as duration.

When there is an MPP during which different individuals lay reproductive eggs, it is not necessary that a mechanism be present that enables the workers to recognize whether the queen's egg has been fertilized or not (Nonacs and Carlin, 1990) and to which they respond by laying unfertilized eggs. A general condition or signal inside the colony related to the start of an MPP would suffice to stimulate both workers and queens to lay haploid eggs.

2.2. MPPs and the ratios of males versus workers and queens

Some population-wide studies on the production numbers of males, workers, and queens have been conducted that cover a long time span. They included the following species: *M. quadrifasciata* (Bezerra, 1995), *M. subnitida* (Koedam et al., 1999, 2005; Alves, unpublished), *M. beecheii* (Moo-Valle et al., 2001), *M. favosa* (Koedam, 1999; Sommeijer et al., 2003; Chinh, 2004), *M. trinitatis* (Sommeijer et al., 2003), *M. asilvai* (Alves, unpublished), and *M. bicolor* (Alves, 2004).

The results of those studies are summarized in Table I.

Alves analyzed 29 *M. subnitida* combs from different colonies, harvested in April, June and July 2003 in their natural habitat. In April, males constituted only 2.4% of the brood and queens 10% of the females. In June, the average male score was 7.5% and that of queens 6%. In July, these values were 11.3% for males and 9% for queens. Queens were present in all combs, usually in low percentages. Males were often absent or occurred in rather low numbers. If they were more frequent, their percentage usually remained below 30%; the maximum found was 36%. This indicates that male production is clustered in time. This result confirms the more detailed observations of Koedam et al. (1999), who found only 31 males on 14 combs having 2 496 cells. Of these 31 males, 29 were produced in only a few combs.

To further study male production, Koedam et al. (2005) manipulated food circulation in two *M. subnitida* colonies. Before manipulation, these colonies produced 3% and 0% males and 9.2% and 8% queens. During the manipulation period, the male proportions increased to 47% and 25% respectively, while the queens scored 9% and 18% resp. These results show that queen numbers remained rather stable despite manipulation, while male numbers fluctuated. In other words, male production was subject to colony conditions.

Ten *M. beecheii* colonies were studied for one year by Moo-Valle et al. (2001). The population produced brood that was 22.9% male, and 14.6% of the female brood were queens. The average male production by the entire population was constant, except for September when it was only 11%. There was, however, a large monthly variation in the frequency of males between the colonies, much larger than between seasons. The percentage of queens fluctuated over the year between 11% and 21%, being low in July and high in May. In a factor analysis, the factor ‘season’ was of equal importance as the factor ‘colony’ in explaining the fluctuation. The average queen/male (q/m) ratio was 1/2. A separate experiment with six colonies studied the effect of food manipulation. The three control colonies were fed during the experiment, while the three experimental colonies were not. Food stored in the experimental colonies was reduced to one-third that in the control group. After a year, these experimental colonies were only one-third the size of the control colonies. The latter were identical to the sample of 10 colonies. The brood of the experimental colonies consisted of only 1% drones, while queens made up 10% of the female brood, thus the q/m ratio was 1/0.1. In comparison to natural conditions, food limitation affected the proportion of drones much more than the proportion of queens, probably as a consequence of colony size reduction.

In *M. favosa* (Sommeijer et al., 2003), 167 brood samples, taken from 78 colonies over a number of years, contained 16 342 pupae. Of these, 2 827 were males (17.3%), 689 were queens (4.2%), and 12 826 were workers (78.5%). Due to the occurrence of male-production periods, the percentage of males in a given comb could be as high as 74.2%, but was often 0% (in 26.5% of the samples). On an annual basis, queen production varied less (4–6%) with exceptions in March (8%) and July (7%). Another study of the same species (Chinh, 2004) included 6 colonies at the same location, studied from October to February. These colonies produced 639 males during a period of 119 days. Males were concentrated in some of the combs (Fig. 1) and constituted about 8% of the total brood production, contrasting with the annual average of 17.3% of the Sommeijer et al. study. The author explained this difference by pointing out that, according to Sommeijer et al. (2003), males were most frequently encountered in the months July and August, reaching populational averages of 25–30%.

Similar figures exist for *M. trinitatis* (Sommeijer et al., 2003). This species was sampled for 4 months: 21 combs from 15 colonies contained 2 567 pupae. Queens were present in 80% of the samples, males in only 45%. Of the females 5.2% were queens. Males amounted to 7.7% of all brood, but made up 31% of the brood of a single comb.

Alves (unpublished) counted the cells in 15 combs of *M. asilvai*, collected between 15 April and 19 July 2003. She found a total of 1 719 cells: 302 males, 102 queens and 1 315 workers. Except for 3 combs, the average proportion of queens in the female brood was 5.8% (4–8%). When all 15 combs were included, the proportion was 8.4%: one small comb contained 23% queens. Males, amounting to an average of 17.6%, were either absent or numbered less than 5 in 8 of the 15 combs.

A sampling of 18 *M. bicolor* colonies (Alves, 2004) during a year period concerned a total of 97 combs containing 11 745 brood cells. Queens made up, on average, 6.5% of the female brood. At population level, this fluctuated between 4.3% and 9.2% per month. Males constituted a monthly average of 3.7% (1.7–6.7%, 10 months) with the exception of August (23.9%) and November (12.5%). At the colony level, male frequencies were found to fluctuate much more than queen frequencies and to differ much more between colonies sampled at the same time. More than 50% of the males were aggregated on a single comb of their respective colony, making up 24–92% of all the cells of that comb, while 70% of the combs contained less than 5 males each.

Comparing the reproductive investments of these species, the percentages of males found varied from 6% to 23%, those of queens from 5% to 15%. Taking both sexes together, *M. bicolor* and *M. trinitatis* were the most prudent (Tab. I). They invested 13% of all brood in reproduction. In contrast, *M. beecheii* was the other extreme with 37.5% of all brood being sexuals. Apparently, there are MPPs for all of these species, and the colonies of a single species are not synchronized in their male production. Also, the maximum proportion of males in the brood sample varies among the species and, consequently, the fluctuations in worker numbers are more prominent in some species than in others.

Queen/worker proportions appear to be more uniform. In the abovementioned studies, a synchrony in the quantitative aspects of the production of the two sexual forms was not reported. However, Koedam (1999) did find a positive significant correlation for *M. favosa*, between the numbers of queens and males per comb. This indicates that a common environmental factor may be involved in the production of queens and males.

2.3. What regulates the occurrence of an MPP?

What kind of information is available to a member of a colony that determines when males can be produced without much harm to the future performance of the colony? We propose that demographic factors play a role (see also Bego, 1982). Tasks like constructing and provisioning brood cells are performed by younger workers, while eggs are produced by the queen. We suggest that there is a certain adjustment in the production capacities of each of the parties, i.e. for the numbers of cells and eggs produced, and that it is conceivable that at a certain rate, the cell construction capacity is higher than the egg production capacity of the queen. In these circumstances, there will be a surplus of young workers. By laying haploid eggs in part of the cells that the workers prepare, the number of workers is down-regulated for the near future, possibly reaching an equilibrium with the egg-laying capacity of the queen. Whether this is a fine-tuned process, keeping worker numbers stable, that can be governed by the queen alone or whether it causes notable fluctuations in worker numbers, in which perhaps laying workers also take part, is left undecided for the moment.

Alternative solutions for repairing such a disequilibrium in the production rates of cells vs. eggs include an earlier shift of the workers from nursing to foraging activities, which leads to an increase in food stored inside the nest, and swarming. The respective limiting factors of these alternatives are pollen and nectar availability outside and storage space inside the nest, and the presence of a new nest site for the swarm. Since stingless bees first find the new nest site and then prepare for swarming, both alternative solutions depend on ecological factors and may not be available for a given colony.

2.4. Fitness aspects of male production

If specific colony conditions favour the occurrence of an MPP and information on these conditions is available to all colony members, then the queen as well as some of the workers may respond by starting the MPP. At this moment a divergence in the fitness interests of queens and workers develops. A reproductive worker shares 25% of her genes with the son of the queen, 37.5% with the son of a sister and 50% with her own son. So, in conformity with Trivers and Hare (1976), we might expect the workers to produce the males. Indeed, monandry is the rule in stingless bees (Peters et al., 1999) and in all *Melipona* species workers are capable of reproducing directly; being unmated, all of their eggs are haploid (Sakagami, 1982). Since the survival of the colony is in their interest, workers should restrict their egg laying in number and to time periods when colony survival is not at stake. Given that the colony can endure only a certain number of males being produced and both queen and workers may respond to favourable colony conditions, the queen and her workers are competitors in the realization of this number of males. The outcome of this competition and the strategies applied vary greatly between the species. For instance, all *M. beecheii* males appear to be the sons of the queen (Paxton et al., 2001), while 95% of the *M. favosa* males are sons of the workers (Sommeijer et al., 1999). Tóth et al. (2002) already discussed part of this plasticity in male production.

All of the above concerns queenright conditions. In queenless conditions, the workers of a number of species produce eggs. This is outside the scope of the present study.

3. THE VARIATION IN WORKER OVARY FUNCTIONS IN THE OTHER GENERA

Annoted above, there is a variation in the proportion of males that are sons of workers. Moreover, there are genera in which reproductive workers are fully absent even though the conditions concerning monogyny and monandry are met that, theoretically, would favour worker-produced sons. However, this does not mean that the worker ovaries are disfunctional.

Apart from the fertile, reproductive eggs, workers of many stingless bee species generate trophic eggs. Trophic eggs are essentially infertile (Akahira et al., 1970; Cruz-Landim and Cruz-Höfling, 1971; Koedam et al., 2001) and are specialized vehicles for the transfer of protein from a worker to the queen, comparable to the glandular secretions that pass from a honeybee worker to the queen during trophallaxis (Velthuis, 1993).

In *Geotrigona* (Lacerda and Zucchi, 1999) and in *Tetragonisca* (Koedam et al., 1996; Grosso et al., 2000) the workers are capable of laying trophic but not reproductive eggs. In *Trigona cilipes* workers have trophic eggs in their ovaries, but do not lay them. In these genera, therefore, workers may have active ovaries, but remain without offspring. *Leurotrigona* (Sakagami and Zucchi, 1974; Terada, 1974) and *Friesella,* on the other hand, have no trophic eggs, but do have reproductive eggs. Only *Friesella,* however, actually lay these eggs (Camillo-Atique, 1971, 1977; Imperatriz-Fonseca and Kleinert, 1998). In even more contrast to the basic theory, the ovaries of *Frieseomelitta* (Zucchi, 1993), *Duckeola* (Sakagami and Zucchi, 1968) and *Tetragonula* (Suka and Inoue, 1993) workers are never activated. In fact, the ovaries of *Frieseomelitta* workers are degenerated (Boleli et al., 1999). The complex situation of stingless bee worker ovaries and the eggs they may produce has been excellently reviewed by Silva-Matos et al. (2000).

4. SEX RATIOS

4.1. Primary sex ratios

The ratio of queens/males at emergence varies in the long-term brood samples of the *Melipona* species of Table I: 10 for experimental *M. beecheii* colonies, 1.1 for *M. subnitida*, 0.9 for *M. bicolor,* 0.6 for *M. trinitatis*, 0.5 for natural *M. beecheii*, 0.3 for *M. asilvai* and 0.25 for *M. favosa*. This is interesting, because one would expect the primary sex ratio to be strongly male-biased in a social insect that multiplies its colonies through swarming: total investments in males on the one hand and in the entire swarm on the other should be in equilibrium (Fisher, 1930). In these *Melipona* bees, it appears as if the workers accompanying the queen during swarming do not count.

There are two explanations for this unusual sex ratio. The first is that, theoretically, there is an overproduction of queens, a maladaptation considering the colony level, that may be the consequence of self-determination (Ratnieks, 2001). In classical terms, this is the interaction between a genotype capable of developmental plasticity and a variable environment, in cases where we do not see the impact of this environmental variation. It is the expression of a conflict between individual selection and selection at the colony level. Under such conditions, larvae are expected to "decide" more often to become a queen. As already mentioned, Kerr (1950) proposed a genetic mechanism that renders 75% of the female larvae of *Melipona* species insensitive to the food stimulus that leads to queen development. The relationship between genome and food condition in the remaining 25% of the female larvae is unknown.

The second explanation for the unusually high frequency of young queens is that the incidence of swarming is low, that mature colonies are usually prepared for swarming already long before they can actually do so, and that an investment in queens is needed to maintain the preparedness of the colony. With this explanation, we try to find the adaptive side of the phenomenon at the colony level. Before a comparison with male investment is made, the continued preparedness, in terms of queen numbers, should be added to the number of workers participating in the swarm. We can expect, therefore, that on average, there should be only a small male bias in the q/m ratio.

In the other Meliponine genera, those with specific larger queen cells, we find the more usual situation for social insects. In a large sample of *Plebeia remota*, Alves (unpublished) found queens in 0.04% of the cells and males in 25%; the primary sex ratio was 0.0016. In a smaller sample from another population, the sex ratio was 0.005. In more than 14 000 *Schwarziana quadripunctata* cells, Alves (unpublished) found 2 900 males, 14 royal cells, and an additional 67 miniature queens emerging from worker cells. Sometimes miniature queens become physogastric and are able to head a colony like normal queens (Ribeiro and Alves, 2001). As the functional difference between these two types of queens remains unknown, the primary sex ratio is 0.028 for all queens or 0.0005 for queens from royal cells only.

In relation to the higher proportions of queens among the female brood in *Melipona* and the proposed ecological explanation we have presented, it must be noted that there are species in other genera that also have a low incidence of swarming. *Scaptotrigona,* for instance, lives in habitats similar to those of many *Melipona*, but appears to swarm more often than *Melipona.* Virgin queens in a number of these genera are often maintained for longer time periods then in *Melipona*, sometimes "emprisoned" in special cells (Engels and Imperatriz-Fonseca, 1990). This may be another way for the colony to remain prepared for swarming. Apparently, there is also more variation in mating age for these queens then for those of *Melipona*.

4.2. Operational sex ratios

The sex ratio at emergence is not very important for the situation at mating. Mortality rates transform the ratio at emergence into the operational sex ratio, i.e. the situation in which a queen and a male will find each other and which might shape their species-specific behaviours. Almost no *Melipona* queens will survive after their emergence and have a chance to partake in a mating flight (Imperatriz-Fonseca and Zucchi, 1995; Koedam et al., 1995; Wenseleers et al., 2004). As can be concluded from the long residency of marked queens, laying queens of *Melipona* may remain in their colony for over a year. Substitution is infrequent. The incidence of swarming is also low, far less than once a year in most species. Taking substitution and swarming together, a queen will depart from a colony for a mating flight on average only once every 8–12 months.

How many males will be available for a queen to select a mate from? Chinh's study (2004) indicated a productivity of 639 males over a period of 119 days, originating from 6 colonies, i.e., on average, 0.895 males per colony per day. If the period of sexual activity of males lasts 14 days, each colony in the area has, on average, 12.5 males on the wing. The operational sex ratio largely depends on the number of colonies in the area. If there are 10, for example, the queen may find 125 males from which to choose. A few other queens searching for a mate at the same time would hardly make a difference. Since all species are monandrous, each of the queens reduces the number of males by just one. Thus, plenty of males remain, provided the males that spend their energy in a fruitless pursuit of a queen soon recover and again pursue with similar vigour, if given a second chance.

For males, however, this operational sex ratio is too optimistic a figure, because many of them are mature in time periods when there is no virgin queen available. Again based on Chinh's study, the annual production of a *M. favosa* colony is around 320 males. With a supposed annual production of just a single queen out for mating, the probability for a male to mate is only 0.003. This is an optimistic perspective, given that the estimate of male production based on Chinh (2004) is well below that of Sommeijer et al. (2003)!

We can obtain a rough estimate of the mating probability for males of the other species by supposing that a new comb is started about every 6 days. This means 60 combs a year. Using the data for the number of cells per comb and male frequency (see Tab. I for refs.), we can then calculate the male numbers per colony per year to vary from 365 in *M. subnitida* to 1 000 in *M. favosa*. Depending on the incidence of swarming and the replacement of old queens, the mating probability for a male might indeed be in the order of 0.01–0.002.

5. LIFE HISTORY OF MALES

Considering the very low probability that a male will ever mate, mating does not appear in activity-time budgets of males. In fact, mating has hardly ever been seen. Males stay inside the colony until the age of about 2–3 weeks (*P. droryana*, Cortopassi-Laurino, 1979; *M. beecheii* and *M. favosa*, van Veen et al., 1997). During that time, they have been reported to be involved in building activities, trophallaxis, nectar dehydration (Imperatriz-Fonseca, 1973; Cortopassi-Laurino, 1979), incubation, and nest defense (Kerr, 1990). According to Nogueira-Neto (1997), some of these activities (building, nest defense) are only incidental, even though males have been observed to secrete wax. Nectar dehydration could also play a role in their preparation for leaving the nest and thus not be a social activity. Van Veen et al. (1997) found that males of *M. beecheii* spent more than 90% of their time walking, standing, self-grooming, and stirring.

Once the males have left the colony, not much is known of their activities. They do not return inside the colony, so it is supposed they live the life of a solitary male bee. Their life expectancy is unknown, but, based on survival under laboratory conditions, they might obtain an age of 4–6 weeks.

While they live on their own, males have to forage and may visit the same flowers as workers of their species. Roubik (1990) suggested that males may follow workers back to their nest and thus learn the locations of conspecific nests. There have been made several observations of stingless bees males that were lured to orchids, where they do not find food but become loaded with the pollinia of the orchid during an act of pseudocopulation (Singer et al., 2004). There is little doubt that males do play a role in the pollination of these orchids as well as other flowers.

6. HOW DO MALES MEET A QUEEN?

Theoretically, all of the mating tactics known for other bees (see Thornhill and Alcock, 1983; Paxton, 2005) can be applied to stingless bees. Are there species, for example, where males maintain a territory or where they jointly attract females to a lek? We do not know. There is, however, a kind of mating strategy that is quite conspicuous and therefore observed for a number of species: the temporary congregation of males near a colony. Such male congregations were described already long ago. More recently, descriptions have been made for *Plebeia droryana* (Cortopassi-Laurino, 1979), *Scaptotrigona postica* (Engels and Engels, 1984; Engels and Imperatriz-Fonseca, 1990; Paxton, 2000), *Trigona (Tetragona) dorsalis* (Roubik, 1990), *Tetragonisca angustula* (Imperatriz-Fonseca et al., 1998; Nogueira-Ferreira and Soares, 1998; van Veen and Sommeijer, 2000), *Trigona collina* (Cameron et al., 2004), *M. fasciata* (van Veen et al., 1997), and were seen in *M. crinita, M. scutellaris, M. subnitida, Nannotrigona testaceicornis, Trigona spinipes, Paratrigona subnuda* (Cortopassi-Laurino, unpublished). Males of different species may even be found together. In all of these cases, it was often noted that the males clustered close to a colony with a queen to be inseminated or nearby a queenless nucleus that just a few days earlier was separated from the mother colony. Apparently, these colonies produce an extremely attractive odour. In fact, 30–50, sometimes even hundreds, of males have been counted near such colonies, supposedly arriving from great distances. They cluster together (*Scaptotrigona*) or remain more dispersed (*Tetragonisca*) near the nest entrance, a smaller number may even fly around the entrance, all awaiting the appearance of the queen. Such clustering begins just a few days before the mating flight and disperses a few days thereafter. Once the virgin queen departs from the nest, the males compete to mate. Some queens may even be mated by two males (Paxton et al., 2003; Imperatriz-Fonseca et al., 1998). Studies by Paxton (2000) and Cameron et al. (2004) have shown that the congregating males come from a large number of colonies. Inbreeding, therefore, is largely prevented. Sommeijer and de Bruijn (1995) described a male congregation of *M. favosa* at some distance from a nest. This group of males had gathered on a wall, a site that was also visited by the virgin queens. The authors reported that the males and virgin queens flew off together. Mating could not, however, be observed. *T. angustula* (Nogueira-Ferreira and Soares, 1998) and *P. remota* (Alves et al., in prep.) males were reported to aggregate at a new nesting site a few days before a young queen arrived with a swarm. The males stayed there until the nuptial flight had taken place.

Long-lasting nuptial flights are known for *M. quadrifasciata* (Silva et al., 1972) and *M. beecheii* (van Veen and Sommeijer, 2000). In both cases, the queens were observed to leave the colony in rapid flight and to return, sometimes with a mating sign, up to 100 and 40 min. later, respectively. Such a long duration of a mating flight indicates that queens also search for males instead of encountering them at the nest entrance.

7. WHO PRODUCES THE MALES?

Recently, male parentage in stingless bees was reviewed extensively (Tóth et al., 2004). We suggest that the reader should refer to that paper for most of the literature on the subject. It shows that worker reproduction is far more common in the genus *Melipona* than in the majority of the other genera. At present, there is no satisfying explanation for this higher frequency or for the important differences between the species of *Melipona*. The Tóth et al. paper discusses 10 predictions for worker reproduction. Since this subject is of great interest from the theoretical point of view of sociobiology, these predictions deserve our comments. Some of the arguments are rather abstract, while others are of a more classical biological nature. This leads to an overlap in the predictions. In the monogynous colony with a monandrous queen, theory predicts that workers, having fitness interests different from those of the queen, should attempt to monopolize male production. However, like in the ants discussed by Trivers and Hare (1976), a solution is often found between the optima for workers versus queens. One group of predictions concentrates on cost/benefits, focusing on the individual egg layer as well as on the colony as a whole, because all colony members have their inclusive fitness interests. The other set of predictions concentrates on the instruments with which one party might control the other, i.e., the direct fitness interests. These instruments, however, are also the means by which the cost/benefit ratio is controlled. It is through the joint effects of these instruments that, in Meliponine bees like in the ants, a compromise is found between the conflicting interests of the parties. This compromise is not a static mean value, it is dynamic, leading to large variations around the mean. The mean values, therefore, may vary over time and between species.

How can we achieve an understanding of the interactions of these instruments? Tóth and coworkers compared observational and molecular genetic methods and preferred the latter because (a) the observer might confuse the trophic and the reproductive eggs of stingless bees; (b) worker egg laying might be cryptic; (c) behavioural observation is time-intensive, therefore observations are often restricted in time with the consequence that variation could escape detection; and (d) queens may also lay male eggs. Genetic studies should circumvent these problems, especially if a queen and a worker lay an egg in the same cell and a male emerges (who laid the egg?). The criticism of the behavioural method concerns the quality of the observations, not the method as such. In fact, several molecular genetic studies, like several behavioural observations, have also missed the variation or presented no explanation for the variation found. We believe that it is only through behavioural observations that the variation, both within and among species, can be interpreted. The understanding will bring the cost/benefit ratios and the mechanisms involved together. In order to improve understanding, the two methodologies are not of different ranks but are instead supplementary.

We have mentioned already that, in the genus *Melipona,* great differences exist in the proportion of males originating from worker-laid eggs, that males are often produced in batches, and that MPPs occur because, in the demography of the colony, a situation can arise in which the queen cannot keep up with the number of cells workers are able to produce. This leads to changes in the details of the provisioning and oviposition process (POP), such as a more rapid provisioning and a more delayed egg laying by the queen and to a lower degree of involvement of the workers of the appropriate age class. These factors might have consequences for the individuals involved.

While such a cause-and-effect chain could explain the overall pattern of male production within the genus, it is through the amplitudes of the process that we might find an explanation for the differences between the species in the relative amounts of males in an MPP. Such differences include the average percentage of males as well as the proportions produced by either the queen or the workers. When measured with molecular techniques, however, these kinds of data are still only the net result of interactions. In fact, the "arms race" among the participants or the "power" of any of the parties could include the elimination of an opponent's offspring.

It must be stressed that a different physiology and behaviour are needed to lay a trophic or a reproductive worker egg. A *Melipona* worker needs five to six days to produce and lay a trophic egg, while reproductive eggs may be laid with intervals of only one day (Koedam et al., 2001; Koedam, unpublished data). In general, a worker laying a trophic egg does so prior to egg laying by a queen. She then flees from the cell. A worker that lays a reproductive egg stays on the cell and closes it, resisting the queen or other laying workers that try to remove her (Sakagami, 1982). Morphologically and physiologically, the two types of egg also differ (see Koedam et al., 2001). The distinction, however, does not imply that an individual should lay either trophic or reproductive eggs; some individuals lay both types in distinct phases of their life (Koedam and Imperatriz-Fonseca, 2004b; Koedam, unpublished data).

A few examples of such intricate interactions that might remain obscure in genetic studies may illustrate our case. They revolve around the POP, subdivided into a pre-provisioning phase, a provisioning phase, and a post-provisioning phase, followed by oviposition by the queen and, subsequently, cell closure by a worker (see Zucchi et al., 1999, for definitions of POP elements). All of these phases are characterized by interactions among the parties. In normal situations the queen will lay her egg after the cell has received enough food and a worker will close the cell. Beig (1972) observed that this closing worker could be a reproductive one and that her egg is then in the same cell as the one of the queen. He concluded that 85% of the males in *Scaptotrigona postica* were sons of workers. Bego (1982) studied the same species and found that, during brief periods, up to 70% of the cells contained 2 or more eggs. Paxton et al. (2003), using genetic markers, concluded that almost all males were sons of the queen.

Laying an egg while sealing the cell also occurs in many species of *Melipona.* Competition among the hatched larvae determines what will eventually be produced. Another mechanism is that the reproductive worker lays her egg before the queen can do so, thus preventing the queen from laying. This was observed in *M. favosa*, *M. subnitida, Scaptotrigona barrocoloradensis,* and *S. postica*. This sequence prevents the two descendants from competing for food and implies that no eggs are lost. There is also a third possibility: namely that a reproductive worker disturbs the cell closure of another worker. This has been reported in *M. bicolor*, *Friesella schrottkyi,* and *S. postica.* A fourth mechanism of reproduction is that the worker opens an already sealed cell some time after it is closed, occasionally eats the egg, oviposits, and seals the cell again. These different strategies are illustrated in Table II.

With regard to the rates of cell production and the rates of egg laying, it is only when a worker lays her egg prior to the queen that no eggs are lost. Indeed, the only study that compares the rates before and during the MPP found that the egg-laying rate of the queen remained constant while the cell construction rate increased (Koedam et al., 2005).

Interestingly, it is always a reproductive worker that closes the cell, although theory would allow her to leave this task to her non-reproductive sisters! This demonstrates that there is selfishness involved: reproductive workers competing for the use of the same cell, thereby destroying each other's eggs, diminish the proportion of males that could be workers' sons. This suggests that direct competition is the driving force. Cells to oviposit in are scarce for *Melipona* workers.

It should be underlined here that the queen responds to the egg laying of a worker, prior to the moment she would do so herself, by vigorously tapping the worker. Usually, this is not successful. If the worker lays after the queen, however, the latter may notice but not respond; often she passes by and may antennate the worker during egg laying and cell sealing as well as during the re-opening of cells. We are not certain whether the queen notices that worker reproduction occurs, but we do not exclude it.

Why does the queen allow a reproductive worker to lay an egg and to monopolize that cell, before she herself has oviposited? Explanations such as the queen is aging, tired, or unattentive (Camillo-Atique, 1977; van Buren and Sommeijer, 1988; Sommeijer and van Buren, 1992) are not appealing. Queens depend on trophic eggs for their nourishment, eggs that are laid by workers once the provisioning is completed. The *Melipona* queen may solicit such egg laying by withdrawing from the cell. Sometimes, she may have to wait for minutes for a trophic egg to be laid. A reproductive worker may then take advantage of the situation and lay an egg before the queen can do so. The worker then seals the cell. The queen, being physically inferior (she has a smaller head and thorax compared to workers and a much heavier abdomen), cannot prevent this.

There are a few ways in which the queen may interfere with worker reproduction. One is passive: i.e., she also produces haploid eggs during an MPP. In *M. subnitida*, for instance, plenty of cells still remain available for oviposition by the queen despite the activity of reproductive workers. One study by Koedam et al. (2005) showed that two-thirds of the males were the sons of the queen (or 3:2, Contel and Kerr, 1976). Outside the MPP, only a few males are produced, all by the queen (Fig. 2, from Koedam et al., 2005). The same low number of males produced outside the MPP has been reported for other species. They are absent, however, in *M. favosa*.

There appears to be an even more intriguing interference in *M. bicolor*. During an MPP many reproductive workers may be present at

Table II. The laying of reproductive eggs by stingless bee workers during the provisioning and oviposition process (POP) under queenright colony conditions as documented for various species. As a rule, such workers operculate the cell immediately following on their egg laying. See Zucchi et al. (1999) for definitions of POP elements.

Species	After cell provisioning, excluding the queen	Immediately after queen oviposition	While cell is sealed by another worker	Some time after cell has been sealed	Authors
Melipona bicolor	no ($)	28.2%	30.8%	41.0%	Koedam et al., unpubl. data.
M. favosa	yes (§)	at least < 0.2%	no	no	Chinh et al., 2003
M. marginata	no	yes	?	?	da Silva, 1977
M. subnitida	66.7%	33.3%	no	no	Koedam et al., in press
M. quadrifasicata	no	yes	?	?	da Silva, 1977
Friesella schrottkyii	no	yes	yes	yes	Imperatriz-Fonseca and Kleinert, 1998
Paratrigona subnuda	no	no	no	100% (&)	Tóth et al., 2002
Scaptotrigona barrocoloradensis	100%	no	no	no	Suka et al., 1994
S. postica	yes (#)	yes	yes	yes	Bego, 1990

$ A former study on this species by Koedam et al. (2001) showed that reproductive workers occasionally excluded the queen.

§ Various workers may compete for oviposition, each trying to operculate after its oviposition.

& Worker oviposition could occur as late as two days after cell provisioning.

This includes cells exclusively oviposited in and sealed by a reproductive worker, thus containing a single egg, and cells in which the queen laid her egg next to that of a reproductive worker, after which the cell, now having two eggs, was sealed.

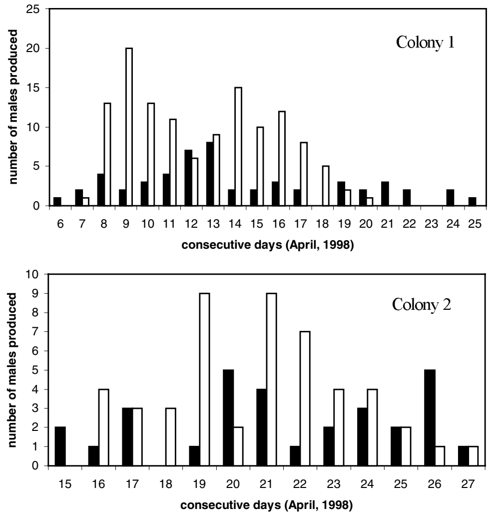

Figure 2. The sharing of the production of males by the queen (open bars) and workers (closed bars) in two laboratory-kept colonies of *Melipona subnitida*, over a period of up to two weeks in the month of April 1998, São Paulo. Up to the date when sharing began, in both colonies the queens produced males occasionally. For details, see Koedam et al., 2005.

a given cell at a given time. They repeatedly push each other from the cell, before as well as after worker oviposition. They also re-open cells in which a worker has oviposited, eat that egg, and oviposit themselves. In fact, sequences of up to 16 workers laying one after the other in the same cell have been observed. Meanwhile, just a few cells away, a regular POP may be occurring with queen oviposition and cell closure by a non-reproductive worker. The competing laying workers nearby are, this time, not interested in the cell containing the queen's egg. This suggests that some cells are protected from being used by workers, while others are not. Perhaps the queen protects a cell by adding a larger amount of a pheromone? By varying this amount in a series of cells, the queen may concentrate worker egg laying and egg destruction in some of the cells. This would protect a number of her own eggs and simultaneously cause damage to worker reproduction. During the observed MPP, the mortality rates for reproductive worker eggs were twice as high as those for queen eggs (Velthuis et al., 2002).

Thus, the battle is fought almost without overt aggressiveness between queen and worker. Only in *M. subnitida* was it once observed that a worker pulled the queen from a cell by grasping her mandibles. The worker then laid her own egg and sealed the cell. In *Melipona*, and also in a number other genera, the outcome depends on the environmental details within the colony as a whole, details which change constantly. In this dynamic context, each of the parties has successes and failures. If we had a nose as fine and sensitive as bees, we would certainly be impressed by the variety of signals that contain messages of threat and submission.

ACKNOWLEDGEMENTS

Our studies of stingless bees have received long-lasting financial support from FAPESP (São Paulo) and from the Dobberke Foundation (Amsterdam), for which we are grateful. While preparing this paper we had stimulating discussions with, and obtained information included in this paper from Dr. Paulo Nogueira-Neto, Dr. Marilda Cortopassi-Laurino, and Denise de Araujo Alves. Furthermore, we acknowledge the suggestions made by the referees for the improvement of this manuscript. Linguistic help was given by Laura Cobb.

Résumé – Les mâles des abeilles *Melipona*, et des autres abeilles sans aiguillon, et leurs mères. Cet article considère le modèle de reproduction et l'origine des mâles chez les abeilles sans aiguillon (Apidae, Meliponini), en particulier chez le genre *Melipona*. On présente des arguments selon lesquels des facteurs écologiques, tels que la saison, combinés aux facteurs internes à la colonie, déterminent la présence des mâles dans le temps. Les facteurs écologiques sont souvent si déterminants que les colonies d'une population sont hautement synchronisées quant à leurs périodes de production de mâles et que la production de mâles est limitée à une saison donnée. Pourtant, sous certaines conditions tropicales, ce synchronisme se perd et, au niveau de la population, des mâles sont produits tout au long de l'année. Néanmoins chaque colonie ne les produit que dans certaines conditions et des lots de mâles apparaissent dans des périodes distinctes de production de mâles (Fig. 1). Quand la production de mâles se fait aux dépens de la production d'ouvrières, les périodes de production de mâles peuvent conduire à des fluctuations dans le nombre d'ouvrières et l'on suggère que ce facteur démographique est l'un des facteurs de la régulation de la production de mâles. Un autre facteur est l'existence d'une disparité entre le taux de construction des cellules d'ouvrières et le taux de production d'œufs de la reine.

La production des mâles est indépendante des mécanismes de production des reines. Les mâles constituent un moyen pour transférer des gènes à une autre colonie, alors que les reines servent soit à multiplier les colonies par essaimage, soit à les maintenir par remplacement de la reine. Chez six espèces bien étudiées de *Melipona*, il existe des différences énormes en ce qui concerne l'investissement dans la reproduction. Ces différences portent à la fois sur le sex-ratio primaire et sur l'investissement total en sexués par rapport à l'investissement en ouvrières (Tab. I). Pour chaque espèce le nombre de mâles fluctue beaucoup plus d'un mois à l'autre que le nombre de reines.

Les mâles proviennent des œufs pondus par les ouvrières et aussi des œufs haploïdes pondus par la reine. Chez certaines espèces la reine et l'ouvrière reproductrice sont en compétition directe pour la possession de la cellule dans laquelle elles peuvent pondre leur œuf : un seul œuf est pondu par cellule. Chez d'autres espèces pourtant, la compétition a lieu entre les larves de la descendance, quand à la fois la reine et l'ouvrière ont pondu un œuf dans la cellule. De plus, les ouvrières peuvent détruire les œufs de la reine, ou des autres ouvrières, avant de déposer elles-mêmes leur œuf. Et finalement une reine peut réagir à la ponte des ouvrières en pondant elle-même des œufs haploïdes, plutôt que diploïdes. Il existe donc de nombreuses façons par lesquelles les deux castes femelles entrent en compétition pour leur propre fitness. C'est le résultat d'interactions comportementales complexes pendant le processus d'approvisionnement de la cellule et de ponte, qui sont caractéristiques des abeilles sans aiguillon. Même au sein du genre *Melipona*, il existe des différences importantes entre les espèces concernant le moment où cette compétition reine/ouvrière s'exprime (Fig. 2 ; Tab. II). Cela pourrait expliquer les résultats contrastés des études portant sur la paternité des mâles parmi les abeilles sans aiguillon.

Les sex-ratios primaires des abeilles du genre *Melipona* sont proches de l'unité. Il s'agit d'une valeur remarquable pour un insecte social qui se multiplie par essaimage. On suppose qu'il s'agit de l'adaptation, au niveau de la colonie, au fait que les sites de nidification libres sont très rares et que les colonies doivent se maintenir prêtes à essaimer sur un longue période.

Les sex-ratios secondaires sont par contre très asymétriques. On s'attend à ce qu'ils soient de l'ordre de 1–0,1 % de reines/mâles.

abeille sans aiguillon / sex ratio / conflit reine-ouvrière / rassemblement de mâles / processus d'approvisionnement et de ponte / cycle évolutif

Zusammenfassung – Drohnen der *Melipona* und anderer stachellosen Bienen und ihre Mütter.
Diese Arbeit beschäftigt sich vor allem mit dem Produktionsmuster und der Abstammung der Männchen bei Stachellosen Bienen, mit besonderer Berücksichtigung der *Melipona*. Es werden Argumente aufgezeigt, dass Umweltfaktoren wie Saisonalität in Kombination von Bedingungen im Volk das zeitliche Muster im Auftreten der Drohnen bestimmen. Häufig dominieren die Umweltfaktoren, sodass die Drohnenerzeugung in den Völkern einer Population stark synchronisiert wird. In diesen Fällen gibt es Männchen nur zu festgelegten Zeiten. Unter bestimmten tropischen Bedingungen geht diese Synchronisation jedoch verloren und in Bezug auf die Population werden das ganze Jahr über Drohnen erzeugt. Trotzdem gibt es auf der Volksebene nur unter speziellen Bedingungen Männchen; in so einem Volk treten Männchen nur während relativ kurzen Perioden auf (Abb. 1). Weil in einem Teil der Zellen Männchen statt Arbeiterinnen produziert werden, führt diese Periode zu einer Fluktuation in der Anzahl der Arbeiterinnen. Es wird angenommen, dass dieser demographische Faktor einer der Komponenten zur Regulation der Männchenproduktion ist. Ein weiterer Faktor ist das Auftreten einer Diskrepanz bei der Rate beim Zellbau im Vergleich zur Rate der Eiproduktion der Königin.

Die Drohnenerzeugung ist unabhängig vom Mechanismus der Königinnenproduktion. Männchen dienen der Übertragung von Genen auf andere Völker, während Königinnen entweder zur Vermehrung der Völker durch Schwärme beitragen, oder zum Erhalt des Volkes als Nachfolgerinnen ihrer Mütter. Bei sechs gut untersuchten Arten von *Melipona* treten deutliche Unterschiede in Bezug auf die Investition in die Reproduktion auf. Diese Unterschiede betreffen beides, sowohl das primäre Geschlechtsverhältnis als auch die Gesamtinvestition in Geschlechtstiere im Vergleich zur Investition in Arbeiterinnen (Tab. I). Bei jeder Art ändert sich die Zahl der Männchen während des Jahres viel stärker als die Zahl der Königinnen.

Drohnen können aus Eiern von Arbeiterinnen oder aus haploiden Eiern der Königin entstehen. Bei einigen Arten, bei denen es pro Zelle nur ein Ei gibt, konkurrieren Königin und die reproduktiven Arbeiterinnen direkt um eine Zelle. Bei anderen Arten jedoch findet die Konkurrenz zwischen den Larven statt, nachdem sowohl die Königin als auch die Arbeiterin ein Ei in die Zelle gelegt haben. Außerdem kommt es vor, dass Arbeiterinnen das Ei der Königin oder anderer Arbeiterinnen vernichten, bevor sie ihr eigenes Ei in die Zelle legen. Schließlich ist es auch möglich, dass eine Königin auf eierlegende Arbeiterinnen durch Ablage eigener haploider Eiern reagiert. Es gibt also viele verschiedene Möglichkeiten, wie die beiden weiblichen Kasten um ihre individuelle Fitness konkurrieren. Das Ergebnis sind komplexe Verhaltensweisen und Interaktionen während der Verproviantierung der Zelle und des Ablaufs der Eiablage, ein sehr charakteristischer Vorgang bei Stachellosen Bienen. Selbst innerhalb der Gattung der *Melipona* gibt es wichtige Unterschiede zwischen den Arten in Bezug auf den Moment in dem der Königin- /

Arbeiterin- Konflikt stattfindet. (Abb. 2, Tab. II). Hiermit könnten sich die widersprechenden Ergebnisse bei Untersuchungen über die Abstammung der Männchen bei den Stachellosen Bienen erklären.

Das ursprüngliche Geschlechtsverhältnis bei *Melipona* liegt nahe bei 1:1, ein Wert, der bemerkenswert für soziale Bienen ist, die sich durch Schwärme vermehren. Es wird angenommen, dass dies eine Adaptation auf dem Volksniveau auf Grund von selten vorhandenen Nistplätzen ist. Aus diesem Grund müssen die Völker über lange Zeiträume jederzeit in der Lage sein zu schwärmen. Sie ziehen jederzeit junge Königinnen heran, die meistens von ihnen getötet werden, sowie sie adult sind, sofern keine neue Nistmöglichkeit entdeckt wurde. Sekundäre Geschlechtsverhältnisse sind jedoch sehr asymmetrisch. Sie liegen wahrscheinlich im Bereich von 1–0,1 % Königinnen im Vergleich zu Drohnen.

Stachellose Bienen / Drohnen / Geschlechtsverhältnis / life history / Drohnenansammlungen / Königinnen / Arbeiterinnen-Konflikt

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