

Research article

Colony reproduction in *Tetragonisca angustula* (Apidae, Meliponini)

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Summary. Colony multiplication of the neotropical stingless bee *Tetragonisca angustula* started with the finding of a new nesting site by scout bees, followed by the cleaning of the cavity. Cerumen was flown in from the mother colony for the sealing of crevices and the construction of an entrance tube. Major investment of the mother colony in the daughter nest was in workers and cerumen. Almost negligible amounts of pollen were transported from the mother colony after arrival of the gyne in the founding colony. Small quantities of honey were transferred as well. Workers from the daughter nest foraged actively for pollen. Some 500 to 1000 workers entered in the daughter nest, following the virgin queen. This is only a relatively small proportion of the population of the mother colony. Two to four days after the nuptial flight the young queen started egg-laying, and storage pots, mainly filled with honey and some pollen were encountered. In the mother nest, ample pollen and honey stores were present during the months preceding the swarming process. Shortly before swarming took place brood (and adult) populations were 20 to 50% higher than in the other non-swarming colonies, whereas the production of royal cells and males was not different. Data were compared with those got in literature.

Key words: Stingless bees, *Tetragonisca angustula*, swarming, founding.

Introduction

In the highly eusocial honey bees (Apini) and stingless bees (Meliponini), colonies are founded through swarming. The sequence of the swarming process in stingless bees was first described by Nogueira-Neto (1954), and is interestingly different from that of honey bees (Michener, 1974; Sakagami, 1982). Whereas swarming is quite abrupt for honey bees, – thousands of workers leave the original colony with the old queen, a new nest location is selected by scouts from the

departing swarm, and the relation with the mother colony is broken –, for stingless bees it is a long lasting process. In stingless bees the following steps are described (Da Silva et al., 1972; Engels and Imperatriz-Fonseca, 1990; Michener, 1974; Nogueira-Neto, 1954; Sakagami, 1982; Terada, 1972; Wille and Orozco, 1975): scout bees look for a suitable nesting site within the flight range of the colony, it is cleaned and an entrance tube is constructed, resins, cerumen and food resources are transferred from the mother colony to the new nest or partly collected in the field, a virgin queen arrives at the new nest site accompanied by a mass of workers (not always) from where she undertakes her mating flight, and the relation with the mother nest continues for several days up to half a year depending on the species.

The most detailed quantitative information for stingless bees swarming process is available for Indonesian *Trigona* (*Tetragonula*) *laeviceps*, for which species six swarm processes are described (Inoue et al., 1984). These authors found for the first time that about half of the workers that had entered the daughter nest with the swarm returned to the mother colony the next day, a behaviour which probably helps adjusting the number of workers in the daughter nest. Finally about 30% of the adult workers of the mother colony moved to the daughter nest. The workers of the daughter colony of this species carried only small amounts of resources from the mother nest for just one week after the arrival of the virgin queen. During this period active foraging for food was observed by the authors. The quantity of building material transported depended on the state of the cavity and the crevices in it.

In contrast to tropical *Apis mellifera*, which colonies can swarm three to four times during a year, stingless bee colonies reproduce only once a year or even less frequently (Bego, 1982; Roubik, 1989).

The available information about the condition of the mother nest before swarming, the investment in resources and workers in the daughter colony, and the influence of environmental factors such as resource availability, suitable

nesting site and predation is still fragmentary (Engels and Imperatriz-Fonseca, 1990; Inoue et al., 1984; Roubik, 1989). No description of swarming by any species of *Melipona* exists up to day.

This paper describes the process of colony reproduction for *Tetragonisca angustula* in Costa Rica and the investment of the mother colony in resources and workers.

Material and methods

At three locations in Costa Rica, Horquetas de Sarapiquí, Pérez Zeledón and Heredia, the swarming process of colonies of *Tetragonisca angustula* was studied. At all three locations *Mangifera indica* (mango) and secondary natural vegetation were within the foraging range of the colonies.

All colonies were housed in wooden boxes, constructed of at least 18 mm thick timber with a volume between 3.1 and 22.1 liters. All colonies were well established and had representative food stores and adult and brood populations (Michener, 1974; Roubik, 1983), at the moment when the measurements started. All hives were hung under the roofing of the houses to protect them from rain and excessive sunshine. To increase the chances of observing swarming processes, some 20 empty wooden boxes with inside dimensions of about 10 (w) × 20 (l) × 7 (h) cm were set out at each location.

When any signs of swarming activity were observed, such as bees flying out with resin, mass flights around nests or available nest sites, or scout bees entering unoccupied boxes, some of the workers were paint-marked and followed to locate either mother or daughter nest (Inoue et al., 1984). Extranidal behaviour of workers, drones and gyne were observed continuously, and the number of flights was counted daily for five minutes every hour between 7:00 h and 16:00 h, until a relation between mother and daughter colony could be observed no more. A brief description of the behaviour of gynes and drones (Van Veen et al., 1997) is given in this paper in order to complete the swarming behaviour data. Workers carrying pollen and cerumen (corbiculae), waste (mandibles), or nothing at all were recorded separately. Bees scored without apparently carrying anything may have transported nectar, honey or pollen in their crop.

All 21 colonies in Horquetas, whether involved in swarming activities or not, were opened every three or six weeks between October 1994 and May 1995 and from October 1995 to May 1996. The adult and brood populations and food stores were measured. The involucre surrounding the brood combs was taken away partly so the larger royal cells could be observed. Brood samples were taken from combs to measure the number of drone pupae. Since food storage pots in *T. angustula* are constructed in a very compact cluster, the total volume occupied by the pots was measured for each colony, in spite of volumes of individual pots. All measurements mentioned were used to compare the development between swarming and non swarming colonies.

Results

Eight partial cases of swarming processes in *T. angustula* are described below. Of the first swarm the development of the mother nest before and after swarming and its flight activity were measured. The second to the seventh case concern founding colonies and one observation on a mother colony. The eighth case describes a swarming process for a mother and daughter colony at 5 m distance from each other.

1. On 20th of February 1995 workers were observed flying out of a colony with resin in their corbiculae. The daughter nest of this colony was not found. Outflying workers stayed

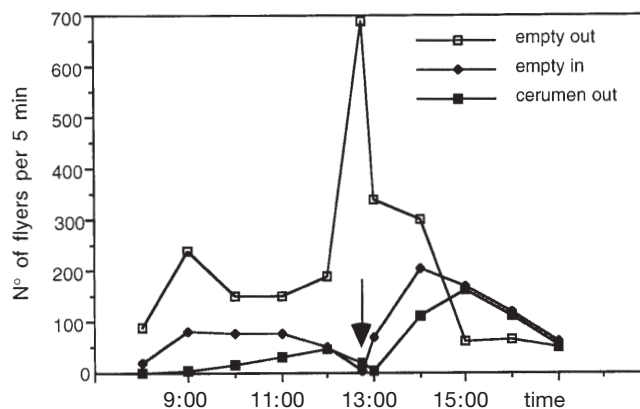


Figure 1. Flight activity on the day of swarming (21 February 1995, moment indicated by arrow) of a colony of *T. angustula*, in Horquetas. Recordings were performed during 5 min about every 45 min. Part of the bees scored as empty out or empty in may have transported nectar (empty in) or honey (empty out) in their honey stomach

away for 396 s (S.D. = ± 36 s, n = 12), so the daughter nest must have been nearby.

The following day, a gyne was seen leaving the mother nest at 12:23 h (outside temperature 30.2°C). She flew out in a straight line, unaccompanied. After a few seconds, hundreds of bees followed the gyne in the same direction. Within 5 min after the gyne left, 687 workers had left the mother colony. This mass out flow had a duration of about 30 min. Three samples of the outflying bees (n = 35 bees each), revealed that only workers followed her, no drones were observed. The flight activities of this colony were measured for the day the gyne left (Fig. 1), and the day afterwards (Fig. 2). These two days flight activities were very different from those performed by other colonies at the same place. A peak of outflying workers was observed (Fig. 1) immediately after the gyne left the mother colony, and a

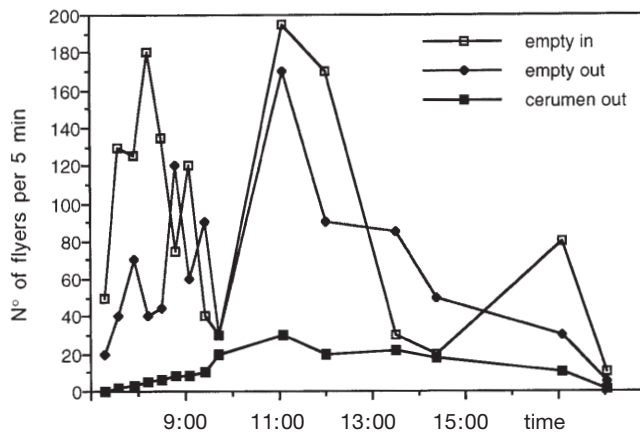


Figure 2. Flight activity on the day after swarming (22 February 1995) of a colony of *T. angustula*, in Horquetas. Recordings were performed during 5 min about every 45 min. Part of the bees scored as empty out or empty in may have transported nectar (empty in) or honey (empty out) in their honey stomach

Date	N° brood cells	N° royal cells	Drones (%)	Honey (ml)	Pollen (cc)
29/10/94	6820	1	N.M	594	18
09/12/94	10656	1	N.M	360	168
23/01/95	14725	1	17.5	425	120
27/02/95	12124	2	1.1	353	112
11/04/95	12552	3	12.5	345	72
17/05/95	4645	4	0	264	30

Table 1. Development of a colony (case 1) of *T. angustula* that swarmed on 20 February 1995 (N.M = not measured). The percentage of drones refers to pupae in emerging brood

growing number of workers leaving with cerumen. A high number of inflights during the first hours of the next morning was observed (Fig. 2), which exceeds the number of outflights. This means that these bees stayed outside overnight. Since this had not been observed before in this nor the other colonies, these bees must have come from the filial nest. After this peak of incoming workers, the cerumen outflights resumed.

The development of this colony was measured at six-weekly intervals between 23th of October 1994 and 17th of May 1995. It was observed that the colony had a high brood production, and surplus honey and pollen stores (Table 1). Royal cells were always present in small numbers and drones were produced in varying quantities. Brood and food store sizes are bigger for this colony than for the average colony of *T. angustula* in this period.

Five weeks before swarming took place, in this colony the mother queen was superseded.

Cases 2 to 7.

In five founding colonies of *T. angustula* it took up to two days before an entrance was constructed in the new hives after scout bees had selected the boxes. During these two days cerumen was flown in from the mother colonies, on average between 1 and 10 times every five minutes. In a sixth case, cerumen was flown out from a mother colony for seven days with a frequency of 18 times every five minutes, after which it gradually diminished until completely ceased 29 days later. Paint marked workers of this colony stayed away for 60 to 70 min ($n = 15$). The development of this colony was measured (Table 2). It always had pollen and honey reserves and the quantity of brood cells tripled between 4th of December and 15th of February.

Once the entrance had been constructed 20 to 56 workers stayed overnight in the hives. It was observed that until the day before a gyne came in, 150 to 300 workers stayed over-

night. Twice a new nest box was abandoned after workers had constructed an entrance tube and some involucrum. In one of these cases it was observed that another nest box at only three meter distance was occupied simultaneously by (marked) bees from the same colony.

The shortest distance found between a mother colony and the filial nest was 2.10 m.

Occasionally some storage pots for honey were constructed and a start made of an involucrum before the swarm entered the hive. These relatively small honey stores were between 15 ml and 60 ml, and occurred in two of the five cases only. Pollen was never stored until the day the swarm occupied the new box.

In four cases it was observed that two to 13 days after scout bees had entered a box the actual swarm, a gyne with a group of worker bees flew in. In one case it was observed that the gyne arrived unaccompanied at the new hive, followed after a few minutes by some 200 workers.

After arrival of the gynes up to 45 workers per five minutes arrived with cerumen. The same day the inflight of pollen started, which was transported by the workers in their corbiculae. Estimates at night when all bees were in the hives ($n = 3$) revealed that between 500 and 800 workers had participated in the swarms. Two to four days after the nuptial flight, which was on the day after the gyne had arrived at the new nest ($n = 4$), the first brood cells were being constructed. At that moment small honey reserves were in the colonies. Hardly ever any pollen reserves were present, so apparently all pollen was used for the provisioning of the brood cells. In two newly established colonies about 540 brood cells were counted three and seven days respectively after the first egg-laying. Two weeks after the nuptial flight honey reserves were between zero and 150 ml.

8. On 14th of November 1991 scout bees were seen entering an empty swarm box, at five meter distance from the

Date	N° brood cells	N° royal cells	Honey (ml)	Pollen (cc)
04/12/92	4450	0	100	100
23/12/92	8093	1	150	120
04/01/93	7885	0	150	120
18/01/93	12772	1	110	85
15/02/93	14923	2	150	50
03/03/93	8140	0	200	50
17/03/93	6075	0	190	5
09/04/93	5998	0	120	45

Table 2. Development of a colony (case 7) of *T. angustula*, that showed cerumen transport between 1 March and 6 April 1993

mother colony. In front of the mother colony between 500 and 1000 worker bees were hovering between 9.00 and 10.30 h. This behaviour was repeated on the following day. On 15th of November the entrance tube was built in the filial nest. On 16th of November many worker bees were again seen hovering in front of the mother colony, but this time the flight activity lasted until 13.45 h, and over 1500 workers participated. At 12.41 h a gyne left the mother colony, and flew straight to the filial nest. The gyne landed on top of the hive, and walked all over it during 7 min before entering. After the gyne had entered, some 300 worker bees came from the “cloud” that was hovering in front of the entrance of the mother colony, and rapidly entered the daughter nest. The next day the gyne made her nuptial flight. During the whole observed period only cerumen and honey inflights were seen coming from the mother colony. Simultaneous observations at the entrance of the mother and daughter colony revealed that workers collected pollen in the field and brought it in on the corbiculae. This pollen collection did not start until after the gyne had arrived at the daughter nest.

On 19th of November the newly established nest was opened. Four brood cells were counted, 11 storage pots filled with honey and three with pollen. An estimated 1000 workers were present. Some involucrum was being constructed.

Colony development for *Tetragonisca angustula*

During the eight months observation period, for two subsequent years, most brood was produced between December and March, coinciding with the best foraging conditions (Fig. 3 top). Maximum brood production was an average of 9624 cells in March.

Royal cells were produced in low numbers in all months (Fig. 3 center). It should be noted that due to the partly removal of the involucrum, only one third of the combs was made completely visible. Actual royal cell numbers could therefore have been about three times as high. In 60% of the recordings, no royal cells were observed in the colonies. No recordings on drone presence in the combs were made in the months of October and December. During the rest of the monthly samplings, between 5.8 and 23.2% of the brood consisted of drone pupae. Exceptionally, in two colonies a percentage of 87 and 83 drone cells were recorded, in April and May. One of these colonies swarmed in that period.

Pollen stores did not vary greatly, and were always smaller than honey stores (Fig. 3 bottom). In 13 out of the 21 colonies at least once no pollen stores were present. Honey stores were always present, and significantly greater in October and from March through May (polynomial regression, $y = 443.9 - 154.982x + 18.113x^2$, $F = 22.69$, $p = 0.0028$). The colony that swarmed had relatively big pollen stores, being 170 cc one month prior to swarming and 120 cc in the week swarming took place. A positive significant correlation was found between the brood production and the amount of pollen and honey stored ($r^2 = 0.045$, $p = 0.001$ and $r^2 = 0.293$, $p = 0.007$ resp., $n = 113$ samples of more than 100 cells

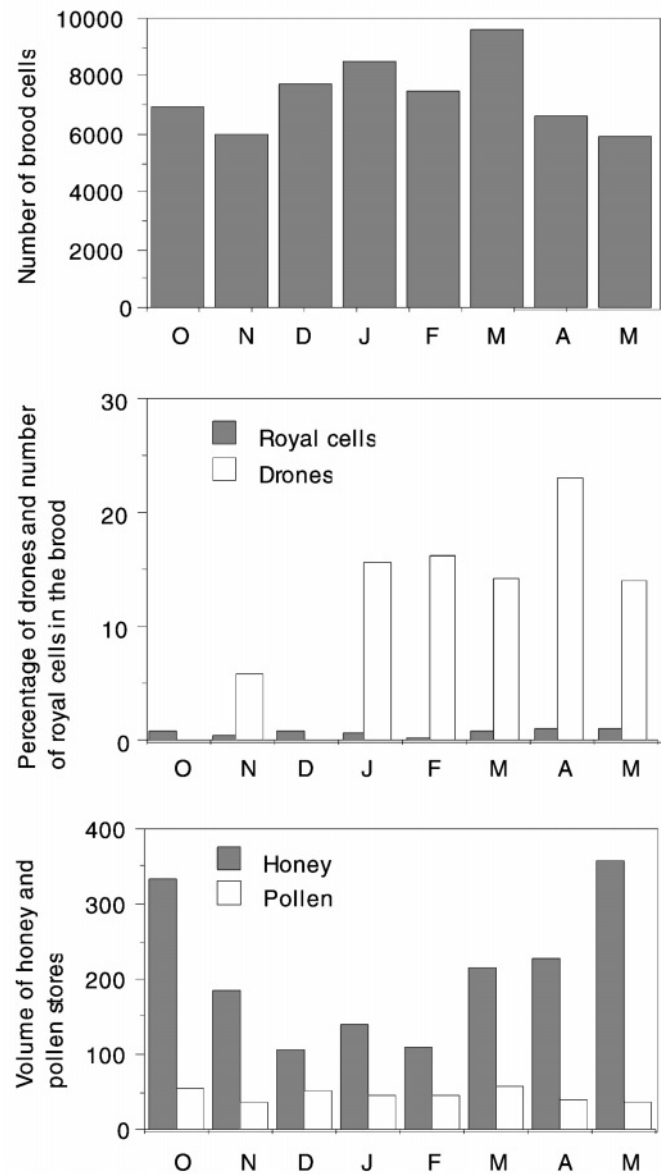


Figure 3. Average number of brood cells (top), percentage of drone producing cells and number of royal cells in the combs (center), and the average volume of honey and pollen stores in cubic centimeters (bottom), recorded at three weekly intervals, between October 1994–May 1995, and October 1995–May 1996, in 21 nests of *Tetragonisca angustula*

each). The amount of pollen stored was not significantly correlated to the production of drones nor royal cells.

Discussion

Nest founding

Colony multiplication started with the finding and preparing of a new nesting site by scout bees. We found for *T. angustula* that this took as long as 13 days or as short as two days (case

8) before the swarm arrived, the latter being the shortest observed for any stingless bee species so far (Inoue et al., 1984; Nogueira-Neto, 1954; Wille and Orozco, 1975). It was found that two potential nesting sites may be cleaned and prepared simultaneously. The criteria by which finally is chosen for one nesting site or the other are not clear. The odour of cerumen present in a cavity might attract scout bees, and the material present might mean an economy in labour and resources (Inoue et al., 1984; Michener, 1946; Nogueira-Neto, 1954). In our study two out of four nest foundings observed were in boxes which had been occupied by another colony of the same species before.

The distance between mother and daughter nests found so far varied from 15 m (Inoue et al., 1984) and 50 m (Terada, 1972) up to 300 m (Nogueira-Neto, 1954). We found very short distances for *T. angustula*, 2.10 m and 5 m. In one case workers that transported cerumen stayed away for more than an hour, indicating a great distance between mother and daughter colony.

Relation between mother and daughter colony

In accordance with what was found for *Frieseomelitta varia* (Terada, 1972), the transport of cerumen is most intense on the day of the virgin queen's arrival at the filial nest, especially during the two hours following upon her arrival. In case of swarm 1, no more transport of building material was observed five days after founding. From our data it is not clear if this also meant the rupture of the mother – daughter nest relation, because transport of honey and or pollen in the honey crop may have taken place for a longer period. Wille and Orozco (1975) found that pollen was collected in the field by *Trigona cupira*, now called *Partamona bilineata*, during the first three months of founding, after which it was transported from the mother nest in the corbiculae, and not, as was found for *T. angustula*, *Nannotrigona testaceicornis*, *Plebeia droyana* and two *Melipona*, as a fluid suspension in the crop (Nogueira-Neto, 1954; Moure et al., 1958). Pollen transported as a suspension in the crop cannot be stored anymore and can serve only for cell provisioning or as food for bees (Sommeijer and De Bruijn, 1994). We also found that pollen was not transported until after the gynes arrival at the new hive. No pollen storage pots were present until then. The transport and collection of pollen not until after the establishment of the swarm in the nest, might be a predation risk reducing strategy. Storage of pollen long before the brood production starts increases the chance of predation. Pollen is known to attract phorid flies and ants (Roubik, 1989). Occasionally honey was transported to the filial nest a few days before a gyne was present in it. For *T. laeviceps* and *Partamona bilineata* no transport of food into the new nesting cavity was found before the swarms had arrived (Inoue et al., 1984; Wille and Orozco, 1975).

Generally spoken it can be concluded that the amount of resources transported to the daughter nest was very small compared to the stores in the mother colony (Inoue et al., 1984).

The swarming colony

Swarms of *Hypotrigona*, *T. laeviceps* and *F. varia* consisted of between 280 and 1300 workers (Darchen, 1977; Inoue et al., 1984; Terada, 1972). We found between 500 and 1000 workers in the recently founded colonies. In case 1 some 700 bees stayed in the filial nest, although initially more workers were involved in the transport of resins and cerumen from the mother colony. After the first night many workers returned to the mother nest the next morning. Based on the assumption that adult population sizes of stingless bee colonies seldom exceed two-third of the brood population sizes (Roubik, 1983), the number of adults of this swarming colony can be estimated at a maximum of 10,000 bees. This means that the final investment of the colony in workers for the swarm was less than ten percent. Inoue et al. (1984) discovered that a mother colony of *T. laeviceps* invested about 30% of her adult population in the daughter colony.

We found that one single gyne left the mother colony to the filial nest. We observed twice that the virgin queens left the mother colony prior to swarm departure. This means that workers that participate in the swarming process communicate to the virgin queen about the location of the new nest site. This is very different from *Paratrigona subnuda* (Engels and Imperatriz-Fonseca, 1990) and *Scaptotrigona postica* (Kerr et al., 1962) where workers departed together with more than one gyne from the nest. Also in *F. varia* one single gyne left with the swarm to the new nest (Terada, 1972).

All nuptial flights we observed were from the filial nest. It is generally accepted that only virgin queens leave the mother colony (Imperatriz-Fonseca and Zucchi, 1995; Imperatriz-Fonseca et al., 1998; Nogueira-Neto, 1954; Sakagami, 1982; Terada, 1972).

The development of the daughter colony after the mating of the gyne was found to be fast. In the newly established colony of case 8 it took only 2 days after the queen had mated before oviposition started, in other cases egg-laying did not start until after approximately one week. These findings are in accordance with the former observations of the start of egg-laying by *T. angustula* of five to six days (Moure et al., 1958).

Reproductive effort of T. angustula

For stingless bees the reproductive effort is basically indicated by three parameters: the investment of the mother colony in the workers that swarm to the daughter colony, the amount of resources transported from the mother to the daughter colony, and the length of the dependence of the daughter colony on the mother nest (Inoue et al., 1984).

A length of dependence of 36 days, as we concluded from the cerumen transport by one colony, was quite short if compared with half a year for *P. bilineata* (Wille and Orozco, 1975), and long if compared with 2–3 days for *T. varia* (Terada, 1972). Another observation of a half year dependence of *T. angustula* (Nogueira-Neto, 1954) illustrates the great variation even within species. The length of depen-

dence may vary with the number of bees in the new nest and the abiotic conditions. During the period of dependence, the mother colony cannot produce another swarm.

The transport of resources from the mother colony consisted mainly in cerumen, and very little in food. Pollen was collected actively in the field by several swarms, which was also found for *T. laeviceps* (Inoue et al., 1984) and *P. bilineata* (Wille and Orozco, 1975).

Between 500 and 1000 bees were invested in the daughter colony. The total investment in bees is not so high and less than the 30 percent of the adult population as was found for *T. laeviceps* (Inoue et al., 1984). In *Apis mellifera* about 50% of the workers leave with a swarm (Michener, 1974).

Condition of swarming colonies

It is not known under what intranidal conditions, concerning adult and brood population sizes and food stores, a stingless bee colony may swarm. We found that the colonies of *T. angustula* that came to swarming had 20 to 50% more brood cells and similar to more than double honey and pollen stores if compared with the data for non-swarving colonies in the same period. Since pollen is the major component of the larval food, the surplus availability may have been a key factor in the prosperous development of the population of these colonies. We found that in 13 out of 21 colonies at least once during the study period no pollen stores were present, and assumed that this could have represented a limiting factor in the development of these colonies.

The production of gynes and drones in the swarming colonies was similar as for the non-swarving colonies. For *F. varia* it was found that three to six virgin queens were produced in the mother colony during the swarming process (Terada, 1972).

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