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Observations on the founding of a new colony by Trigona cupira (Hymenoptera: Apidae) in Costa Rica

by

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ABSTRACT: New colonies of *Trigona* (*Partamona*) *cupira* Smith, the most common bee in Mesoamerica, are founded in progressive stages and not in one swarming as those of the honey bee, as observed in Costa Rica. Pollen was collected in the field during the first three months, and not transported from the mother nest. Daily observations during six months showed that while the ambient temperature fluctuated between 15 and 28 C, and between 15 and 46 C on the outside of the nest proper, the temperature in the brood chamber was almost constant (23-29 C). Although the connection between the two nests lasted six months, the longest recorded among the Meliponidae, dependence of the daughter nest during that period was usually less than 50 % and in some instances less than 10 %.

The present paper summarizes six months' observations on the formation of a new colony of the most common bee in Mesoamerica, *Trigona* (*Partamona*) *cupira* Smith.

Relatively little is known about the founding of new colonies among the stingless bees. SPINOLA (11) was the first to suspect, in 1840, that new colonies were formed in progressive stages. This was stated quite clearly, almost at the end of his paper, in the following paragraph: "Le défaut d'espace nécessitera l'émigration; mais, comme il se fera sentir aux premiers individus qui ne sauront ou se placer a leur aise, l'émigration pourra etre lente, successive, pour ainsi dire insensible, et elle ne sera accompagnée d'aucune des circonstances éclatantes qui signalent les essaims de nos *Abeilles*." Although gradual colony founding was actually observed by NOGUEIRA-NETO during the years of 1947 to 1951 (7), his observations were not published until 1954 (8).

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This author can be regarded as the real discoverer of this method of founding new nests, so different from that of the honey bees. Further observations on this matter were made at about the same time by KERR (3), KERR *et al.* (5), and more recently by JULIANI (2) and TERADA (12). The species of stingless bees on which these observations were made are the following:

Trigona (*Plebeia*) *mosquito* Smith
T. (*P.*) *julianii* Moure
T. (P.) *droryana* Friese
T. (*P.*) *schrottkyi* Friese
T. (*Nannotrigona*) *testaceicornis* Lepeletier
T. (*Scaptotrigona*) *postica* Latreille
T. (*Tetragona*) *varia* Lepeletier
T. (Tetragona) *jaty* Smith
T. (*Trigona*) *hyalinata* Lepeletier
Melipona fasciata melanoventer (Schwarz)
M. favosa orbignyi Guerin

To summarize their findings, we can recognize from their data the following steps:

1) When a colony of stingless bees is ready to form a new nest, several bees undertake the task of finding an appropriate nest site. These scouts seem to prefer a place formerly occupied by another stingless bee nest and not too far from the mother nest, usually no more than 300 m away.

2) As soon as the scouts have found an acceptable site, they start sealing up all the cracks and holes, leaving only one as the entrance, which can be simple, funnel-shaped, or a tube, according to the species. The construction of the entrance appears to be the most important of the early steps, at least in *Trigona* (*Scaura*) *Latitarsis* Friese (13), which establishes its colony in an active termite nest. The material used to seal the nest and to make the entrance is brought from the mother nest.

3) Bees then start to carry cerumen, wax, pollen and honey from the mother nest. At this time more bees join the new nest.

4) In a few days males start arriving at the daughter nest, possibly from the mother colony as well as from other nearby colonies. The males do not participate in building the new nest but just fly around or alight on it or on vegetation close by.

5) When the new nest is furnished, and there are enough workers and males, the virgin queen arrives, accompanied in some cases by a great number of workers and males. This phenomenon has been reported by Peckolt (SCHWARZ, 9). KERR, *et al.* (5) have shown that in many cases more than one virgin queen flies from the mother colony to the new one,

6) The mating of a stingless queen bee was observed for the first time by KERR and KRAUSE (4) in *Melipona quadrifasciata quadrifasciata* Lepeletier in a nuptial flight of 4.5 minutes. It seems logical that the nuptial flight of any species should vary considerably, since it depends on the distances of the mating flights, behavior of the males, and accidents during the flight. In *Melipona quadrifasciata anthidioides* Lepeletier and *Melipona quinquefasciata* Lepeletier, "Four nuptial flights had an average duration of 78 min. 18s. The shortest one was 33 min. long and the longest 102 min." (SILVA *et al.*, 10: 128). The queen arrives at the nest with the whole genitalia of the male attached to the vagina; apparently all the stingless queen bees can be inseminated only once in a single mating flight (KERR, *et al.*, 5). After a virgin queen is successfully mated, and if there are more virgin queens in the nest, those remaining may be imprisoned in isolated waxy cells, where they eventually die, as observed in T. *jaty* (5) and other species (1,2), but this is not characteristic of all the species.

7) After 5 to 30 days, the queen starts laying eggs (3). The connection between the mother and daughter nests can be maintained during weeks and even months and is only severed when the new colony has all the necessary elements for independence.

In the present study the connection between the mother and daughter nests lasted six months, the longest recorded for any stingless bee.

A doubtful connection of six months was reported by NOGUEIRA-NETO (8) in *T. jaty* in an attempt to colonize in an electric meter box, from August 19 to November 21, 1947. During all this time (three months) the bees did not build much, except for deposits of cerumen, an unfinished involucrum and an empty pot. At the end the bees abandoned their efforts, which can be explained by the frequent opening of the box (2). On February 29, 1948, however, a new colony with 13 combs and 30 food pots was found in this same box.

MATERIAL AND METHODS

This study was favored by unplanned happenings. The whole sequence of events started a few months before April of 1972, when the senior author took a nest of *Trigonia (Scaura) latitarsis* to the back yard of his house. The nest, as is usual in this species, was located inside of a live nest of *Nasutitermis* sp. A week later, however, all the termites died, and later on all the bees also perished. Notwithstanding, the empty nest was left where it was originally placed (Fig. 1). Several weeks later, the first scout bees of *T. cupira* were observed inspecting the abandoned nest, which was soon occupied by a new colony. The mother nest, 110 m away, was found two days later.

All the observations were made outside of the nests, and no endeavours were made to open them. The opening of nests in formation may cause the bees to abandon them, as has been recorded by JULIANI (2). The observations were made from April 3 to October 21, 1972.

Daily observations were carried out during April and May, and during June and July only relatively few days were spent in the study, mainly to avoid many routine repetitions. An average of ten days in each of the following months (August, September, October) was spent in observations.

During the study 419 bees were marked with model airplane paint, to investigate some details of the colonization. During the whole study we used two waterproof transceivers (walkie-talkies). One of us (A.W.) stayed at the daugther nest while the other was at the mother nest. A soil thermometer was placed well down in the center of the new nest (Fig. 2) to obtain general data on the fluctuations of inside temperatures. For outside temperatures a very accurate infrared field thermometer was used.

SEARCHING AND SEALING ACTIVITIES

On April 3, at noon, the first group of scout bees of *T. cupira* was observed inspecting the abandoned *Scaura* nest (Fig. 3). There were slightly more than 100 bees, none carrying any material. Late in the afternoon most of the beees were moving in and out actively through all the cracks and holes.

On the second day there were many more bees at work, carrying yellowish cerumen, resin and mud. The sealing of the *Scaura* nest had begun. Most of bees were busy around the large cracks encircling a couple of branches that went through the original termite nest (Fig. 4). Others were closing minor cracks and holes.

On the third day most of the openings had been sealed and two entrances were constructed, one (closed three days later), 12 mm in diameter, at the base of the major tree branch (Figs. 5, 6); the other, 3 cm from the first entrance, corresponded to the former *Scaura* exit, but it already had the general appearance of a typical *T. cupira* entrance (Figs. 7, 8); it was 7 cm long by 2.5 cm wide. This entrance was further modified four days later (Figs. 9-12) by the construction of outside swellings of mud and resin around the inferior and posterior areas (Figs. 11, 12).

Apparently still more bees had joined the new colony during the third day, and there were more workers carrying materials, mostly cerumen. In general, the bees became much better organized and showed their typical aggressive behavior.

In the afternoon of the third day the mother nest was found, 110 m away (Figs. 13-16). Actually three nests of *T. cupira* were located only a few feet apart from each other. It was rather easy to determine which was the mother nest by the bees emerging with cerumen and other construction materials on their hind legs. Later, when several bees were marked, the bees coming out of the mother nest could be easily identified on arrival at the daughter nest.

ARRIVAL OF THE QUEEN AND MALE SWARMING

The first few males were seen on April 5, resting on the major tree branches of the nest (Fig. 18), on neighboring rose bushes (Fig. 17), and close to the smaller entrance, which was still open (Fig. 19); apparently they were premature males that follow the workers.

At night, as well as in the morning of April 6, only one male was seen (Fig. 20). However, at 11:55 AM a very interesting phenomenom was observed; an estimated 800 bees were seen flying around the new nest, it looked like a real swarming (Figs. 21, 22). This type of behavior was apparently what led several investigators, like Peckolt, to believe that the founding of a new colony was accomplished by a true swarming like that of the honey bee.

The swarm was composed mostly of males, but there were also many new workers resting on the nest (Fig. 23). Unfortunately no one was at the mother nest at that critical moment, and when checked, nothing unusual was observed, except for some bees carrying construction materials.

The swarming males kept flying around the new nest for an hour, then rested on the major tree branch of the nest (Fig. 24-26), and on the neighboring rose bushes (Fig. 27).

At 2:00 PM of April 6, 229 males were left at the new nest; at 3:45 PM there were only 140. Next day (April 7) there were 108 males; on April 8 there were 15 males; on April 9, two males; and on April 10, only one male was seen and thereafter no more were observed.

It seems reasonable to assume that the male swarming and the arrival of more workers were the direct result of the queen's arrival. Unfortunately, the queen could not be easily differentiated among so many bees, nor was the nuptial flight observed. Assuming that the queen was among the swarming bees, it would mean that she arrived four days after the beginning of colonization. According to KERR *et al.* (5), the queen of *Trigona* (*Scaptotrigona*) *postica* arrives five days after colonization begins.

CONNECTION BETWEEN THE MOTHER AND DAUGTHER NESTS

Progressive transportation of construction materials and food from the mother to the daughter nest is fundamentally different between the Meliponini and the Apini. Not all the materials, either for construction or for food, used during the early stages of the new colony by *T. cupira,* came from the mother nest. It was quite evident, even from the very beginning, that the bees were also collecting material elsewhere. During the first three months *T. cupira* was never observed to transport pollen from the mother nest, but on April 7 they were seen collecting it in the field. During July, however, bees were seen transporting pollen from the mother nest for the first time. On July 7, for instance, from 7 to 8 AM 20 bees were observed coming out of the mother nest carrying pollen on the hind tibiae. At the same time 29 bees arrived at the daughter nest with pollen (some marked bees came from the older nest). From 8 to 10 AM ten bees with pollen arrived at the daugther nest, five from the mother nest. These and further observations showed that during and after July the bees collected pollen from the field as well as from the mother nest. According to KERR (3), NOGUEIRA-NETO (8), and MOURE *et al.* (6), pollen from the mother nest is carried in a fluid suspension in the crop by *Trigona (Tetragona) jaty*, *T.* (*Nannotrigona*) *testaceicornis*, *T.* (*Plebeia*) *droryana*, *T.* (*Plebeia*) *schrottkyi*, *T.* (*Trigona*) *hyalinata*, *Melipona fuscata melanoventer* and *Melipona favosa orbignyi*; *T. cupira* may also use the same method during the first three months, although the few dissections made during this study do not confirm this hypothesis.

During the first days of colonization the bees logically transported mostly construction material. Apparently most of these materials, like cerumen, resin, and gum or sticky material were collected from the mother nest and mud from the field. Later it was obvious that the bees gathered construction material not only from the mother nest, but also from the field, while some materials were collected exclusively in the field. On April 5, for instance, several workers were seen collecting pieces of rose leaves (Figs. 28-31) found close to the new nest. The collection of material from the field became quite evident after May 13 when one of us (E.O.) reported (8 to 8:10 AM) three bees coming out of the mother nest with greenish cerumen, whitish cerumen, and transparent gum. Meanwhile A.W., at the daughter nest, reported the entrance of these three specific bees, plus ten more carrying resin, mud and other material. From 8 to 9 AM only three bees were seen coming out of the mother nest with construction material while 22 were seen bringing material to the daugther nest. From similar observations throughout the study, it was evident that more than 50 per cent of the material carried to the daughter nest was not from the mother nest. The amount of material taken from the original nest varied markedly from month to month, and even from week to week.

As would be expected, the connection between both nests was very strong throughout the first month of colonization. From April 4 to 15, for instance, an average of 6.1 bees per minute came out of the mother nest carrying construction material. However, during the last half of April and the beginning of May the average number of bees started to fluctuate between 20 and 15. Table 2 summarizes the observations made. During the second half of May and the whole month of June the connection between both nests was extremely weak, with an average of four bees every two hours carrying material from the mother nest (0.16 bees/5 min); apparently the new nest was becoming independent. This phenomenon changed, however, in a very spectacular way during July when the connection strengthened considerably, with an average of 40 bees coming from the mother nest every hour (3.3 bees/5 min) with material for the new nest. At this time the bees also started to collect pollen from the mother nest, or at least to carry it externally in the corbiculae. This type of connection was more or less maintained until the last half of September, when the nests became independent from each other.

The average time spent by the bees flying between both nests (110 m) was 31.7 seconds (range 25-45 seconds, N=36). At the end of June a small corn field, about 25 x 40 m, was planted close to the mother nest. On August 22 the plants were 4 m high, increasing the average flight time to 81 seconds between nests (range 60-107 seconds, N=55).

The average time spent in the mother nest loading material was 12.54 minutes (range 10.30-13.40 min, N=15) and 3.78 minutes unloading in the daugther nest (range 2.0-6.0 min, N=16). The bee that spent 2 minutes unloading had a rather small load, while the one which spent 6 minutes had a very large load; loading therefore took three times longer than unloading (see Table 1 for trips made by a particular marked bee).

TABLE 1

Activity of a particular bee (marked red on the thorax) between the mother and daughter nests (April 13, 1972; 7:55 to 9:38 AM)

Time (min) in mother nest (loading)	Amount of cerumen carried	Duration (sec) of flight to daughter nest	Time (min) in daughter nest (unloading)	Duration (sec) of flight to mother nest
12	normal	30	3	30
10.30	normal	30	3.45	30
11.15	normal	30	3	30
13.40	very large	30	6	30
11.58	very small	30	2	30
12	small	30	3	30
3.38	none	30	stayed	

OBSERVATIONS ON THE GENERAL BEHAVIOR OF THE BEES IN THE DAUGHTER NEST

From the very beginning about ten bees usually stayed around the ear-shaped entrance of the nest (Fig. 12), sporadically making short semicircular flights. These bees, regarded as sentinels or guards, behaved quite differently from the others; they were ready, at the slightest provocation, to defend the nest, presumably releasing alarm pheromones. One of the sentinels was marked and its behavior observed: it lingered at the entrance platform, and frequently flew around the nest for a few seconds and then returned; sometines it went inside the nest but promptly reappeared. This behavior was repeated over and over. At about 5.00 PM all the guards began to retreat toward the inner part of the ear-shaped entrance platform, and half an hour later only a few bees could be seen at the bottom of the entrance. All these observations were made at 1.7 m from the nest to avoid any possible disturbance.

We may speculate as to when the queen started to lay eggs and when the first bees hatched. We know that the workers took possesion of their new nest on April 3, we presume that on April 6 the queen arrived, and that on April 7 the bees first started to transport pollen from the field to the new nest. We may assume (3) that the queen began to lay eggs a few days later, about April 15. On May 31 the first callow, or newly emerged adult bee was seen to come out of the nest. Although we do not know exactly when the egg which gave origin to that callow was laid, we can assume, with some approximation, that the life cycle from egg to adult takes between 30 to 40 days.

The longevity of the adults is apparently greater than that of the honey bee. For instance, a fully mature field bee was marked green on the thorax on April 8; it was found again on May 16, one month and eight days later.

Pollen collecting trips to the field during the first three months had the following duration (in minutes): 8, 5, 4, 4.40, 4.35.

Taking into account only data from the morning, during April there was an average of 32.38 bees entering the daughter nest; on May 12, 13 and 17 the counts were low (average of only 6.65 bees). The highest records were during September, with an average of 84 bees. On September 2, from 9:00 to 9:05 AM, 219 bees were counted coming into the daughter nest with material on their hind legs (the highest recorded during the six-month study).

Data on the total number of bees coming to the nest every five minutes, with or without any material, were obtained only for the months of April and May (Table 3); it is interesting to note the great differences in activity between months: the average during April was of 142.94 bees, while during May it was of 38.30 bees. Note also that if we calculate from Table 2 the total number of bees (including morning and afternoon counts) coming with material to the daughter nest, the average is 30.3 bees for April and only 13 for May. Due to causes we could not discern, throughout May the activity of the bees was much lower than in any other month during our study.

While the fluctuations of the temperature on the outside of the nest (15-46 C) and that of the environment (15-29 C) were very variable, the inside temperature (in the brood chamber) was very constant (Table 4 and Fig. 33) with a minimum of 25 C and a maximum of 29.5 (average 26.5 C). Since the inside temperature was taken with a soil thermometer, there was a question as to its accuracy. However, later investigations with a very precise electric thermometer in the brood chamber of *Melipona flavipennis* gave quite similar results (unpublished data).

TABLE 2

Number of bees carrying material to daughter nest from April to September, 1972

Date		Time	Count*	Date		Time	Count*
Apr.	8	8 AM	5 + 39 = 44	May	26	10:30 AM	7 + 14 = 21
	8	11:15 AM	5 + 27 = 32		26	10:35 AM	0 + 18 = 18
	11	9:10 AM	34		31	7:05 AM	32 + 0 = 32
	11	9:15 AM	37		31	7:15 AM	62 + 0 = 62
	11	11:55 AM	39		31	7:30 AM	41 + 7 = 48
	12	3:10 PM	5		31	7:40 AM	63 + 6 = 69
	14	1 PM	53		31	8 AM	50 + 6 = 56
	15	7:35 AM	45		31	9 AM	28 + 5 = 33
	15	7:40 AM	39		31	10 AM	8 + 3 = 11
	15	7:45 AM	29		31	10:05 AM	9 + 2 = 11
	15	7:50 AM	33		31	1 PM	1 + 1 = 2
	26	9:55 AM	14		31	1:05 PM	1 + 0 = 1
	26	10 AM	3 + 15 = 18		31	1:10 PM	2 + 0 = 2
	27	8:35 AM	5 + 23 = 28		31	2:30 PM	0 + 0 = 0
	27	8:40 AM	4 + 25 = 29				
	27	2:20 PM	1 + 5 = 6	June	7	7 AM	10 + 4 = 14
					7	7:25 AM	24 + 5 = 29
May.	5	7:35 AM	4 + 24 = 28		7	8:35 AM	30 + 6 = 36
	5	2:05 PM	1 + 1 = 2		16	7:20 AM	25 + 5 = 30
	5	2:35 PM	1 + 0 = 1		16	7:40 AM	17 + 2 = 19
	12	9:45 PM	0 + 3 = 3		16	9:05 AM	12 + 3 = 15
	12	9:50 AM	1 + 4 = 5				
	13	5:35 AM	9 + 0 = 9	July	7	7:30 AM	20 + 3 = 23
	13	5:40 AM	9 + 1 = 10		7	8:30 AM	9 + 3 = 12
	13	6:40 AM	5 + 0 = 5		7	8:45 AM	4 + 1 = 5
	13	7:05 AM	0 + 3 = 3		7	9:40 AM	4 + 0 = 4
	13	7:35 AM	0 + 7 = 7				
	13	8 AM	0 + 6 = 6	Aug.	3	8:45 AM	45 + 0 = 45
	13	8:15 AM	0 + 2 = 2		22	6:25 AM	8 + 0 = 8
	13	8:45 AM	0 + 2 = 2		22	9:10 AM	17 + 2 = 19
	15	5:03 AM	1 + 1 = 2		22	9:20 AM	17 + 6 = 23
	15	5:15 AM	5 + 7 = 12		24	9:55 AM	16 + 4 = 20
	16	5:08 AM	0 + 1 = 1		24	10:15 AM	23 + 0 = 23
	17	5 AM	11 + 1 = 12				
	17	6 AM	7 + 4 = 11	Sept.	2	6:15 AM	3 + 29 = 32
	17	7 AM	7 + 5 = 12		2	7 AM	22 + 71 = 93
	17	8 AM	1 + 7 = 8		2	7:25 AM	22 + 81 = 103
	17	9 AM	2 + 8 = 10		2	8 AM	28 + 96 = 122
	17	10 AM	3 + 4 = 7		2	9 AM	73 + 146 = 219
	17	11 AM	2 + 4 = 6		2	10 AM	60 + 96 = 156
	17	12 M	1 + 3 = 4		2	11 AM	34 + 84 = 118
	17	1 PM	0 + 0 = 0		16	7 AM	57 + 8 = 65
	17	2 PM	1 + 1 = 2		16	7:50 AM	63 + 8 = 71
	17	3 PM	0 + 0 = 0		21	6 AM	4 + 6 = 10
	17	4 PM	0 + 1 = 1		21	6:30 AM	9 + 3 = 12
	17	5 PM	0 + 0 = 0		21	7 AM	32 + 4 = 36
	26	8:15 AM	25 + 0 = 25		21	7:30 AM	59 + 3 = 62
	26	8:40 AM	25 + 0 = 25		21	8 AM	71 + 6 = 77

* A number alone represents the number of bees carrying material in the corbiculae. When three numbers are used, separated by + and = signs, the first number represents the bees carrying pollen, the second, the bees carrying construction material, and the third is the total.

TABLE 3

Total number of bees coming to the daughter nest during five minute periods in April and May, 1972

Date		Time	Number of bees	Date		Time	Number of bees
April	8	11:40 AM	102	May	5	7:30 AM	136
	9	9:30 AM	134		5	2 PM	38
	11	9 AM	142		5	2:30 PM	44
	11	11:40 AM	145		12	9:30 AM	80
	12	3 PM	33		12	9:35 AM	61
	13	7:45 AM	212		13	6:35 AM	57
	13	7:55 AM	219		13	7 AM	43
	13	8 AM	220		15	5:30 AM	49
	13	10:05 AM	107		15	6:10 AM	42
	14	7:35 AM	181		17	5:15 AM	50
	14	8 AM	190		17	6:15 AM	53
	14	12:45 PM	96		17	7:15 AM	39
	26	9:45 AM	124		17	8:15 AM	36
	26	9:50 AM	129		17	9:15 AM	42
	27	8:30 AM	211		17	10:15 AM	42
	27	1:45 PM	97		17	11:15 AM	27
	27	2:15 PM	88		17	12:15 PM	13
					17	1:15 PM	0
					17	2:15 PM	7
					17	3:15 PM	6
					17	4:15 PM	7
					17	5:15 PM	5
					17	5:50 PM	4

TABLE 4

Inner nest temperature fluctuations during May, 1972

Day	Time	Temp. C.	Day	Time	Temp. C.	Day	Time	Temp. C.
5	7:30 AM	26.5	9	9:30 AM	28	17	11 AM	28.2
5	12:15 PM	27.5	13	5 AM	26	17	12 M	28.5
5	2 PM	27.5	13	6:20 AM	26	17	1 PM	28.8
5	9:15 AM	27	13	10 AM	27	17	2 PM	28.5
7	3:15 AM	26	14	8:20 AM	27	17	3 PM	28.5
7	5:35 AM	25	15	3:30 AM	25.3	17	4 PM	28
7	9:15 AM	28	15	4:55 AM	25	17	5 PM	27.5
7	10:40 AM	28.5	15	6 AM	25	17	6 PM	27.5
7	1:40 PM	29	15	7 AM	25	17	7 PM	27.4
7	3:30 PM	28.5	15	10:30 AM	28.5	17	8 PM	27.3
7	4:40 PM	28	16	7:30 AM	27	17	9 PM	26.7
7	5:30 PM	27.7	16	12 M	29	17	10 PM	26.5
7	6:30 PM	27.7	17	2 AM	26.2	17	11 PM	26.3
7	8:30 PM	27.5	17	3 AM	26	18	0	26.3
8	4:20 AM	26.3	17	4 AM	25.5	18	1 AM	26.5
8	7:15 AM	26.5	17	5 AM	25	18	2 AM	26
8	8 AM	27.5	17	6 AM	25.2	18	3 AM	26
8	10:50 AM	28.5	17	7 AM	25.2	18	4 AM	26
8	5:45 PM	27.5	17	8 AM	26.2	19	3:30 PM	29.5
9	5 AM	25	17	9 AM	27.2			
9	7 AM	25	17	10 AM	28			

On September 3 an estimate of the population which was active outside of the nest was made; three days before, 400 bees were captured on arrival, marked and then released. The estimate was made using the following equation:

$$P = \frac{400 \times \text{total number of bees recaptured in five minutes}}{\text{number of marked bees recaptured in five minutes}}$$

This was done three times, from 7 to 8 AM, with the following results:

$$\frac{400 \times 165}{97} = 680\,; \quad \frac{400 \times 171}{95} = 720\,; \quad \frac{400 \times 120}{62} = 774$$

which gave an average of 724 bees.

STUDY OF THE INSIDE OF THE DAUGHTER NEST

On December 1 the daughter nest was opened, eight months after its foundation. The following data were obtained:

Total population of adult bees = 3125
Total number of cocoons (with pupae and prepupae) = 1628
Total number of cells (with eggs and larvae) = 1273
Total number of empty cells = 29
Approximate number of food pots = 228
Space occupied by the nest = 20 × 20 cm
Space occupied by the brood chamber = 12 × 12 cm
Number of laminated batumen sheets = 4 (in some places 5)
Number of involucrum sheets = 3 to 4
For the general architecture of the nest see Figure 32.

CONCLUSIONS

The founding of new colonies among stingless bees is quite different from that of the honey bee, as suggested by SPINOLA in 1840 and actually observed by NOGUEIRA-NETO (8) from 1947 to 1951, and later by KERR (3), KERR *et al.* (5), and JULIANI (2). All these authors had demonstrated that the new colonies are formed in a progressive way, transporting all the necessary material, either for construction or for food, from the mother nest. The connection between the mother and daughter nests can last for weeks and even months.

Although our studies on *T. cupira* agree with those of other authors, we found a few important differences. The most important, in our opinion, was that, while dependence on the mother nest was not as strong as suspected, it was the longest connection recorded for any stingless bee (6 months). It was quite obvious, even from the beginning, that the bees were also collecting material elsewhere. The dependence of the daughter colony was, at its highest, less than 50 per cent; sometimes it was even less than 10 per cent of the total material being brought to the daughter nest on workers' corbiculae.

In *T. cupira* the bees transported all the pollen, from the very beginning, from the field. We are not sure whether they also carried pollen in liquid suspension in the crop, as do other species (3, 6, 8); at least, the few dissections did not show any pollen in their crops. However, three months later, some bees started to collect pollen from the mother nest, which they carried on the hind tibiae.

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RESUMEN

Se resume una serie de observaciones, llevadas a cabo durante seis meses, sobre la formación de una nueva colonia de una de las abejas más comunes de Mesoamérica: *Trigona* (*Partamona*) *cupira*, conocida en Costa Rica con el nombre de arragre.

El 3 de abril de 1972 se notó por primera vez a un grupo de abejas exploradoras inspeccionando un nido abandonado de termitas (comejenes) *Nasutitermes* sp. que antiguamente albergó un nido de *Trigona* (*Scaura*) *latitarsis*. Las abejas pronto tomaron posesión del nido e iniciaron el trabajo de sellar todas las rajaduras y agujeros. Dos días después el nido madre fue encontrado a 110 metros. Al tercer día el nuevo nido ya estaba en buenas condiciones y tenía una entrada bien formada y típica de *T. cupira.* El 6 de abril varios cientos de abejas, la mayoría machos, llegaron del nido madre, y al día siguiente comenzaron a acarrear polen del campo a la nueva colonia. Se supone que la reina llegó con este grupo. Los machos desaparecieron por completo el 14 de abril.

El promedio de tiempo en volar las abejas entre los dos nidos fue de 31.7 segundos. Al final de junio se plantó un área de 25 x 40 m de maíz cerca del nido madre. El 22 de agosto las plantas de maíz tenían una altura de 4 m, y las abejas tenían por fuerza que volar sobre dicha plantación. Por este motivo se hizo otro promedio de tiempo de vuelo, dando como resultado 1.21 minutos. Las abejas tardaron un promedio de 12.54 minutos colectando material del nido madre y 3.78 minutos descargándolo en el nuevo.

Aunque nuestros estudios sobre *T. cupira* son similares a los de otros investigadores sobre especies afines, encontramos algunas diferenicas de importancia. La más interesante fue que, aunque la conexión entre los dos nidos fue muy larga, la dependencia con el nido madre no fue tan fuerte como se esperaba; era bastante obvio, aún desde el comienzo, que las abejas también colectaban material en el campo. La conexión entre ambos nidos fue siempre (exceptuando los primeros días) mucho menos del 50 por ciento y algunas veces menos del 10 por ciento. No obstante, esta conexión duró seis meses, la más larga que se conoce hasta ahora entre los Melipónidos.

Otra diferencia interesante fue que las abejas de *T. cupira* desde el principio colectaban todo el polen del campo y nunca del nido madre. Sin embargo, tres meses después, algunas abejas comenzaron también a colectar polen del nido madre. El transporte del polen del nido madre, a diferencia de lo observado hasta ahora en otras especies, se hizo aparentemente en la forma normal, es decir, sobre las tibias posteriores, y no en el buche en suspeción fluida.

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Fig. 1. Abandoned termite nest formerly occupied by *Scaura.*

Fig. 2. Nest showing a soil thermometer placed well down in the center.

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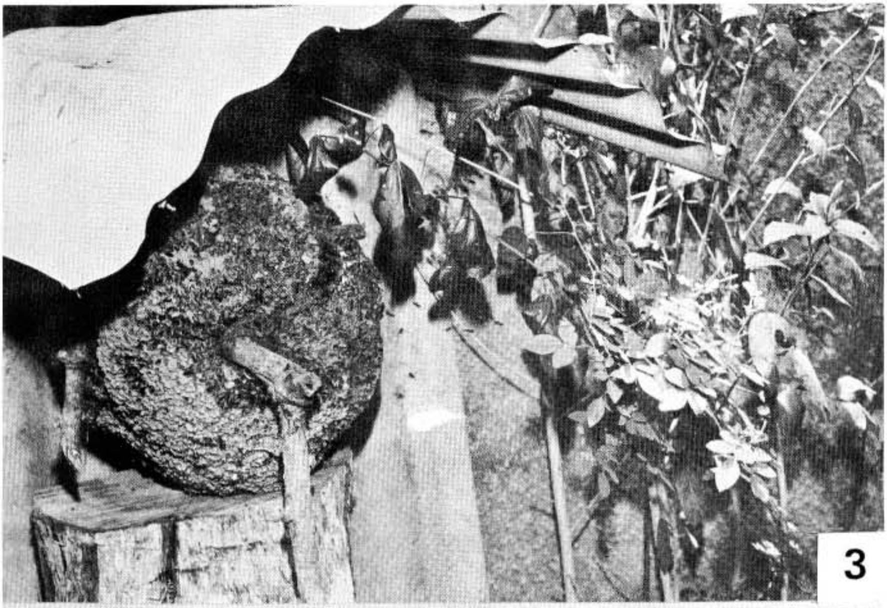
Fig. 3. The first group of scout bees inspecting the abandoned *Scaura* nest.

Fig. 4. Bees sealing the large cracks encircling a tree branch.



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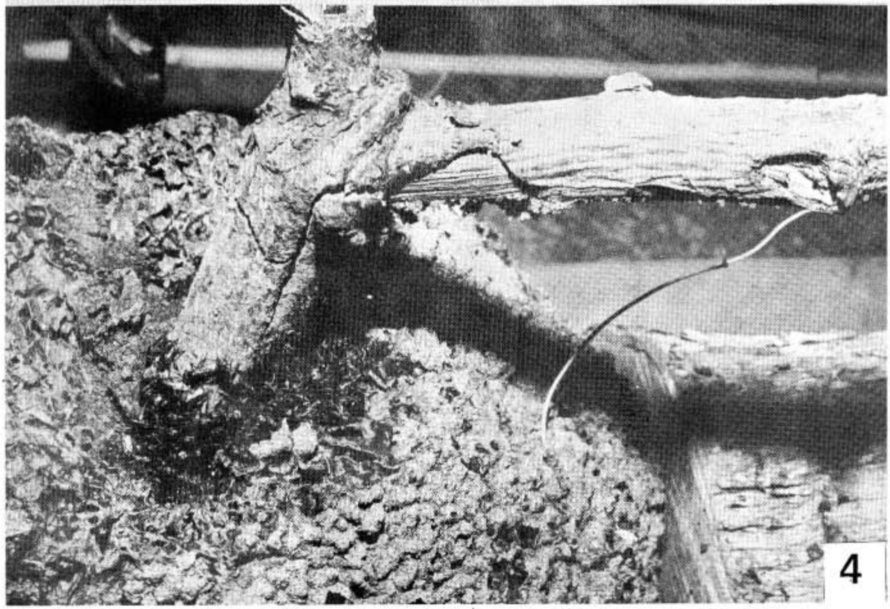

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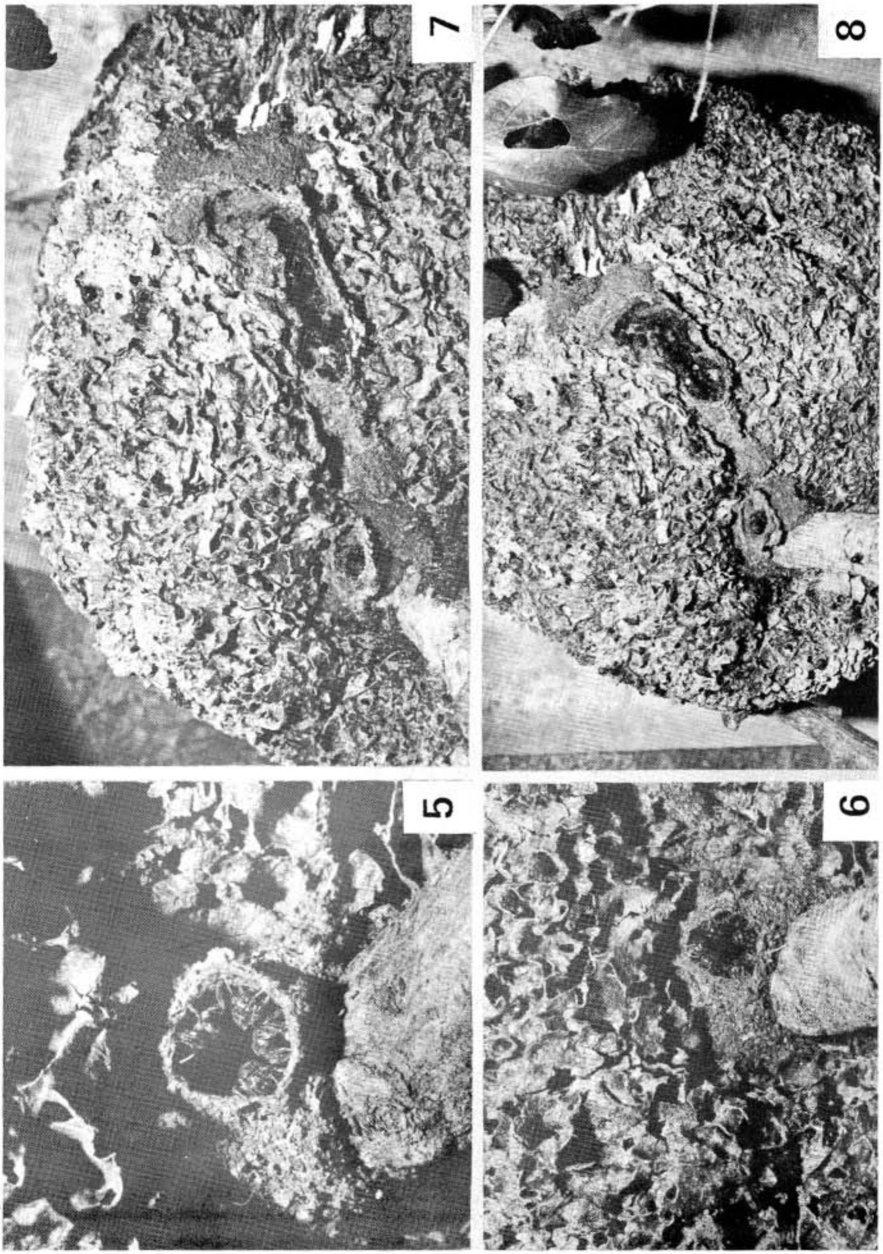
Figs. 5-8 Daughter nest showing two entrances. Figs. 5 and 6 show only the smaller entrance at the base of the major tree branch. Figs. 7 and 8 show both entrances, the largest has the general appearance of a typical *T. cupira* entrance.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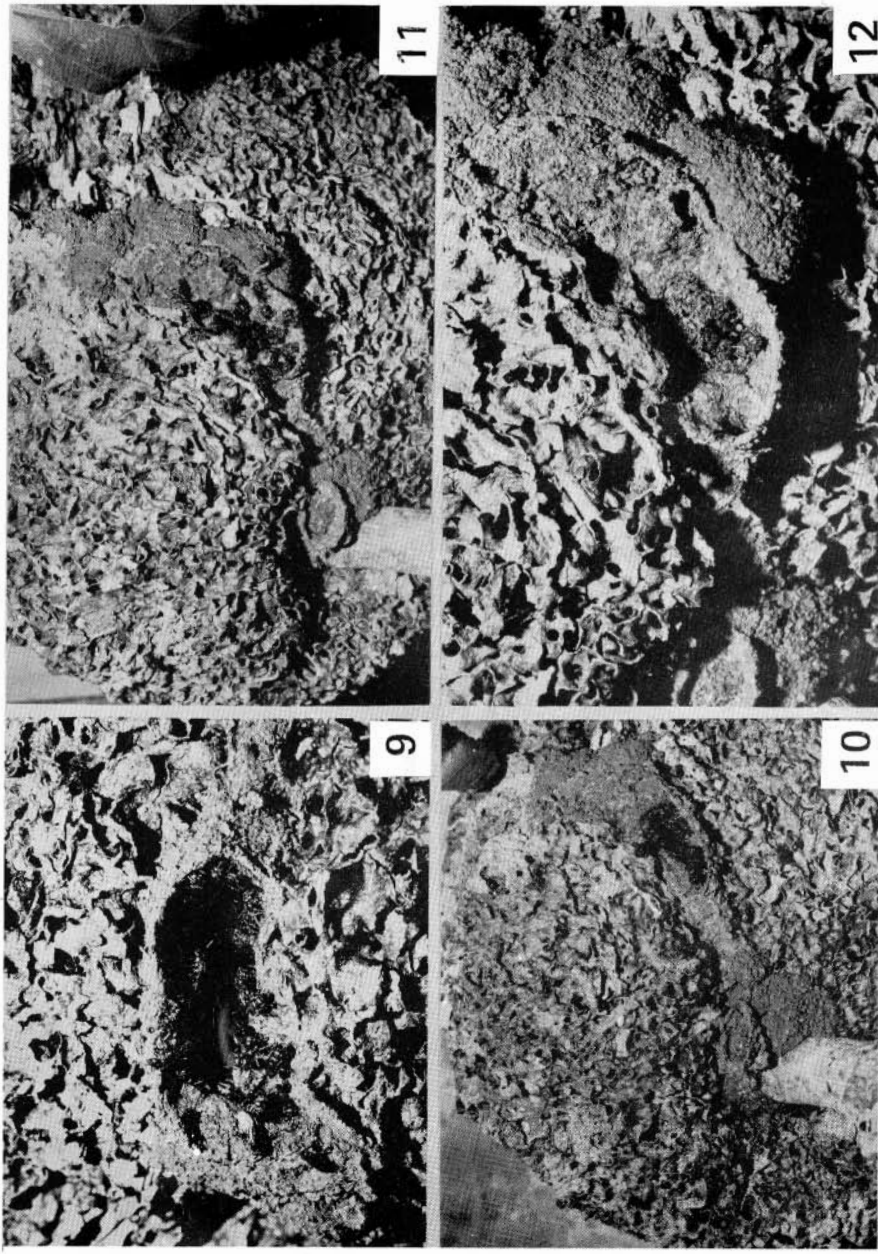
Figs. 9-12. Modification of the main entrance by the construction of outside swellings made of mud and resin. Fig. 9, bees commence modifying the larger entrance. Figs. 10 and 11 represent intermediate stages. Fig. 12 shows the final modification. Note that the smaller entrance, at the base of the major tree branch is already closed (Figs. 10 and 11).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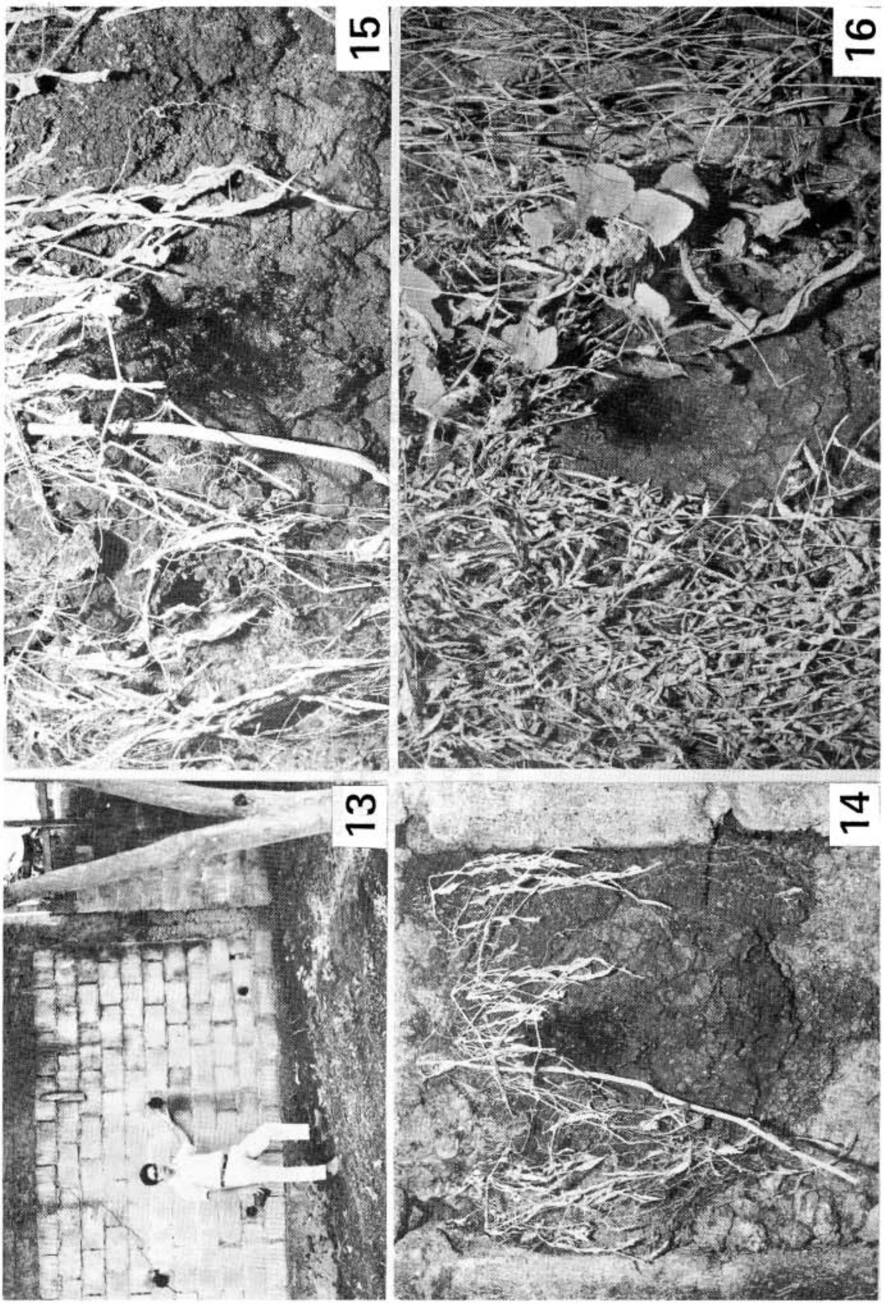
Figs. 13-16. The mother nest. Fig. 13 shows the hole occupied by the mother nest, other holes also contain different nests of *T. cupira.* Figs. 14 to 16 show the entrance of the nest surrounded by vegetation.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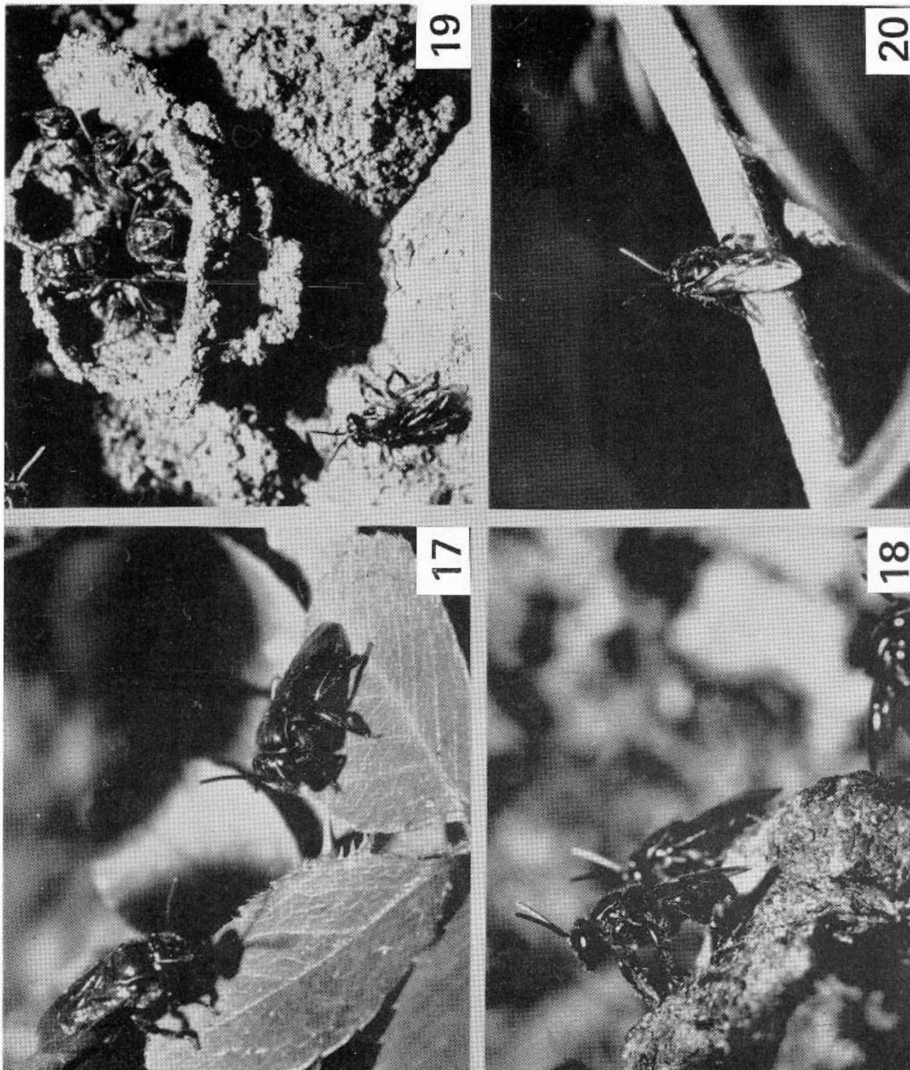
Figs. 17-20. Arrival of the first males; apparently they were premature males that followed the workers. Figs. 17 and 18, males resting on neighboring rose bushes and on the major tree branch. Fig. 19, male close to the smaller entrance, which was still open. Fig. 20, the only male left after the first males disappeared from the daughter nest.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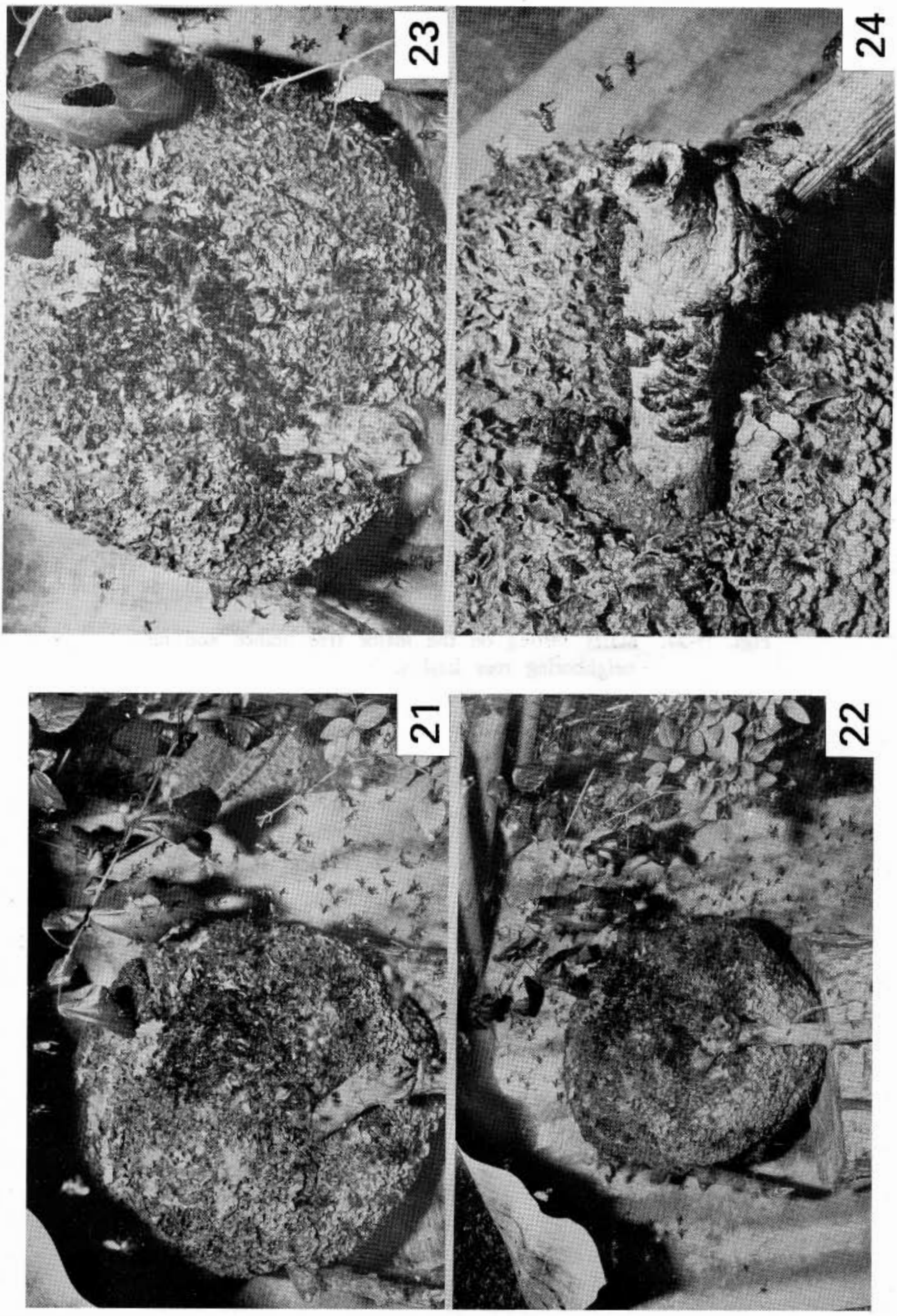
Figs. 21-24. Males and workers around the new nest. Figs. 21 and 22, males swarming around the new nest Fig. 23, the arrival of new workers, resting on the nest. Fig. 24, males flying toward the major tree branch.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Figs. 25-27. Males resting on the major tree branch and on neighboring rose bushes.

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Figs. 28-31. Worker bees collecting pieces of rose leaves near the daughter nest.

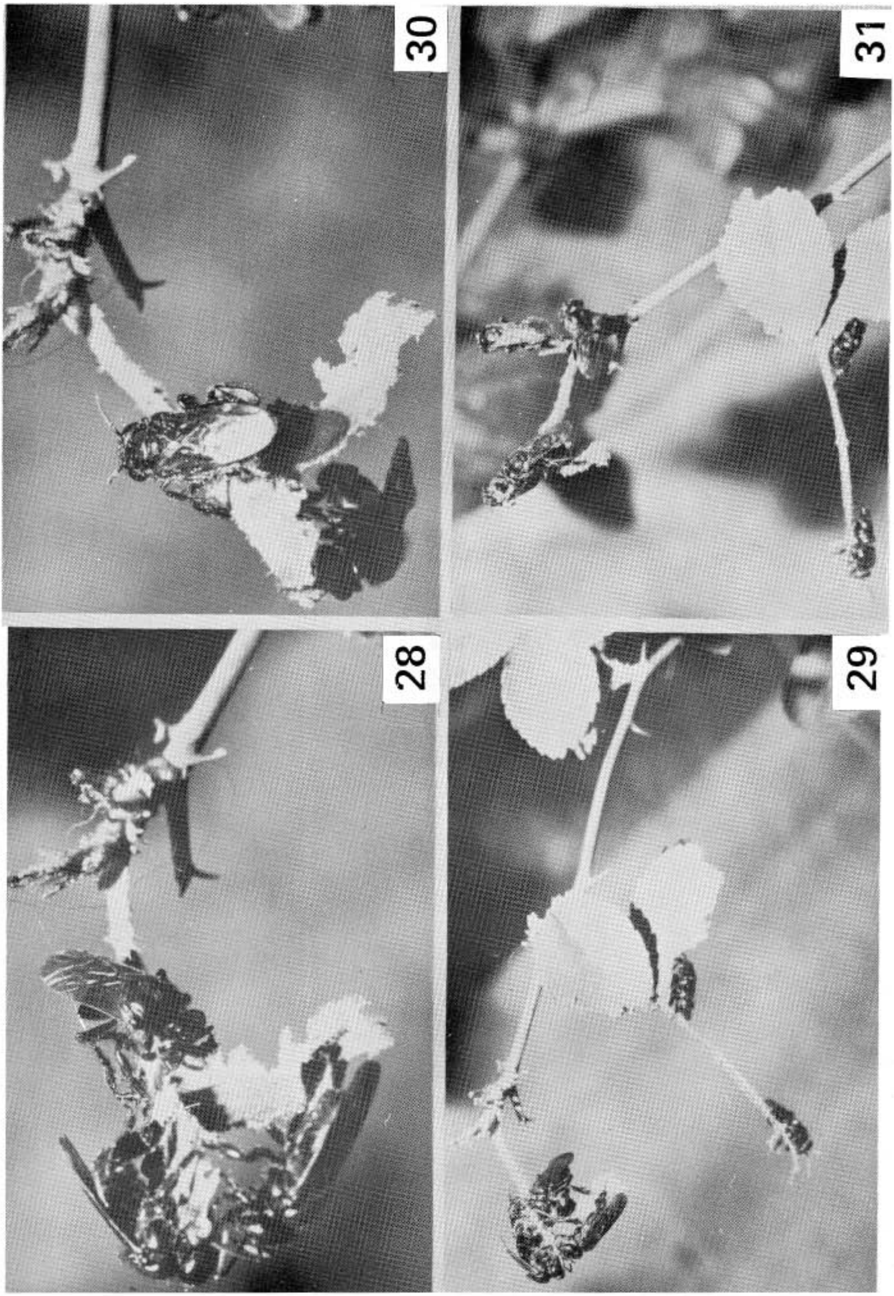
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Fig. 32. *T. cupira*, diagram of nest. Cocoons are drawn with thin lines, cells with thick lines.

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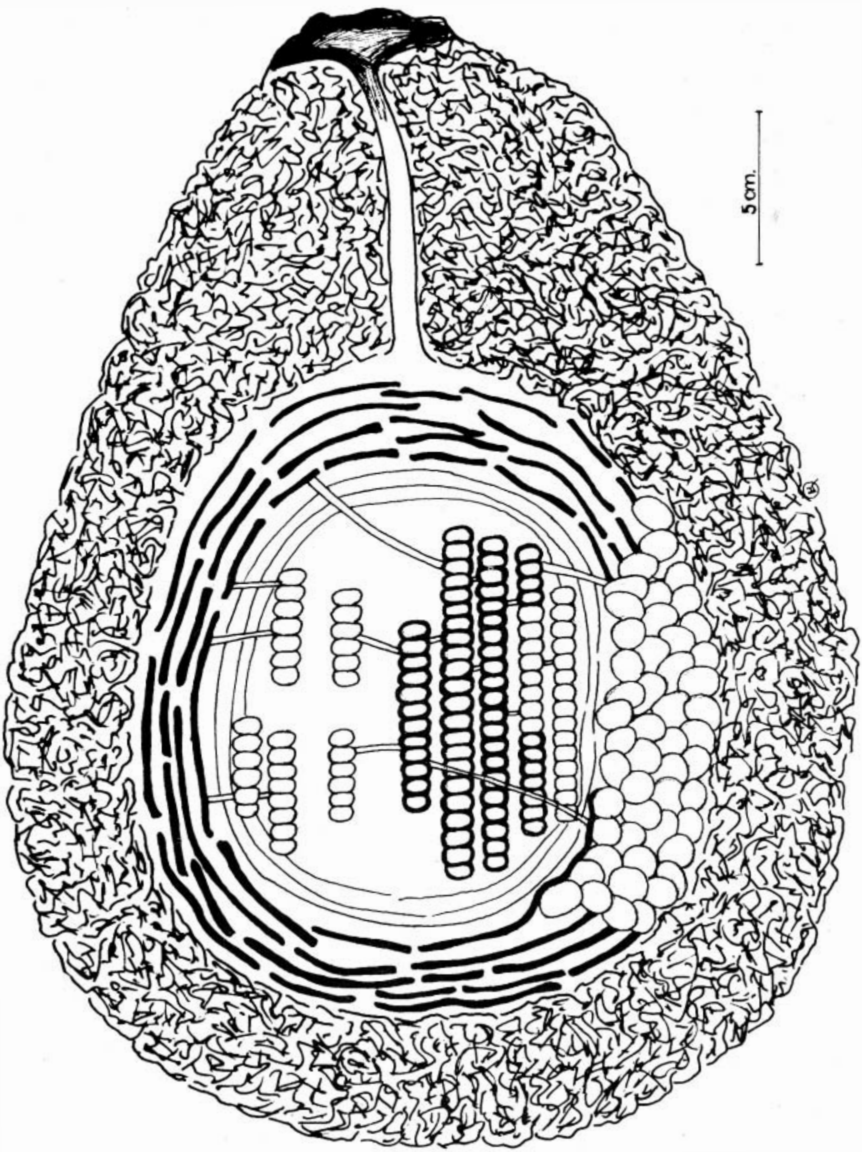
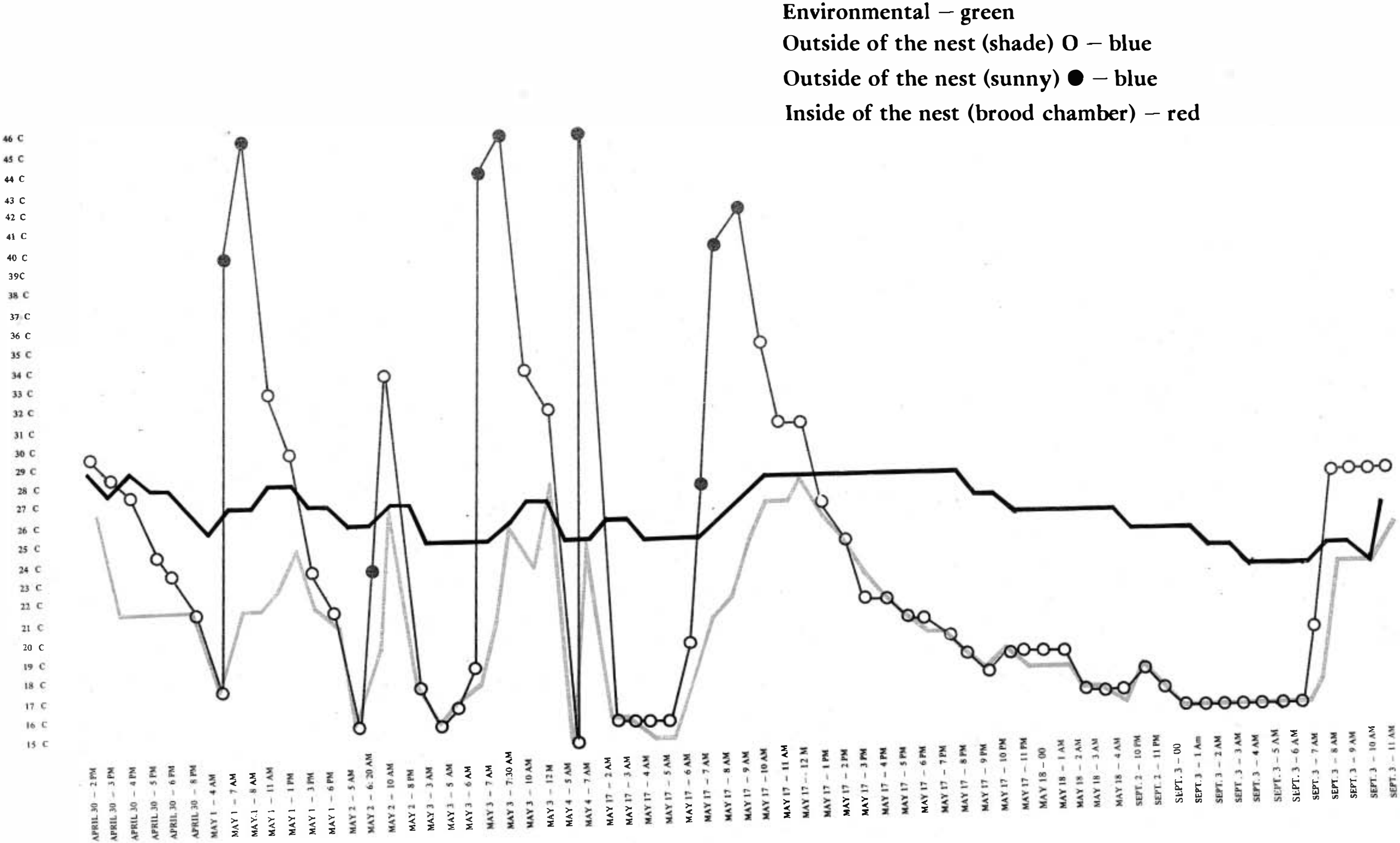


Fig. 33. Graph of temperature fluctuations (Centigrade).


Environmental – green
Outside of the nest (shade) O – blue
Outside of the nest (sunny) ● – blue
Inside of the nest (brood chamber) – red