



# A COMPARATIVE STUDY OF FORAGING BEHAVIOR AND POLLEN RESOURCES OF VARIOUS STINGLESS BEES (HYM., MELIPONINAE) AND HONEYBEES (HYM., APINAE) IN TRINIDAD, WEST-INDIES

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M. J. Sommeijer, G. A. de Rooy, W. Punt, L. L. M. de Bruijn. A COMPARATIVE STUDY OF FORAGING BEHAVIOR AND POLLEN RESOURCES OF VARIOUS STINGLESS BEES (HYM., MELIPONINAE) AND HONEYBEES (HYM., APINAE) IN TRINIDAD, WEST-INDIES. *Apidologie*, 1983, 14 (3), pp.205-224. hal-00890599

**HAL Id: hal-00890599**

**<https://hal.science/hal-00890599>**

Submitted on 11 May 2020

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**A COMPARATIVE STUDY OF FORAGING BEHAVIOR  
AND POLLEN RESOURCES  
OF VARIOUS STINGLESS BEES (*HYM., MELIPONINAE*)  
AND HONEYBEES  
(*HYM., APINAE*) IN TRINIDAD, WEST-INDIES**

M. J. SOMMEIJER\*, G. A. DE ROOY, W. PUNT\*\*, L. L. M. DE BRUIJN

**SUMMARY**

A comparative palynological analysis of pollen resources of various stingless bees and honeybees revealed a considerable overlap of pollen spectra of these bees. However, certain pollen types were of different importance to the various bee species. Colonies of the same *Melipona* species had a very similar spectrum. The widths of the pollen spectra of the different bee species appeared more related to the natural population size of the colony than to the body size of the bees. At the start of the rainy season we recorded in some bees a shift to other pollen resources. However, certain plants continued as a major pollen resource for other bees, e.g. coconut for the honeybees.

The stingless bees principally collected pollen in the morning and nectar in the afternoon. In individual foragers of *Melipona favosa* we could not observe a sequence in the collecting of nectar and pollen. Exclusive pollen foragers and exclusive nectar foragers had a different trophallaxis behavior. Pollen returnees solicit for food before unloading their corbiculae and nectar returnees offer spontaneously. This is the only occasion in which we observed spontaneous food donations by workers of stingless bees.

**INTRODUCTION**

The honeybee, *Apis mellifera*, was introduced into the New World by early settlers several centuries ago, since then European races of these bees have been kept intensively by apiculturists in both continents of America. It is mainly due to the

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recent, uncontrolled, hybridization of the South American populations of domesticated *A. mellifera* with *A. mellifera scutellata* from Africa (MICHENER, 1975; GONÇALVES, 1982) that the ecological research of native pollinators has been emphasized.

Most abundant bees in the neotropics are members of the diverse group of stingless bees (Apidae, Meliponinae). The ecology of these bees and, more recently the impact on their biology by the introduction of the honeybee from Africa has been given some attention (HUBBELL and JOHNSON, 1977 A, 1977 B, 1978; HEITHAUS, 1974, 1979 A, 1979 B; ROUBIK, 1978, 1979 A, 1979 B, 1980, 1981, 1982, 1983).

Both groups of eusocial bees, the honeybees and the stingless bees, share various characteristics. Considerable food reserves are stored inside their perennial nests. Comparable patterns of social behavior such as division of labor, communication concerning food sources and recruitment of nest mates, learning behavior etc., are related to the cooperative collection of food (MICHENER, 1974; SAKAGAMI, 1982; LINDAUER and KERR, 1958, 1960; JOHNSON and HUBBELL, 1974, 1975). Aspects of their social behavior related to brood production have been studied in detail in various species by SAKAGAMI (see : review, 1982) and SOMMEIJER *et al.* (1982). Foraging in bees is generally studied by the analysis of the visitation of flowers or artificial feeders. Most reports on pollen resources of stingless bees that are based on palynological methods, either treat only one bee species, or are of little use for interspecific comparative analyses because of sampling at different locations or at different times (ABSY *et al.*, 1977, 1980; IWAMA and MELHAM, 1979; ENGEL and DINGEMANS-BAKELS, 1980). Comparative data on inter- and intra-specific differences in pollen foraging are scarce. IWAMA and MELHAM (1979) found that the nectar foragers of two colonies of *Tetragonisca angustula angustula* were attracted to the same floral resources. ABSY, BEZERRA and KERR (1980) analyzed the nectar resources of 2 *Melipona* species. They found considerable differences in pollen species contained in the nectar samples of both bees. The study on pollen resources of *Melipona* by ABSY and KERR (1977) discusses only one species.

Competitive interactions between stingless bees and Africanized honeybees at flowers and at artificial feeders were studied by ROUBIK (1978, 1980, 1983). After his experimental introduction of Africanized honeybees near flowers, stingless bees became less abundant or harvested less, yet in another study, no disruption of colony food storage and reproductive activity occurred. However, the colonizing Africanized honeybees may lead to a shift in resource for the neotropical stingless bees and this eventually may lead to a population decline of these native pollinators. In another study the same author recorded the flower visitation for different bee species in undisturbed tropical forest and savanna (ROUBIK, 1979 A). Bees that were taxonomically related were found to be similar in floral preference. The similarity in the nectar and pollen use of these groups was further

analysed. It was concluded from this that the *Trigonini* (*Trigona* s. lat.) form the most generalized pollen collecting group. The most generalized pollen collecting species included in ROUBIK's study were, however, *Melipona fulva* and *Apis mellifera*.

The objective of our study was to investigate comparatively the foraging behavior of stingless bees in Trinidad, West-Indies. In this paper we will specifically report on our analysis of pollen foraging by various colonies of different stingless bees and one colony of the European honeybee, *A. mellifera* at the same locality. We studied the composition and the temporal variation of the pollen diet of these colonies. Further we will report here some results concerning certain related behavioral aspects such as flight behavior and division of labor in foraging in *Melipona*.

### MATERIAL AND METHODS

The observations were carried out in 1979 on 5 species of bees: *Melipona scutellaris trinitatis* Cockerell\* (4 colonies), *M. favosa* Fabricius\* (3 colonies), *Trigona* (*Nannotrigona*) *mellaria* Smith\*\* (1 colony), *Trigona* (*Tetragona*) *nigra* var. *paupera* Provancher\* (1 colony) and *Apis mellifera* (1 colony).

The honeybee colony was collected as a natural swarm several weeks before the observations started and was housed in a single story Langstroth beehive. At the beginning of the observation period the population was estimated at 5,000 individuals. The length of a honeybee worker is about 13-17 mm. The colonies of the stingless bees were estimated to consist of the following numbers of bees: *M. scutellaris* (all colonies): 400-500, *M. favosa* (all colonies): 200-300, *Tetragona*: 400-500, *Nannotrigona*: about 1,000. Workers of *M. scutellaris* and *M. favosa* measure in length about 9 mm and 7-8 mm respectively, workers of *Nannotrigona* 3-4 mm and workers of *Tetragona* about 5 mm. The stingless bee colonies were housed in wooden hives according to the size of the natural nests. All colonies were placed at the compounds of the Commonwealth Institute of Biological Control at Curepe, on a 50 m stretch of land. At the compounds several West-Indian fruit-trees are grown in addition to patches of Teak and Mahogany trees. This institute is located in a residential area in Curepe and a variety of useful and ornamental plants were available, next to weeds and other wild second growth vegetation.

In one *M. favosa* colony the workers were marked upon emergence. In this colony frequency and duration of the pollen collecting flights could be measured through the recording of the successive pollen depositing acts of single bees inside the nest. The age of the foragers of this colony and their relative contribution to the collection of different plant products was also studied through intranidal observations on division of labor. In the latter observation series the individual foraging behavior was registered during 15 minutes of observation every hour, for 12 hours daily, every other day. Possible temporal differences in the collection of the different food and building materials, over the day, could thus be analyzed.

Pollen samples were taken from the colonies by collecting the loads in the corbiculae of returning foragers, intercepting these bees before they entered the hive. Samples were taken weekly at a fixed day around 08.00 and around 17.00 from 23 March to 17 August 1978. Sampling from the *Tetragona* colony was not started before July. The samples of each colony contained the loads of 2 to 5 individuals. The pollen samples were later processed by a standard acetolysis method (REITSMA, 1969) and analyzed at the

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\* Ident. F. Dingemans-Bakels. *T. nigra paupera* is now generally recognized as belonging to the subgenus *Frieseomelitta* (D. W. Roubik, pers. comm.).

\*\* Ident. J. S. Moure and C. D. Michener.

laboratory of Palaeobotany and Palynology of the State University of Utrecht. Pollen types were identified by the use of the reference collection at the palynological institute. This slide collection, resulting from the work of ENGEL (ENGEL and DINGEMANS-BAKELS, 1980), was further expanded. The relative occurrence of various pollen types in the samples was expressed by the use of four within-sample-frequency categories. These categories, 1-4, indicate the relative incidence of specific pollen types among a random number of 100 pollen grains in a microscopic specimen of the sample (see also : ENGEL and DINGEMANS-BAKELS, 1980). Cat. 1 : « abundant », more than 30 %; cat. 2 : « frequent », 5-30 %; cat. 3 : « incidental », less than 5 %; cat. 4 : « sporadic », encountered on the microscope slide, but not present among the 100 counted pollen grains.

## RESULTS

### A. Activities of foraging bees in *M. favosa*

#### 1. General remarks about the behavior of returning foragers inside the nest

It was of interest to note that bees returning to the hive with pollen behaved differently from those returning with nectar. Returning nectar foragers expose a drop of nectar between their mandibles. Generally this drop is already visible at the very moment of entering the hive. The swollen abdomen of these bees clearly indicates their filled honey stomach. The behavior of these arriving bees is characterized by excited movements. A returnee apparently provokes as many interactions as possible with surrounding workers by means of rapid erratic movements, involving several sharp turns. Meanwhile, the returnee continuously offers food to nestmates. The continuous offering of food at that stage may lead to situations in which two nestmates take food at the same time from one returnee. After several of such trophallactic interactions, and about 1.5 minutes after arriving in the nest, the returnee proceeds to the food storage cells and regurgitates the main nectar load in an open nectar storage pot by one firm abdominal contraction, followed by one or more brief contractions. Generally this bee leaves the hive again shortly afterwards. Returning pollen foragers demonstrate excitement to much the same degree. However, it is remarkable that instead of offering food, they beg for it. They are often rewarded. Their excited locomotive pattern prior to going to the storage pots is rather similar to that of nectar collecting returnees. The surrounding bees antennate the pollen loads in the corbiculae and also contact these loads frequently with their extended glossa. The pollen loaded bee proceeds also after 1 or 2 minutes to an open pollen storage pot, rests at its mouth with her hind legs hanging inside and scrapes the load from her corbiculae by moving both hind legs against each other in a very brief moment lasting from one to a few seconds.

#### 2. Intervals between pollen load deposits of single bees

Flight intervals between successive pollen deposits of single bees were registered for 45 min. from 06.15 to 07.00 on 9 and 11 April. Weather conditions

were somewhat different on these days because of the drizzling rain on 11 April. On the first day, 56 workers deposited 124 pollen loads into the storage pots. Of these, 23 workers deposited only once during this observation period. During the less favorable conditions 2 days later 35 individuals were observed depositing 47 loads. Of these 24 workers deposited only once (Table 1). The duration of the intervals between successive deposits by the same individuals ranged from 1'05" to 34'43" min. in the first series with an average of 12'52" ( $n = 68$ ,  $SD = 5'.58''$ ). In the second observation, intervals ranged from 1'58" to 36'26" with an average of 18'11" ( $n = 13$ ,  $SD = 8'.0''$ ) (Fig. 1).

TABLE 1. — *Number of pollen deposits of stingless bees of a M. favosa colony from 06.15 - 07.00 hrs on two days in 1979*

No. deposits	1	2	3	4	5	6
No. bees, April 9 :	23	11	13	6	2	1
April 11 :	24	11	1			

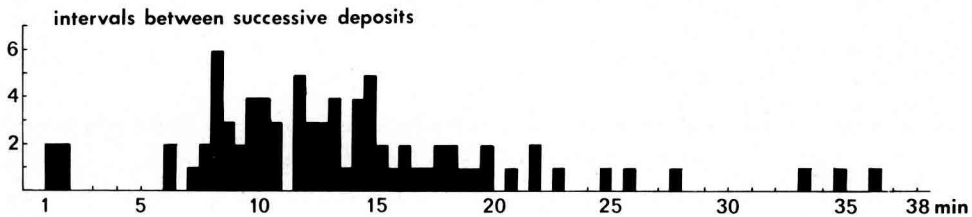


FIG. 1. — *Pollen depositing frequency of individual bees during two periods of 45 min*

The frequency distribution of in-between-pollen-deposit-interval-durations of individuals that deposited at least twice during the total observation period of 45 min is indicated.

### 3. Daily temporal distribution of foraging activity

It appeared that foraging activity in the *Melipona* colonies is not synchronous for nectar and pollen. The general pattern was that pollen flights took place in the early morning, between 05.30 and 09.00. Generally, this activity was maximum at around 08.00 hours. Pollen flights after 12.00 were uncommon. Nectar flights occurred generally between 10.00 and 16.00 and were most prevalent around noon. Foraging was hampered by rainfall. A short early morning shower delayed pollen foraging and continuous rain caused a drop of foraging activity, although not much disturbed by a light rain as shown above. During earlier observations on one

colony of *M. scutellaris* (during 10 days in February, in observation periods of 20 min. duration, at varying times of the day) we recorded a similar flight pattern and the same circadian organization of pollen- vs. nectar foraging.

The *Apis* colony distinguished itself from these *Melipona* bees by collecting pollen throughout the day.

#### 4. Individual participation in pollen and nectar foraging in a *M. favosa* colony

TABLE 2. — *Subsequent participation of individual bees in the collection of pollen (P) and nectar (N) in whole days*

	% of observed foragers (n = 85)
exclusive N	38
exclusive P	37
N and P at same day (s)	6
N preceding P	8
P preceding N	4
P preceding and succeeding N	2
N preceding and succeeding P	0
N and P at same day(s) succeeded by N	0
N and P at same day(s) succeeded by P	1
N preceding N and P at same day(s)	2
P preceding N and P at same day(s)	2
Number of trips recorded : 289	

Both pollen- and nectar collecting were observed to be carried out by workers of the same age group. The ages of nectar foragers ranged from 24-63 days and of the pollen foragers 23-63 days old. The individual ontogenetic participation in the collection of these two floral products was analyzed. This revealed that only 25 % of the 85 observed foragers collected both nectar and pollen, but did so in separate flights. We did not observe a consistent succession of one type of foraging followed by the other in bees involved in the collection of both commodities (Table 2).

## B. Analysis of pollen resources of different species and colonies

### 1. General diversity of collected pollen

A total number of 191 samples were collected. These contained 44 different pollen types, occurring in such quantities that they could safely be assumed to represent pollen resources (Table 3). Some other pollen types occurred at a very

unsignificant level in a few samples. 20 Types could be identified to species, 4 to genus, 15 to family and 4 to a two-family level (Sapotaceae/Meliaceae and Sapindaceae/Myrtaceae). Only one of the common types remains unidentified.

## 2. Inter- and intra-specific differences in pollen collecting

The relative importance of various pollen types during the total observation period was determined for all colonies. The results (Table 3) indicate the frequency with which each pollen type occurred, in each of the 4 within-sample-frequency categories, among all the scores of all pollen types encountered in all the samples of each colony.

These results demonstrate a selective and consistent flower visiting pattern for the respective bee species. However, the differences between the available colonies of the same species appeared minimal. The differential occurrence of the various pollen types in samples from the various colonies of the same bees is also shown in table 3.

Some pollen types were prevalent in successive samples of a certain bee species but did not occur, or were only of minor importance, in samples of other species. For example « hogplum », *Spondias mombin*, formed a major pollen supply for an extended period for all bee species, except for *Tetragona*. It is, however, remarkable that this pollen was not present in the afternoon samples of *Apis*. In contrast, *Delonix regia* was for a considerable time of major importance to *Apis*, but exclusively in the afternoon. *Delonix* was only of minor importance to the stingless bees, which all had their major pollen collecting in the morning.

The pollen of the coconut, *Cocos nucifera*, represented another remarkable interspecific difference. This was of major importance to *Apis* and was collected during the whole observation period, both in the morning and afternoon, but was only incidentally collected by the stingless bees. Other palm pollen was also frequently encountered in samples of *Apis* and *M. scutellaris* and in very small quantity in only one sample of *Nannotrigona*. One unidentified palm pollen type was especially important to *Apis* in the afternoon. These palm pollen types were not found in samples of *M. favosa* nor in those of *Tetragona*. Pollen from Sapotaceae/Meliaceae was only found to be collected by *M. scutellaris*, *Tetragona* and *Nannotrigona*. For the latter it represented a major supply. Teak, *Tectona grandis*, represented a major pollen supply for *Nannotrigona*. However, it was only once found to be of minor importance to *M. favosa*, and was not at all encountered in the samples from *Apis*, *M. scutellaris* and *Tetragona*.

Pollen from the Compositae, including the common *Bidens pilosa*, was for some weeks prevalent in *Apis* samples. *Nannotrigona* collected this a few times, but it was not found in the samples of any of the *Melipona* hives nor in those from *Tetragona*.

TABLE 3. — *Identified pollen types and their relative importance to the various colonies*

The relative importance of various pollen types in the respective within-sample-frequency in all samples of each colony. The number of samples containing a certain pollen type, in one of the 4 frequency categories, is indicated in the percentage of all scores for all pollen types encountered in all samples of each colony. (Values for the percentages are rounded to integers!) The 4 categories for within-sample-frequency are as those commonly applied in Melisso-palynology (see also ENGEL *et al.*, 1980).

cat. 1 — « abundant » : more than 30 %;

cat. 2 — « frequent » : 5-30 %;

cat. 3 — « incidental » : less than 5 %;

cat. 4 — « sporadic » : encountered on the microscopic slide, but not present among the 100 coated pollen grains.

Colony	Apis AM	Apis PM	Nannorigona	Tetragona	scu. 2	scu. 3	scu. 6	scu. 7	fav. 1	fav. 2	fav. 3
within-sample-frequency cat. :	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4	1 2 3 4
ANACARDIAC. <i>Spondias mombin</i> L.	6		2 2		4 2 10 2	3 3 3 2	2 11	5 3 3 6	11 3 3	10 6 3	3 3 3
CAESALPINIAC. <i>Delonix regia</i> (Bojer) Raf.		4 4 2	2 2	4 4							
<i>Tamarindus indica</i> L.				7 4		2					
COMPOSITAE <i>Bidens pilosa</i> L.	1 2										
type 1		9 4 2 2	2								
type 3		2	4 2								
CUCURBITAC. <i>Momordica charantia</i> L.	1 2 4			4		2	2			3	
CYPERAC. type				7							
EUPHORBIAC. <i>Hura crepitans</i> L.	1 2 1	2		4 4		2					
GRAMINEAE <i>Zea mays</i> L.	1										
other cultivated grain	2 3		2					3		3	
LECYTHIDAC. <i>Couroupita guianensis</i> Aubl.										3	
MALPIGHIAC. type			6 6		2						

[illegible]

*Mimosa pudica* pollen occurred in samples of all bee species. It was of major importance to *Apis* but even moreso to all colonies of *Melipona*. In addition, the *Melipona* colonies collected various other mimosaceous pollen types.

*Cecropia* pollen was of major importance to *Apis*. It was collected by these bees for a considerable time; where as three *Melipona* colonies collected it only once in moderate quantity.

The width of the plant-spectra appeared to be different for the various bee species. *Apis* and *Nannotrigona* had about 10 major plant species and *M. favosa* only 5 (Table 4). The variation of the spectrum of a certain species was also reflected in the degree by which the pollen types in the samples were mixed. The percentages of samples containing only one pollen type in abundance (over 30 %), possibly accompanied by only (an) incidental other pollen type(s) (less than 5 %), were analyzed for each species. In general such samples contained over 95 % of one pollen type. All colonies of *Melipona* spp. had over 50 %, *Apis* only 17 %, *Tetragona* 13 % and *Nannotrigona* 32 % of their samples in this category.

TABLE 4. — Number of pollen species collected by the various colonies.

	colony	samples	species	Species minimal	
				cat. « 1 »	cat. « 2 »*
<i>Apis mellifera</i>	1	22	27	14	18
<i>M. scutellaris</i>	2	18	17	9	13
	3	21	21	9	13
	6	17	13	8	10
	7	17	14	6	9
<i>M. favosa</i>	1	17	7	3	5
	2	10	14	3	7
	3	12	8	3	3
<i>Tetragona</i>	1	8	12	8	13
<i>Nannotrigona</i>	1	18	19	10	11

### 3. Variation in pollen collected throughout the observation period

A distinct fluctuation could be observed in the collection of several pollen types. Table 5 indicates that a number of major pollen types was collected throughout the observation period by the five bee species. Certain plants appeared to occur consistently throughout the observation period, e.g. guava for *M. scutellaris* and *M. favosa*, and coconut as well as miscellaneous palm pollen for *Apis*. Other plants were only of importance for a limited period, e.g. hogplum in April. The short interruption in the continuous collection of guava pollen by the *Melipona*

TABLE 5. — Seasonal variation in the collection of eight major pollen types.

Colonies of some bee species are taken together. Included are only the scores of minimal within-sample-frequency category é (at least 5 %).

	March	April	May	June	July	Aug.
	2330	6 7 12 20 27	4 11 25 31	8 14 15 22 23 29	9 15 23 27	4 10 17
Spondias mombin	A N T S F	● ● ● ● ○ ▲ ▲ ▲ △ △	● ● ▲		▲ ▲	
Mimosa pudica	A N T S F	●		● ○ △ △	X ▲ △ △ △ △	○ ▲ ▲ ▲
Cecropia peltata	A N T S F	●	● ● ▲	● ● ●	X ● ● ●	●
Psidium guajava	A N T S F		● ○ ○ X		● ▲ ▲ ▲ ▲	▲ ▲ ▲ ▲
Cocos nucifera	A N T S F	● ● ●	● ● ● ● ●	● ● ● ● ●	● ● ● ● ●	● ● ● ●
misc. Palmae	A N T S F	● ● ● ● ●	●	● ●	● ▲	● ▲
Citrus spp.	A N T S F	●		● ●		
Tectona grandis	A N T S F				○ ○ ○ ○ ○	○ ○ ○ ○

colonies may in fact be caused by a liberal supply of hogplum pollen in that period. Although guava forms a permanent major supply for the two *Melipona* spp., it is only of major importance to other bees in April and May, e.g. for *Nannotrigona*. The latter bee shifts in June to the pollen of teak. The pollen of these tall trees (20-30 m) is from then a major resource, exclusively for this bee. *Mimosa pudica* was a major bee plant to all bees, but only in the months June, July and August. This plant is then, next to guava, of great importance to *M. favosa*. This partial switch from guava and hogplum towards, respectively teak and mimosa as major pollen resources coincided with the onset of the « rainy season » which started in 1979 with considerable rainfall in the first days of June (Fig. 2, see also Fig. 3). We were not able to collect comprehensive comparative data on seasonal variation since the sampling was restricted to a limited period.

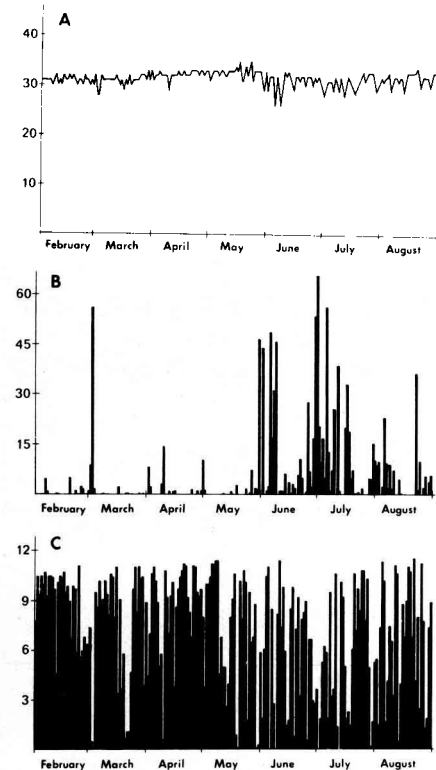


FIG. 2. — Daily weather conditions, during observation period, Piarco Airport, Trinidad, W.I.. Latitude 10° 37' N, longitude 61° 21' W, elevation 14 m, February -August 1979.

- A. Max. air temperature, °C.
- B. Rainfall, mm.
- C. Hours of sunshine.

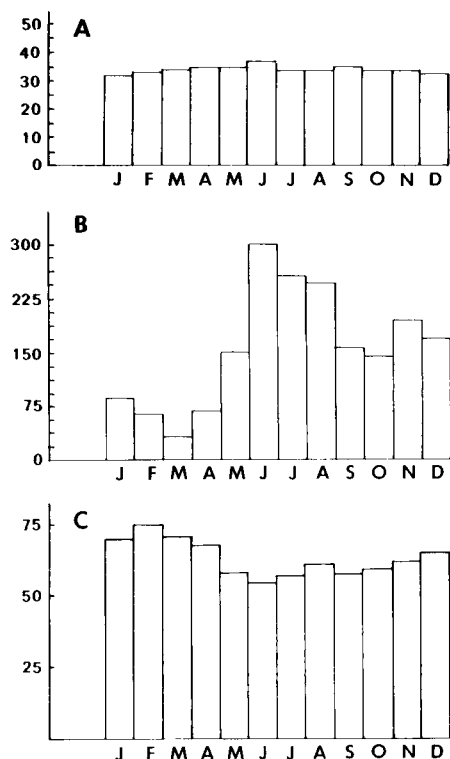


FIG. 3. — Mean monthly climatological conditions Trinidad, West-Indies.

- A. Max. air temperature °C, Piarco Airport.
- B. Precipitation, mm., Piarco Airport.
- C. Monthly percent sunshine.

## DISCUSSION

**A. The trophallactic behavior of foragers**

The differential trophallactic behavior of returning foragers, depending on the selective delivery of either pollen or nectar, has not been observed before in the stingless bees. The spontaneous offering by returning nectar foragers is of itself a remarkable feature of stingless bee behavior and although we have made several detailed observations on the intranidal behavior of various stingless bees, we have not observed this behavior in any other situation. This is in sharp contrast to the trophallactic behavior of *A. mellifera*, where spontaneous offerings occur everywhere in the nest including those by incoming foragers.

**B. Inter- and intra-specific differences in pollen foraging**

Our palynological results demonstrate a considerable overlap in the pollen resources of different bees. This is not surprising since both stingless bees and honeybees are known to be generalists (MICHENER, WINSTON and JANDER, 1978).

However, next to the recorded overlap, we also found considerable differences in the pollen resources of the bee species. The evident intraspecific similarity between the various colonies of *M. favesa* and *M. scutellaris* respectively, makes it likely that the relatively small sample size is not a major cause of these interspecific differences (thus weekly sampling from corbicular loads may be considered as a satisfactory method). Since no additional colonies of the other species were available, our observations on intraspecific differences in foraging behavior were restricted to the two species of *Melipona*. However, for *Tetragonisca angustula* it was found that two colonies, only being 140 m apart, were both attracted to the same floral supplies (IWAMA and MELHAM, 1979). This is in accordance with the intraspecific similarity observed in *Melipona*. The difference we found between the colonies of the different species should be considered to at least to some degree representative interspecific differences. These interspecific differences, despite the above mentioned generalistic nature of eusocial bee foraging, may reflect a form of limited specialization (see : EICKWORT and GINSBERG, 1980). Even though the different bee species forage on the same plants, the hour of the day when visitation occurs may be different. The pollen samples collected by ENGEL and DINGEMANS-BAKELS (1980) from *M. favesa* colonies in Surinam represented a longer list of pollen types. However, their samples (from intranidal pollen stores, corbicular loads, and nectar) were collected at different locations and times. Guava, *Psidium guajava*, which is also a common fruit tree in Surinam, is remarkably absent from their samples. This tree formed a major and continuous pollen resource for our *M. favesa* colonies in Trinidad. *Mimosa pudica*,

representing the most important pollen resource for our *M. favosa* colonies, was recorded only once as abundant pollen in the Surinam samples. This difference suggests that concentration to particular pollen resources does not represent an inherent oligolectic tendency but probably a partial adjustment according to local conditions, including kinds and abundance of competitors, relation between flight radius and distance to pollen sources etc. (cf. SAKAGAMI *et al.*, 1973). It should be stressed that comparisons between pollen analyses for different regions should be made with caution. The adaptive plasticity of highly eusocial bees may result in considerable seasonal and regional differences, even within the same country. Comprehensive and long-term sampling is needed, especially when such research is expected to have practical implications.

### C. Factors determining the width of a pollen spectrum

Comparing the results for the different bee species it appears that the widths of their pollen spectra are not positively correlated with their body size. *Nannotrigona*, the smallest bee included in our study demonstrated a considerable wider pollen spectrum than *Melipona favosa*. This relatively wide spectrum was demonstrated by *Nannotrigona* in combination with fairly homogeneous samples; possibly an indication for flexibility in collective sampling. The results may lead to the suggestion that the widths of the pollen spectra of eusocial bee species depend largely on their natural colony size. Although our experimental colonies were under their normal natural population size, the natural interspecific differences in colony strength for these species (WILLE and MICHENER, 1973; ROUBIK, 1979 B) are in accordance with the observed differences in pollen spectrum widths. The results are in agreement with IWAMA and MELHAM (1979) who found in nectar samples of *Tetragonisca angustula* a wide range of pollen species. *Tetragonisca angustula* colonies are composed of large numbers of bees : 2,000-5,000 (NOGUEIRA-NETO, 1970). This is 5-10 times the population of *M. favosa* colonies. The results are in agreement with ROUBIK (1979 A), who found that the Trigonini were the most generalized bees. The majority of the species of this group are small sized bees, living in populous to very populous colonies (see also : ROUBIK, 1979 B). Of the stingless bees, the Trigonini are generally the most abundant in individuals as well as in species. That in ROUBIK's study, however, *M. fulva* was found to be most generalized species, next to *A. mellifera*, may be a result of the fact that *M. fulva* builds up relatively large colonies for *Melipona* spp. The width of the pollen spectrum may also be influenced by the size of the home range. ROUBIK *et al.* (1983) investigated differential homing capacity in two species from Panama. As maximum distances from which bees still returned to their nest were found : 2.1 KM for *M. fasciata* and 1.5 KM for *Trigona capitata*. *M. fasciata* is 10 mm long and lives in colonies of

400-800 adults and *T. capitata*, which is among the largest *Trigona*, measures 9 mm long and lives in colonies of 1,000-2,000 individuals.

HUBBEL and JOHNSON (1977) assumed that home range size can be estimated approximately by the inverse of colony density. MICHENER (1974), however, mentions that home range probably increases in a general way with the size of the bees. Comparison of our data obtained for the small-sized *Nannotrigona*, naturally living in populous colonies and for which we found a relatively wide spectrum, and for *M. favosa*, a larger-sized bee living in small colonies and demonstrating a relatively narrow spectrum, may indicate the importance of colony density. A specific width of pollen spectrum may also be a result of other factors, such as for example specific pollen foraging behavior. JOHNSON and HUBBELL (1975), studying the foraging strategies and coexistence of *Trigona fuscipennis* and *T. fulviventris* in Costa Rica by analyzing nest density and flower visiting behavior, proposed the terms « low-density and high-density specialists ». These terms stand for bees that either forage as individuals or in small groups on isolated or widely spaced floral resources or, respectively, forage in large groups monopolizing plants and restricting their visits to large clumps of floral resources. The latter type of foraging was found in *T. fuscipennis*, a species in which, in contrast to *T. fulviventris*, an effective pheromone communication in the recruiting and leading of nestmates to food sources is known to exist. Interspecific competition and differences in competitive ability may also account for differences in the pollen spectrum. ROUBIK (1979, 1980) found that Africanized *A. mellifera* in Guyana had at rich compact resources a competitive ability superior to that of native stingless bees. This author considered this as a result of the properties of the *Apis* communication system and of its larger worker- and colony size. Finally, morphological differences related to specific pollen packing mechanisms might also attribute to differential pollen spectrum widths.

#### **D. Ontogeny and temporal variation of foraging behavior**

Our results on the subsequent foraging of different plant products indicate that there is no definite ontogenetic sequence in nectar and pollen foraging in single individuals. This concurs with what is known from the honeybee in this respect. In *A. mellifera* the absence of an ontogenetic sequence of different foraging types appears in contrast to the succession of house activities. However, SEKIGUCHI and SAKAGAMI (1966) emphasized the flexibility of division of labor in *A. mellifera*. The supposed similarity in the absence of ontogenetic sequence in foraging tasks of *M. favosa* may account, together with our observation that most recorded foragers collected exclusively pollen or nectar, for a general plasticity of the colony, by means of more or less further permanent division of labor among foragers; which of itself is not irreversible. The supposition that meliponines

resemble *A. mellifera* in this respect has already been made by MICHENER (1974). The individual specialization of foragers that may preliminarily be deduced from these results, may be a result of flower constancy of individual workers. The advantages of this fidelity to a certain flower and the fact that this more or less permanent division of labor is based on individual bees, are also discussed by MICHENER. In relation to this it is of interest to note that individual workers of *Apis* possess a greater host specificity for pollen collecting than for nectar foraging, but have next to that a general preference for the collecting of nectar.

The obvious preference of *Melipona* colonies for collecting pollen principally in the morning versus principal nectar collection in the afternoon, is remarkable. This has also been observed by KERR and SANTOS NETO (1965). They found for a small number of marked workers in colonies of *M. quadrifasciata* : « usually they collected pollen from 8.30 AM to 12.30 PM and nectar from 11.00 AM to 6.00 PM ».

This may be related to a specific way of pollen manipulation by *Melipona* workers (BUCHMANN, 1973; WILLE, 1963). We observed these bees commonly « buzzing » through the tuft of anthers of flowers of *Mimosa* and the like. Certain conditions (humidity?) may facilitate such type of pollen collection. *Mimosa* flowers also appeared shrivelled in the afternoon. It should be realized that pollen samples collected from returning pollen foragers in the morning, may not be fully representative for all the plants visited by these colonies. Other plants may be visited exclusively for the collection of nectar in the afternoon.

The clear temporal separation of nectar and pollen foraging throughout the day in stingless bees, may well represent a consistent difference from the foraging behavior of *Apis* colonies. This could be attributed to differences in pollination effect between introduced *Apis* and native *Melipona*. This should be taken into consideration not only when designing methods for the study of food resources of stingless bees, but also when investigating the interrelations between foraging stingless bees and honeybees in the field.

*Received for publication in May 1983.*

#### ACKNOWLEDGEMENTS

This study was supported by travel grants of the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) and the Utrecht University Foundation. We are very grateful to Dr. F. D. BENNETT, general director CIBC, for permission to work at the CIBC compounds in Trinidad. Special acknowledgement is due to Dr. C.D. MICHENER, Padre J.S. MOURE and Mrs. F. DINGEMANS-BAKELS, for their assistance in the identification of the bees. Dr. D.W. ROUBIK is acknowledged for supplying some of his unpublished data. Meteorological data were kindly supplied by the Meteorological Office at

Piarco International Airport, Trinidad. Drs H.H.W. VELTHUIS, S.F. SAKAGAMI and V.C. QUESNEL are thanked for their valuable comments the manuscript.

## RÉSUMÉ

### ÉTUDE COMPARATIVE DU COMPORTEMENT DE BUTINAGE ET DES RESSOURCES POLLINIQUES DE DIVERSES MÉLIPONINÉS (HYM., MELIPONINAE) ET ABEILLES DOMESTIQUES (HYM., APINAE) A TRINIDAD, ANTILLES

Cette étude comparative des ressources polliniques de diverses abeilles eusociales comprend les mélipones *Melipona scutellaris trinitatis*, *M. favosa*, *Trigona (Nannotrigona) mellaria*, *T. (Tetragona) nigra* var. *paupera* et l'abeille domestique, *Apis mellifica*. On a étudié 10 colonies, toutes placées au même endroit. L'analyse pollinique des échantillons de pollen, prélevés chaque semaine sur les butineuses qui rentrent, montre qu'il existe un recouvrement considérable pour les diverses abeilles. Les différences dans l'importance relative des divers types de pollen pour chaque colonie prouve néanmoins que chaque espèce visite les fleurs selon un schéma sélectif et uniforme. Les colonies d'une même espèce d'abeille se comportent de façon semblable dans la récolte du pollen. Les résultats montrent que l'étendue des spectres polliniques des diverses espèces d'abeilles est corrélée positivement avec la taille de la population de la colonie, mais négativement avec la taille corporelle des abeilles. Au début de la « saison des pluies » un déplacement vers de nouvelles ressources polliniques s'observe chez certaines abeilles. Mais on observe aussi un butinage continu de certains types de pollen; par exemple le cocotier constitue une source principale et permanente de pollen pour les abeilles domestiques.

L'observation, à l'intérieur du nid, du comportement des butineuses de *M. favosa* révèle qu'il n'y a pas d'ordre ontogénétique dans la récolte du nectar et du pollen. La récolte du pollen a lieu principalement le matin, tandis que le nectar est surtout récolté en fin de journée. Les abeilles qui rentrent au nid avec du pollen n'ont pas le même comportement que celles qui rapportent du nectar. Les abeilles qui rentrent avec du nectar l'offrent spontanément aux autres abeilles de la colonie avant de le décharger dans la cellule de stockage. Nous avons observé des offres spontanées de nourriture uniquement de la part des butineuses de nectar, puisque les autres interactions trophallactiques sont toujours initiées, chez les mélipones, par sollicitation.

## ZUSAMMENFASSUNG

### VERGLEICHENDE STUDIE ÜBER DAS SAMMELVERHALTEN UND DIE POLLENRESSOURCEN VERSCHIEDENER STACHELLOSER BIENEN (HYM., MELIPONINAE) UND DER HONIGBIENE (HYM., APINAE) VON TRINIDAD, WESTINDIEN.

Diese vergleichende Studie der Pollenressourcen verschiedener eusozialer Bienen umfaßt die stachellosen Bienen, *Melipona scutellaris trinitatis*, *M. favosa*, *Trigona (Nannotrigona) mellaria*, *T. (Tetragona) nigra* var. *paupera* und die Honigbiene, *Apis mellifera*. Insgesamt wurden 10 Kolonien untersucht, die alle auf einem Stand plaziert waren. Die palynologische Untersuchung der wöchentlichen Pollenproben, die von zurückkehrenden Sammelbienen genommen wurden, ergab eine bemerkenswerte Überlappung bei den verschiedenen Bienen. Differenzen in der relativen Wichtigkeit der verschiedenen Pollentypen für jede Kolonie zeigten, gleichwohl, ein selektives und übereinstimmendes Blütenbesuchsmuster für die jeweilige Bienenart. Kolonien der gleichen Bienenart verhielten sich beim Pollensammeln sehr ähnlich. Die Ergebnisse weisen darauf hin, daß die Breite des Pollenspektrums der verschiedenen Bienenarten positiv korreliert ist mit der Populationsgröße der Kolonie aber negativ mit der Körpergröße der Bienen. Zu Beginn der Regenzeit konnte bei einigen Bienen ein Wechsel zu neuen

Pollenressourcen beobachtet werden. Aber auch kontinuierliches Sammeln von bestimmten Pollentypen konnte beobachtet werden, z.B. bildet die Kokospalme den ständigen Haupt-Pollenlieferanten der Honigbiene.

Beobachtungen des Verhaltens der Sammlerinnen von *M. favosa* innerhalb des Nestes zeigten, daß keine ontogenetische Reihenfolge im Nektar- und Pollensammeln besteht. Pollensammeln fand prinzipiell am Morgen statt, während Nektar hauptsächlich später am Tag gesammelt wurde. Bienen, die mit Pollen zum Stock zurückkamen, verhielten sich anders als solche mit Nektar. Zurückkehrende Nektarsammlerinnen offerieren spontan Nektar den Stockgenossen bevor sie ihr Futter in die Futterspeichertöpfe entladen. Pollensammlerinnen offerieren nie trophallaktisch Futter sondern betteln bevor sie ihre Körbchen in die Speichertöpfe entleeren. Wir beobachteten spontanes Futteranbieten nur bei zurückkehrenden Nektarsammlerinnen. Alle anderen trophallaktischen Interaktionen bei stachellosen Bienen wurden immer durch Betteln eingeleitet.

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