# POLLEN HARVEST BY AFRICANIZED APIS MELLIFERA AND TRIGONA SPINIPES IN SÃO PAULO BOTANICAL AND ECOLOGICAL VIEWS

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## SUMMARY

During one year, monthly samples of pollen were taken from one colony of *Apis mellifera* and one colony of *Trigona spinipes*. A great number of pollen types was observed in each of the samples (approximately 40), although few sources were intensively visited each month. *T. spinipes* collected significantly from *Eucalyptus* spp., *Aloe* sp. and *Archontophoenix* sp., and *A. mellifera* visited mainly *Eucalyptus* spp., *Tipuana speciosa, Caesalpinia peltophoroides, Mikania glomerata* and *Cecropia* sp.

The high values obtained for niche size (H') and the low values found for evenness (J') point to the fact the bees collected their food in a very heterogeneous manner. The overlap values (PS) were found between 0.1 and 0.5, as a result of intense gathering from abundant resources.

## INTRODUCTION

Few examples are known of bee genera with polylectic habits. It can be observed, however, that the most noteworthy characteristic of social and subsocial species compared with solitary species is their polytrophy, probably due to the perenniality of the colonies and the consequently longer foraging period. Nevertheless since degrees of polylecty constitute a relative problem in themselves, and the pollen preferences of the species of many genera are unknown, it is important to study and discuss with precision the degrees of polylecty found for the different groups of bees in varying environmental conditions.

The neotropical region provides an opportunity to investigate the inner dynamics of the complex pollinator plant community in the context of the recent proliferation of africanized *Apis mellifera* L. (Am) (ROUBIK, 1978a). This bee's polytrophic nature and its ability to take the place of native pollinators make it a very important biotic factor, which may become limiting for certain taxa, either for reasons which are intrinsic to the interaction process in flowers, or through human intervention in the form of beekeeping practice (favoring Am) and deforestation (by destroying natural nests of stingless bees).

Among neotropical stingless bees, some Trigonini are conspicuous flower-visitors because of the relatively large populations in their colonies (MICHENER, 1974), aggressive and monopolistic behavioral strategies in the sharing and exploitation of floral resources (JOHNSON and HUBBELL, 1974, 1975 ; HUBBELL and JOHNSON, 1978), and the highly developed systems of communication between foragers (LINDAUER and KERR, 1960 ; KERR and ESCH, 1965 ; KERR *et al.*, 1981). For ROUBIK (1978b) the *Trigona* near Kourou comprises what might be called the pivotal forager guild. *Trigona spinipes* Fabricius (Ts), a native species, combines all these features which enable it to interact profoundly with Am.

Am and Ts are the Apidae of greatest relative abundance in the gardens of the Bioscience Institute of São Paulo University - IBUSP (KNOLL, 1985), with natural nests of relatively large population. Recently, CORTOPASSI-LAURINO (1982) conducted a field study on this site and found that Am and Ts were the most generalistic plant-visitors among the Apidae. This was an estimate of flower-visiting at the population level. Here, we make a colonial approach, by inferring the utilization of floral resources during a one-year period through palynological analysis of pollen gathered by these two bee species.

The object of the present paper is to describe the pollen niche of two similar polytrophic species of eusocial bees — one native and the other introduced to Brazil in 1957, 110 miles away from the place of study — and their foraging relationships. It is also intended to contribute to furthering the knowledge of bee plants and of the relative importance of each of these plant species.

## MATERIALS AND METHODS

Am and Ts colonies were located 50 meters from one another in the gardens of the Bioscience Institute of the University of São Paulo (IBUSP), on the outskirts of the city of São Paulo (23° 33′ S, 46° 43′ W). The floral composition of the area is varied, with an expressive presence of trees and bushes of the Leguminosae (*Tipuana, Schizolobium, Caesalpinia, Piptadenia, Mimosa, Leucaena, Acacia* and *Cassia*), some species of *Eucalyptus, Archontophoenix Tibouchina,* and others. There is an equally diversified group of herbaceous shrubbery, with many ornamental, invasive and annual species, and hence it is very disturbed. There are also many species of Compositae, Liliaceae, and other families. The region also contains a small secondary grove of semi-deciduous vegetation, covering some 10 hectares and rich in native species.

Pollen samples were collected over a 13-month period (Aug. 1980-Aug. 1981). Weekly pollen samples were collected from a colony of Am, with the help of a pollen trap fixed at the entrance of the nest during a one-day period. Monthly pollen samples were collected from a colony of Ts from new storage pots (20 to 30). The new pollen pots are easily recognized by their soft cerumen and colorful pollen. In colonies of Ts, like other Trigonini such as *Scaptotrigona* spp. (M. RAMALHO, unpublished) the stored pollen grains acquire a dark color when they become progressively older. The pollen grains were acetolyzed using ERDTMAN's technique (1960), and identified by comparing them with the material in the Institute's reference collection of local plants. The occurrence of pollen types in the samples was estimated on the basis of a count of 1000 grains on three microscopic slides (VERGERON, 1964 ; RAMALHO and KLEINERT-GIOVANNINI, 1986).

The pollen niche overlap was calculated as follows (CODY, 1974) :

$$a_{AmTs} = n_{AmTs_t}/(n_{Am_t} \cdot n_{Ts_t})^{1/2}$$

where : $n_{AmTs}$ is the number of plants in common in the diets of the species Am and Ts during the period t, and $n_{Am_t}$ or $n_{Ts_t}$ the total number of plants visited by the species in question over the same period. This index may vary from 1 to 0, i.e. from total overlap to complete segregation in terms of resource utilization.

The pollen niche size is expressed by the SHANNON-WEAVER diversity index (1949) :

$$H' = - \Sigma \, ph \cdot \ln ph$$

where : ph = the pollen proportion of the h plant species visited in the month in question.

The evenness index was calculated in accordance wih PIELOU (1977) :

$$J' = \frac{H'}{H' \, max.}$$

where : H' max. is the neperian logarithm of the total number of pollen types present in the sample. J' may vary from 0 to 1, i.e. from heterogeneous utilization to homogeneous utilization of plant species.

If the species do not share the resources equally, their trophic niches overlap to a greater or lesser extent, depending on the intensity with which they visit common sources. The percentage similarity can be expressed by SCHOENER's index (1968) :

$$PS = 1 - \frac{1}{2} \Sigma \, |ph_{Am} - ph_{Ts}|$$

where : $ph_{Am}$ is the proportion of pollen from species h collected by species Am, and $ph_{Ts}$ is the respective value for the species Ts.

## RESULTS

Pollen foraging during the seasons is shown in Table 1 (A and B) as the pollen types with over 1 % and in Figure 1 (A and B) as the pollen types with over 10 %. If plants with over 1 % frequency are considered, the number of species visited by Am was 41 and those visited by Ts was 34. It was clearly demonstrated that the important plants (> 10 %) which supplied pollen represented a small proportion of the whole floral population ; a total of 13 species for Am and 8 for Ts.

For Ts winter (June, July and August) and early spring (September) were characterized by the predominance of *Eucalyptus* pollen (Table 1A and Figure 1A). Around mid-spring (October), there was a small amount of *Eucalyptus* pollen. The diversity of Leguminosae pollen was highest in spring, but the predominant pollen type collected was from *Aloe* sp. The end of this season (November) was characterized by a greater decrease in the numbers of *Eucalyptus* and Leguminosae pollen, and increased foraging of pollen from *Archontophoenix*. The most frequently visited plant in this month was an unidentified Compositae.

TABL. 1 A. — *Phenology of bee plants represented over 1 % in pollen samples from* Trigona spinipes *(Letters at the top indicate months from August 1980 through August 1981).*
× = pollen represented over 10 %.
::: = pollen represented over 1 %.

| A | S | O | N | D | J | F | M | A | M | J | J | A 1981 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | ::: | | | | | | | | AGAVACEAE | Fourcroya gigantea |
| | | | | ::: | | | | | | | | | BALSAMINACEAE | Impatiens balsamina |
| | | | | | | | | | | ::: | | | BALSAMINACEAE | Impatiens sultanii |
| | | | × | × | ::: | | | | | | | | COMPOSITAE | Sp 1 |
| | | | ::: | ::: | ::: | | | | | | | | COMPOSITAE | Sp 2 |
| | | | | ::: | | | | | | | | | GRAMINEAE | Zea mays |
| | | ::: | | | | | | | | | | | LEGUMINOSAE | Caesalpinia peltophoroides |
| ::: | ::: | | | | | | | | | | | | LEGUMINOSAE | Erithryna speciosa |
| | | ::: | ::: | ::: | ::: | | ::: | ::: | ::: | | | | LEGUMINOSAE | Leucaena leucocephala |
| | ::: | ::: | | | | | | | | | | | LEGUMINOSAE | Schizolobium parahybum |
| | | | | | | | | | ::: | | | | LEGUMINOSAE | Schizolobium parahybum s.l. |
| ::: | ::: | × | | ::: | | × | × | | × | ::: | | | LILIACEAE | Aloe sp |
| | | | | | | | | × | | | | | LILIACEAE | Asparagus s.l. |
| | | ::: | ::: | ::: | | | | | | | | | LILIACEAE | Hemerocallis spp |
| | | | ::: | | | | | | | | | | LORANTHACEAE | Struthanthus spp |
| | | | | | | | | | | | ::: | | MORACEAE | Morus nigra |
| × | × | ::: | ::: | ::: | | × | ::: | × | ::: | × | × | × | MYRTACEAE | Eucalyptus blackelyi |
| ::: | ::: | | | | | ::: | | ::: | ::: | ::: | ::: | ::: | MYRTACEAE | Eucalyptus cinerea |
| × | × | ::: | | ::: | | ::: | ::: | ::: | | × | ::: | ::: | MYRTACEAE | Eucalyptus robusta |
| ::: | ::: | | | | | | | | | | | | MYRTACEAE | Eucalyptus tereticornis |
| ::: | ::: | | | | | | | | | | | | MYRTACEAE | Sp 1 |
| | ::: | | | | | | | | | | | | MYRTACEAE | Sp 2 |
| | ::: | | | | | | | | | | | | MYRTACEAE | Psidium guayava s.l. |
| | | ::: | ::: | | | | | | | | | | MYRTACEAE | Sigizium jambo |
| | | | | | | ::: | | | | | | | MYRTACEAE | Sigizium jambo s.l. |
| ::: | ::: | | × | × | × | × | × | × | × | ::: | | ::: | PALMAE | Archontophoenix cunninghamiana |
| | | | | | | | ::: | ::: | ::: | ::: | × | ::: | PALMAE | Archontophoenix cunninghamiana s.l. |
| | | | ::: | × | ::: | | | | | | | | ULMACEAE | Trema micrantha |
| | | | | | | ::: | | | | | | | undetermined | Sp 1 |
| | | | | | | | ::: | | | | | | | Sp 2 |
| | | | | | | | ::: | | | | | | | Sp 3 |
| | | | | | | | | | | ::: | | ::: | | Sp 4 |
| | | | | | | | | | | | ::: | | | Sp 5 |
| | | | | | | | | | | | ::: | | | Sp 6 |

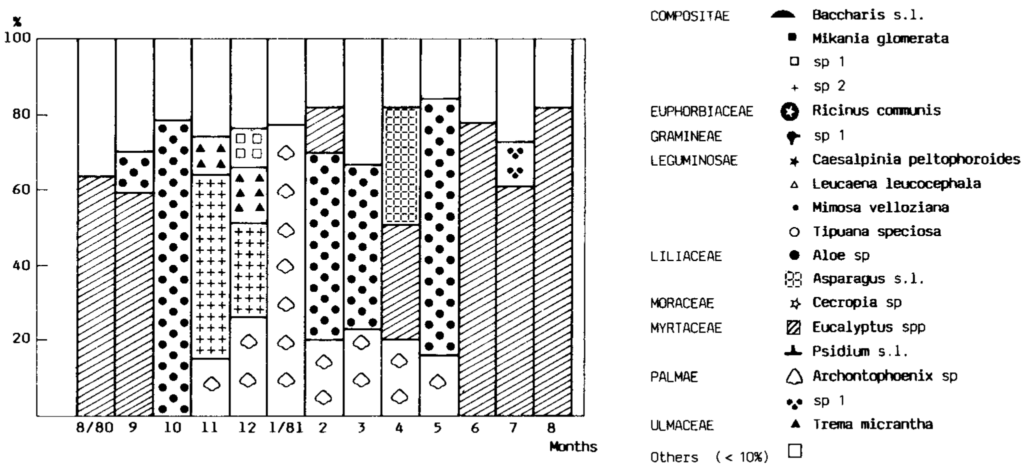


FIG. 1A. — *Relative frequency of pollen types with percentage higher than 10 % - pollen samples from* Trigona spinipes.

At the beginning of summer (December), this same Compositae shared the pollen preference of Ts bees with *Archontophoenix.* During this period, pollen diversity remained high, including many low-density plants, among them Gramineae, which is considered anemophilous. During the rest of the summer (January and February) there was less pollen diversity. January was the only month in which no *Eucalyptus* pollen was collected, and *Archontophoenix* was the main source. At the end of the summer — as at the beginning and end of autumn (March and May) — *Aloe* pollen was again predominant, followed by *Archontophoenix.* At this time, *Eucalyptus* species reappeared.

In April *Asparagus* pollen occurred, and as was the case throughout winter, *Eucalyptus* pollen was the most collected, thus being highly characteristic of this period.

For Am (Table 1B and Figure 1B), foraging was very constant during autumn and winter (March-August 1981). The most frequently collected pollen grains were from two species of *Eucalyptus.* Early and mid-spring (September-October) were characterized by the predominance of guapuruvú *(Schizolobium parahybum)* and tiputree *(Tipuana speciosa),* which are Leguminosae, as well as by an increase in the diversity of species from this family.

In November foraging was mostly from *Cecropia* sp., which appeared in different proportions from August 1980 to February 1981, except for October. It is considered anemophilous, like Gramineae, which were foraged upon in January, February, May and June. Three species of Compositae were represented during this period.

TABL. 1 B. — *Phenology of bee plants represented over 1 % in pollen samples from* Apis mellifera *(Letters at the top indicate months from August 1980 through August 1981).*
× = pollen represented over 10 %. ⁝⁝⁝ = pollen represented over 1 %.

| A | S | O | N | D | J | F | M | A | M | J | J | A 1981 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | | | | BIGNONIACEAE | Spathodea campanulata |
| | | | | | | | | | | | | × | COMPOSITAE | Baccharis s.l. |
| × | | | | | | | | | | | | | COMPOSITAE | Mikania glomerata |
| | | ⁝⁝⁝ | | | | | | | | | | | COMPOSITAE | Mikania hirsutissima |
| | | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | | | | | | | | | COMPOSITAE | Taraxacum officinale |
| | | | ⁝⁝⁝ | | | | | | | | | | COMPOSITAE | Tithonia speciosa |
| ⁝⁝⁝ | ⁝⁝⁝ | | | | | | | | | | | | COMPOSITAE | Vernonia sp 1 |
| | | | | ⁝⁝⁝ | | | | | | | | | COMPOSITAE | Vernonia sp 2 |
| | ⁝⁝⁝ | | | | | | | | | | | | COMPOSITAE | Sp 1 |
| | | | ⁝⁝⁝ | × | | | | | | | | | COMPOSITAE | Sp 2 |
| | | | | ⁝⁝⁝ | | | | | | | | | COMPOSITAE | Sp 3 |
| | | | | | | ⁝⁝⁝ | | | | | | | COMPOSITAE | Sp 4 |
| ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | | ⁝⁝⁝ | ⁝⁝⁝ | × | ⁝⁝⁝ | ⁝⁝⁝ | × | EUPHORBIACEAE | Ricinus communis |
| | | | | | × | ⁝⁝⁝ | | | ⁝⁝⁝ | ⁝⁝⁝ | | | GRAMINEAE | Sp |
| | × | | | | | | | | | | | | LEGUMINOSAE | Caesalpinia peltophoroides |
| | | | | | ⁝⁝⁝ | | | | | | | | LEGUMINOSAE | Desmodium sp |
| | | | | | | ⁝⁝⁝ | | | | | | | LEGUMINOSAE | Erithryna s.l. |
| | | ⁝⁝⁝ | × | × | ⁝⁝⁝ | ⁝⁝⁝ | | | | | | | LEGUMINOSAE | Leucaena leucocephala |
| | | | | | | ⁝⁝⁝ | | | | | | | LEGUMINOSAE | Mimosa bimucronata |
| ⁝⁝⁝ | | | | | | | | | | | | | LEGUMINOSAE | Mimosa daleoides |
| | | | | × | × | × | | | | | | | LEGUMINOSAE | Mimosa velloziana |
| | | | ⁝⁝⁝ | ⁝⁝⁝ | | | | | | | | | LEGUMINOSAE | Piptadenia gonoacantha |
| | | ⁝⁝⁝ | | | | | | | | | | | LEGUMINOSAE | Schizolobium parahybum |
| | | × | ⁝⁝⁝ | ⁝⁝⁝ | | | | | | | | | LEGUMINOSAE | Tipuana speciosa |
| | | ⁝⁝⁝ | | | | | | | | | | | LILIACEAE | Aloe sp |
| ⁝⁝⁝ | | | | | | | | | | | | | MORACEAE | Morus nigra |
| ⁝⁝⁝ | ⁝⁝⁝ | | × | ⁝⁝⁝ | × | ⁝⁝⁝ | | | | | | | MORACEAE | Cecropia sp |
| ⁝⁝⁝ | | | | | ⁝⁝⁝ | × | × | × | × | × | × | × | MYRTACEAE | Eucalyptus blackelyi |
| | | | | | ⁝⁝⁝ | | | | | | | | MYRTACEAE | Eucalyptus blackelyi s.l. |
| | | | | | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | MYRTACEAE | Eucalyptus cinerea |
| | | | | | ⁝⁝⁝ | × | | × | × | × | ⁝⁝⁝ | | MYRTACEAE | Eucalyptus robusta |
| | | | ⁝⁝⁝ | ⁝⁝⁝ | | | | | | | | | MYRTACEAE | Eucalyptus robusta s.l. |
| | | | | | | | | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | ⁝⁝⁝ | MYRTACEAE | Eucalyptus tereticornis |
| | × | ⁝⁝⁝ | × | | | | | | | | | | MYRTACEAE | Psidium guayava |
| | | | | ⁝⁝⁝ | | | | | | | | | MYRTACEAE | Sigizium jambo |
| | | ⁝⁝⁝ | | | | | | | | | | | PALMAE | Archontophoenix cunninghamiana |
| | ⁝⁝⁝ | | | | | | | | | | | | RUTACEAE | Citrus spp |
| | | | | ⁝⁝⁝ | | | | | | | | | UMBELLIFERAE | Foeniculum vulgare |
| | | | ⁝⁝⁝ | | | | | | | | | | undetermined | Sp 1 |
| | | | | | ⁝⁝⁝ | | | | | | | | | Sp 2 |
| | | | | | ⁝⁝⁝ | | | | | | | | | Sp 3 |

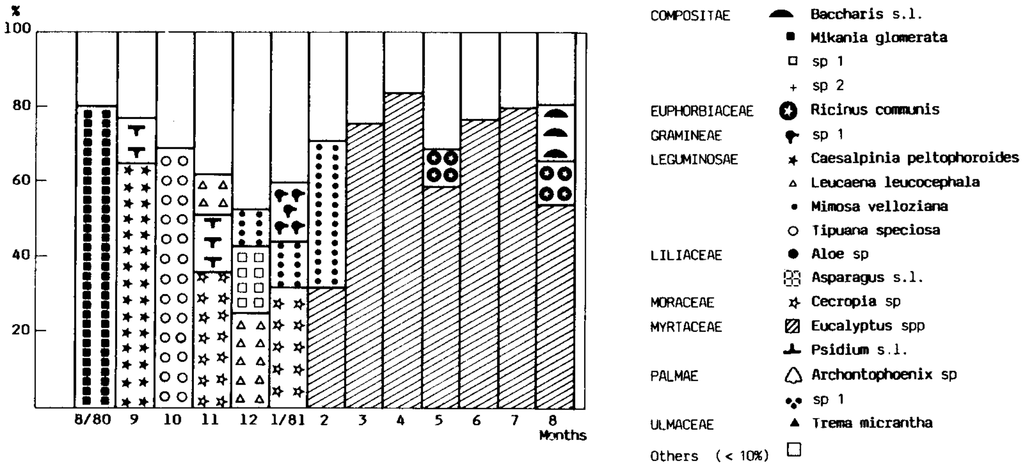


FIG. 1B. — *Relative frequency of pollen types with percentage higher than 10 % - pollen samples from* Apis mellifera.

Early and late summer (December and February) were the months when pollen diversity was highest. The highest annual diversity of Leguminosae and Compositae occurred in December. *Mimosa velloziana* began being visited in this month, but reached a peak in January and February, proving to be the plant most visited by Am together with *Cecropia* sp. and *Eucalyptus.*

If the grain size of the pollen collected from these flower visits is analyzed, both bee species collected pollen with grain sizes between 20-30 µm. In the Am samples, no grain sizes larger than 71 µm occurred, whereas in the Ts samples there were grains over 100 µm. Grains of less than 10 µm are not only rare in nature but were not collected by either of the bee species studied.

Annual pollen preferences were estimated by adding up the percentages for monthly pollen foraging by bees. Myrtaceae (47.0 %), Leguminosae (19.0 %), Compositae (16.0 %), and Moraceae (7.0 %) were greatly preferred by Am. and were represented not only as most collected pollen but also by the large diversity of species. Ts tended to prefer flowers from Myrtaceae (37.0 %), Liliaceae (24.0 %), Palmae (18.0 %), and Compositae (8.0 %).

As to the annual diversity of these two bee species (Fig. 2), January was the month with the highest value, while the lowest values occurred in August 1980 and July 1981. The number of monthly pollen types collected by both species varied from 42 to 81. October 1980 showed the lowest pollen diversity rate for Ts, and August 1980 and July 1981 showed the lowest for Am. The months with the least diversity were the coldest periods in the year.

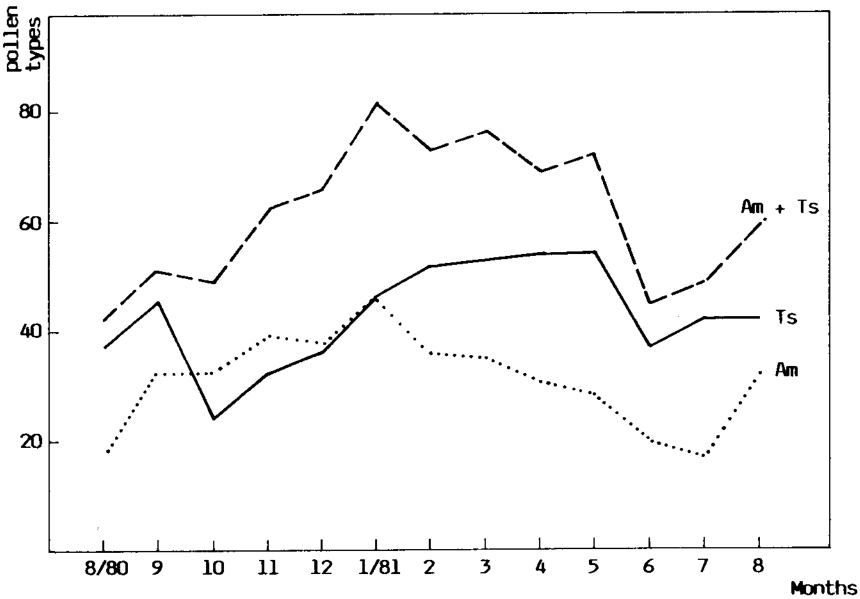


FIG. 2. — *Niche size (in number of species).*

Ts = number of pollen types in *Trigona spinipes* samples ;
Am = number of pollen types in *Apis mellifera* samples ;
Ts + Am = total number of pollen types in both bees samples.

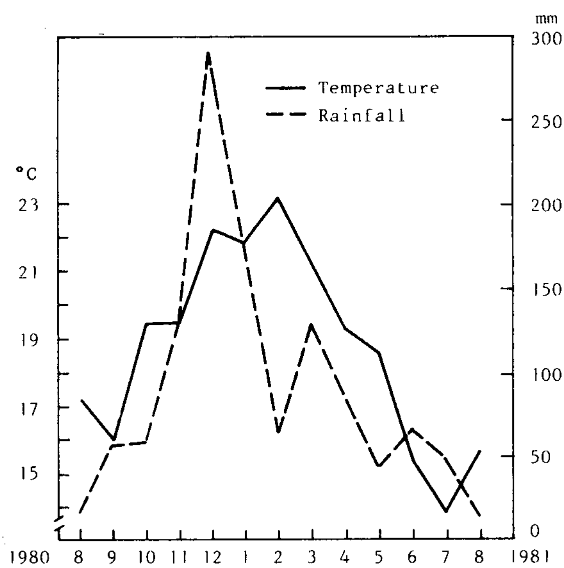


FIG. 3. — *Rainfall (mm), and temperature (°C) during the period analysed.*

For Am, the months with the highest pollen diversity — November, December, January and February — were months of higher temperatures and rainfall. For Ts April and May were the months with the greatest pollen diversity, which showed a slight decrease in temperature and rainfall (Fig. 3).

The percentage similarity in gathering (PS) remained well below the qualitative overlap (a), although there were fluctuations in the order of magnitude of these parameters (Fig. 4). In August and September 1980, the highest proportions of pollen types in common occurred in the samples (high value for « a »), but the sources were not highly shared (low value for PS). In June, July and August 1981, the opposite occurred : intense visits to a few common sources. In general, overlaping was low for both « a » and PS (less than 0.5).

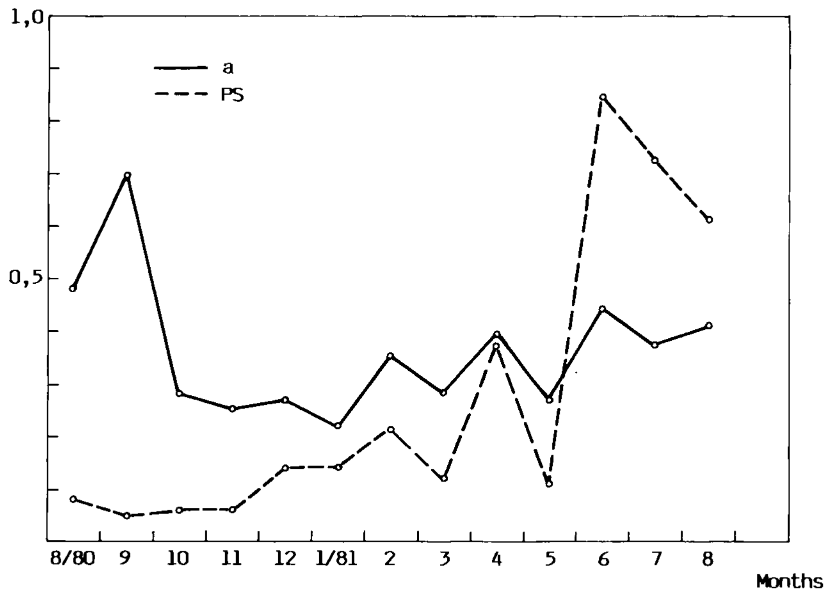


FIG. 4. — *Resource overlap (PS and a) between* Trigona spinipes *and* Apis mellifera.

Pollen niche width (H') varied from 1 to 2.5 for both bee species (Fig. 5). The high values are due more to the large number of pollen types than to their representation in the samples, for the exploitation of the floral resources actually visited was very heterogeneous (low evenness values) throughout the period analyzed.

Table 2 shows that there is no correlation between the qualitative overlap (a) and the percentage similarity (PS), i.e. the number of pollen types in common in the two diets was not related to the intensity of visits to floral resources. Neither was any significant correlation found between niche size (H′) and PS, for Ts and Am alike. The significant positive correlation between H′ and the evenness index (J′) shows that the number of sources visited has some effect on the intensity of exploitation of each resource.

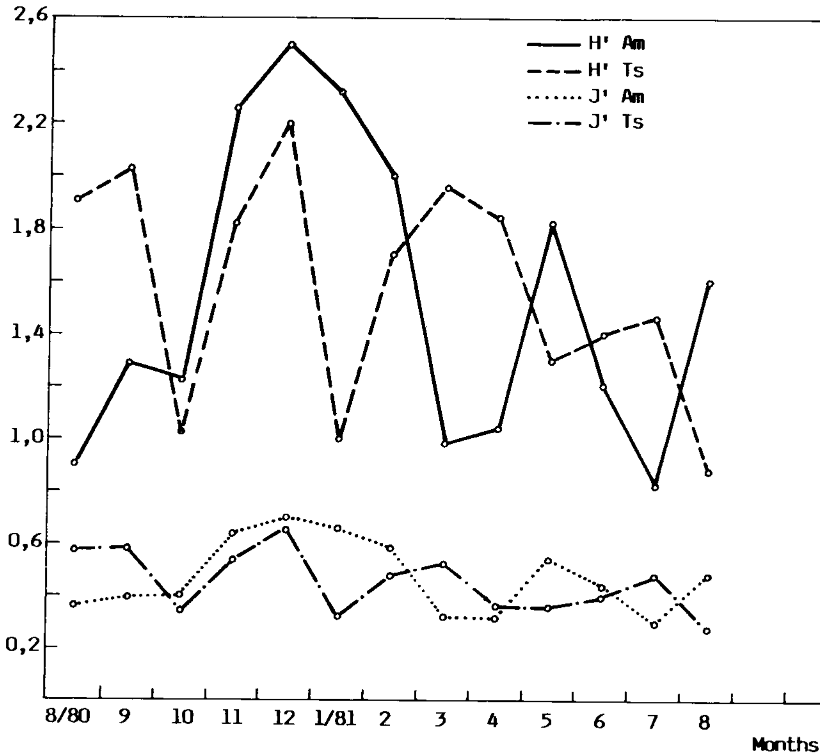


FIG. 5. — *Niche size (H′) and evenness (J′).*

TABL. 2. — *SPEARMAN ordinal correlation coefficients (rs) for various ecological parameters relating* Apis mellifera *and* Trigona spinipes (see text).

| | a × PS | H′ × PS | | H′ × J′ | |
|---|---|---|---|---|---|
| | | Ts | Am | Ts | Am |
| rs | 0.1669 | − 0.2920 | 0.1873 | 0.8953 | 0.9560 |
| sl | > 0.05 | > 0.05 | > 0.05 | < 0.05 | < 0.05 |

sl = significance level.

## DISCUSSION

### 1) *Botanical aspects*

Pollen spectra for Am and Ts samples show that both these species had similar behavior in terms of pollen collection, i.e., they gave preference to collecting from few plant species (considered as « important food resources » when over 10 %). However, they collected small amounts of pollen from a wide range of plants grouped at the top of Figure 1 called « alternative food sources ». But it is in fact the large diversity of pollen types below 1 % that accounted most for the degree of polylecty of each species of bee.

The number of species of each plant visited for pollen by the two bee species is shown in Figure 1 (A and B). It was observed that the most frequent for Am were Compositae, Leguminosae and Myrtaceae, and for Ts Myrtaceae and Leguminosae. HEITHAUS (1979) found that in Costa Rica Leguminosae are the bee plants most visited, as well as being abundant and diversified in the region. However, when the amount of pollen supplied by each family is calculated, it can be seen that this order is changed or even inverted. Thus, for Am the family which supplied most pollen was Myrtaceae, Followed by Leguminosae and Compositae. For Ts, the families were Myrtaceae, Palmae and Compositae in decreasing order.

The Myrtaceae were represented almost exclusively by several species of *Eucalyptus* (Fig. 6). SANTOS (1964) and BARTH (1970a) have shown that this genus is often overrepresented in honey, as it is an excellent grain producer. For NOGUEIRA-NETO (1953), *Eucalyptus* not only produced an abundance of nectar, but also provided nestbuilding sites for Meliponinae in hollow parts of the trunk. Of all Myrtaceae genera, *Eucalyptus* are considered excellent for bees owing to the great variety of flower species for visiting year round (BARTH, 1970a ; JULIANO, 1970). For Am, Myrtaceae were followed by Leguminosae, represented in decreasing order of importance : *Mimosa velloziana, Tipuana speciosa, Caesalpinia peltophoroides, Leucaena leucocephala, Piptadenia gonoacantha, et al.* For Ts, the pollen grains of Leguminosae were not so attractive : species worthy of mention include *Leucaena leucocephala, Schizolobium parahybum, Erythrina speciosa,* and *Caesalpinia peltophoroides.*

KUHLMANN and KUHN (1947) mentioned *M. velloziana* (Fig. 6) as one of the various species of the genus which is visited not only by wild bees but also by Am. They also mention *Piptadenia gonoacantha* (Fig. 8). GIORGINI and GUSMAM (1972) referred to various *Mimosa* as being visited for pollen and for nectar.

Several authors have already proved the importance to bees of *Tipuana speciosa* (Fig. 7) in Brazil (GIORGINI and GUSMAN, 1972) and in tropical

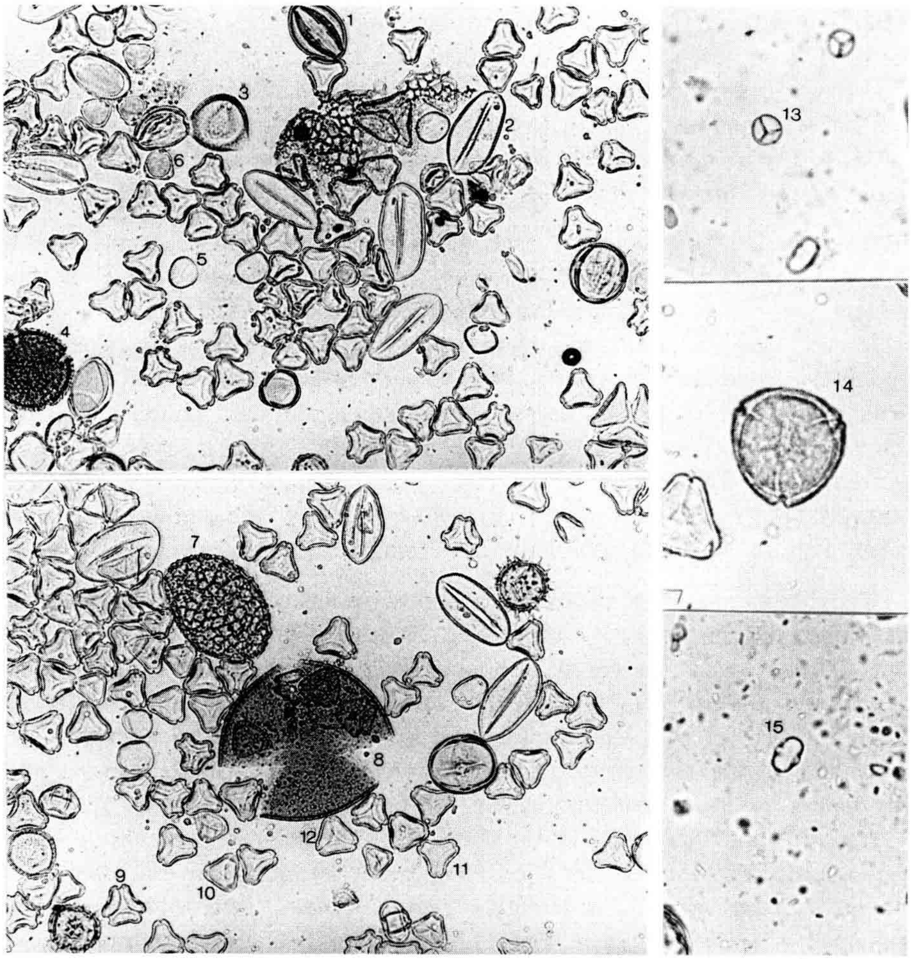


FIG. 6. — *Photomicrographs of the pollen grains collected by the bees* Apis mellifera *and* Trigona spinipes :
*1.* Euphorbia splendens, *2.* Archontophoenix cunninghamiana, *3.* Erythrina speciosa, *4.* Chorisia speciosa, *5.* Aloe *sp.*, *6.* Eucalyptus *sp.*, *7.* Hemerocallis *sp.*, *8.* Mesembryanthenum *type,* *9.* Eucalyptus tereticornis, *10.* Eucalyptus cinerea, *11.* Eucalyptus blacklyi, *12.* Eucalyptus robusta, *13.* Mimosa velloziana, *14.* Ricinus communis, *15.* Cecropia *sp.*

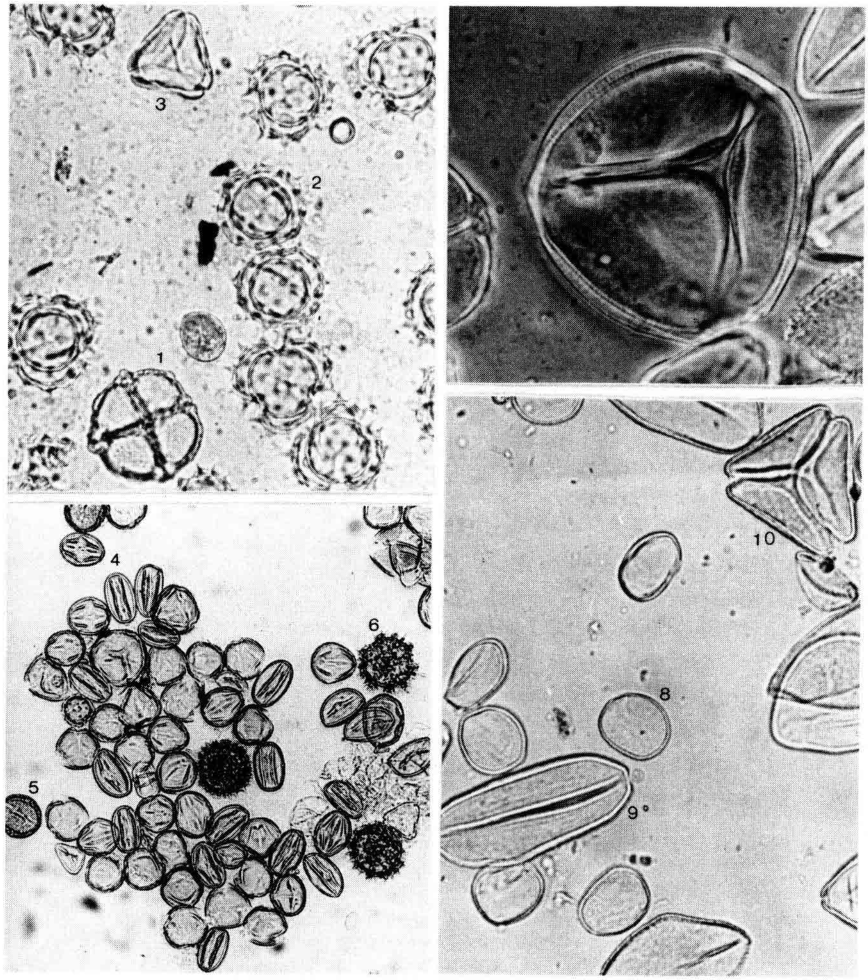


FIG. 7. — *Photomicrographs of the pollen grains collected by the bees* Apis mellifera *and* Trigona spinipes :
*1.* Mimosa daleoides, *2.* Mikania glomerata, *3.* Eucalyptus rudis, *4.* Tipuana speciosa, *5.* Citrus *sp.*, *6.* Vernonia *sp.*, *7.* Leucaena leucocephala, *8.* Aloe *sp.*, *9.* Archontophoenix cunninghamiana, *10.* Struthanthus *sp.*

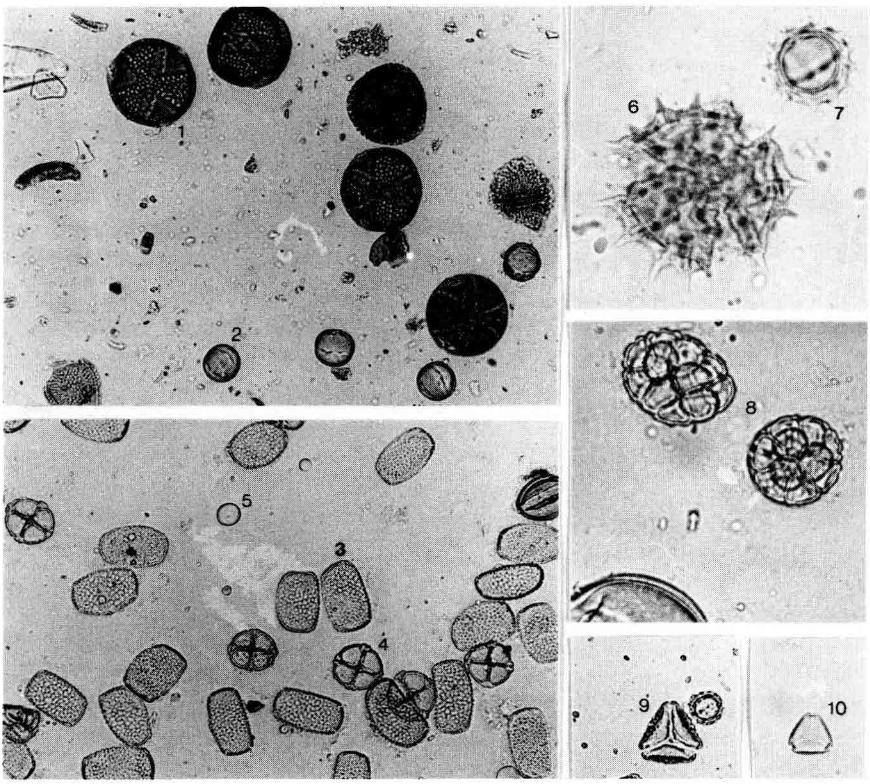


FIG. 8. — *Photomicrographs of the pollen grains collected by the bees* Apis mellifera *and* Trigona spinipes :
*1.* Caesalpinia peltophoroides, *2.* Citrus *sp.*, *3.* *Impatiens sultanii*, *4.* Mimosa daleoides, *5.* Morus nigra, *6.* Vernonia *sp.*, *7.* Baccharis *type*, *8.* Piptadenia gonoacantha, *9.* Struthanthus andrastylus, *10.* Psidium guayava.

America (ORDETX-ROS, 1952). In the present study, the trees planted under urbanization programs consist almost entirely of this species.

*Leucaena leucocephala* (Fig. 7) is another plant which has been proved to be frequently visited by bees (AMARAL, 1970). It is cultivated in the area, but also grows wild and bears flowers from a very early age. This is not the case with *Schizolobium parahybum,* however, as it takes many years to flower with inflorescences at about 10 meters above the ground. This species appears with relative frequency in *Apis* honey (BARTH, 1970c). *Erythrina speciosa* (Fig. 6) and *Caesalpinia peltophoroides* (Fig. 8) also have proven value for bees, and occur in the honey made by *Tetragonisca angustula* (IWAMA and MELHEM, 1979).

The Compositae was the third most frequent family for Am. The most frequently visited species for Am were *Mikania glomerata* (Fig. 7), *Vernonia* sp. (Fig. 8) (including the species *polyanthes* and *scorpioides,* which flower almost at the same time), and *Taraxacum officinale.* For Ts, this family was represented by two pollen types which were not identified. The four species of Compositae mentioned are recognized as being visited by bees in a number of lists of bee plants made by various authors ; *Mikania* sp. is nectariferous for *Tetragonisca angustula* (IWAMA and MELHEM, 1979), and the other are also polliniferous (GIORGINI and GUSMAN, 1972).

Writing about the Compositae, LOUVEAUX (1968) said that it is not visited a great deal by bees but it is always included in foraging ; BARTH (1970a) remarked that its grains are very frequently found in Brazilian honey samples, and that almost no samples are found to be without at least one or two pollen grains. She also mentions that the number of species is very high, and that specific pollen identification is very difficult to perform. SOMMEIJER *et al.* (1983) saw that *Bidens pilosus* was prevalent in *Apis* samples for some weeks.

The Moraceae were represented for Am by *Cecropia* sp. (Fig. 6) and *Morus nigra* (Fig. 8). For Ts the latter was less frequently. Pollen from *Cecropia* sp., regarded as anemophilous by BARTH (1970a), was found in the pollen loads of *Melipona seminigra* (ABSY and KERR, 1977) as well as in the nectar from this bee, and from *Melipona rufiventris* (ABSY *et al.*, 1980). ENGELS and DINGEMANS-BAKELS (1980) found *Cecropia* sp. in pollen storage pots from *Melipona favosa.* SOMMEIJER *et al.* (1983) identified *Cecropia peltata* in pollen collected by *Apis* and Meliponinae. *Morus nigra* is known to be visited by Am and stingless bees in our area.

The Euphorbiaceae were represented for Am by *Ricinus communis* (Fig. 6) only ; this was so throughout the year, except for March 1981. BARTH (1970b) found it in the honey from *Apis,* and GIORGINI and GUSMAN (1972) mentioned this species as nectarifereous. ENGELS and DINGEMANS-BAKELS (1980) registered *Melipona rufiventris* in these flowers.

The Gramineae, little represented for both bee species, were separated by size, following a suggestion by SALGADO-LABORIAU (1973).

The Bignoniaceae, represented by *Spathodea campanulata* (bell flambeau), were collected by Am, but very little by Ts. PORTUGAL-ARAÚJO (1963) studied these trees and found that their flowers kill a large number of stingless bees. In Brazil, NOGUEIRA-NETO (personal communication) observed that here these flowers are also poisonous for stingless bees. In our observations, the mucilage inside flowers was found to contain dead *Tetragonisca angustula, Plebeia* sp., Ts, ants and beetles, but only very rarely Am.

The Palmae, represented by an ornamental coconut tree (Fig. 6) which is native to the area *(Archontophoenix cunninghamiana)* were not frequently collected by Am ; in the case of Ts, however, this family contained the second most frequently collected pollen type. For BARTH (1970c), species from this family were principally visited by bees for pollen, which was occasionnaly found in their honey, such as in the case of *Cocos nucifera,* as isolated pollen.

The Rutaceae, represented by *Citrus* sp. (Fig. 7), were only visited by Am. Its value as a source of nectar is much greater than as a pollen supply, and as a pollen source it is probably underrepresented (BARTH, 1970a).

The Umbelliferae, represented by *Foeniculum vulgare,* grow wild and flower early in life. In the area involved in this study, they are also visited by small stingless bees and wasps, as well as by Am.

The following families were also visited by Ts : Ulmaceae, represented by *Trema micrantha* — this appears relatively often as isolated pollen in the honey of Am (BARTH, 1970c) and of *Tetragonisca angustula* (IWAMA et MELHEM, 1979) ; Liliaceae represented by *Hemerocallis* spp. (Fig. 6), including *H. flava* and *H. fulva,* which flower together and have very similar pollen. BRAGA and MOREIRA (1962) mentioned the latter species as being visited for nectar. Ts bores into the base of the receptacle and then ingests nectar. This opening is then used by Am and other bees. *Aloe* and *Asparagus* are cultivated because of their beautiful flowers.

The Balsaminaceae were represented by *Impatiens balsamina* and *I. sultanii* (Fig. 8). NOGUEIRA-NETO (1953) said that these two species were very attractive for small native bees. BRAGA (1961) saw *P. emerina* collecting principally pollen, while BARTH (1970c) found isolated pollen in honey. IWAMA and MELHEM (1979) found the second species as isolated pollen in honey during two months of the year. These plants flower all year round and do not need much attention when cultivated.

The Loranthaceae were represented by *Struthanthus* sp. (Fig. 8). KUHLMANN and KUHL (1974) mentioned that the flowers of various species of this genus were visited by wild bees and by Am. The *S. andrastylus* has been seen being visited for nectar (IWAMA and MELHEM, 1979).

The Agavaceae were represented by *Fourcroya gigantea*. This species produces enormous pollen grains of about 127 μm. However, the plants of this family observed to be most visited by Ts were *Agave americana* and *A. attenuata*. They are highly valuable plants in economic terms, and are visited by bees in tropical America (ORDETX-ROS, 1952).

2) *Ecological aspects*

Am and Ts are conspicuous in relation to the degree of polylecty if we compare them with some stingless bees studied in the gardens of IBUSP, such as *Tetragonisca angustula* (IMPERATRIZ-FONSECA *et al.*, 1984, *Melipona marginata* (KLEINERT-GIOVANNINI, 1984), *Paratrigona subnuda* (MOUGA, 1984), *Plebeia remota* (RAMALHO *et al.*, 1985) and *Melipona quadrifasciata* (L.S. GUIBU, personal communication). This general pattern, revealed by palynological analysis of stored food, has confirmed an earlier field study. CORTOPASSI-LAURINO (1982) found that of 190 plant species surveyed in the gardens of IBUSP, Am visited 104 belonging to 44 families, while Ts visited 105 from 48 families ; other bee taxa attained half of these numbers in the same time.

SOMMEIJER *et al.* (1983) remarked that for some species of stingless bees and the honeybee studied in Surinam, the pollen spectrum was related to the size of colony population rather than the size of the foragers. Our data corroborate this finding, for although Ts is smaller than Am, their colony populations are equivalent and very large (around 50,000 bees), compared with those of the other stingless bees mentioned above. Thus the greater availability of workers may determine the degree of dispersion over the countryside, thereby contributing to the location of alternative sources and the elevation of the degree of polylecty.

We found that both species were very active throughout the year in pollen collection, but there were quantitative variations in diversity. The peak for pollen diversity that occurred between December and May may be related to the greater plant availability at this time of year. Although the gardens of IBUSP do not have well-defined flowering seasons (FUKUSIMA-HEIN, personal communication), during warm wet periods it is possible to see the proliferation of many invasive species, especially of Leguminosae and Compositae, which are less frequent during cold dry periods. In this context, sporadic fluctuations in the number of sources available may be the main factor behind the diversification of gathering by Am and Ts, even if they have a negligible role in the diets of these bees.

The months when diversity was lowest corresponded to the shortest days and coldest temperatures of the year. In winter less pollen may be ingested by Am which also could reduce foraging activity. Another justification for lower diversity of pollen harvest in cold months is the fact that *Eucalyptus,* the major source of pollen for Am and Ts is flowering during this period.

High pollen niche size (H′) together with low evenness values (J′) show great diversity of collection with intense exploitation of few sources. This was also observed for the other stingless bees mentioned above *(Melipona marginata, Tetragonisca angustula, Paratrigona subnuda, Plebeia remota,* and *Melipona quadrifasciata),* although H′ values were far lower. We conclude that in terms of collecting pattern, these species of Apidae can be differentiated basically as far as the number of sources visited is concerned, since just a few sources are intensively used by each. Am and Ts are similar species.

The high degree of polylecty of Ts and Am must be a factor which enhances potential interactions in the flowers, if just a few and most productive sources would be chosen by foragers from large colonies. PERCIVAL (1974) found that of 225 plant species surveyed in the Cardiff region, 86 were used by Am, and only 17 were really well exploited in a radius of 400 meters from the nests. Similar results were obtained by ANDREJEW (1928), SYNGE (1947), and LOUVEAUX (1968), all for Am. Other field studies have shown a tendency for few more productive sites or flower sources to be chosen by *Trigona* (JOHNSON and HUBBELL, 1974, 1975 ; HUBBELL and JOHNSON, 1978), and Am (JHAJJ and GOYAL, 1979 ; VISSCHER and SEELEY, 1982).

By comparing two communities RANTA *et al.* (1981) remarked that when one of them is more stable in terms of flowering (a certain number of species flowers for longer periods), there is more likelihood of segregation between species of bumble bees (less overlap). In this study it was found that long-lasting flowering contributes both to segregation (Ts gathering from *Archontophoenix* sp.) and to overlapping (gathering from *Eucalyptus* spp.) for both species, probably depending on their attractiveness.

We found only one period when there was considerable qualitative overlap (a), another period when similarity (PS) was high. Both were associated with relatively low values for pollen type diversity in samples : in the former case, the low supply of resource types could moderate the effect of chance in the differentiation between gathering by Am and Ts, while in the latter the abundance of some sources could facilitate simultaneous exploitation (gathering from *Eucalyptus* spp. for example). We believe that intense sharing of a single large source, and analogously common visiting of many smaller shared sources, point to the occurrence of mutual shifts depending on the food available from each source and on the floral preferences by Ts and Am. The tendency for « PS » to remain below the values of « a » during most of the extensive period analyzed corroborates this assumption, all the more so because the former index is more indicative of the real utilization of each source by both species. In constrast, the lack of correlation between the fluctuation patterns of the « PS » curve and the H′ and J′ curves reveals the lack of a strict and generalized influence between the ways in which Am and Ts visit flowers, probably due to the excessive food supply from most shared sources compared with demand during most of the year, and the possibility of exploiting alternative preferential sources.

Floral concentration seems to be a determining factor in the attraction of Ts foragers. Since Ts has the features of the species which JOHNSON and HUBBELL (1975) call « specialists in high floral densities », which tend to be effective monopolists, the idea put forward by JOHNSON and HUBBELL (1974) that the first to arrive at a source « takes all » may be a premise which Ts maximizes, especially in the flowers of *Archontophoenix* sp. and *Aloe* sp. These plants have very large flowerings which are very compact and limited to a small area. This strategy would be not successfull for the exploitation of resources with flowers which are more spread out in the crown of the plant, as in *Cecropia* sp., *Mimosa velloziana, Tipuana speciosa,* and even in *Eucalyptus* spp., all visited by Am.

The success of Ts as a polytrophic species is due to its biology and behavior in flowers. In addition to its highly developed system of communication and its relatively large colonial populations, Ts increases its trophic niche by robbing floral nectar after biting a hole in the base of floral corollas (GIORGINI and GUSMAN, 1972). We observed this in 5 % of 190 plant species. We also observed the four levels of aggression (JOHNSON and HUBBELL, 1974) among individuals from rival colonies of Ts and against Am in the flowers where Ts predominated *(Euphorbia grandicornis, Agave americana* and *Dombeya burgessiae)* (CORTOPASSI-LAURINO, 1982).

For SAKAGAMI and LAROCA (1971) the predominance of Ts in the flowers near Curitiba (PR) is easily understood because of its construction of aerial nests and independence from tree hollows.

All these factors suggest that Ts has a great degree of adaptability to different environments. This is confirmed by its extensive geographic distribution in Latin America (SCHWARZ, 1948).

On the basis of the high degrees of polylecty and the strategy of chosing and exploiting just a few abundant resources, we conclude that (Am and Ts) have a similar impact on the plant-pollinator community in the site considered. Furthermore they are of outstanding importance in regard to their potential for reducing the availability of food for other species, mainly social Apidae.

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## RÉSUMÉ

### ÉTUDE BOTANIQUE ET ÉCOLOGIQUE DU POLLEN RÉCOLTÉ PAR L'ABEILLE AFRICANISÉE (*APIS MELLIFICA* L.) ET *TRIGONA SPINIPES* A SÃO PAULO

*Apis mellifica* L. et *Trigona spinipes* Fabricius sont les Apidae les plus abondants dans les jardins du Bioscience Institute de l'Université de São Paulo (23° 33′ S, 46° 43′ W, 735-765 m d'altitude), où il existe une grande diversité d'espèces végétales (près de 400 ont été déjà recensées). Une petite forêt de feuillus, riche en espèces indigènes, couvre 10 ha (Fig. 3).

On a analysé des échantillons prélevés mensuellement du pollen récolté par *A. mellifica* et *T. spinipes.* Vu la diversité totale des plantes récoltées, peu de ressources ont été bien exploitées par les 2 espèces d'abeilles (Fig. 1, Tabl. 1). Le pollen d'*Eucalyptus* spp. d'*Aloe* sp. et d'*Archontophoenix* sp. a été récolté par *T. spinipes,* tandis qu'*A. mellifica* a principalement exploité *Eucalyptus* spp., *Tipuana speciosa* et *Cecropia* sp. Les familles botaniques qui ont fourni la plus grande quantité de pollen à *T. spinipes* sont les Myrtaceae, les Liliaceae et les Palmae ; à *A. mellifica,* les Myrtaceae, les Leguminosae et les Compositae (Fig. 6-8).

On a trouvé près de 40 types polliniques chaque mois dans les échantillons de chacune de ces abeilles (Fig. 2). Le chevauchement des ressources a oscillé en général entre 0,1 et 0,5 (Fig. 4). Le pourcentage de similarité de la récolte (PS) s'est maintenu en-dessous du chevauchement qualitatif (a), ce qui dénote l'existence possible de préférences florales ou d'interactions compétitives. La diversité des ressources disponibles à un moment donné paraît être l'une des variables les plus importantes dans la détermination de la polylectie d'*A. mellifica* et de *T. spinipes,* malgré la grande hétérogénéité de leur exploitation, caractérisée par des valeurs élevées de H′ (taille de la niche) accompagnées de valeurs basses de J′ (constance) (Fig. 5, Tabl. 2).

Vu le degré élevé de polylectie d'*A. mellifica* et de *T. spinipes* et leur tendance à exploiter d'autant plus intensément les ressources les plus abondantes, on peut supposer que ces espèces ont une influence semblable sur la communauté plante-pollinisateur de cette région.

## ZUSAMMENFASSUNG

### POLLENERTRAG BEI AFRIKANISIERTEN *APIS MELLIFERA* UND *TRIGONA SPINIPES* IN SÃO PAULO — BOTANISCHE UND ÖKOLOGISCHE ASPEKTE

*Apis mellifera* Linneus und *Trigona spinipes* Fabricius sind die am meisten vorhandenen Apiden in den Gärten des Bioscience Institute der Universität von São Paulo (23° 33′ S ; 46° 43′ W, 735-765 m ü.d.M.). Die Gärten weisen eine große Vielfalt an Pflanzenarten auf (ca. 400 Arten katalogisiert). Außerdem gibt es ein Areal von ca. 10 Hektar mit sekundärer Vegetation (Mischwald), reich an einheimischen Arten (Fig. 3).

Die Untersuchung umfaßte monatliche Stichproben des von *A. mellifera* und *T. spinipes* gesammelten Pollens (Versuchsdauer : 13 Monate). Angesichts der allgemeinen Sammelvielfalt wurden während der gesamten Zeitdauer relativ wenige Ressourcen von beiden Species ausgenutzt (Fig. 1 und Tab. 1). Bei *T. spinipes* wurden häufig Pollenkörner von *Eucalyptus* spp., *Aloe* und *Archontophoenix* sp. in den Stichproben gefunden, bei *A. mellifera* hauptsächlich *Eucalyptus* spp., *Tipuana speciosa* und *Cecropia* sp. Die Pflanzenfamilien, die *T. spinipes* mit dem meisten Pollen versorgten, waren die Myrtaceen, Liliaceen und Palmen ; bei *A. mellifera* die Myrtaceen, Leguminosen und Kompositen (Fig. 6-8).

Bei beiden Bienenarten wurden monatlich etwa 40 Pollentypen in den Stichproben gefunden (Fig. 2). Der Überlappungsbereich der Ressourcen betrug im allgemeinen zwischen 0.1 und 0.5 (bei 1 = totale Gleichheit der Ressourcen und 0 = totale Divergenz) (Fig. 4). Die Ähnlichkeit im Sammelverhalten (PS), ausgedrückt als Anteil des Pollens von gemeinsamen Ressourcen in Prozent, blieb meist unterhalb des qualitativen Überhangs (a), was auf mögliche Präferenz bestimmter Blüten oder auf konkurrierende Interaktionen schließen läßt.

Die Vielfalt der zur Verfügung stehenden Ressourcen zu einem bestimmten Zeitpunkt scheint eines der wichtigsten Kriterien für die Polylectie von *A. mellifera* und *T. spinipes* zu sein, obwohl ihre Art der Ausnutzung sehr heterogen ist, mit hohen Werten für H′ (Pollen-Nischen-Größe) und niedrigen Werten für J′ (Stetigkeit) (Fig. 5 und Tab. 2).

Angesichts des hohen Grads an Polylectie bei beiden Arten *A. mellifera* und *T. spinipes* und ihrer Tendenz, die am meisten vorhandenen Trachten intensiver auszunutzen, kann angenommen werden, daß beide Arten einen etwa gleich großen Einfluß auf die Pflanzen-Bestäuber-Gemeinschaft dieses Areals haben.


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