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Wild Bee Biocoenotics in São Jose dos Pinhais (PR), South Brazil. Preliminary Report¹⁾²⁾

By

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(With 3 Text-figures and 7 Tables)

The present paper deals with the results of one year's periodical sampling of wild bees on flowers, made in São José dos Pinhais near Curitiba, Paraná. The primary purpose of the survey was to obtain information about the annual cycles of various bee species, in order to have a general background to their comparative bionomics. As many species are still not accurately determined and many of them are new to science, the detailed results at the specific level must be published later. These results, however, can serve to show an outline of the relative abundance and phenology of the local bee assemblage, with some quantitative value.

The relation between bees and flowers is worthy of study as one of the best examples of mutualism between plants and animals, as well as for the economic importance of bees as unrivalled pollinators. Up to the present, there are some studies dealing with ecological aspects of local bee assemblages (Stoekherth, 1933; Pearson, 1933; Graenicher, 1935; Popov, 1956, *cf.* Linsley, 1958). But there is still no work in which a local bee assemblage was studied with a standardized sampling method. In 1959, one of us (SFS) made a regular quantitative sampling of all bee species on flowers at the campus of Hokkaido University, Sapporo (the part dealing with andrenid bees is published in Sakagami & Matsumura, 1967). The purpose of this survey was to obtain data concerning the annual cycle of each species and to gain a perspective of the structure of the bee assemblage as a whole in the area studied. This paper deals with the preliminary results of the survey made by the same purpose, using the same procedure, when SFS stayed at Univers-

1) Wild bee biocoenotics in Eastern Paraná, South Brazil I.

2) A joint contribution from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan (No. 779, SFS) and Departamento de Zoologia, Faculdade de Filosofia, ciências e Letras, Universidade do Paraná, Curitiba, Brasil (No. 203, SL and JSM).

3) Research Fellow of Universidade do Paraná (Curitiba) and Campanha Nacional de Aperfeiçoamento de Pessoal de Nível Superior (Rio de Janeiro) during the work.

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idade do Paraná, Curitiba. The survey was planned by him, the field work was made by SL and SFS while most species collected were identified by JSM.

Methods

1. *Area studied:* Regular sampling was made at a secondary grassland near Airport Afonso Pena in São José dos Pinhais, about 10 km from the center of Curitiba, the State Capital of Paraná. Most parts of the region surrounding Curitiba were primarily covered with famous coniferous forests, with *Araucaria angustifolia* as the dominant tree species (Maack, 1950; Michener *et al.*, 1958; Klein & Hatschbach, 1962). The region adjoins the primary grassland zone surrounding Ponta Grossa, and patches of primary grassland are scattered within the forest zone. The area southeast of Curitiba, where São José dos Pinhais is located, seems to be a zone of such mixture. The occurrence of a previous forest is revealed by the scattered remnants of *Araucaria*. The area surveyed, about 2.1 km. sq. is a secondary grassland. The dominant grasses are *Paspalum notatum*, *Panicum subjunceum* and *Andropogon virgatum*, with an abundant mixture of herbs and semishrubs, especially Compositae, visited by many bees. Patches of shrubs are scattered within the area, but it is virtually free from tall trees and remote from any forest areas nearby. The area is generally flat but with numerous shallow depressions and ditches, which become watercourses during heavy rains. In general the area studied shows the characteristics of so called *Campo sujo* (Heterogenous or uneven grassland).

The bees were sampled on flowers of 67 plant species, which covered most entomophilous species and probably most dominant species in bloom during one year. Among these plants only 35 were identified to species, including two introduced species, *Ulex europaeus* (Leguminosae) and *Tritonia crocosmiflora* (Iridaceae). The predominance of native plants, even in the secondary vegetation, shows a marked contrast to similar situations in the north temperate region, where the ratio of feral species is often very high. Thirteen of 35 identified species were herbs, 13 were shrubs or semishrubs, and 9 intermediates.

The climate of the area is Cfb (Köppen), BB'r (Thorntwaite) or A'₄ (Kira), that is, corresponding to the warm, rainy zone of the north temperate region. The faunal lists of Curitiba region include numerous decidedly tropical elements such as some butterflies (*Morpho*, *Heliconia*, etc.) and stingless bees (about 20 spp., according to Michener *et al.*, 1958). Apparently, the Curitiba region received in the past many tropical elements from the previous subtropical rainforest zone situated northward, but now greatly destroyed.

The relatively mild summer and cool winter, considering the latitude, are mainly due to the altitude (ca. 900 m), the area being on the south Brazilian plateau system. The mean maximum, mean, and mean minimum temperatures of each 10 days during the year are given in Fig. 1, B. The absolute maximum

and minimum were 33.6°C (Jan. 7) and -3.6°C (May 30). In general, the temperature is high in December to February and low during May to August. Rainfall is abundant, the mean annual rainfall during 1955-'65 (excl. '56, '59, '60) was 1,305.7 mm (max. 1,803.7; min. 974) and the mean annual rainy days were 150.9 (max. 164; min. 145). While the seasonal change of temperature does not markedly differ from year to year, the distribution of annual rainfall is quite variable. The total rainfall, measured once each 10 days during the year, is given in Fig. 1, C. Rain was scarce in April to August and abundant in September to March, with a decrease in November to December. This tendency, the dry season in middle autumn to winter and rainy season in spring to early summer with intermediate drop, is generally seen in other years. But the mean monthly rainfall during 8 years shows relatively much rain in June and December: I (156.0 mm), II (114.2), III (116.0), IV (93.3), V (47.9), VI (110.4), VII (69.7), VIII (55.6), IX (126.8), X (110.6), XI (89.4), XII (135.8). Moreover, the difference among years is remarkable. As to the dry months, the maximum and minimum rainfalls in May are 130.8 mm ('55) and 6.6 mm ('64) and in July 338.3 mm ('57, the maximum monthly rainfall during 8 years!) and 10.1 mm ('61). As to the rainy months, maximum and minimum are 270.0 mm ('56) and 58.0 mm ('61) in January.

2, *Sampling procedure:* Sampling was made from March, 1962 to February, 1963, 3 times per month and 4 hours per time, mostly from 9-10:00 to 14-15:00. Actual sampling dates are as follows:

March 5+7, 19,28; April 10, 20, 26; May 3, 14, 24; June 12, 20, 26; July 20, 31;
August 4, 19, 28; September 6, 18, 27; October 10, 20, 31; November 3, 14, 24;
December 9, 17+20, 27; January 9, 21, 30; February 10, 20, March 3.

These dates are henceforth abbreviated IIIe, IIIm IIIl (early, middle and late March), etc. We tried to keep the interval between two sampling dates, if possible, longer than 6 days and shorter than 12 days, though this was often impossible. The interval was too short in VIII-VIIIe, and XI-XIe, while too long in VI-VIe. The final sampling, III, could not be undertaken within February but was made on March 3. Furthermore, the regular procedure was not fulfilled in the following cases: 1) In IIe and XIII, a total of 4 hours sampling was made on two days, not within one and the same day. 2) Sampling was made only 1 hour in VIe, VIIm, only 2 hours in VIIe, due to cold weather, and only 2 hours in XI due to rain (*cf.* Fig. 1, A)

Before and after each hourly sampling, air temperature was measured by a shaded thermometer hung at ca. 1.2 m above ground. Intensity of insolation, cloud amount and wind classes were estimated by eye. The sampling technique is the same as that adopted by one of us in 1959 (SFS, *cf.* Sakagami & Matsumura, 1967). At each hourly sampling, any wild bees on any kinds of flowers or in flight were captured at random, without choice. Each bee was captured by net individually or in groups *when discovered*, that is, not by means of random sweeping on flowers. The captured individuals were separately preserved according to the flower species visited. (Therefore, we used to bring as many killing tubes as the approximate number of flower species found at the time.). Care was taken to walk about approximately 1/4-1/3 of the area studied within each one hour's sampling, thus covering the whole area during one day's sampling of 4 hours. For this purpose, prolonged stay at one particular spot was avoided. For instance, when one flower species was in full bloom in a restricted area, attracting a large number of bees, we captured as many specimens

as possible at one time, then moved away to other places, without awaiting the arrival of further individuals.

In the laboratory, each specimen was labelled according to sampling date, sampling time (1-4), and flower visited. All the following results were obtained based upon sorting and counting of these specimens. All specimens were classified according to the system of one of us (JSM). He believes that his system is valid, but admits that the genera are relatively more subdivided than the systems adopted by some other melittologists.

3. *Possible sources of sampling biases*: To give an unbiased measure of relative abundance among species, our sampling procedure is not free from criticisms. Some of these possible sources of biases are enumerated below, hoping further improvements of the procedure:

3.1. *Influence of removal of individuals upon the total assemblage*. This defect is important but inevitable in a preliminary survey such as ours. Linsley & MacSwain (1959) adopted the capture-release method in estimating the number of andrenid bees visiting *Ranunculus* flowers. Such a procedure could be employed only after the faunal makeup of the given assemblage, especially the distribution of dominant species, was more or less clarified. The influence of removal may vary according to the individual and species numbers. We believe that this influence is not too large in our case, but we have no objective estimation of this aspect.

3.2. *Adoption of individual capture instead of random sweeping*: Apparently, individual capture enhances the errors due to various specific differences as enumerated below. The efficiency of random sweeping is, except for some limited cases, relatively low in sampling wild bees. They are very active and sensitive, *visiting, not inhabiting*, flowers of various types under diverse situations. But random sweeping is useful for getting a sample of small, inconspicuous bees, that otherwise would be missed. Probably combined methods would be best in future.

3.3. *Relative ease of capture due to specific difference*: In general, the larger, slower, less sensitive bees with some conspicuous coloration or other morphological peculiarities are more easily discovered and caught than those with opposite features. The species with painful stings, for instance, bumblebees, carpenter bees, etc. require much time per individual for capture and preservation, thus affecting the sampling efficiency within a definite interval, especially when the population density is high. The specific difference due to weather conditions is also important. Excessively hot or cold weather conditions inhibit the activities of some stenothermal species. The nocturnal or crepuscular species are usually ignored by daytime sampling.

3.4. *Differences due to different flower visiting habits*: The estimation of the relative abundance of oligotrophic species tends to deviate from the real density, because the distribution of flower species preferred by them is often sporadic or patchy, thus the chance of discovery varies greatly from case to case. The bees visiting flat, open and pale coloured flowers are easier to discover and to catch than in the opposite case. The capture of bees visiting spinous plants is often inefficient. Finally the bees visiting arboreal flowers are difficult to discover and to catch. The last mentioned item is not important as far as the grassland bee fauna is concerned, but may become one of the most serious obstacles in determining the relative abundance objectively, when the bee assemblages of various types of vegetation, including woodland types, are compared.

3.5. *Different efficiency due to personal differences of collectors*: Obviously the ability to discover and to catch the bees greatly varies among persons. This is partly compensated for by converting the results into the relative values. But some primary

knowledge on the bees, their flower visiting habits and motor patterns are indispensable. We cannot also underestimate the fatigue of the collector due to continuous field work. This is one of the reasons why we divided each sampling period into 4 separate hours.

Our results at São José dos Pinhais are not free from the biases mentioned above. Some of them will be removed by improving the procedure, but some others are difficult to eliminate. However, in spite of these defects, we believe that our results present an approximate estimation of the relative abundance of various bees, and that the performance of this kind of survey in various areas is useful to compare the composition and phenology of local bee assemblages.

Results and discussions

1. Relative abundance: Table 1 shows the number of species and individuals collected at a generic level. The result can be regarded as a sample taken from an assemblage. But the assemblage can be regarded at various levels. At the lowest level, the table shows a sample from the wild bee assemblage peculiar to the secondary grassland surveyed during 1962-63. Or, it may represent the bee assemblage in and near Curitiba, or that of South Brazilian plateau system. Further it may be a fraction taken from the unusually rich Neotropical bee fauna. For the lack of any comparable data, it must be mentioned that the following comments cannot definitely be focussed at any particular levels.

The faunal characteristic is clear from the distribution patterns of the genera collected, even if such patterns are always more or less arbitrary and depend on the classificatory system. Among 48 genera in total, more than half (56.3%) are Neotropical, about 18.8% are Neotropical with some Nearctic representatives. Most of the other genera are large groups with wide distribution, either cosmopolitan or nearly so. Any melittologists in Northern Hemisphere could point out the lack of predominantly north temperate elements such as Melittidae or some large genera, *Andrena*, *Lasioglossum*, *Eucera* and *Panurginus*. Further faunistic comparison will be given in the concluding remarks.

Comparing the data in table 1 with the general perspective of the bee fauna in and near Curitiba, after long years' experience by one of us (JSM), there is an obvious lack or poverty of some bee groups, perhaps explained by the absence of arboreal strata and by the unbalanced flora, especially by the lack of legumes. The poverty of *Xylocopa* both in species and individual numbers and stingless bees in species number are apparently caused by the lack of suitable nesting sites for these principally arboricolous groups. It is noteworthy that the unique flourishing stingless bee species, *Trigona (Trigona) spinipes* (Fabricius), occupying the top rank among bees in individual number captured, makes free aerial nests, hence does not need hollow trees for nidification.

As to the number of species, the overwhelming dominance of Halictidae (occupying 58.6%) is remarkable. The ratios of the other families are: Anthophoridae 16.3 (Anthophorinae 6.1, Xylocopinae 4.8, Exomalopsinae 3.0, Nomadi-

Table 1. Numbers of species and individuals of wild bees sampled in São José dos Pinhais, 1962-63

Family & subfamily	Genus	Distribution pattern ¹⁾						Number of species		Number of individuals		
		Nt	Ne	Pa	Et	Or	Au	Total	Known in ♀	♀	♂	Total
COLLETIDAE	6							10	8	15	28	43
	<i>Hylaeus</i>	±	+	+	+	±	+	3	2	3	16	19
	<i>Colletes</i>	±	+	+	±	±		3	3	8	9	17
	<i>Hoplocolletes</i>	+						1	1	1	1	2
	<i>Ptiloglossa</i>	+	±					1	1	1	0	1
	<i>Tetraglossula</i>	+						1	0	0	1	1
	<i>Oediselisca</i>	+						1	1	2	1	3
HALICTIDAE	15							88	70	1,746	693	2,439
	<i>Paroxystoglossa</i>	+						4	2	313	286	599
	<i>Dialictus</i>	+	+	±				41	30	464	90	554
	<i>Augochloropsis</i>	+	±					15	14	266	97	363
	<i>Pseudagapostemon</i>	+						4	4	250	75	325
	<i>Augochlora</i>	+	±					4	3	134	14	148
	<i>Caenohalictus</i>	+						1	1	91	57	148
	<i>Cerathalictus</i>	+						2	2	96	36	132
	<i>Neocorynura</i>	+						3	2	29	19	48
	<i>Thectochlora</i>	+						1	1	44	3	47
	<i>Augochlorodes</i>	+						2	2	39	1	40
	<i>Augochlorella</i>	+	+					4	3	7	10	17
	<i>Pseudaugochloropsis</i>	+	±					1	1	7	3	10
	<i>Rhynocorynura</i>	+						2	2	3	1	4
	* <i>Sphecodes</i>	±	+	+	+	±	±	3	2	2	1	3
* <i>Temnosoma</i>	+	±					1	1	1		1	
ANDRENIDAE	6							17	16	108	29	137
	<i>Psaenythia</i>	+	±					6	6	46	6	52
	<i>Anthrenoides</i>	+						6	5	32	15	47
	<i>Rhopitulus</i>	+						2	2	16	1	17
	Gen. ³⁾	+						1	1	8	3	11
	<i>Acamptopeum</i>	+						1	1	4	2	6
<i>Callonychium</i>	+						1	1	2	2	4	
MEGACHILIDAE	3							19	14	60	23	83
	<i>Megachile</i>	+	+	+	+	+	+	14	10	48	17	65
	* <i>Coelioxys</i>	+	+	+	+	+	+	4	3	11	6	17
<i>Epamthidium</i>	+						1	1	1	0	1	
ANTHOPHORIDAE	14							27	26	290	142	432
	3							5	5	26	2	28
	<i>Exomalopsis</i>	+	±					3	3	18	0	18
	<i>Tapinotaspoides</i>	+						1	1	5	2	7
<i>Lanthanomelissa</i>	+						1	1	3	0	3	

Table 1 (Continued)

*Nomadinae	3						4	3	9	6	15	
	<i>Isepeolus</i>	+					2	1	7	5	12	
	<i>Trophocleptia</i>	+					1	1	1	1	2	
	<i>Nomada</i>	±	+	+	±	-	±	1	1	1	0	1
Anthophorinae	5						10	10	59	54	113	
	<i>Gaesischia</i>	+	±				4	4	13	38	51	
	<i>Melissoptila</i>	+					3	3	41	16	57	
	<i>Thygater</i>	+					1	1	3	0	3	
	<i>Centris</i>	+					1	1	1	0	1	
	<i>Anthophora</i>	-	+	+	±	±	1	1	1	0	1	
Xylocopinae	3						8	8	196	80	276	
	<i>Ceratina</i>	+	±	±	+	+	±	3	3	145	38	183
	<i>Centinula</i>	+					2	2	42	39	81	
	<i>Xylocopa</i>	+	±	±	+	+	+	3	3	9	3	12
APIDAE	4						6	6	1,012	71	1,083	
	<i>Bombus</i>	±	+	+	-	±	3	3	327	69	396	
	<i>Trigona</i>	+					1	1	675	0	675	
	<i>Melipona</i>	+					1	1	9	2	11	
	<i>Plebeia</i>	+					1	1	1	0	1	
Total	48						167	140	3,231	986	4,217	

1) Nt(Neotropical), Ne (Nearctic), P (Palaeartic), Et (Ethiopean), Or (Oriental), Au (Australian). Symbols + ± - show approximate relative abundance.

2) In Apidae, queens and workers combined.

3) An undescribed genus.

* Parasitic groups.

nae 2.4), Megachilidae 11.4, Andrenidae 10.2, Colletidae 5.9, and Apidae 3.6. In the table, the species number of each genus is given in two ways, by the total number and that known only in females. The latter presentation is often useful or even necessary, because in many bee groups females are much more sampled than males due to their longer life spans and lasting foraging activities. It must be stressed that in biocoenotic studies of bees, both sexes are not equivalent as sampling units and in the significance of their influence upon flowers. In five genera, *Augochlorella*, *Sphecodes*, *Augochloropsis*, *Dialictus* and *Anthrenoides*, there are certain unidentified species known only by one sex. It is probable that species A, known by male, is conspecific to B, known by female. In these genera, the real species number lies between the two values mentioned in the table.

The number of genera (A) represented by various numbers of species (B) in the total number of species, not that known by females alone, is given as follows (B/A): 1/22, 2/6, 3/9 4/6, 6/2, 14/1, 15/1, 41/1. These values may be useful for further comparative studies. It is clear that most genera are represented by a restricted

number of species, but some genera involve a large number of species. The number of species in *Dialictus* is of special interest, occupying nearly 1/4 of the total number of species. It is unlikely that the flight radius of this genus much exceeds 1 km (Batra, 1966), so that most of the 30–40 species collected are the inhabitants of the 2 km. sq. area studied, a quite high species density within a limited area.

Concerning the relative abundance in terms of individual number, a peculiar difficulty occurs in biocoenotic studies of bees, due to the occurrence of various social patterns, by which the significance of the *individual* as a sampling unit is unequal among groups. In Apidae, all species collected are social. For instance, a well developed colony of *Trigona spinipes* contains 100,000–150,000 individuals (Lindauer & Kerr, 1958, cited as *T. ruficurus*). In such case, the occurrence of a single nest within a given area is sufficient to distribute an enormous number of individuals throughout the area, and the number of sampled individuals may become very large near the nest. The problem is qualitatively the same in *Bombus*, although the colony size is far smaller, probably not or rarely reaching 1,000 in the local climate. Even in Halictidae, a number of species collected are certainly social or subsocial, with less than 10 females per nest. Moreover, the makeup of the sample becomes different according to the social pattern. In bumblebees and social halictine bees, queens, workers and males are captured on flowers. In stingless bees, however, males are captured only exceptionally, and queen, in all probability never, on flowers. Therefore, in addition to the different modes of life between both sexes, biocoenotic studies of bees (and vespid wasps) are complicated by the occurrence of various social patterns.

Nevertheless, the comparison of various groups in terms of individual number is of some value. Relative abundance among various families is given as follows:

	Total	Female	Male
Halictidae	57.9%	54.6%	70.0%
Apidae	25.7	31.2	7.2
Anthophoridae	10.2	8.7	14.4
Xylocopinae	6.5	6.0	8.0
Anthophorinae	2.5	2.2	5.0
Exomalopsinae	0.8	0.2	0.7
Nomadinae	0.4	0.3	0.7
Andrenidae	3.2	3.3	2.9
Megachilidae	2.0	1.9	2.3
Colletidae	1.0	0.6	2.8

The dominance of Halictidae is evident in individual number. Some genera of this family outnumber most other families: *Paroxystoglossa* 14.3%, *Dialictus* 13.2, *Augochloropsis* 8.7, and *Pseudagapostemon* 7.7 (both sexes combined). This abundance may partly but not exclusively be caused by the occurrence of social species. For instance, the most abundant species, *Paroxystoglossa jocasta* (Schrotky) is solitary (Michener & Lange, 1958a). On the other hand, the second rank occupied by Apidae is apparently caused by their social mode of life as seen by the makeup of females: 287 workers and 40 queens in bumblebees and 685 workers and no queen in stingless bees (*Trigona*, *Melipona* and *Plebeia*). Among other groups,

Xylocopinae are relatively abundant in part by the reason given in the next section. The other groups occupy in combination only about 10% of the total individual number.

How these ratios vary in the other areas must be clarified through further comparative studies. The abundance of halictine bees could probably be seen in various districts of the World. The abundance of Apidae is also evident by their mode of life. Their relative importance may be quite variable among different districts. The family contains three social groups with different geographic distributions and ecological niches: Stingless bees as pantropical arboricoles, honeybees as Palaetropical arboricoles with considerable extension to temperate zones and bumblebees as Holarctic terricoles with Neotropical extension. Of course the picture may vary completely when the European honeybee, *Apis mellifera* Linné, is involved. In most cultivated lands, this domestic species outnumbers the wild bees. This was also true in our survey in São José dos Pinhais, although no quantitative sampling was made of this species.

The numerical inferiority of another biological group, the parasitic bees, is also recognized from the table. The total individual number of parasitic bees, including *Sphecodes*, *Temnosoma*, *Coelioxys* and Nomadinae is 36, that is, only 0.85% of the total sample. This agrees with the assertion so far empirically presented.

As a whole, the number of species (A) represented by different individual numbers (B) is arranged as follows (B/A):

1. Total individual number: 1/53, 2/13; 3/11; 4/10; 5/8; 6/3; 8/4; 9/6; 10/2; 11/6; 12/1; 13/2; 14/3; 15, 16, 17, 18/2; 20/1; 21/1; 22, 25, 31/1; 33/2; 36/4; 39, 40, 43, 45, 47, 51/1; 59/2; 67, 70, 75, 77, 82, 95, 99, 130, 148, 160, 273, 328, 582, 675/1.

2. Number of females (Apidae excluded); 1/88, 2/11; 3/12; 4/8; 5/9; 7/5; 8/8; 9/4; 10/1; 11/2; 13/1; 14, 15/3; 18, 19, 20/1; 21, 27/2; 29, 31, 32, 33, 35/1; 39/3; 41, 44, 46, 50, 60, 69, 70/1; 91/2; 122, 125, 230, 309/1.

The occurrence of many bee species represented by a single specimen and of a few species with enormous numbers of individuals are clear. When the logarithm of individual number of each species is arranged in a descending order, a linear relation is obtained except for several dominant species, whose individual numbers are excessively large. The occurrence of numerous species known only by a few specimens suggests further increase of the total number of species by repeated surveys.

2. Phenology: The data basic to phenological trends are given in Fig. 1. The abscissa shows month divided into three 10 day periods. All values are plotted on the mid-point of the period, not on the actual calendar dates. Some additional explanations are given as follows:

A. Cloud amount is the mean of 8 measurements taken at beginning and end of each one hour sampling.

B. Mean temperatures were calculated from the observatory records measured hourly (24 times per day). The free end of vertical bar given for each 10 day period shows the mean air temperature at sampling (=mean of 8 measurements as in cloud amount).

E. Anthophoridae include Exomalopsinae, Nomadinae and Anthophorinae, but exclude Xylocopinae.

F and G. In Apinae, queens and workers are combined as females.

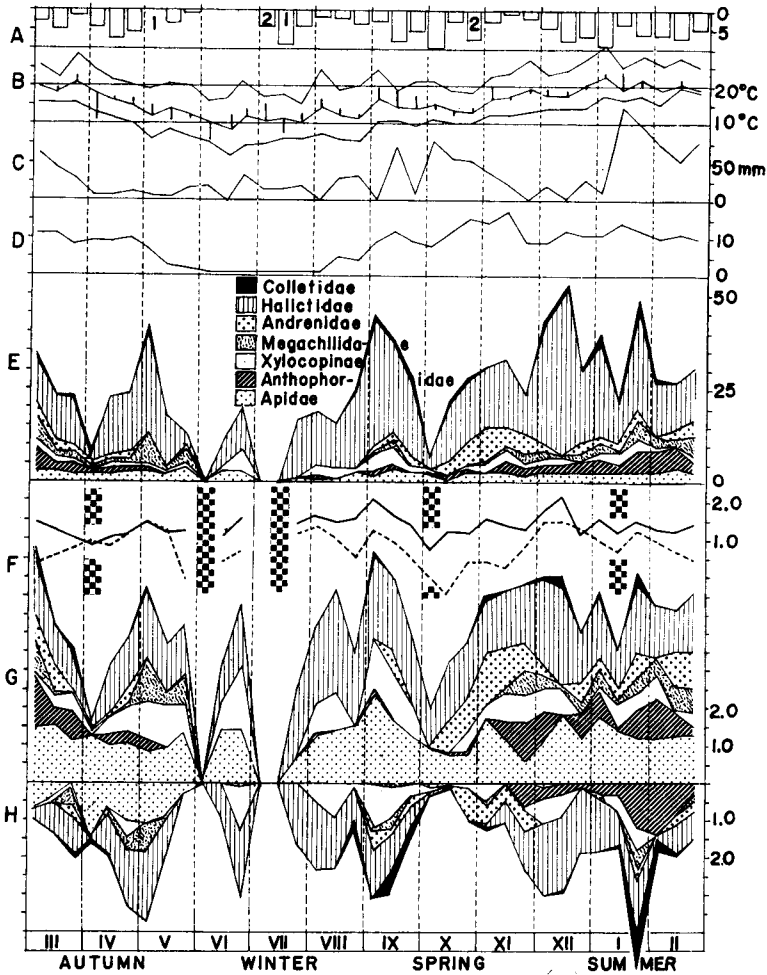


Fig. 1. Phenology of species and individuals during one year. *A.* Mean cloud amount during 4 hours' sampling in each 10 day period. Numerals 1, 2, mean only 1 or 2 hours' sampling was made. *B.* Mean maximum, mean and mean minimum air temperatures in each 10 day period (from records by Airport Observatory). Vertical bars on mean temperature show deviation of mean air temperature on each sampling day from corresponding mean temperature of the 10 day period. *C.* Total rainfall in each 10 day period (from records by Airport Observatory). *D.* Number of flower species visited by bees. *E.* Number of bee species collected. Each taxonomic group is differently shaded. *F.* Total individual number (solid line, females; broken line, males) by logarithmic scale. Checkerboard bars show the possible influence of adverse weather in corresponding 10 day periods. *G.* Relative abundance of each taxonomic group (females), given by logarithm of individual number. Shading as in *E.* *H.* Ditto (males). Shading as in *G.*, but in opposite arrangement.

2.1. *General accounts of phenology:* Fig. 1, B shows the climate type governed by temperature, though not as conspicuously variable as in typically temperate zones. The hottest months are January and February and the coldest June and July. The mean maximum temperature in the coldest months is slightly higher than the mean temperature of, and distinctly higher than, the mean minimum temperature of the hottest months, indicating a rather mild annual change of temperature. The rainfall in 1962-63 (Fig. 1, C) was scarce in the cold months (IV-VIII) but abundant in the hot months (IX-III), with a distinct decrease in late spring to early summer. The occurrence of such a relatively dry period within the rainy season are observed in other years. The seasonal change in the number of flower species visited by bees (Fig. 1, D) well reflects the climatic trends, flowers being scarce in autumn-winter and numerous in spring-summer. During the winter, *Senecio* sp. 1 is the only species which attracts bees (*cf.* Fig. 3) and virtually the only plant in bloom. After August, the number increases steadily, reaching the maximum (17 spp.) in middle November, then drops to about 10 spp. and, except for a second peak in middle January (14 spp.), keeps this level until late April.

On the other hand, the bee activities do not show such definite seasonal trends. Both species and individual numbers (Fig. 1, E, F) are characterized by rather erratic ups and downs. This partly depends on the weather conditions on sampling days.

When the population density of some active animal groups is measured utilizing their activity, two kinds of populations, from which the sample is extracted, must be considered: A, total individual (in our case, total adult bees inhabiting the area), and B, total active individuals (in our case, total adult bees flying). The ratio B/A varies according to weather conditions, especially in animal groups such as bees, which are in general very sensitive to weather conditions. Sampling on fine, warm and calm days alone is practically impossible, so that fluctuation of ratio B/A is inevitable. The tolerance range of each bee species to weather conditions is practically unknown. To partly compensate this defect, the possible influence of adverse weather during sampling, taken from Fig. 1, A and B, was shown in Fig. 1, F with checkerboard bars. It is suggested that poor results are probably caused by cold weather in IVe, VIe, VIIm, by rains in Xe and by excessive heat and rains in Im.

However, even when such influence of adverse weather is considered, there is no clear correspondence between species and individual numbers and seasons as is characteristic in typically temperate climates. The cold temperature in winter seems to inhibit flight activities, yet under favorable conditions, many species and individuals are flying (VII, 20 spp. and 186 individuals).

Concerning the number of species, four maxima are recognized: late autumn (Ve), early spring (IXe), early and middle summer (XIIIm, II). Although drops between these peaks are partly caused by adverse sampling conditions given above,

Table 2. Phenology of

Month & period	III			IV			V			VI		VII	VIII			
	e	m	l	e	m	l	e	m	l	m	l	l	e	m	l	
<i>Melissoptila</i>	♀	12	*	*		*										
<i>pterocauli</i>	♂															
<i>M.</i>	♀	12														
<i>aureocincta</i>	♂															
<i>Augochloropsis</i>	♀	11	*	*		*	*	*	*					*	*	*
<i>iris</i>	♂	+	+			+	8	5								
<i>A.</i>	♂	6	*	*		*	*	*	*		*	*				*
<i>sp. 1</i>	♂			+		+	+	+	+							
<i>Augochlora</i>	♀		*			12	*	4	+	*		5		*	*	*
<i>amphitrite</i>	♂					+	+	+	+							
<i>Augochloropsis</i>	♀		*			*	*	4	*					*		
<i>sp. A</i>	♂					+	25	9								
<i>Paroxystoglossa</i>	♀						10	*			*	15	28	21	20	34
<i>jocasta</i>	♂					+	+	+		+	28	38	34	20	+	
<i>Ceratina</i>	♀		*	*		*	8	8	33	19	21	17		*	6	
<i>asuncionis</i>	♂			+		+		+				6		+	+	
<i>Pseudagapostemon</i>	♀	*	*			*		*			*		18	31	23	19
<i>sp. 2</i>	♂		+	+		*	*	6	*	48	+		*	*	*	*
<i>Augochlora</i>	♀			*		*	*	6	*					*	*	*
<i>semiramis</i>	♂							*		*						
<i>Pseudagapostemon</i>	♀	*						*		*						
<i>fluminense</i>	♂					+	13				+	+		+	*	
<i>Ceratina</i>	♀											6		*	*	
<i>sp. 3</i>	♂											+				
<i>Caenohalictus</i>	♀	*	*										*		6	5
<i>implexus</i>	♂					+						+		+	+	
<i>Neocorynura</i>	♀	*											*			8
<i>sp. 2</i>	♂															
<i>Ceratinula</i>	♀										*					
<i>oxalidis</i>	♂	+	+								+			+	+	+
<i>Cerathalictus</i>	♀					*	*						*	*	*	*
<i>theia</i>	♂					+	+									
<i>Augochloropsis</i>	♀		*											*	*	
<i>sp. G</i>	♂															+
<i>Dialictus</i>	♀	*														*
<i>phleboleucus</i>	♂												*			
<i>D.</i>	♀					*										
<i>opacus</i>	♂					+										
<i>Paroxystoglossa</i>	♀														*	
<i>sp. 2</i>	♂															
<i>Augochlorodes</i>	♀			*		*	*	*	*							*
<i>sp. 1</i>	♂					+										

the peaks seem to represent, in some extent, real phenological phases. Peaks Ve and IXe are apparently separated by periods, characterized by the poverty of species and individuals and by the lack of some major groups as explained below.

dominant "forms"

IX			X			XI			XII			I			II		
e	m	l	e	m	l	e	m	l	e	m	l	e	m	l	e	m	l
														*	*	*	
															+	+	
														5	*	*	
*	*	*				*	*		*	*							16
									+					5	*	*	*
												+		*	*	*	+
						*	*		*	*							7
9	9	8	77		*	*	*	*	15	8		*	*	*	*	*	9
+	+	+				*	*	+	22	5					*	*	+
5	5	*				*	*		*					14	*	*	*
+	+	+				+		+				*		+	*	*	*
14	*	*			*	*	*	25	4	*		*		8	*	*	*
						*	*	12	4	5		+	+	+	14		7
*	*	*			*	*	*	+	4	*		*	*	*			*
									+					+			+
*	*											+		+			
6	+	11			*	*			*	6				14			
+	+	*				+			*	+	20	+	+	+			
*	*								*	*		*	*	*			
4	5	*			*		*		+	+	+	+		*			+
4	+		+		+				+	+		*		*			
6	6	*			*	*	*	*	+	+	*	*	*	*			*
									+	11		+					+
4	*	*							4	*		*					+
+		+				*											
4		7						+	4	8				*	*		
*	13	8			*				+	10		+	+	*			
					*				*	*	*			*			
*									+	+							*
+	5	+										*			*	*	*
*	*		24	18					*					*			*

The drop between peaks IXe and XIIIm is partly caused by sampling conditions, but partly reflects a real decrease, because it corresponds to the experience by one of us (JSM) in and near Curitiba during many years, and represent the transi-

Table 2. Continued.

Month & period	Dominant form	III			IV			V			VI		VII	VIII			
		e	m	l	e	m	l	e	m	l	m	l	l	e	m	l	
	<i>Cerathalictus</i>	♀						*				*				*	
	sp. B	♂		+				+									
	<i>Anthrenoides</i>	♀															
	sp. A	♂															
	<i>Rhopitulus</i>	♀															
	sp. A	♂															
	<i>Psaenythia</i>	♀															
	<i>collaris</i>	♂															
	<i>Thectochlora</i>	♀					*										
	<i>alaris</i>	♂				+			+								
	<i>Melissoptila</i>	♀															
	<i>bonaerensis</i>	♂					+										
	<i>Dialictus</i>	♀													*	*	
	sp. I	♂							+								
	<i>D. anistisianus</i>	♀										*				*	
	<i>D. sp. T</i>	♂															
	<i>Gaesischia</i>	♀	*														
	<i>fulgrans</i>	♂															
	<i>Anthrenoides</i>	♀															
	sp. A	♂															
	% ratio of non dominants		59	100	100	100	88	49	57	54	33	79	13	16	14	25	34
	Total indiv. number of non apid bees		65	32	37	6	42	61	172	46	31	24	156	125	187	102	92
	Total species number of non apid bees		30	20	21	6	21	21	39	16	9	8	17	16	17	15	23
	<i>Bombus</i>	♀			*												
	<i>bellicosus</i>	♂	38	31	30	284	17	16	4	*	32	21	*		*		
		♀	+	+		450	+	16	5	15	+		+				*
	<i>B. atratus</i>	♂						*									
		♀	*			*											
		♂	+	+					+		+						
	<i>Trigona</i>	♀	*	69	*		*	*				83	14	*	9	25	38
	<i>spinipes</i>	♂							11	29							

tion from spring to summer makeup of the bee assemblage. The drop between the two summer peaks, XIIIm and II is again caused by adverse weather at sampling. But excessive hot and rainy weather is rather a rule in mid summer, even if not so inhibitory to bee activities as low temperatures in winter. The corresponding differentiation of early and middle summer assemblages is conceivable. Finally the period between II and Ve represents the transition from summer to autumn assemblage, but it is open to question whether or not the autumnal peak

IX			X			XI			XII			I			II		
e	m	l	e	m	l	e	m	l	e	m	l	e	m	l	e	m	l
*	*		15	*		*	*			*	*	*	*				
			*	*				*									
			10			+	+	+									
			*	*		16	*										
			*	*				+									
								10									
						8	7		*			31	14				
								12	*								
								+	+								
*					*				6	22	*			*			
									+	+				+			
*	*				*				*	11	*			*			*
									+	9		+		+			
												+		6	29	+	
															17	+	
															+		
44	57	66	23	61	72	84	82	44	40	44	42	69	72	62	57	83	61
219	126	71	13	46	50	61	62	75	247	450	90	81	36	133	73	48	68
43	35	26	4	21	25	28	30	22	41	50	27	38	20	46	25	23	28
*		*	*	11	*	*	11	*				57	72	6	10	17	*
	*		*	*	*	*	*	*	*	*	8						
			+									17	*	*	*	*	13
	*	*	*		*	*			*	*							
128	40	21	*		*	92	*	*	4	12	*	*	6		8	17	7

represented by Ve is constantly seen in every year.

The seasonal fluctuation of individual number has two distinct peaks in females, IXe and XIIm. The former peak was partly caused by the large number of *Trigona spinipes* workers (281 out of the total of 675 individuals of this species captured throughout the survey), caught exclusively on *Croton* sp. (being more than 40% of all bees visiting this plant during the survey). But the sample in IXe is also rich in other groups, especially in halictine bees. The second peak in XIIm

is due to the burst of halictine bees, apparently indicating the emergence of new generations. Two species, *Dialictus anistisianus* (Strand) and *Dialictus* sp. 1, both represented by relatively scarce individuals in other seasons, are very numerous in this sample. Besides these peaks, the individual number fluctuates rather irregularly. The relative abundance of females and males goes in parallel, except for IIIe ($\hat{\sigma} > \hat{\varphi}$), VI, VIII, and Xm ($\hat{\varphi} > \hat{\sigma}$), mostly caused by the fluctuation in halictine bees.

However, the seasonal trends described above must be less constant in comparison with those in temperate zones. Due to the mild thermal condition and variable distribution of rainfall, the levels of peaks and depressions as well as their times may vary from year to year. In the absence of a well demarcated inactive period, the phenological trends are intermediate between temperate and humid tropical patterns. The assemblage is very rich in December, both in species and individuals. Graph C show relatively scarce rains in this month. The rainfall in XI-I in different years are:

	1955	1956	1957	1958	1961	1962	1963	1964	1965
XI	27.4	18.7	94.3	50.0	186.5	60.0	141.8	103.7	123.2
XII	213.4	224.4	187.0	70.2	106.0	48.9	150.2	38.1	184.2
I	171.3	270.0	210.6	141.5	58.1	130.1	229.1	61.5	231.8

Apparently such fluctuation may affect bee activities either directly or indirectly through the flowering plants.

The relative abundance of various taxonomic groups, both in species and individuals (Fig. 1, E,G,H), shows the occurrence of two distinct phenological groups. The *first group* consists of Colletidae, Andrenidae, Megachilidae and non-xylocopine Anthophoridae, the *second one*, of Halictidae, Xylocopinae and Apidae. The first group is not captured in winter. This agrees with the phenology of their temperate relatives, which do not winter as active adult forms. The phenology approaches to the temperate pattern by the winter assemblage, consisting of the second group alone, and to the tropical pattern by the absence of a complete cessation of adult activities in winter.

As to the relative abundance of various taxonomic group, the absolute dominance of Halictidae is confirmed from the phenology. The seasonal change of the total species number (graph E) is mostly governed by the fluctuation in this group. They are also the dominant and most stable group in individual number, occupying, in most 10 day periods, the conspicuous part of the whole assemblage. Apidae are a minority group in species number but important in individuals, characterized by the stable appearance both in species and (in females) in individuals, obviously caused by their social mode of life. By the occurrence of two dominant species, *Ceratina (Crewella) asuncionis* Strand and *Ceratinula oxalidis* (Schrottky), Xylocopinae behave as do Apidae, though they are less abundant and stable. Among the other groups, Andrenidae have many species and individuals in spring, and Anthophoridae in summer. Colletidae and Megachilidae do not show marked

seasonal concentration, although the latter is richer in summer to autumn.

2.2. *Phenology of dominant species:* Table 2 shows the dominant 'forms' of non-apid bees in each 10 day period. Considering different modes of life between sexes, females and males are regarded different 'forms'. In each 10 day period, such 6 non-apid dominant 'forms' were chosen by the descending order of individual number. The forms with less than 5 individuals are omitted, even if they are ranked within 6. On the other hand, more than 6 forms are chosen, when the 6th rank is occupied by more than one form with the same individual number. The individual numbers of these dominant forms were converted to the percentage ratio to the total individual number of non-apid bees and are shown in the table. The ratio occupied by all non-dominant forms is given at the bottom, followed by the absolute individual and species number of non-apid species collected. In the table, the percentage ratios of dominant forms are given with erect letters in females, and italic letters in males. When some forms, being dominant in some periods, appear in other periods as non-dominants, their occurrence is shown by asterisks in females and by crosses in males. When one species was at least once dominant in one sex, the opposite sex of the same species is cited even if it was never dominant. The lowest part of the table shows the phenology of dominant apid forms (queens, workers and males separately). The forms comparable in individual number to that of dominant non-apid forms were chosen and their individual numbers were converted, for the sake of comparison, to the percentage ratio of the total individual number of *non-apid bees* given above. Their occurrence as non-dominants is shown by asterisks or crosses. From the table, and partly from Fig. 1, the assemblage structure in each month, starting with winter is given as follows:

June-July: The coldest months in the area. Bees flying only on warm days. Assemblage poor in species and individuals, consisting of only Halictidae, Apidae and Xylocopinae. *Paroxystoglossa jocasta* (♀ ♂) very abundant, often being more than half of non-apid bees. Among other species, *Ceratina asuncionis* (♀) abundant earlier, and *Pseudagapostemon* sp. 2 (♀) later. In Apidae *Bombus* (*Fervidobombus*) *bellicosus* Smith (workers) active in earlier periods but ceasing activities thereafter. *Trigona spinipes* active on warm days.

August: Earlier part as in July. Later, assemblage becoming richer, both in species and individuals, parallel to increased temperatures and flower species. But assemblage structure still simple, virtually dominated by *Paroxystoglossa jocasta* (♀ ♂), *Pseudagapostemon* sp. 2 (♀), followed by *Ceratina asuncionis* (♀) and *Caenohalictus implexus* Moure (♀). In Apidae, *Trigona spinipes* constantly active.

September: Assemblage becoming richer, later poorer. *Paroxystoglossa jocasta*, *Pseudagapostemon* sp. 2, *Caenohalictus implexus*, *Ceratina asuncionis* (all ♀♀) continuously dominant. But some others becoming abundant: *Ceratinula oxalidis* (♀ ♂), *Cerathalictus theia* (Schrottky), *Dialictus* (*Chloralictus*) *phleboleucus* (Moure), *D. (C.) opacus* (Moure). Besides increase of halictine species, 3 previously inactive groups, Andrenidae, Megachilidae and Anthophoridae were beginning to appear, though not yet abundant. In Apidae, bumble-bee queens beginning to appear and *Trigona spinipes* very active.

October: Assemblage dropping both in species and individuals, in spite of favorable thermal and floral conditions. Most previously dominant forms, including those active since winter, disappearing except for *Paroxystoglossa jocasta* (♀). Activities of Andrenidae increasing with *Anthrenoides* sp. B (♀) as dominant, together with two halictine bees, *Augochlorodes* sp. 1 and *Ceratalictus* sp. 1 (both ♀♀). In Apidae, besides queens, *Bombus bellicosus* workers beginning to appear, while activities of *Trigona spinipes* decreasing.

November: Assemblage again enriched both in species and individuals. Andrenidae at the peak with dominant forms, *Rhophitulus* sp. A and *Psaenythia* (*Psaenythia*) *collaris* Schrottky, together with a halictine species, *Thectochlora alaris* (Vachal) (all ♀♀). At the end of the month, one anthophorine species, *Melissoptila bonaerensis* (Holmberg) (♀) dominant and *Pseudagapostemon* sp. 2 (♀) again becoming dominant. Ratio occupied by dominant forms very low. No marked difference in Apidae from October, except for sporadic dominance of *Trigona spinipes*.

December: Assemblage at the peak of summer activities, mainly due to numerous halictines. In earlier part, *Paroxystoglossa jocasta* (♀♂) occupying the top rank and *Pseudagapostemon* sp. 2 (♀) continuously dominant. Later, *Caenohalictus implexus* (♀♂), *Ceratalictus theia* (♂) and *Dialictus phleboleucus* (♀) again dominant. Further, some halictine bees, relatively scarce in other months, becoming quite active, in particular, *Dialictus anistisibeas*, relatively scarce in other months, becoming quite active, in particular, *Dialictus ananus* and *Dialictus* sp. 1. In Apidae, bumblebee queens absent but worker activity gradually becoming conspicuous.

January: Assemblage decreasing at middle but still rich. In Halictidae, *Thectochlora alaris* dominant in earlier half, while *Caenohalictus implexus* and *Pseudagapostemon* sp. 2 later (all ♀♀). The abundance of *Ceratina asuncionis* (♀) in middle period also conspicuous. Later period characterized by increased activities of Megachilidae and Anthophoridae, with two dominant species, *Gaesischia fulgrans* (Holmberg) and *Melissoptila aureocincta* Moure (both ♂♂). Activities of bumblebee workers very high, but activity of *Trigona spinipes* low.

February: Assemblage still keeping the same level in individual number but dropping in species number. Activities of Anthophoridae continuous as shown by *Gaesischia fulgrans* (♂) as dominant. Andrenidae again active with late summer species, notably *Anthrenoides* sp. A (♀). In Halictidae, *Augochloropsis iris* (Schrottky) and *Augochlora semiramis* (Schrottky) dominant, followed by *Paroxystoglossa jocasta* (♀♀). Bumblebee workers continuously active.

March-April: Both species and individual numbers of non-apid bees decreasing. Anthophoridae active only in earlier part, with dominants *Melissoptila pterocauli* (Bertoni & Schrottky) and *M. aureocincta* (♀♀). In Halictidae, *Augochloropsis iris* (♀) dominant earlier, while *Augochlora amphitrite* (Schrottky) (♀), *Augochloropsis* sp. A (♂) and again *Paroxystoglossa jocasta* (♀) later. But throughout these months, the lack of particular dominant forms notable, due to the small number of individuals captured. On the other hand, bumblebee workers very active, suggesting, together with appearance of males, the climax phase of their colony development. Activity of *Trigona spinipes* sporadic.

May: Late autumn characterized by a peak of species and individual numbers, followed by rapid decline. But the constancy of such peak, whether a regular event or not, still uncertain. As far as the result obtained is concerned, *Ceratina asuncionis* (♀) and *Augochlora semiramis* (♀) regarded as dominant, together with *Augochloropsis* sp. A (♀♂) and *Augochlora amphitrite* (♀). Appearance of males of two *Pseudagapostemon*, *P.* sp. 2 and *P. fluminense* (Schrottky) in this period noteworthy. *Bombus bellicosus* (workers and ♂) still active in this month but *B. (Fervidobombus) atratus* Franklin not. *Trigona spinipes* more active than in April.

Some phenological trends in the succession of dominant "forms" given above may be only particular to the year and area surveyed. On the other hand, some others may appear regularly in the area, or even in the Curitiba region in general. Further comparative data are required to confirm the principal, stable phenological trends.

2.3. *Annual cycles of particular species*: A clear understanding of phenological trends could not be achieved by the analysis of the assemblage in each period alone. This is particularly true in bees, which include various species having different types of annual cycles. In Table 2, the numerals diagonally running from left-top to right-bottom show the seasonal alternation of dominant "forms". If the numerals concentrate along this line alone, it means the successive appearance of univoltine species with more or less limited adult longevity. The scattered occurrence of numerals in the right-top part indicates that some species become dominant twice within the year.

In the previous section (2.1.), two phenological groups were distinguished, based upon the occurrence or not of active adults in winter. From Table 2, it is clear that all dominant species belonging to the first group (no active adults in winter) are characterized by a short active stage, indicating their univoltine appearance (*Melissoptila*, *Gaesischia*, *Anthrenoides*, *Rhophitulus*, *Psaenythia*). A similar tendency is seen in many, if not all, other species belonging to this group. Table 3 shows the monthly distribution of captured specimens in some species, sampled relatively abundantly, and shows the monovoltinism in most species cited. In Anthophoridae, *Melissoptila bonaerensis* is probably a monovoltine spring species, but there is a single record of one male in April! All other anthophorid species in the table are univoltine summer to early autumn species. The individual number of other species is too small. Probably *Lanthanomelissa* sp. 1 belong to the spring type and most others belong to the summer type. The continuous appearance of Anthophoridae (excl. Xylocopinae) from August to May is, therefore, understood as the succession of these two phenological types, though with a considerable overlap. The abundance of the summer type, both in species and individuals, is evident from Table 3 and Fig. 1, E,G,H. In Andrenidae, three types are distinguished: 1) Spring type. *Rhophitulus* sp. A, *Anthrenoides* spp. B and C, *Psaenythia collaris* and probably *Callonychium* sp. 1, 2) Summer type. *Psaenythia* (*Psaentia*) *quadrifasciata* Friese, *P. (P.) bergi* Holmberg and, though rather transitional to the former type, *P. (P.) annulata* Gerstäcker. 3) Irregular type. This includes the species whose annual cycles cannot be determined with certainty, as represented by an undescribed species representing a new genus, and *Acamptopeum prini* (Holmberg). These species were captured sporadically during a prolonged period. Such irregularity may be the outcome of one of the following possibilities or the combinations of them: 1) multivoltinism, 2) long adult life span, 3) marked variation in individual life history and resulting obscurity of generations. Andrenid phenology is mainly

Table 3. Monthly distribution of specimens of some representative species of Andrenidae, Anthophoridae (excluding Xylocopinae) and Megachilidae

Family	Species		Month					Type				
			IX	X	XI	XII	I		II	III	IV	V
ANTHOPHORIDAE	<i>Melissoptila bonaerensis</i>	♂			3	1				1		Spring
		♀			9	4						summer
	<i>Isepeolus</i> sp. 1	♂			1	3						"
		♀			1	4	2					"
	<i>Exomalopsis</i> sp. 1	♀				1		2	3	2		Summer
	<i>Ex.</i> sp. 2	♀				1	1		4	1	2	autumn
	<i>Tapinotaspoides</i> sp. 1	♂					2					"
		♀					1	2	1			"
	<i>Gaesischia fulgrans</i>	♂					9	25				"
		♀					1	6	2			"
	<i>Melissoptila pterocauli</i>	♂						3				"
	♀					1	4	12	1		"	
<i>M. aureocincta</i>	♂					7	1				"	
							2	8			"	
ANDRENIDAE	<i>Anthrenoides</i> sp. C	♂	2	1								Spring
		♀		4	5							"
	<i>Psaenythia collaris</i>	♂	1									"
		♀	1	4	10							"
	Gen. sp. ¹⁾	♂	3									Spring-
		♀	4	2					2			autumn
	<i>Anthrenoides</i> sp. B	♂		5	2							Spring
		♀		2	3							"
	<i>Rhopitulus</i> sp. A	♂			1							"
		♀		2	12							"
	<i>Psaenythia annulata</i>	♂			1							Spring
		♀			1	2	2					-summer
	<i>Acamptopeum prinii</i>	♂			1				1			?
		♀			1	1			1		1	"
	<i>Psaenythia capito</i>	♂					1					?
	♀			3		1	2		2		"	
<i>Ps. bergi</i>	♂						1				Summer	
	♀				1	2	1	3			-autumn	
<i>Ps. quadrifasciata</i>	♂							1			"	
	♀					2		3	2		"	
<i>Anthrenoides</i> sp. A	♂							3			Summer	
	♀							14			"	
MEGACHILIDAE	<i>Megachile terrestris</i>	♂								1	1	"
		♀			2	2				1	3	"
	<i>M. franea</i>	♂							2			"
		♀			2	3	3	5			2	"
	<i>M. lentifera</i>	♂					1					"
		♀						3	2		3	"
<i>M. nigropilosa</i>	♂	2		2						2	2	"
	♀					1	2	1	1	2	"	

1) Undescribed genus and species.

explained by the succession of univoltine and short-lived species, intervened by some species with less simple life history. By their abundance in late spring to early summer, this group behaves as do their Holarctic cousins in the enormous genus *Andrena* (cf. Sakagami & Matsumura, 1967).

The phenology of Megachilidae is more difficult to interpret, because many species appear irregularly during a prolonged period. In this group, the degrees of wing wear were examined in most females in order to estimate their relative ages, but the results did not show any definite tendency. For instance, in *Megachile* (*Pseudocentron*) *framea* Schrottky, the wing conditions vary as follows:

Month	XI	XII	I	II.....V
Intact			1	
Slightly worn	1	3	1	1
Moderately worn	1		1	1
Heavily worn			1	

The appearance of worn females in February could be regarded as the end of one generation, followed by a second one, which is continuous to autumn. But the distribution is irregular and covers a prolonged period and the number of specimens is insufficient to make further analysis. The individual number of Colletidae is also too small to make any definite conclusion.

Among the second phenological group, possessing an active adult stage in winter, the life cycle is much more complicated. Leaving detailed analysis of the data for other articles, here are given only a few comments.

In Xylocopinae, the dominant species, *Ceratina asuncionis* appears to have two generations per year; first hibernating and producing the second in summer, and the latter producing the hibernating population in autumn. The capture records are distributed rather irregularly and require closer analysis. The annual cycles of other species are difficult to determine. The bees belonging to this subfamily are well known for their prolonged adult life span, characterized by a long juvenile adult stage before sexual maturity. It is conceivable many species are univoltine in the area studied, in spite of the appearance of adults in various months.

The annual cycle is difficult to determine in Halictidae. This group outnumbers all other groups in abundance, both in species and individuals. In table 2, 21 out of 32 dominant species belong to this group, appearing as dominants at 81 out of 106 positions in the table. Many of them become twice or more often dominants during the year. Moreover, some species are captured in diverse periods of year, even if not as dominants. For instance, *Augochlora semiramis* and *A. amphitrite* appear virtually every month, unless adverse weather inhibits their flight. The three possibilities and their combinations referred to above will be applied in these instances. As gradually clarified by recent advances in the sociological analysis of this group, the situation is here complicated by the occurrence of an extremely rich social spectrum characteristic of this group, ranging from a strictly solitary

Table 4. Number of bee individuals visiting various plant

Plant family	Number of plant species	Number of bee species visiting						Total number of bee individuals visiting			Colletidae		
		Total			Non-halictids			♀	♂	T	♀	♂	T
		♀	♂	T	♀	♂	T						
Compositae	34	106	76	128	53	38	62	1,580	660	2,240	3	14	17
Non compositae combined	33							1,602	318	1,920	10	14	24
Euphorbiaceae	1	45	27	61	10	10	16	576	79	655	2	11	13
Saxifragaceae	1	33	19	39	9	3	8	342	83	425	3	1	4
Labiatae	3	35	19	43	15	7	18	188	96	284			
Rosaceae	2	22	3	22	3	1	3	127	2	129			
Xyridaceae	1	33	7	36	7	2	8	114	9	123	1	1	2
Borraginaceae	1	13	4	17	4	4	8	71	7	78			
Umbelliferae	2	18	7	24	2	2	4	39	13	52			
Rubiaceae	3	17	6	19	8	3	9	31	5	36	2		2
Iridaceae	4	21	1	22	6		6	35	1	36			
Verbenaceae	3	18	3	19	8		9	31	3	34			
Solanaceae	3	12	2	12	6	2	6	13	5	18	1		1
Melanostomaceae	2	5		5	2		2	11		11			
Anacardiaceae	1	6	3	7		2	2	11	6	17		1	1
Lobeliaceae	1	3	3	5	1		1	3	8	11			
Onagraceae	1	3	1	3	2	1	2	3	1	4	2	1	3
Leguminosae	1	2		2	2		2	3		3			
Lytraceae	1	1		1	1		1	2		2			
Amarantaceae	1	1		1	1		1	1		1			
Rhamnaceae	1	1		1				1		1			
Total								3,182	978	4,160	15	28	43

to an elaborated social mode of life. Some species mentioned in the table may be solitary. For instance, the phenology of the most dominant species, *Paroxystoglossa jocasta*, agrees with the observations by Michener & Lange (1958a), suggesting two solitary generations per year and wintering of both female and male adults. In many other species, the occurrence of diverse social patterns is suggestive (*Augochloropsis*, *Dialictus* cited as *Chloralictus*, *Augochlora*, *Necorynura*, *Caenohalictus* cited as *Caenaugochlora*, Michener & Lange, 1958-'59). Each nest can continue for a lasting period, either by the prolonged life span of the nest foundress or by her replacement by her daughters. In such cases, nests can produce successively females which often have undeveloped ovaries. Consequently the correspondence between generations and seasons is not as simple as in solitary species.

All species of Apidae captured are social. In this case, the phenological order is understood better than in Halictidae, because of the advanced social differentiation. In two bumblebee species, *Bombus bellicosus* and *B. atratus*, the seasonal trends may be outlined as follows: Posthibernating queens appear in

families (Sexes given separately and in combination (=T))

Halictidae			Andrenidae			Megachilidae			Anthophoridae (excl. Xylocopinae)			Xylocopinae			Apidae		
♀	♂	T	♀	♂	T	♀	♂	T	♀	♂	T	♀	♂	T	♀	♂	T
931	481	1,412	56	12	68	58	18	76	73	54	127	151	46	197	308	35	343
807	208	1,015	48	16	64	2	5	7	18	6	24	45	34	79	602	35	707
179	46	225	1	1	2		3	3		2	2	25	16	41	369		369
272	76	348							2	1	3	3	5	8	62		62
58	54	112	9	5	14	1	2	3	5		5	11	2	13	104	33	137
74		74										2	2	4	51		51
89	7	96										1	1	2	23		23
16		16	13	3	16				2		2	2	3	5	38	1	39
30	8	38								1	1		4	4	9		9
20	3	23	1		1				3	1	4				5	1	6
26	1	27	4		4				3		3				2		2
14		14	13	2	15				1		1	1	1	2	2		2
6		6	4	5	9	1		1							1		1
8		8							1		1				2		2
11	5	16															
2	8	10													1		1
1		1															
			2		2										3		3
			1		1												
1		1															
1,738	689	2,427	104	28	132	60	23	83	89	60	149	196	80	276	980	70	1,050

spring (IX-X), each of them founding her own nest. Workers produced by the queen begin to forage in spring (*bellicosus*) or early summer (*atratus*). Colony development and worker foraging activities increase in mid summer to early autumn. Sexual forms are produced in autumn and males are abundant on flowers. Worker activities continue to early winter but not to mid winter. Therefore, the annual cycle of those species at São José dos Pinhais does not essentially differ from that in north temperate *Bombus*, except for the reversal in calendar date and worker activities lasting until early winter (*cf.* Moure & Sakagami, 1962; Sakagami & Zucchi, 1965; Sakagami, Laroca & Moure, 1967). Finally, *Trigona spinipes* has no "phenology" in the sense so far used. By the possession of enormous and perennial nests, the life cycle is virtually independent of the season. Only the intensity of foraging and probably brood rearing is affected by adverse weather conditions.

3. Flower visits: Among 4,217 specimens sampled, 4,160 (3,182 ♀♀ and 978 ♂♂) were captured on some of 67 flower species belonging to 20 families. The basic data are given in Table 4. The relationships among the 67 flower species and

more than 160 bee species are quite complicated, so that here only relative flower visits at the family level and the phenology of the predominantly visited flower species are described.

It is well known that many bee species possess a rather narrow preference range for pollen foraging (oligolecty), even if they visit a variety of flowers for nectar. The distinction between these two types of flower visits is important but not regarded here, because it can be analysed better at a specific level.

3.1. Relative visits to various plant families in species number: The number of flower species visited in each plant family is given in the second column of Table 4. Two facts are soon recognized: Predominance of Compositae (50.7%) and poverty of Leguminosae. The first fact agrees with the dominance of Compositae, particularly in Brazil. According to Angely (1960), among 222 Brazilian phanerogamous plant families, the families with more than 100 genera are, Compositae (number of genera, 226), Leguminosae (220), Orchidaceae (185), Gramineae (135), Rubiaceae (127) and Euphorbiaceae (104). In our results, however, the number of species of Compositae visited by bees larger than in other families. This may be explained by the success of this family as entomophilous plants (Graenicher, 1935) and the ability of many species of this family to become dominant herbs in secondary grassland. Among Compositae, 4 genera are particularly rich in species, *Baccharis* (9), *Eupatorium* (5), *Vernonia* (5) and *Senecio* (4), occupying 38.8% of the total species number. The poverty of Leguminosae is also remarkable when their richness in the Brazilian flora is considered. Only two worker specimens, one *Trigona spinipes* and one *Bombus bellicosus*, were caught on *Ulex europaeus*, an introduced species! Apparently the scarcity of legumes must affect the species and individual numbers of bees in the present survey.

The number of species (sexes separately and in combination) visiting each plant family is represented in the third column of Table 4. As the ratio occupied by Halictidae is very high, the number of non-halictid species is given in the fourth column. The relative visits of each bee family to various plant families is better shown by the visiting individual number given in the next section. The total number of visits to Compositae and non-Compositae by each bee family is given at the top of the table. The predominance of visits to Compositae is obvious in most bee families, especially in Megachilidae and Xylocopinae. The ratio of visits to non-Compositae species are (both sexes combined): Colletidae (50.0%) > Halictidae (46.4) > Apidae (43.8) > Andrenidae (42.9) > Anthophoridae excl. Xylocopinae (41.6) > Xylocopinae (33.3) > Megachilidae (25.9).

3.2. Relative visits to various plant families in individual number: The tendencies of relative visits are given better in terms of individual number sampled, as given in the fifth column in Table 4. Based upon these data, the relative abundance of various bee families visiting some predominant plant families is presented, females and males separately, in the left side of Fig. 2. Two graphs given at the top show the ratios of various bee groups visiting all flower species. The deviation

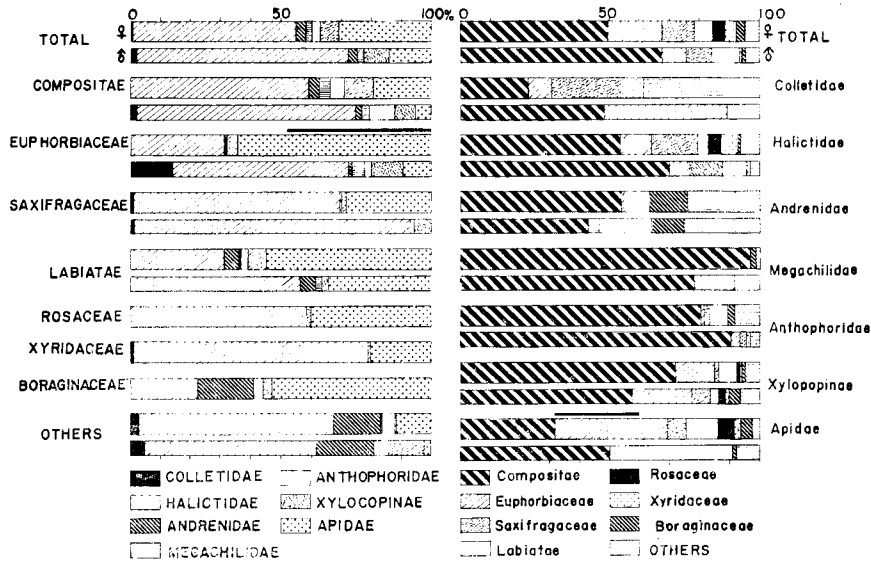


Fig. 2. Bee-flower relationship at family level. *Left*: Relative ratios of visits of various bee groups to the mainly visited plant families. *Right*: Relative ratios of plant families visited by various bee groups. Females and males separately given by thick and thin bars. Anthophoridae include the groups other than Xylocopinae. Thin bars in Euphorbiaceae (left) and Apidae (right) mean the ratios of *Trigona spinipes* caught on a single day (cf. text).

of each plant family from this standard spectrum is briefly commented on:

Compositae: No essential deviation. This is reasonable because more than half of the total specimens were caught on *Compositae*.

Euphorbiaceae (only one species, *Croton* sp.): In females, the portion occupied by Apidae is very high, caused by a large sample of *Trigona spinipes* caught on a single day (281 workers, shown with black bar). Except for this, the ratios are more or less similar to the standard spectrum. The paucity of andrenid and anthophorid bees and lack of megachilid bees partly depends on the phenological discrepancy, that is, the scarcity of these bees at the time of bloom. In males, the relatively high ratio of Colletidae is noteworthy.

Saxifragaceae (only one species, *Escallonia montevidensis*): As in the standard spectrum, except for the first phenological group (cf. Section 2.1.) explained by the phenological discrepancy as in *Euphorbiaceae*.

Labiatae: The ratio Apidae/Halictidae as in the standard in males but higher in females, partly caused by the phenological discrepancy but partly by a real difference in preference. *Salvia lachnostachys* is frequently visited by Apidae but almost ignored by Halictidae.

Rosaceae (mostly on *Prunus* sp. 1) and *Xyridaceae* (only one species, *Xyris* sp. 1): Virtually visited only by females of the second phenological group, not by the first phenological group, because of phenological discrepancy (cf. Figs. 1 and 3). Poor visits by males are noteworthy.

Table 5. Number of bee individuals visiting predominant

Plant species	Total			Colletidae			Halictidae		
	♀	♂	T	♀	♂	T	♀	♂	T
<i>Senecio</i> sp. 1	682	300	982				425	248	673
<i>S. brasiliensis</i>	65	21	86				46	12	58
<i>Eupatorium</i> sp. 7	136	84	220				116	78	194
<i>E. littorale</i>	135	34	169				40	15	55
<i>E.</i> sp. 2	44	27	71				20	17	37
<i>Baccharis spicata</i>	83	43	126	2		2	21	43	64
<i>B. cylindrica</i>	67	14	81				52	12	64
<i>Vernonia</i> sp. 2	70	52	122				25	5	30
<i>Croton</i> sp. 1	576	79	655	2	11	13	179	46	225
<i>Escallonia montevidensis</i>	342	83	425	3	1	4	272	76	348
<i>Prunus</i> sp. 1	125	2	127				72		72
<i>Cunila gallioides</i>	78	86	164				43	52	95
<i>Salvia lachnostachys</i>	88	9	97				1	2	3
<i>Xyris</i> sp. 1	114	9	123	1		2	89	7	96
<i>Moritzia dusenii</i>	71	7	78				16		16
Total	2,576	850	3,526	8	13	21	1,417	613	2,030
% to total visits	81.0	87.0	84.9	53.3	46.4	48.8	81.7	89.0	84.0

Boraginaceae (only one species, *Moritzia dusenii*): The high ratio of visits by Andrenidae is partly caused by the phenological coincidence between plant and bees, but the high ratio of Apidae / Halictidae seems to indicate a real difference in preference here (cf. Figs. 1 and 3).

Other families: The relatively high ratios of Andrenidae and Colletidae are noteworthy. This is also partly caused by the phenological coincidence but partly reflects a real specificity in preference, probably suggesting a rather oligotrophic nature in some species of these bees.

3.3. *Relative visits among various bee groups*: The graphs at the right of Fig. 2, show the relative visits to different plant families by all bees sampled. The overwhelming predominance of Compositae is again recognized. Within this family, the 4 genera mentioned in 3.1. are of particular importance. The ratios occupied by them and by some other important families are:

	Females	Males	Total
Compositae	49.5%	67.2%	53.9%
<i>Senecio</i>	23.7	33.2	26.0
<i>Eupatorium</i>	11.6	16.1	12.6
<i>Baccharis</i>	9.1	9.4	9.2
<i>Vernonia</i>	3.4	5.9	4.0
Other genera	1.7	2.6	2.1
Non-Compositae	50.5	32.8	46.1
Euphorbiaceae	18.1	8.1	12.7
Saxifragaceae	10.7	8.5	10.2
Labiatae	5.9	9.8	6.8

flowers species (Sexes given separately and in combination (T))

Andrenidae			Megachilidae			Anthophoridae (excl. Xylocopinae)			Xylocopinae			Apidae		
♀	♂	T	♀	♂	T	♀	♂	T	♀	♂	T	♀	♂	T
3		3	19	8	27	1		1	117	30	147	117	14	131
5	2	7	3	1	4	10	4	14		2	2	1		1
3		3	3		3	6	1	7	5	4	9	3	1	4
21	3	24	8	2	10	11	4	15	2	2	4	53	8	61
5	1	6	3	3	6	7		7	3		3	6	6	12
									4		4	56		56
						5		5	2	2	4	8		8
	3	3	7	3	10	20	41	61	6		6	12		12
1	1	2		3	3		2	2	25	16	41	369		369
						2	1	3	3	5	8	62		62
									2	2	4	51		51
1		1	1	1	2	4		4	4		4	25	23	58
7	5	12				1		1	7	2	9	77		77
							1	1	1	1	2	23		23
13	3	16				2		2	2	3	5	38	1	39
59	18	77	44	21	65	69	53	123	183	69	252	901	63	964
56.8	64.4	58.5	73.4	91.2	78.3	77.4	88.3	82.5	93.7	86.3	91.6	92.0	90.2	91.8
			Rosaceae			4.0		0.2			3.1			
			Xyridaceae			3.6		0.9			2.9			
			Boraginaceae			2.2		0.7			1.9			
			Umbelliferae			1.2		1.3			1.2			
			Rubiaceae			1.0		0.5			0.8			
			Iridaceae			1.1		0.1			0.8			
			Vervenaeeae			1.0		0.3			0.8			
			Other families			2.7		2.4			4.9			

The ratios in various groups are similar for females and males except for Labiatae ($\delta > \text{♀}$), Rosaceae, Xyridaceae, Boraginaceae, Rubiaceae and Verbenaceae ($\text{♀} > \delta$). Probably these cases partly show the different requirements between sexes, females needing both pollen and nectar, but males visits mainly for nectar.

Compared with the standard spectrum, the relative visits in various bee families (Fig. 2, right) differ in the following points: 1) Overwhelming predominance of visits to Compositae in Megachilidae and non-xylocopine Anthophoridae, and 2) Deviation in Colletidae and Andrenidae from the standard spectrum, especially in the relatively high ratios occupied by the plant families rather neglected by other bees. These peculiarities are partly explained by phenological coincidence or discrepancy, but partly may reflect a specific preference, especially in Colletidae and Andrenidae.

3.4. *Predominantly visited plants and their phenology:* The results so far described give only a preliminary perspective to bee-flower relationships. Flower visting habits of bees and attractiveness of flowers may vary greatly

at infrafamilial levels. Moreover, the ratios occupied by visiting bee groups and visited plant groups are affected by phenological coincidence and discrepancy. The ratios calculated would not always reflect the real preference, which had to be determined by the ratio of visits of each bee group to the total flower species in bloom during its active period. Leaving aside detailed analysis at the specific level, the phenology of predominantly visited flower species is briefly commented on here.

Table 5 shows the visits of bees to 15 predominantly visited plants. The visits to these plants occupy 84.9% (both sexes combined) of the total visits: about 80% (1,847/2,240) in Compositae, and 100% in Euphorbiaceae, Saxifragaceae, Xyridaceae and about 100% in Rosaceae. Therefore, it is certain that relative visits at the family level given in section 3.1-3.3. are mostly determined by these plants. The % ratios occupied by these predominantly visited species among various bee groups are:

Females: Xylocopinae (93.7%) ≥ Apidae (92.0) > Halictidae (81.7) ≥ Total (81.6) > Anthophoridae (78.0) > Megachilidae (73.4) ≫ Andrenidae (56.8) > Colletidae (53.3)
 Males: Megachilidae (91.2) ≥ Apidae (90.2) ≥ Halictidae (89.0) ≥ Anthophoridae (88.6) > Total (86.3) = Xylocopinae (86.3) ≫ Andrenidae (53.6) ≫ Colletidae (46.4).

Two families, Andrenidae and Colletidae, visit with relatively high ratios plants ignored by other dominant bee families.

The ratios of bee specimens caught on these predominantly visited flower species to the total visits were calculated for each month. The resulting phenological sequence is shown in Fig. 3, showing total visits and visits in some dominant bee groups, when the total number of specimens captured in each and visits month was 30 or more. In contrast to the phenology of bee activities, the sequence of predominantly visited flower species was distinct. The ratio occupied by non predominant flowers was high in October-November, which corresponds to the increase of flower species visited, as given in Fig. 1, D. The most conspicuous feature was the monopoly by *Senecio* sp. 1 during winter, which was, in the area studied, virtually the only food source for late autumn to early spring bees.

The seasonal sequence of predominantly visited flower species was as follows (Plants given parenthetically are those not visited by male bees. Others visited by both sexes, except for *Croton* sp. 1 in January, which was visited by males but ignored by females):

March: *Eupatorium littorale*
 April: *E.* sp.2, *Cunila gallioides*
 May: *C. gallioides*, *Senecio* sp.1
 June-July: *S.* sp.1
 August: *S.* sp.1, *Prunus* sp.1
 September: *Croton* sp.1
 October: No predominant flowers
 November: (*Baccharis spicata*), *Senecio brasiliensis*
 December: *Escallonia montevidensis*, *Eupatorium* sp.7, *Xyris* sp.1
 January: (*Salvia lachnostachys*), *Escallonia montevidensis*, *Croton* sp.1
 February: *Vernonia* sp.2, *Eupatorium littorale*

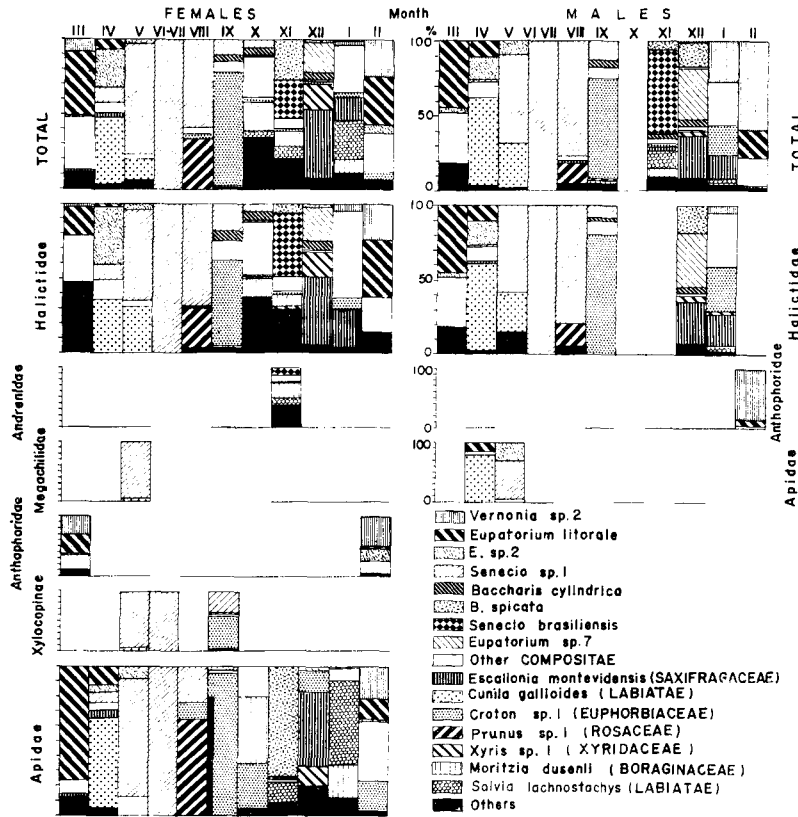


Fig. 3. Phenology of predominantly visited flower species by all wild bees and by dominant bee groups. Females (left) and males (right) separately given. Colletidae excluded. In other groups, the ratios are given only in months, in which more than 30 specimens of respective groups were captured. Thin black bar in Apidae (females, September) means the ratio of *Trigona spinipes* caught on a single day (cf. text).

The preference tendency of Halictidae and female Apidae more or less agrees with that of the total sample, but minor deviations were found, especially in the latter group, for instance, in the preference to *Prunus* sp. 1 in August and *Baccharis spicata* in December. Apart from such deviations, there is an interesting tendency in Apidae. Comparing top and bottom graphs in Fig. 3, left, it is seen that the ratios occupied by the predominantly visited flower species (for instance, *Eupatorium littorale* in March, *Cunila galioides* in April, etc.) are, except January, always higher in Apidae than in the total sample. Here the distinction of two kinds of flower constancy (Linsley, 1958) is of particular importance: constancy characteristic of species (oligotrophy, incl. oligolecty) and that of particular individuals.

In spite of their polytrophic nature at the specific level, many species of Apidae tend to concentrate on particular kinds of flowers at a given time; the resulting high foraging efficiency may be one of the prerequisites for their social mode of life.

The oligotrophic tendency at the species level cannot exactly be determined by the procedure adopted in the present paper, which favors the clarification of preference tendency in dominant species, mostly polytrophic or only moderately oligotrophic, but rather ignores that of rare species, many of which may be oligotrophic. But there are some flower visiting records of non-dominant bee species, probably suggesting an oligotrophic tendency. To call attention for further studies, the records of flower species not frequently visited by halictid bees are cited as follows:

- Petunia* sp. 1 (Solanaceae): *Anthrenoides* sp. C, 13 ♂♂; *Psaenythia collaris*, 1 ♀; *Callonychium* sp. 1, 2 ♀♀ 1 ♂; *Trigona spinipes*, 1 ♀; *Augochlorella iopoesila* Moure, 1 ♀.
- Verbena hirta* (Verbenaceae): *Psaenythia collaris*, 1 ♂; *P. bergi*, 1 ♀; *Rhophitulus* sp. A, 4 ♀♀; *Bombus bellicosus*, 1 ♀.
- Lippia turneifolia* (Verbenaceae): *Acamptopeum prinii*, 1 ♀; *Rhophitulus* sp. A, 2 ♀♀; *Callonychium* sp. 1, 1 ♀; *Augochlora semiramis*, 1 ♀; *Cerathalictus theia*, 1 ♀.
- Salvia lachnostachys* (Labiatae): *Psaenythia collaris*, 1 ♀; *P. annulata*, 1 ♀; *Rhophitulus* sp. A, 1 ♀; *Anthrenoides* sp. B, 4 ♀♀ 5 ♂♂; *Anthophora paranaensis* Holmberg, 1 ♀; *Pseudaugochloropsis graminea* (Fabricius), 1 ♂; *Pseudagapostemon fluminense*, 1 ♂; *Dialictus* (*Dialictus*) *ypirangensis* (Schrottky), 1 ♀; *Xylocopa* (*Neoxylocopa*) *augusti* Lepelletier 2 ♀♀ 1 ♂; *X. (Nannoxylocopa) ciliata* Burmeister, 1 ♀; *Ceratina asuncionis*, 4 ♀♀ 1 ♂; *Bombus bellicosus*, 8 ♀♀, 54 ♀♀; *B. atratus*, 2 ♂♂ 2 ♀♀.
- Jussiaea sericea* (Onagraceae): *Hoplocolletes ventralis* (Friese), 1 ♀ 1 ♂; *Hylaeus rivalis* (Schrottky), 1 ♀; *Pseudagapostemon* sp. 1, 1 ♀.

Concluding remarks

The present study was attempted for two purposes. It was primarily carried out in order to obtain a background for the life history studies of various bee species. A preliminary approach to analyse the bee fauna in the Curitiba region was made.

The faunal makeup of an animal group has been studied in different ways. There are many local catalogues which enumerate various species with no reference to their relative abundance. On the other extreme, there are some studies which give a precise estimation on the relative abundance of each species in terms of individual number or biomass per given spatiotemporal unit. The application of such procedures is often limited by the lack of appropriate data. In sedentary animals with a relatively high density per unit area, or those which can be sampled by special traps, the relative abundance is not difficult to estimate. On the other hand, there are few reliable data concerning such active and alert animals as bees. The use of museum specimens is ineffective, because of the obvious defect that rare species are relatively more often procured, deposited and recorded than common ones. Leclercq (1964 a, b), mentioning this "cult of trophy", attempts to clarify the distribution of Hymenoptera in Western Europe, based upon sampling unbiased

as to season and relative abundance. The present study is intended to clarify the assemblage structure more precisely by standardizing the sampling. This procedure cannot be applied to large areas, because of obvious limitations of facilities. Thus, two approaches are complementary each other and can be used in combination: Within the area surrounding a laboratory, the radius of which may be determined by the transport facilities, several localities of preferably different environmental conditions are chosen, and the procedure adopted in the present survey is applied. These surveys may serve as the foundation showing the structure of the local bee fauna and may be complemented by the occasional surveys in other spots, as stressed by Leclercq, sampling always both common and rare species without bias. The performance of such synthetic sampling in various climatic and vegetational zones in the world may ultimately result in the global comprehension of the bee fauna. For the time being, we have only one set of data described above, so that we can give only some tentative comparisons.

The number of species inhabiting a limited area may vary according to various causes. Some values are given as follows: Sapporo, North Japan ca. 97 spp. (Sakagami, unpubl.); Chicago, Illinois, 169 spp., (Pearson, 1933); Carlinville, Illinois, ca. 297 spp. (Robertson, 1928, after Linsely, 1958), Riverside, California, 439 spp. (Timberlake, after Linsley, 1958). The data in Sapporo were taken by the procedure of the present study, except for 8 hours per week sampling instead of 4 hours per 10 days (*cf.* Sakagami & Matsumura, 1967). All other figures are the outcome of many years' collecting at various habitats. The sampling of 167 spp. during a single year at a single habitat, a secondary grassland of about 2km. sq. in São José dos Pinhais thus indicates a rich bee fauna in the Curitiba region. As mentioned in the results, section I, many species are represented by a few specimens, suggesting duplication or perhaps more species if the whole bee assemblage of Curitiba region should be surveyed during several years. Unfortunately, we have no accurate estimate of the number of bee species inhabiting this region. The following data are suggestive of a rich fauna. In 1963-64, a survey similar to the present study was made by one of us (SL) at Boa Vista, a suburb area of Curitiba. Among various bee groups sampled, only the data of Megachilidae are cited:

	<i>Megachile</i>	<i>Coelioxys</i>	<i>Epanthidium</i>	Total
Spp.collected in S.J.P.	14	4	1	19
Spp.collected in Boa Vista	26	7		33
Spp.common to both areas	7	2		9
Total numberof species	33	9	1	43

Therefore, only about 21% of species were common to both areas.

As to the relative abundance of various bee groups in terms of species number, we have still no sufficient data to compare. Table 6 was compiled to give a preliminary perspective on the relative abundance in different regions of the world at subfamily level. The sources of the data basic to the table were rather arbitrarily chosen without a systematic bibliographical survey. The areas covered by these

studies are variable in extent, from continental to only a few km. sq., and the procedures by which the specimens were sampled are also different, as commented in the table. Nevertheless the table indicates some tendencies, which are suggestive for further studies.

A remarkable difference of the Australian Region from any other areas is immediately recognized. The predominance of Colletidae, the most primitive bees, being never dominant in other continents, and the complete absence of Andrenidae are noteworthy. The relatively rich fauna of Xylocopinae reflects the occurrence of humid tropical forests within the region (compare with Panama). The data II-VI are all taken from the Holarctic Region, so that some basic resemblances are seen, for instance, the presence of Melittidae, and quantitatively the predominance of Andrenidae, principally caused by the genus *Andrena*, and resulting increase of Nomadinae, the dominant genus of which, *Nomada*, is primarily parasitic on *Andrena*. Some interesting tendencies are found when II, the data at continental scale, are compared with III-VI at lower levels. At a glance in the table, the higher ratio occupied by Halictidae in limited areas is obvious. The ratio is distinctly $III > II$, where III is a part of II, and highest in VI, taken from the most limited area. Probably this relates to the dominance of Halictidae in individual numbers. The more the sampling is restricted in area and time, the more the species with numerical abundance would be sampled. A similar tendency is, though less conspicuous, seen in Colletidae and Apidae, but the opposite tendency is seen in Andrenidae (excl. Andreninae, that is, *Andrena*), Anthophoridae and, to some degree, in Megachilidae, explained by the inference given as to Halictidae. The low species number in Sapporo may be due to four causes, operating at different levels to decrease the number of species: Insular poverty in Japan, relatively humid climate in Japan, being inadequate for many bee groups, cold climate in Sapporo, and sampling in a very limited area within a growing city.

The data in Panama show, though less remarkably than in the Australian Region, a clear contrast to the Holarctic data, by the absence of Melittidae, paucity of Andrenidae, Nomadinae and predominance of Exomalopsinae and Apidae, indicating the faunal makeup of the Neotropical Region, which will later be confirmed by the comprehensive catalogue of Neotropical bees now in preparation by one of us (JSM). Obviously our data in São José dos Pinhais, given in the final column, differ markedly from the Australian and Holarctic data and show a basic resemblance to the Panamanian data. Differences between Panama and São José dos Pinhais may be determined geographically (Euglossinae, Andreninae) or by habitat difference (Xylocopinae, Megachilidae), or by the combination of both. The remarkable predominance of Halictidae in São José dos Pinhais, comparable to that in Sapporo, may partly be explained by the reason given in the preceding paragraph. The differences of relative abundance in various groups depend on different causes, operating at different levels. The separation of these causes in a particular set of data could be achieved by promoting biocoenotic studies

Table 6. Relative abundance in % species number of diverse bee groups in various localities of different extents, given at subfamily level (Classification system after Michener, 1965. Subfamilies not represented in any of source data are omitted. Horizontal bars mean the very probable absence from the district concerned)

Family & subfamily	I Austral- ian Region	II North America north of Mexico	III Chicago and vi- cinity	IV Franco- nia, Ger- many	V West. Steppes of Ukr- aina	VI Sapporo Japan	VII Repu- blic of Panama	VII S. Joé dos Pinhais
COLLETIDAE	44.5	5.8	8.3	6.7	7.3	9.2	4.3	6.0
Colletinae	15.4	4.0	5.3	1.6	2.9	1.0	3.7	4.0
Hylaeinae	16.7	1.8	3.0	5.1	4.4	8.2	0.6	1.8
Stentorinae	0.9	—	—	—	—	—	—	—
Euryglossinae	11.5	—	—	—	—	—	—	—
HALICTIDAE	26.8	14.2	26.6	21.2	21.2	46.4	26.6	58.6
Halictinae	20.7	11.0	26.0	19.0	18.7	46.4	23.6	58.6
Nomiinae	6.1	0.8	0.0	0.0	0.7	—	—	—
Dufoureae	—	2.4	0.6	2.2	1.8	—	—	—
ANDRENIDAE	—	25.9	20.1	23.4	20.1	17.5	1.2	10.2
Andreninae	—	16.3	17.2	22.9	18.3	17.5	0.6	—
Panurginae	—	9.4	2.9	0.5	1.8	0.0	0.6	10.2
Oxaeinae	—	0.2	—	—	—	—	0.0	0.0
MELITTIDAE	0.1	0.9	1.2	2.2	1.8	0.0	—	—
Melittinae	—	0.1	0.0	1.2	1.1	0.0	—	—
Dasypodinae	—	0.6	0.0	0.5	0.7	0.0	—	—
Macropidinae	—	0.2	1.2	0.5	0.0	0.0	—	—
Ctenoplectrinae	0.1	—	—	—	—	—	—	—
MEGACHILIDAE	13.8	19.4	15.9	19.5	19.0	8.2	18.2	11.4
Lithurginae	0.6	0.2	0.0	0.0	0.7	0.0	—	—
Megachilinae	13.2	19.2	15.9	19.5	18.3	8.2	18.2	11.4
ANTHOP- HORIDAE	13.2	30.3	19.6	20.2	25.2	13.5	32.8	16.2
Exomalopsinae	—	0.9	0.0	—	—	—	6.8	3.0
Anthophorinae	5.8	10.3	8.9	3.7	14.6	2.1	13.9	6.0
Nomadinae	0.5	18.2	8.9	15.5	8.4	9.3	3.9	2.4
Xylocopinae	7.0	0.9	1.8	1.0	2.2	2.1	8.2	4.8
APIDAE ¹⁾	1.6	3.5 ₁₎	8.3	6.6	5.4	5.2	19.9	3.6
Euglossinae	—	0.0	—	—	—	—	4.8	0.0
Bombinae	—	3.5	8.3	6.4	5.0	5.2	2.2	1.8
Apinae	1.6	—	—	0.2	0.4	—	12.9	1.8
Total number of species	1,920	3,380	169	406	274	97	352	167

1) In Apidae, introduced species (*Apis* in Extra-palaeartic data and *Bombus* in Australian data) are omitted. There is a single record of Euglossinae from the United States.

Sources of data.

I. Michener (1965). The area concerned covers from Halmahera and Buru westward to Tahiti eastward. Systematic revision, data from previous records, museum specimens and the author's own collecting.

II. Musebeck, Krombein & Townes (1951). New names were added to, and synonymous ones were omitted after Krombein (1958). Compiled catalogue of all previous records.

in various areas and comparing these data.

To compare the relative abundance in terms of individual number is more difficult due to the lack of reliable data. Table 7 presents only three sets of data, taken from the studies cited in Table 6. The numerical predominance of Halictidae is evident even in Ukraina, where Andrenidae occupy an important place. The actual ratio of Halictidae in Chicago is apparently higher than that given in the table, because only females of many species were counted, with the note "and numerous males". The ratio of this group is much higher in São José dos Pinhais, probably caused by the sampling in a limited area as mentioned above, and also by the rich differentiation of this group in the Neotropics. The importance of Andrenidae is variable, very high in Ukraina, decreasing in Chicago and of no particular significance in São José dos Pinhais. A similar but less conspicuous tendency is found in Megachilidae and Anthophoridae, and the opposite tendency is seen in Apidae.

The mean individual numbers per species of various bee groups in these three areas are given as follows:

	W.Ukraina	Chicago	Sao José dos Pinhais
Colletidae	12.1	30.0	4.4
Halictidae	31.8	36.8	27.7
Andrenidae	31.8	20.6	8.1
Megachilidae	14.4	20.9	4.4
Anthophoridae	22.1	33.1	15.5
Apidae	26.1	62.4	181.0

The rich individual number of Halictidae is again evident, being only outnumbered by Apidae. The relatively low number in São José dos Pinhais may reflect the rich specific differentiation of Halictidae in the Neotropical Region. The very high values of Apidae do not have the same significance as in other, principally solitary bee groups as mentioned in Results, section I. Summarizing, the dominance of Halictidae, both in species and individuals, and of Apidae in individuals, seem to be the general features of bee assemblages in various areas of the world, to which some other groups add a local tint, e.g., Andrenidae in the Holarctis and Colletidae in the Australian Region.

III. Pearson (1933). Results of two years' sampling in the area surrounding Chicago, Illinois. Sampling is not biased as to relative abundance but not standardized as to the sampling time.

IV. Stoeckert (1933). Results of long years' survey and bibliographical analysis. Comparable to I and II, though the extent of the area concerned is smaller.

V. Osychnyuk (1959). Sampling of several years. Procedure comparable to III.

VI. Sakagami (unpublished): Standardized sampling in the University Campus, Sapporo. Procedure as in the present study in São José dos Pinhais (VIII). The part concerning Andrenidae was published (Sakagami & Matsumura, 1967).

VII. Michener (1954). As in I, but the ratio of the specimens collected by the author would be higher.

Table 7. Relative abundance in % individual number of various bee groups in three localities, given at subfamily level (Sources of data are given in Table 6)

Family & subfamily	Ukraina (Osy-chnyuk 1959)	Chicago (Pearson 1933)	Sao José dos Pinhais
COLLETIDAE	3.7	7.8	1.0
Colletinae	2.6	3.9	0.4
Hylaeinae	1.1	3.9	0.6
HALICTIDAE	27.2	31.0	57.9
Halictinae	22.6	30.3	57.9
Nomiinae	0.9	—	—
Dufoureae	3.7	0.7	—
ANDRENIDAE	26.6	13.2	3.2
Andreninae	21.2	11.5	—
Panurginae	5.4	1.7	3.2
MEGACHILIDAE	11.5	10.6	2.0
Lithurginae	0.1	—	—
Megachilinae	11.4	10.6	2.0
MELITTIDAE	2.7	0.3	—
Melittinae	1.0	—	—
Dasypodinae	1.7	—	—
Macropidinae	—	0.3	—
ANTHOPHORIDAE	22.9	20.5	10.2
Exomalopsinae	—	—	0.7
Anthophorinae	18.7	14.6	2.8
Nomadinae	2.7	1.6	0.4
Xylocopinae	1.5	4.3	6.5
APIDAE	5.4	16.6	25.7
Bombinae	5.4	16.6	9.4
Apinae (excl. <i>Apis</i>)	—	—	16.3
Total individual number	6,559	5,332	4,217

Concerning phenology, the present study shows a pattern intermediate between temperate and tropical types in São José dos Pinhais, resembling the tropical type in the absence of marked seasonal change and the appearance of some dominant species nearly every month, but being similar to the temperate type in the absence in winter of some groups, which do not hibernate in active adult stage in temperate zones. The correct evaluation of the pattern in São José dos Pinhais is possible after the accumulation of comparable data. Here it may be legitimate to point out one aspect, often uncritically generalized.

Among popular writings, or sometimes in some high quality work, we find a comment indicating the absence of clear phenology and of succession of generations in the tropics, resulting in a synchronous occurrence of different developmental stages in many species. This comment is correct if it means a general tendency to such synchronism, though the statement must be restricted to the humid tropics. The idea becomes incorrect if applied uncritically. First, the responses of various species to the same climatic conditions are often quite different, as suggested by the different phenology of halictid bees in a

humid tropical climate in Rio de Janeiro (Michener & Seabra, 1958). Moreover, even in the areas regarded as humid tropics, the occurrence of some, even if slight, seasonal variation in rainfall is rather a rule, which affect the phenology of the local biota. Concerning the bee fauna of Panama, Michener (1954) writes, "It is widely believed that in a tropical climate such as that of Panamá seasonal variation in the activity of animal life are at a minimum. This may indeed be true, but the minimum is nonetheless considerable. In most parts of Panamá there is a dry season beginning in mid-December and continuing to April or May". After explaining the influence of this seasonal change, he adds, "In other areas, such as the Caribbean coast of the Canal Zone, where the annual rainfall is about twice that of the Pacific coast and the dry season is only relatively dry, the contrast between seasons is not so great". But even in such areas, hatched as *Rainforest zones* in most large scale vegetation maps, the phenological trends do not disappear completely. To show this fact, the number of bee species collected in each month from Barro Colorado Island and C6lon Province, representing the most humid climate within the Republic of Panamá, was selected from his monograph as follows (Social Apidae excluded):

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Colletidae	2											
Halictidae	5	4	6	2	2	6					4	9
Megachilidae		4	8	1	2	1					1	1
Nomadinae		3	2	1	2							
Xylocopinae	1		1						1	1	3	3
Anthophorinae	3	4	13	1	1	4	3	1			4	2
Euglossinae	4	4	7		3		2	3			1	3
Total	15	19	37	5	10	11	5	5	1	0	13	18

Of course, the source of the data was not gathered according to a definite plan to show phenology. Nevertheless, the paucity of most groups, except Anthophorinae (mostly *Centris*) and Euglossinae, during July to October is obvious, indicating the occurrence of bee season, however poorly differentiated. In this connection, the necessity of sampling unbiased as to seasons is again stressed.

Our analysis of flower visits is still of a preliminary nature, so that only four remarks are added to, which are, in our opinion, important for further studies. At first, the flower "preference" must be determined not only based upon the flowers visited, but also upon those not visited. The flower preference list of bees usually does not refer to the flowers not visited. The absence of visits may be caused by the phenological discrepancy between bees and flowers or by a real avoidance. The latter instance has a biological significance not much less than the positive preference. The best way may be to make qualitative notes of all flowering plants in bloom at sampling, as did by Sakagami & Matsumura (1967).

Secondly a comment is given about the nature of oligotrophy. It is a recent tendency to stress the importance of oligolecty in bee-flower relationships, based upon the fact that many bee species visit a variety of flowers for nectar but confine themselves to a restricted number of flower species for pollen. When this aspect alone is stressed, it might lead to the underestimation of the preference range for nectar, which, even if not so remarkable as that for pollen, certainly exists in some bee groups, as partly shown in the present study, especially in relative visits by males.

Thirdly, the relative ignorance of the polytrophic species in recent studies must be pointed out. Certainly the relation between oligotrophic bees and flowers preferred by them is one of the fascinating problem in evolution, often leading to an admirable coadaptation. Nevertheless, it must be mentioned that such bee groups are numerically of rather minor importance. On the other hand, the polytrophic or moderately oligotrophic species occupy the important position of "key industry" (Elton) with respect to the bee-flower relationship, offering a background from which various oligotrophic groups have evolved. For this aspect, the procedure adopted in the present study is complementary to the studies of oligotrophic bees (*cf.* Lisle, 1958). In our procedure, the strictly oligotrophic groups tend to escape from sampling. On the other hand, the data on the polytrophic and moderately oligotrophic species are quantitatively obtained, which may serve as the basis upon which oligotrophy is precisely understood.

Finally, it must be stressed that the so-called polytrophic bees do not always visit every flower indiscriminately at given time and area. On the contrary, many polytrophic species, especially those belonging to Halictidae and Apidae, tend to concentrate on particular flowers, as is partly shown in the present study. The best example of this tendency is given by the best known bee, *Apis mellifera*. In spite of a lengthy list of flowers visited by this species, the European honeybee seldom forages on all flower species in bloom homogeneously.

Summary

Relative abundance, phenology and flower visits of wild bees were studied at a secondary grassland in São José dos Pinhais, Paraná, South Brazil, during one year (1962-63), by sampling bees mainly on flowers, three times per month and four hours each time.

The total sample, consisting of about 167 species and 4,217 individuals, shows the predominance of Halictidae both in species and individuals, and of Apidae in individuals. The percentage ratios of various groups in species and (in parentheses) individual numbers are: Colletidae 5.9 (1.0), Halictidae 58.6 (57.9), Andrenidae 10.2 (3.2), Megachilidae 11.4 (2.0), Anthophoridae 16.3 (10.2) Apidae 3.6 (25.7). The relative abundance at a species level is characterized by the occurrence of numerous species represented by a limited number of individuals, and of a few excessively abundant species.

The phenology shows a type intermediate between typically tropical and temperate patterns. It resembles the tropical pattern in 1) Irregular variation in species and individual numbers, 2) Occurrence of flight activities in some species of Halictidae, Xylocopinae and Apidae in winter, and 3) Flight activities of some dominant non-apid species nearly every month. On the other hand, some seasonal trends are recognized in the relative abundance of dominant species, especially of Andrenidae and Anthophoridae, and the absence of winter flight activities in Colle-

tidae, Andrenidae, Megachilidae and non-xylocopine Anthophoridae, showing a resemblance to the temperate type.

The analysis of flower visits was made in the present paper only as to the relative frequency of visits at the family level and the phenology of visits to some predominant flower species. Among 67 flower species belonging to 20 families, upon which most bees were sampled, Compositae take an outstanding position in the number of species visited (34 spp.), as well as in the number of bee species (128) and individuals visiting (2,240, about 54% of total bees captured on flowers). On the other hand, the practical absence of Leguminosae in the area studied must limit the structure of the wild bee assemblage to some extent. The seasonal sequence of predominantly visited flower species is distinguished by the monopoly by *Senecio* sp. 1 during winter.

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