Apidologie (1991) 22, 397-415

Original article

Interactions on floral resources between the Africanized honey bee *Apis mellifera* L and the native bee community (Hymenoptera : Apoidea) in a natural "cerrado" ecosystem in southeast Brazil

SR de Menezes Pedro, JMF de Camargo

Depto de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto – USP 14049, Ribeirão Preto, São Paulo, Brazil

(Received 26 September 1990; accepted 15 May 1991)

Summary — Interactions between *Apis mellifera* and the native bee community, in 1 hectare of a regrowth "cerrado" with typical open-scrub vegetation and tropical climate, at Cajurú, São Paulo state, Brazil, were analysed for relative abundance, phenology and flower visits. Bees on flowers were netted every 14 d for a year, totalling 624 h of sampling. 4 086 individuals, representing 192 species and 6 families of Apoidea, visited 140 of the 184 plant species sampled in the area. *A mellifera*, the second most abundant bee species, was present in a small proportion of the floral sources visited by bees, some of them not primarily melittophilous. Most of the Anthophoridae, Halictidae and Megachilidae exploited plants not visited by *A mellifera*. Even the Meliponinae, the most similar in morphological and behavioral attributes to *Apis mellifera* overlapped with *Apis* on few plant species.

Africanized honeybee / Apoidea / Meliponinae / food competition / bee plant

INTRODUCTION

After the introduction of African honey bees to South America in 1956 (Nogueira-Neto, 1972), studies of their influence on native bee species have been published (eg Roubik 1978, 1979, 1980, 1981, 1983, 1988; Someijer *et al,* 1983; Posey and Camargo, 1985; Roubik *et al,* 1986; Imperatriz-Fonseca *et al,* 1987; Boreham and Roubik, 1987; Cortopassi-Laurino and Ramalho, 1987; Knoll *et al,* 1987; Gottsberger *et al,* 1988; Roubik and Moreno, 1990). Surveys on flower visitors, pollen analyses and data from museum collections have revealed the "generalist" habits of the highly social bees in different regions of America (Sakagami and Laroca, 1971; Roubik, 1979, 1988; Engel and Dingemans-Bakels, 1980; Sommeijer *et al,* 1983; Absy *et al,* 1984; Knoll *et al,* 1987). In French and Guyana, *Trigona*

(s lato) and *Apis mellifera* showed the highest generalization index for floral "preference" and the highest overlap with several other potential guilds (Roubik, 1979). In Trinidad, West Indies, a palynological analysis of *A mellifera* and various stingless bees colonies placed in a residential area with second growth vegetation revealed a wide spectrum and considerable overlap in pollen resources for these bees (Sommeijer *et al,* 1983). The interspecific differences should be to some degree representative and, despite the generalist nature of eusocial bee foraging, these differences may reflect a form of limited specialization. It has been assumed that highly social bees are competitively superior to "less social" or solitary species in the discovery and harvest of floral resources, and that extensive competition between *A mellifera* and stingless bees for nectar and pollen is likely, since they present a high degree of generalization and overlap in flower species visited, time and place of foraging (Roubik 1978, 1979, 1980, 1988). According to Roubik *et al* (1986) extinction of some stingless bee colonies must occur as a result of honey bee competition. The best record on impact of Africanized bees (AHB) has been provided by the Kayapó Indians, who report quite exactly the arrival date of the African honey bee (during full moon in February, 1966) in the region of Gorotire, Pará, Brazil (Posey and Camargo, 1985). These bees began to attack and pillage the nests of the Meliponinae, and other bees at flowers and water sources, but the aggressiveness of the Africanized bee is said to have diminished, allowing the native bees to gather pollen and nectar (Posey and Camargo, 1985).

This paper provides information about the interactions of Africanized *A mellifera* with the native bee community in terms of relative abundance, phenology and flower visits in a natural "cerrado" ecosystem.

MATERIALS AND METHODS

The study area was located at the Santa Carlota Farm, Cajurú, São Paulo State, Brazil (21°18'–21°27' S and 47°12'–47°20' W), 700 m alt. The original vegetation of this site is spread among several patches, amounting to ≈ 2 000 ha, and the remaining areas (*ca* 3 000 ha) are occupied mainly by sugar cane, coffee and pastures. The study site has a typical open-scrub "cerrado" vegetation, with scarce trees 3–5 m high and a predominance of shrubs and grasses. Until 1960, the site was used as pasture, after which it has been preserved, recovering naturally through seeding from adjacent areas. These "cerrados" are peripherical disjunctions at the southern limits of the *"core"* area (plateau of central Brazil).

Within *ca* 600 ha of a continuous "cerrado" range, 1 ha (400 x 25 m) was plotted and subdivided into 8 sub-areas (100.0 x 12.5 m) along each side of a pre-existent path.

The local climate is "savanna" tropical, with 4 defined seasons. In the winter (May–August) the daily mean temperature is 18.6° C; the minimum drops down to 0° C, and the monthly rainfall is 30.5 mm. During the warmest months (December–February) the daily mean temperature is 24.6° C, the maximum reaches ≈ 36–38° C on the warmest days, and the monthly rainfall is 247.7 mm. Annual mean rainfall for the last 30 yr is 1 528.0 mm. Rainfall data for the region was provided by the Usina Amália Station and photoperiod data by the Instituto Agronômico de Campinas (fig 1).

Samples were taken every 14 d for 1 yr, from 5–6 May 1988 to 20–21 April 1989 (fig 1). Each sampling was subdivided into 2 periods of 6 h: 12.00–18.00 on the first day and 06.00–12.00 the second day, totalling 624 h in 26 sampling units. The sampling procedure was modified from that of Sakagami *et al* (1967). Two collectors alternately visited each sub-area for 30 min, walking randomly and catching any bees on any kind of flower, and staying ca 3 min at every flowering plant, which was examined regularly every 2 h. Bees were captured individually or in groups by net and were separately preserved according to flower species and time. Plants were collected for identification and notes were taken on flowering time and resource available (nectar, pollen, oil). Air temperature and relative

humidity were measured 2.4 m above the ground every 2 h. Nest numbers of *A mellifera* and stingless bees were estimated, in and close to the study site (within 50 m). Voucher specimens of the plant and bee species were deposited at the Department of Biology, University of São Paulo, Faculdade de Filosofia, Ciências e Letras de Riberão Preto.

RESULTS

Relative abundance and phenology

The total numbers of bees (species and individuals) per family of Apoidea collected at Cajuru are summarized in table I.

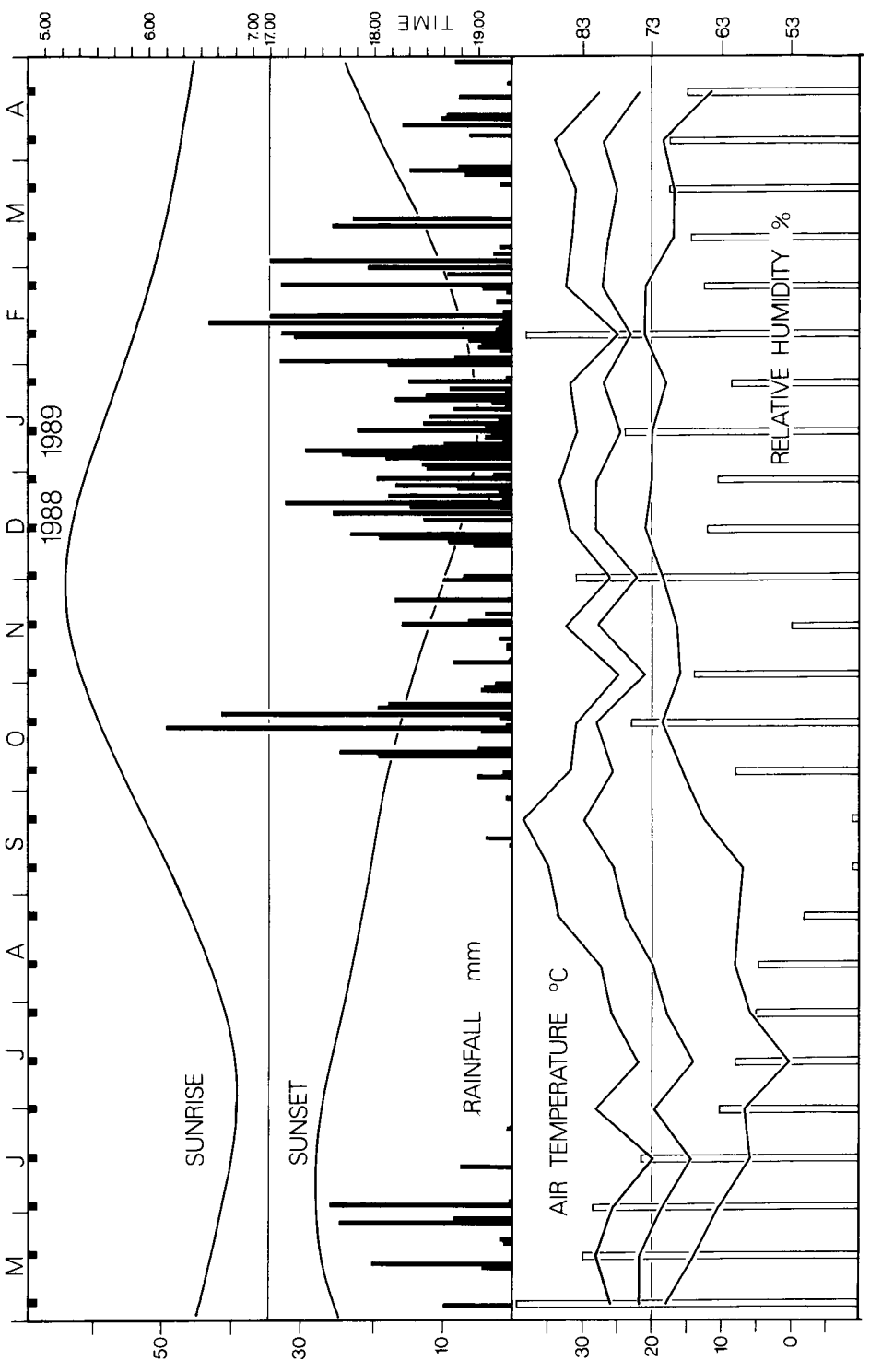
The predominant Apidae bee species were: *Trigona spinipes* (Fabricius), 697, 17.1%; *A mellifera*, 656, 16.0%; *Tetragona clavipes* (Fabricius), 356, 8.7%; *Paratrigona lineata* (Lepeletier), 259, 6.3%; *Scaptotrigona depilis* (Moure), 197, 4.8%; *Tetragonisca angustula angustula* (Latreille), 157, 3.8%; *Trigona hyalinata* (Lepeletier), 109, 2.7% (*cf* table II). Of the ≈ 38 Meliponinae species that occur in southeastern Brazil, all have been observed in and near the study site, although only 19 were collected during this survey.

Throughout the year, the relative abundance of *A mellifera* changed from 0% to 61.4%, showing fluctuations unlike the general trends of the other bee (fig 1). Three abundance peaks were observed for *Apis*, in September, October and April. The other bees, however, were most abundant in August and January, when the Meliponinae were predominant (87.7% of the bees sampled on 11 and 12 August 1988 and 70.9% on 12 and 13 January 1989). *S depilis* was especially abundant in August (35.6%) and *T spinipes* in January (67.4%). Bee activity was reduced during the coldest months (June and July) and *A mellifera* was absent, though over 100 individuals of other species were caught at times (2–3 June 1988). Absence of *Apis* activity was also observed in late February and March, although during the same period the activity of the other bees was only reduced.

Table I. Total numbers of bees (species and individuals) per Apoidea family collected at Cajuru-SP, Brazil (5 May 1988–21 April 1989).

Families	*Individuals*	*Species*
Apidae	2 663 (65.2%)	26 (13.5%)
Anthophoridae	900 (22.0%)	84 (43.8%)
Halictidae	278 (6.8%)	33 (17.2%)
Megachilidae	212 (5.2%)	38 (19.8%)
Colletidae	24 (0.6%)	10 (5.2%)
Andrenidae	9 (0.2%)	1 (0.5%)
Total	4 086	192

Fig 1. Relative abundance of Apoidea at Sta Carlota Farm, Cajuru-SP, Brazil, from 5 May 1988–21 April 1989 and climatic data.


TIME
5.00
6.00
7.00
17.00
18.00
19.00
SUNRISE
SUNSET
RAINFALL mm
AIR TEMPERATURE °C
RELATIVE HUMIDITY %
83
73
63
53
50
30
10
30
20
10
0
M
J
J
A
S
O
N
D
J
F
M
A
1988
1989

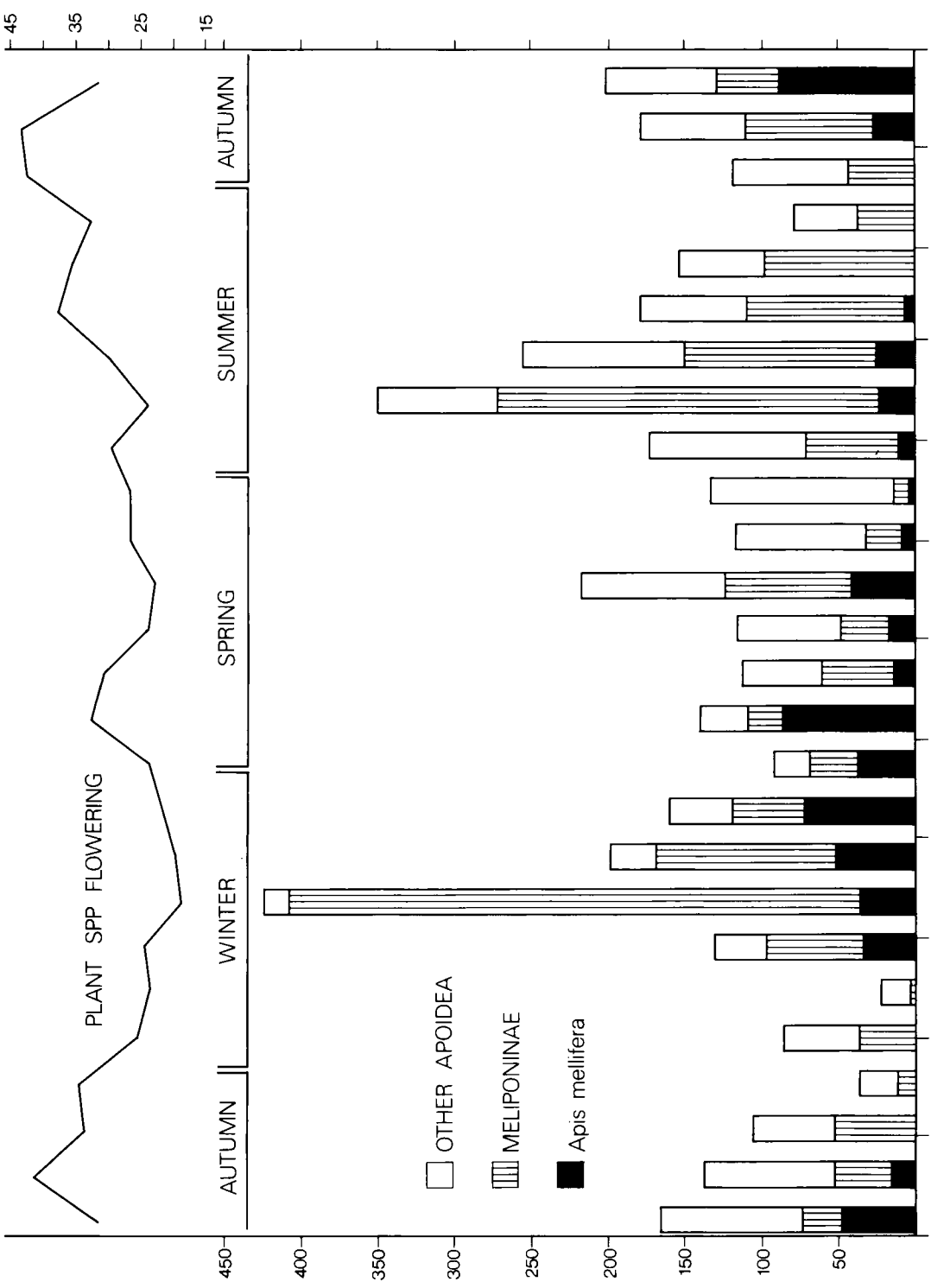

45
35
25
15
PLANT SPP FLOWERING
AUTUMN
WINTER
SPRING
SUMMER
AUTUMN
OTHER APOIDEA
MELIPONINAE
Apis mellifera
450
400
350
300
250
200
150
100
50

Table II. Relative abundance of Apoidea and resource offered on flowers visited by *Apis mellifera*, Sta Carlota Farm, Cajurú - SP, Brazil (5 May 1988–21 April 1989). (*cf* legends in the footnote).

Plants	*Resource*	*Am*	*(%)*	*AP**	*AN*	*HA*	*ME*	*CO*	*AD*	*T cl*	*P li*	*T an*	*S de*	*T sp*	*T hy*	*L mu*	*Mnae**	*B oa*	*B om*	*APOI**	*Total*	*T(%) Am*
(LAB) *Hyptis marruboides* Epl	N	70	(10.7)	168	16	38	7	5	3	-	89	24	-	2	-	-	2	42	9	237	307	22.8
(COM) *Gochnatia barrosii* Cabrera	N	64	(9.8)	134	4	7	2	1	-	8	10	24	81	1	1	8	1	-	-	148	212	30.2
(LYT) *Diplusodon virgatus* Pohl	P	57	(8.7)	31	1	4	-	3	1	4	-	1	-	25	-	-	-	1	-	40	97	58.8
(MYR) *Myrcia alba-tomentosa* DC	P	56	(8.5)	3	-	-	-	-	-	-	-	-	1	-	-	-	2	-	-	3	59	94.9
(RUB) *Rudgea viburnoides* Benth	N	42	(6.4)	1	6	-	-	-	-	-	-	-	-	-	-	-	1	-	-	7	49	85.7
(COM) *Vernonia ferruginea* Less	N	37	(5.6)	351	3	2	3	-	-	88	32	6	105	15	100	-	1	4	-	359	396	9.3
(COM) *Vernonia rubriramea* Mart	N	36	(5.5)	78	24	6	9	-	-	21	18	5	-	1	-	-	5	13	15	117	153	23.5
(ANA) *Lithraea molleoides* Engl	N	33	(5.0)	19	-	2	1	-	-	2	3	4	4	3	3	-	-	-	-	22	55	60.0
(GRA) *Paspalum notatum* Fluegge	P	33	(5.0)	476	6	20	-	-	-	32	1	2	-	441	-	-	-	-	-	502	535	6.2
(MYR) *Campomanesia cambessediana* Berg	P	30	(4.6)	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	31	96.8
(COM) *Eupatorium maximiliana* Schrad	N	24	(3.6)	6	11	-	5	-	-	-	5	1	-	-	-	-	-	-	-	22	46	52.2
(SAP) *Serjania lethalis* St Hil	N	21	(3.2)	7	3	-	-	-	-	-	-	-	-	5	-	1	-	-	-	10	31	67.7
(MAL) *Mascagnia cordifolia* Griseb	O(P)	17	(2.6)	29	5	-	-	-	-	24	-	-	1	1	-	-	3	-	-	34	51	33.3
(LEG) *Acacia paniculata* Willd	N	17	(2.6)	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	2	19	89.5
(VER) *lippia lasiocalycina* Cham	N	14	(2.1)	6	29	-	-	-	-	-	2	-	-	-	-	-	-	2	-	35	49	28.6
(COM) *Trichogonia salviaefolia* Gardn	N	13	(2.0)	14	8	5	10	-	-	3	7	1	-	-	-	-	1	0	2	37	50	26.0
(VOC) *Qualea multiflora* Mart	N	12	(1.8)	15	8	1	-	-	-	-	-	-	-	-	-	-	-	-	14	24	36	33.30
(LAB) *Hyptis multibracteata* Benth	N	11	(1.7)	9	5	1	14	-	-	-	-	-	1	-	-	-	-	8	-	29	40	27.5
(ERY) *Erythroxylum tortuosum* Mart	N(P)	8	(1.2)	4	-	-	6	-	-	3	-	-	1	-	-	-	-	-	-	10	18	44.4
(RUB) *Alibertia sessilis* (Vell) Schuman	N	6	(0.9)	1	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3	9	66.7
(SAP) *Serjania ovalifolia* Radlk	N	6	(0.9)	1	1	2	1	10	-	-	-	-	-	-	-	-	1	-	-	15	21	28.6
(ERY) *Erythrtoxylum campestris* St Hil	N(P)	5	(0.8)	1	-	3	1	-	-	-	1	-	-	-	-	-	-	-	-	5	10	50.0
(COM) *Baccharis dracunculifolia* DC	N	5	(0.8)	1	-	-	0	-	-	1	-	-	-	-	-	-	-	-	-	1	6	83.3
(LEG) *Mimosa tremula* Benth	N	4	(0.6)	-	8	10	-	-	-	-	-	-	-	-	-	-	-	-	-	18	22	18.2
(CYP) *Scleria bracteata* Cav	P	3	(0.4)	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	2	5	60.0
(STE) *Waltheria cf comunis* St Hil	N	3	(0.4)	28	3	1	-	-	-	1	9	15	-	-	-	2	1	-	-	32	35	8.6
(LAB) *Hyptis suaveolens* Poir	N	2	(0.3)	-	30	4	4	-	-	-	-	-	-	-	-	-	-	-	-	38	40	5.0

(DIL) *Davilla elliptica* St Hil	N(P)	2	(0.3)	2	2	-	-	-	-	-	1	-	-	1	-	-	-	-	-	4	6	33.3
(LAB) *Hyptis crinita* Benth	N	2	(0.3)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	100.0
(PRO) *Roupala montana* Aubl	N	2	(0,3)	5	-	-	-	-	-	-	-	2	-	-	2	-	1	-	-	5	7	28.6
(COC) *Cochlospermum regium* (Mart) Pilger	P	2	(0.3)	2	4	2	-	-	-	-	-	-	-	1	-	-	-	-	1	8	10	20.0
(MAL) *Tetrapteris* sp	O(P)	2	(0.3)	7	5	1	-	-	-	4	-	1	-	1	-	1	-	-	-	13	15	13.3
(STY) *Styrax camporum* Pohl	N	2	(0.3)	3	6	-	1	-	2	1	-	-	-	1	-	-	-	-	1	12	14	14.3
(MAL) *Banisteriopsis laevifolia* (Adr Juss) Gates	O(P)	2	(0.3)	6	26	-	-	1	-	4	1	-	-	1	-	-	-	-	-	33	35	5.7
(RUB) *Diodia teres* Walt	N	1	(0.2)	-	7	7	3	-	-	-	-	-	-	-	-	-	-	-	-	17	18	5.6
(MAL) *Byrsonima intermedia* Adr Juss	O(P)	1	(0.2)	23	142	5	-	-	-	1	7	8	-	1	-	3	3	-	-	170	171	0.6
(ARA) *Didymopanax vinosum* (C&S) March	N	1	(0.2)	61	1	6	-	-	-	11	28	1	-	6	-	14	1	-	-	68	69	1.4
(TIL) *Luecea speciosa* Willd	N(P)	1	(0.2)	13	-	1	-	-	-	-	-	-	1	4	3	-	4	-	1	14	15	6.7
(MEL) *Cambessedesia illicifolia* (DC) Triana	P	1	(0.2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100.0
(MYR) *Myrcia lingua* Berg	N(P)	1	(0.2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100.0
(SMI) *Smilax spinosa* Mill	N	1	(0.2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	100.0
(BRO) *Ananas ananassoides* (Baker) LB Smith	N	1	(0.2)	19	3	-	-	-	-	-	-	-	-	19	-	-	-	-	-	22	23	4.3
(STE) *Helicteres brevispira* St Hil	N	1	(0.2)	2	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	2	3	33.3
(COM) *Vernonia herbacea* (Vell) Rusby	N	1	(0.2)	-	15	1	3	-	-	-	-	-	-	-	-	-	-	-	-	19	20	5.0
(LEG) *Platypodium elegans* Vog	N	1	(0.2)	4	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	4	5	20.0
(COM) *Vernonia tragiaefolia* DC	N	1	(0.2)	-	10	1	4	-	-	-	-	-	-	-	-	-	-	-	-	15	16	6.3
(GRA) *Echinolaena inflexa* (Poir) Chase	P	1	(0.2)	54	6	1	-	-	-	5	-	1	-	48	-	-	-	-	-	61	62	1.6
Total 1		656		1585	400	133	75	21	6	218	215	97	195	578	109	29	27	70	43	2218	2876	
Other plants		0		422	500	145	137	3	3	138	44	60	2	119	0	19	5	12	20	1221	1210	
Total 2		656		2007	900	278	212	24	9	356	259	157	197	697	109	48	32	82	63	3439	4086	

Am = *Apis mellifera*; AP* = Apidae less *A mellifera*; AN = Anthophoridae; HA = Halictidae; ME = Megachilidae; Co = Colletidae; AD = Andrenidae; Tcl = *Tetragona clavipes*; Pli = *Paratrigona lineata*; Tan = *Tetragonisca angustula*; Sde = *Scaptotrigona depilis*; Tsp = *Trigona spinipes*; Thy = *Trigona hyalinata*; Lmu = *Leurotrigona mueller*; Mnae* = other Meliponinae; Boa = *Bombus atratus*; Bom = *Bombus morio*; APOI* = Apoidea less *A mellifera*; TOTAL (column) = total number of bees collected on the respective plant species; T (%) Am = percentage of *A mellifera* individuals per plant species; TOTAL 1 (row) = total number of bees collected per Apoidea group; Other plants = total number of bees collected on flowers not visited by *Apis*; TOTAL 2 (row) = total of bees per Apoidea group; Principal reward (resource) for visitors: N = nectar, P = pollen, O = oil, (P) = pollen as principal resource for *A mellifera*. ANA = Anacardiaceae, ARA = Araliaceae; BRO = Bromeliaceae, COC = Cochlospermaceae, COM = Compositae, CYP = Cyperaceae, DIL = Dilleniaceae, ERY = Erythroxylaceae, GRA = Gramineae, LAB = Labiatae, LEG = Leguminosae, LYT = lythraceae, MAL = Malpighiaceae, MEL = Melastomataceae, MYR = Myrtaceae, PRO = Proteaceae, RUB = Rubiaceae, SAP = Sapindaceae, SMI = Smilacaceae, STE = Sterculiaceae, STY = Styracaceae, TIL = Tiliaceae, VER = Verbenaceae, VOC = Vochysiaceae.

Honey bees collected resources on flowers more uniformly during the day, even early in the morning (06.00–08.00 and between 16.00 and 18.00 h. The other bees, however, were most abundant between 10.00 and 14.00 h, with few individuals foraging at 16.00–18.00. The great number of Meliponinae foraging at 06.00–08.00 mainly consisted of *T spinipes* collecting on *Paspalum notatum* flowers (table IV).

Seven honey bee nests were counted at the study area, 3 inside the plot surveyed, and 4 within 50 m of the site. Swarms in transit were observed in late August and early September, and the 3 nests inside the area were initiated during this same period, occupying armadillo holes within termite mounds. On 1 December 1988, two swarms had left the termite mounds. Only one Meliponinae nest (*P lineata*, an underground nesting species) was discovered in the plot. Nests of other species were located nearby. They included: 2 nests of *S depilis*, 1 of *Plebeia droryana* (Friese), 2 of *T angustula* and 1 of *Nannotrigona testaceicornis* (Lepeletier). Nests of *T spinipes*, *T hyalinata*, *Trigona truculenta* Almeida and *T clavipes* were not located. One nest of *Plebeia remota* (Holmberg) and one of the necrophagous stingless bee *Trigona hypogea* Silvestri were found, although they were not collected on flowers.

Flower visits

Of the 184 plant species collected at the study site, bees were sampled on 140 plants belonging to 40 families. Of these, only 47 (33%) were visited by *A mellifera*, ≈ 50% (24 spp) by < 5 individuals (table II). The other 93 plant species, most of them typically melittophilous (Pedro, unpublished data), were visited by 1 210 non-*Apis* bees (29.6% of all bees collected); mostly Anthophoridae, Halictidae and Megachilidae (55.6%, 52.2% and 64.6% of the total for each family, respectively).

A mellifera showed a preference for Compositae (251; 38.3%), Myrtaceae (87; 13.3%), Lythraceae (57; 8.7%) and Rubiaceae (49; 7.5%; *cf* table III); it was the only species with a preference for Myrtaceae. Lythraceae and Rubiaceae also did not receive many visits from the other bee species. Anthophoridae, the second most abundant family in individual numbers, showed a preference for Malpighiaceae and Compositae, Halictidae for Compositae, Labiatae and Sterculiaceae, Megachilidae for Compositae, Leguminosae and Labiatae, Colletidae for Sapindaceae, Labiatae and Lythraceae, and Andrenidae for Labiatae and Solanaceae (table III). Compositae, the most visited plant family, was the most abundant in the area, both in terms of species and individuals.

Not all flowers visited by *Apis* are melittophilous. Some of them present characteristics of myophily/cantharophily, (*Diplusodon virgatus*, *Myrcia* spp, *Campomanesia cambessediana*), ornithophily (*Ananas ananassoides*, *Helicteres brevispira*), psychophily (*Lippia lasiocalycina*, *Alibertia sessilis*) and anemophily (*P notatum* and *Echinolaena inflexa*). Of 13 plant species with anthers with apical poricidal dehiscence sampled in the area, *Apis* (3 individuals) visited only 2, *Cambessedesia illicifolia* and *Cochlospermum regium*. Oil flowers also received visits from honey bees. Among 15 Malpighiaceae species, *Apis* (22 individuals) visited 4, *Banisteriopsis laevifolia*, *Byrsonima intermedia*, *Mascagnia cordifolia* and *Tetrapteris* sp (table II).

The nectar plants preferentially visited by *Apis* were *Hyptis marruboides*, *Gochnatia barrosii*, *Rudgea viburnoides* and *Vernonia* spp, and pollen plants *D virgatus*,

Table III. Relative abundance of bees visiting each plant family Sta Carlota Farm, Cajurú-SP, Brazil (5 May 1988–21 April 1989). The first number in the columns (not in parentheses) gives the percentage of individuals in relation to the total number of bees collected per plant family (total indicated below the plant family names), and the second (in parentheses) the percentages of specimens for each plant family in relation to the total collected per group of bee (indicated below the bee names).

Family *Plants*	A mellifera *656*	*Meliponinae* *1855*	*Other Apidae* *152*	*Anthophoridae* *900*	*Halictidae* *278*	*Megachilidae* *212*	*Colletidae* *24*	*Andrenidae* *9*
Compositae 1219	14.8 (27.6)	57.3 (37.6)	1.5 (11.8)	13.0 (17.7)	5.2 (22.7)	8.1 (46.7)	0.1 (4.2)	0.0 (0.0)
Gramineae 640	5.3 (5.2)	84.5 (29.2)	4.4 (18.4)	2.0 (1.4)	3.8 (8.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Labiatae 403	21.0 (13.0)	29.1 (6.4)	14.6 (38.8)	15.1 (6.8)	11.4 (16.5)	6.9 (13.2)	1.2 (20.8)	0.7 (33.3)
Malpighiaceae 389	5.7 (3.4)	26.7 (5.6)	0.8 (2.0)	64.0 (27.7)	2.6 (3.6)	0.0 (0.0)	0.3 (4.2)	0.0 (0.0)
Leguminosae 192	5.7 (3.4)	28.1 (2.9)	1.6 (2.0)	28.1 (6.0)	11.5 (7.9)	18.2 (16.5)	1.0 (8.3)	0.0 (0.0)
Sterculiaceae 123	3.3 (0.6)	31.7 (2.1)	0.0 (0.0)	32.5 (4.4)	27.6 (12.2)	4.9 (2.8)	0.0 (0.0)	0.0 (0.0)
Myrtaceae 116	75.0 (13.3)	19.8 (1.2)	0.0 (0.0)	0.0 (0.0)	4.3 (1.8)	0.9 (0.5)	0.0 (0.0)	0.0 (0.0)
Vochysiaceae 108	11.1 (1.8)	25.9 (1.5)	15.7 (11.2)	44.4 (5.3)	1.9 (0.7)	1.0 (0.5)	0.0 (0.0)	0.0 (0.0)
Rubiaceae 103	47.6 (7.5)	6.8 (0.4)	0.0 (0.0)	31.1 (3.6)	11.7 (4.3)	2.9 (1.4)	0.0 (0.0)	0.0 (0.0)
Lythraceae 97	58.8 (8.7)	30.9 (1.6)	1.0 (0.7)	1.0 (0.1)	4.1 (1.4)	0.0 (0.0)	3.1 (12.5)	1.0 (11.1)
Oxalidaceae 94	0.0 (0.0)	7.4(0.4)	3.2 (2.0)	46.8 (4.9)	14.9 (5.0)	27.7 (12.3)	0.0 (0.0)	0.0 (0.0)
Solanaceae 90	0.0 (0.0)	1.1 (0.1)	8.9 (5.3)	74.4 (7.4)	10.0 (3.2)	0.0 (0.0)	2.2 (0.9)	3.3 (33.3)
Sapindaceae 52	51.9 (4.1)	13.5 (0.5)	1.9 (0.7)	7.7 (0.4)	3.8 (0.7)	1.9 (0.5)	19.2 (41.7)	0.0 (0.0)
Others 460	16.3 (11.4)	42.4 (10.5)	2.4 (7.2)	28.0 (14.3)	6.9 (11.4)	2.6 (5.6)	0.4 (7.4)	0.4 (22.3)

Myrcia albartomentosa, *Paspalum notatum* and *Campomanesia cambessediana* (table II).

Non-Apidae bees exhibited only a few floral "preferences" in common with *Apis*: Anthophoridae on *Vernonia rubriramea*, and Halictidae on *Hyptis marruboides* and *P notatum*. Apidae other than *Apis* and Meliponinae included *Bombus* spp, which were most abundant on *H marruboides* and *V rubriramea* (table II), and Euglossinae (Pedro, unpublished data).

Meliponinae were most abundant on 6 species preferentially visited by *A mellifera* (> 20 individuals; table II, fig 2): H marruboides *(P lineata, T angustula)*, *Gochnatia barrosii (T angustula, S depilis)*, *D virgatus (T spinipes)*, *Vernonia ferruginea (T clavipes, P lineata, S depilis, T hyalinata)*, *V rubriramea (T clavipes)*, and *P notatum (T clavipes, T spinipes)*; on the latter, 86% of the bees were *T spinipes* and only 6% were *A mellifera*. Other plants such as *Mascagnia cordifolia*, *Waltheria* cf *comunis*, *Didymopanax vinosum*, *A ananassoides* and *E inflexa* had high frequencies of Meliponinae, but *Apis* was an occasional visitor (table II). The flowering periods of the plants shared by *Apis* and Meliponinae and the foraging records are given in figure 2. *G barrosii*, *V ferruginea*, and *V rubriramea* flowered during the same period. *H marruboides*, *V rubriramea* and *D virgatus*, also had overlapping flowering periods. Abundance peaks of *T angustula*, *T hyalinata*, *T clavipes* and *S depilis* were coincident with the flowering of *G barrosii*, *V ferruginea* and *V rubriramea*. *P lineata* was more constant during the year, being abundant mainly when *H marruboides* flowered. *T spinipes* showed a remarkable abundance peak in January coinciding with the blooming of *P notatum*. *A mellifera* was most abundant when *Myrcia albatomentosa* (6 and 7 October 1988), *H marruboides* and *D virgatus* flowered (20 and 21 April 1989).

Pollen flowers *(P notatum, D virgatus)* were primarily visited in the morning, while nectar flowers were visited in the afternoon. *A mellifera* foraged more uniformly throughout the day. On *V ferruginea*, *T hyalinata* foraged especially between 08.00–12.00, *S depilis* between 10.00–14.00 and *T clavipes*, 14.00–16.00 h (table IV).

DISCUSSION

Relative abundance and phenology

A colony of *T spinipes* on average consists of 20 000–30 000 (JMFC, unpublished observations) and an *A mellifera* colony of 2 000 > 50 000 individuals (Boreham and Roubik, 1987). Thus, a single nest inside a given area can provide an enormous number of foragers on flowers, especially near the nest (Sakagami *et al*, 1967). The range exploited by *A mellifera* and *T spinipes* is quite large, considering the large flight range of their workers (2 350 and 840 m, respectively; Kerr, 1959).

During the coldest period (June, July), there was a decrease in bee activity, including *Apis* and the Meliponinae, although Sakagami *et al* (1967) and Sakagami and Laroca (1971) observed that these 2 groups are relatively independent of climatic seasonal change. The increase in *A mellifera* activity in September and October was probably related to swarm movements and the blooming of *M alba-tomentosa* and in April to the flowering period of *D virgatus*. Abundance of *A mellifera* and Meliponinae was not correlated to variation in numbers of flowering plant species (fig 1).

Floral preference

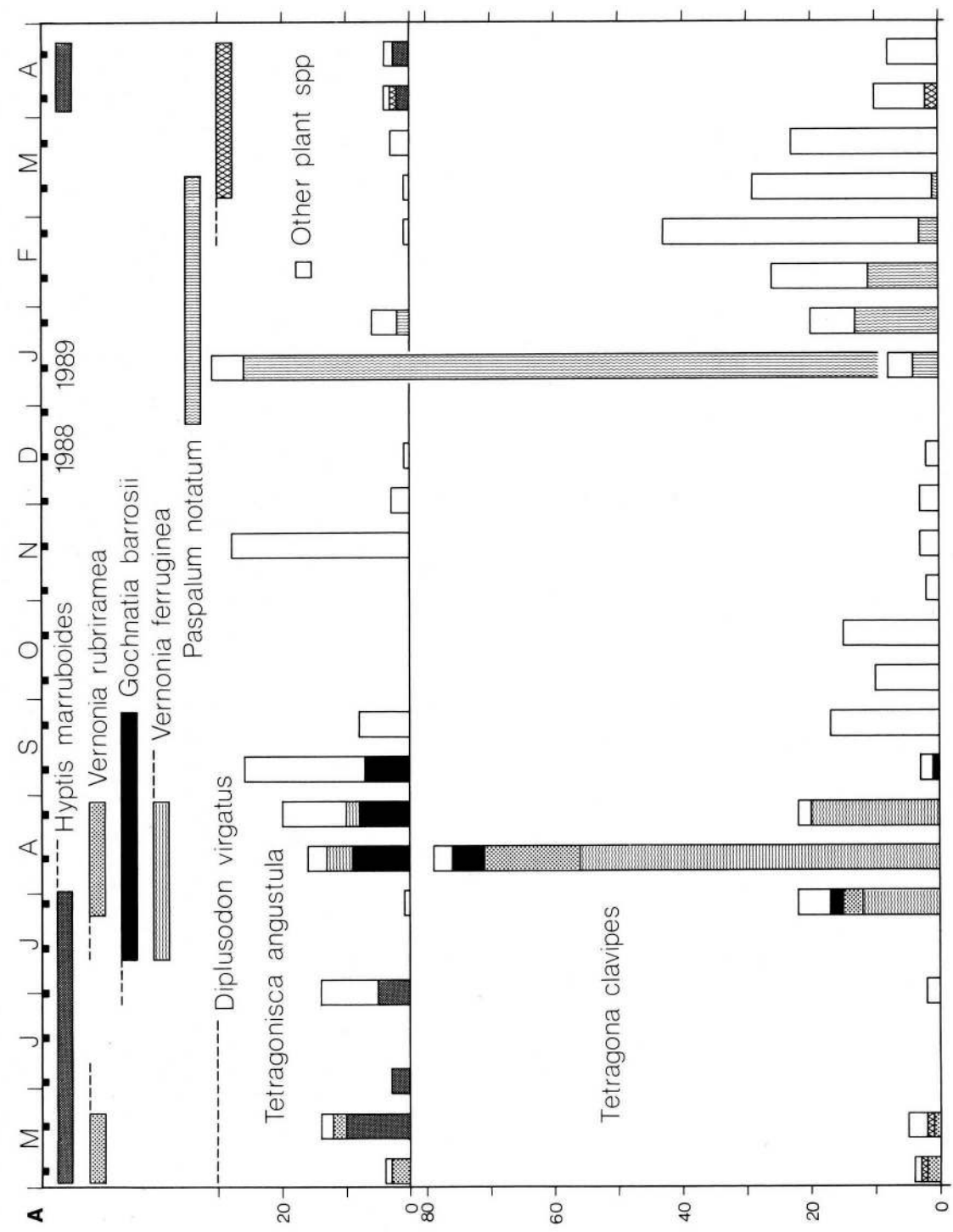
In spite of its "generalist" habits in relation to floral resources, only a small share of all

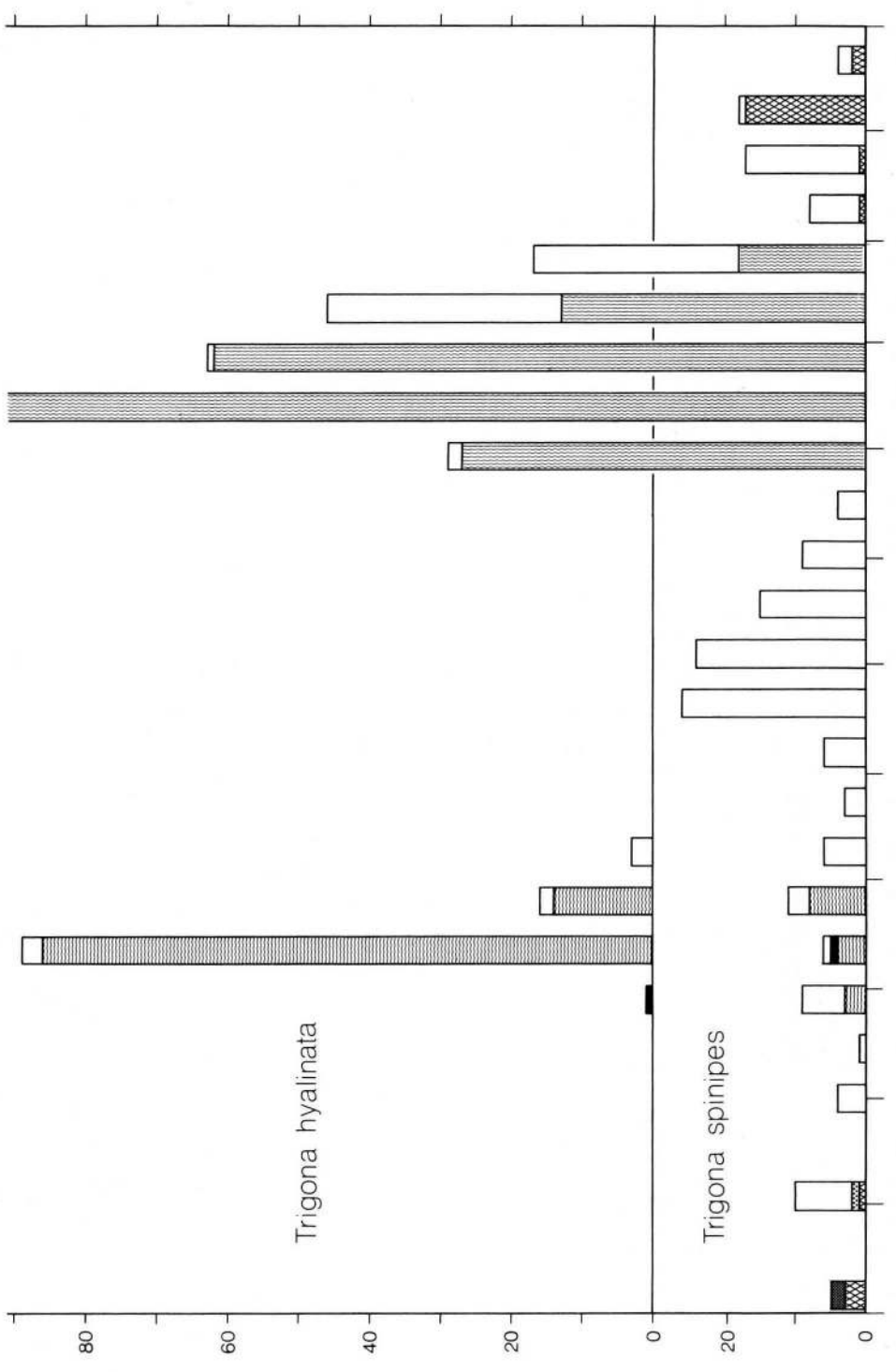
resources available in the study plot was used by *A mellifera*. Although a large degree of overlap has been observed by Roubik (1979), our data show that *Apis* does not share floral resources with most other bees. *Apis* was concentrated on floral types not attractive to the other Apoidea, including *M alba-tomentosa* and *D virgatus*, resources which are not primarily melittophilous. Nectar flowers like *H marruboides* and *V rubriramea* that were intensively frequented by several bee species of different families were the most abundant, and largely distributed throughout the area. Stingless bees, the group most similar in morphological and behavioral attributes to *A mellifera*, also exhibited some floral preferences in common with the latter. *T spinipes* overlapped with *Apis* in pollen foraging of *D virgatus* and *P notatum*, although the latter was only occasionally used as a pollen source for *A mellifera*. Because of its size and flight pattern, *T spinipes* can be a more efficient collector on *P notatum*. *V ferruginea* was intensively used by the Meliponinae, particularly *T hyalinata*, *T clavipes*, *S depilis*; and somewhat by *A mellifera*. In spite of the overlap among *A mellifera, T angustula, T clavipes* and *S depilis*, on *G barrosii, V rubriramea* and *H marruboides*, competitive interactions could not be assessed, since most of the factors that reveal the occurrence of this process were not observed. Although aggressive interactions between *T hyalinata* and *T spinipes* have been observed several times on different plant species and in different places (JMFC, unpublished data) this was not observed in the study area.

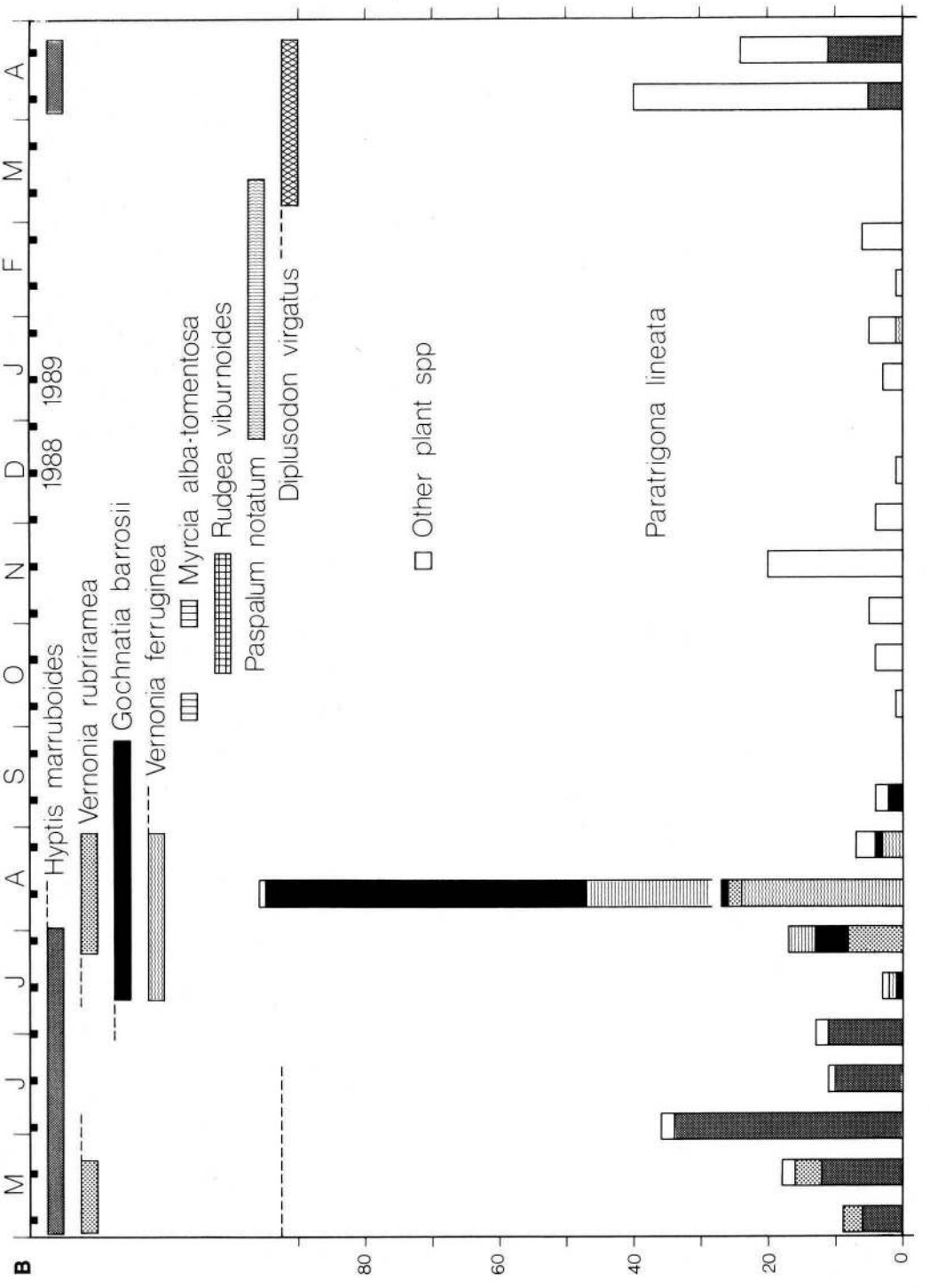
As a whole, Meliponinae seem to be quite ecletic in terms of foraging styles: small bees like *Nannotrigona testaceicornis perilampoides* (Cresson), *Tetragonisca jatl* (= angustula), *Frieseomelitta nigra* (Cresson), *Scaura latitarsis* (Friese) and *S longula* (Lepeletier), *Tetragona clavipes* and *Plebeia* sp (cf Wille, 1963; Laroca and Lauer, 1973; Roubik, 1979), *Leurotrigona muelleri* (Friese) and *P lineata* (personal observation) harvest pollen grains left by other bees on petals and leaves. Others like *Trigona* spp, are able to perforate the bases of long corolla flowers to obtain nectar (Giorgini and Gusman, 1972; Roubik, 1979, 1982), and small Meliponinae *(Trigonisca and Plebeia)* have been observed exploiting the perforations (Roubik, 1982). They also bite poricidal anthers to collect pollen (Wille, 1963). Even "buzzing" behavior is present in the genus *Melipona* (Buchmann, 1983). Therefore, interference of *Apis* in the food niche of the Meliponinae must be minimal.

We conclude that in the study area, *A mellifera* occupies a small share of the available resource (33%), half of them visited only occasionally (< 5 visitors), despite the abundance of these plants. Furthermore, most of the bee plants present in the area have attributes that do not permit efficient exploitation by *Apis* (*eg* oil flowers, flowers with apical poricidal anthers, etc). Some of the pollen flowers primarily visited by *A mellifera* are "peripheral" for the other bees. In this sense, the interference of the Africanized honey bee on food niche of the native bees must be minimal.

Fig 2. A–B. Relative abundance, phenology and plants preferentially visited by honey bees and the most abundant Meliponinae at Sta Carlota Farm, Cajuru-SP, Brazil. **A.** *Tetragonisca angustula, Tetragona clavipes, Trigona hyalinata, Trigona spinipes.* **B.** *Paratrigona lineata, Scaptotrigona depilis,* and *Apis mellifera.* Horizontal bars indicate the annual flowering phenoloy of the plant species preferentially visited; dashed lines indicate low number of flowers.


A
M J J A S O N D J F M A
1988 1989
Hyptis marruboides
Vernonia rubriramea
Gochnatia barrosii
Vernonia ferruginea
Paspalum notatum
Diplusodon virgatus
Other plant spp
Tetragonisca angustula
Tetragona clavipes
20
0
80
60
40
20
0


Trigona hyalinata
Trigona spinipes
80
60
40
20
0
20
0


B
M
J
J
A
S
O
N
D
J
F
M
A
1988
1989
Hyptis marruboides
Vernonia rubriramea
Gochnatia barrosii
Vernonia ferruginea
Myrcia alba-tomentosa
Rudgea viburnoides
Paspalum notatum
Diplusodon virgatus
Other plant spp
Paratrigona lineata
80
60
40
20
0

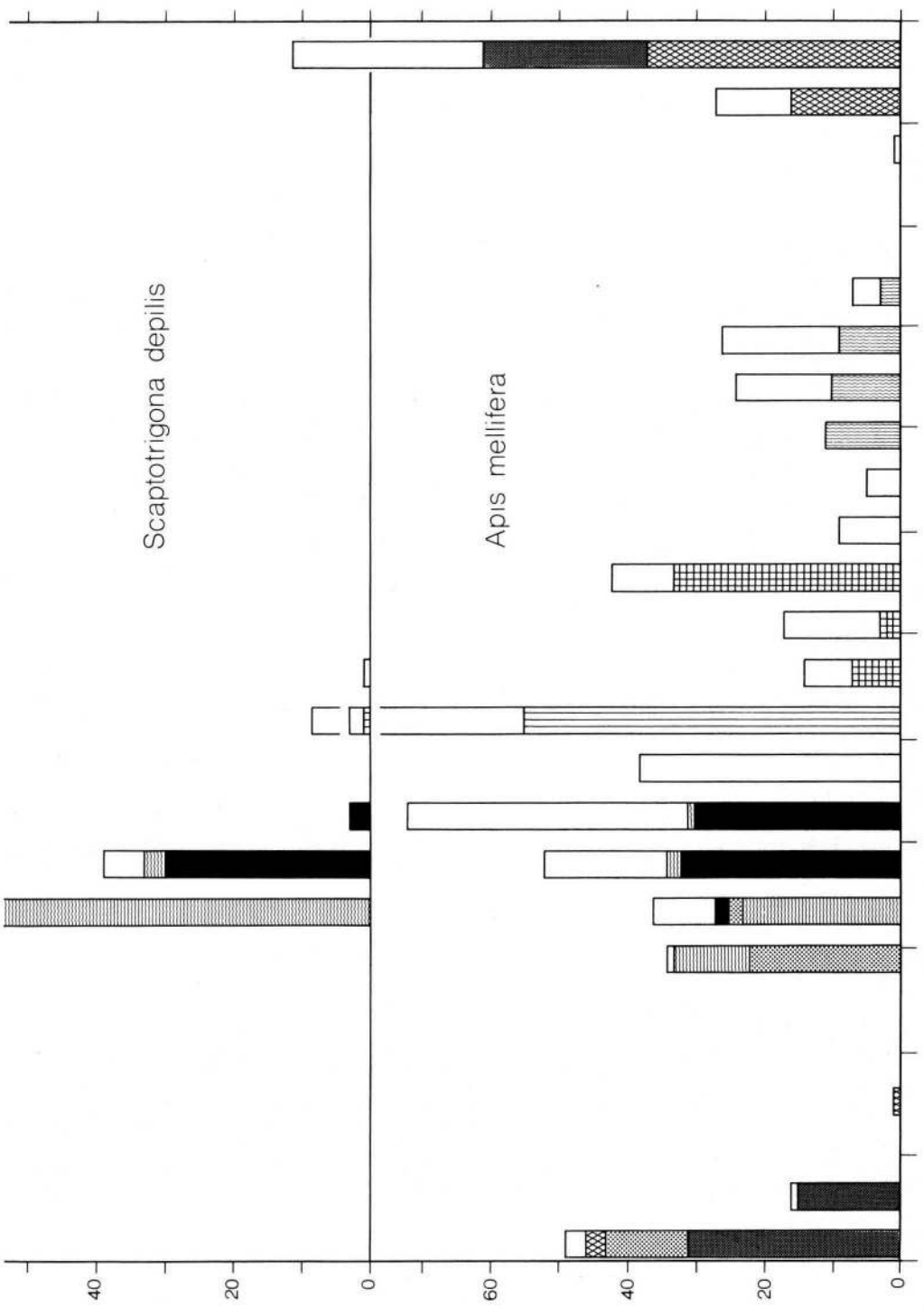

Scaptotrigona depilis
Apis mellifera
40
20
0
60
40
20
0

Table IV. Relative abundance of bees per daily period. Plants flowered from 06.00 to 18.00 h. Sta Carlota Farm, Cajurú-SP, Brazil (5 May 1988–21 April 1989).

Bees	*06.00–08.00 h*	*08.00–10.00 h*	*10.00–12.00 h*	*12.00–14.00 h*	*14.00–16.00 h*	*16.00–18.00 h*
			Hyptis maruboides			
Apis mellifera	-	14	19	14	13	10
paratrigona lineata	-	-	38	36	7	8
Tetragonisca angustula	-	-	6	12	6	-
			Gochnatia barrosii			
Apis mellifera	-	1	11	22	17	13
Tetragona clavipes	-	-	5	2	1	-
Paratrigona lineata	-	-	-	6	4	-
Tetragonisca angustula	-	-	4	8	10	2
Scaptotrigona depilis	–	–	1	47	31	2
Leurotrigona muelleri	-	-	-	8	-	-
			Vernonia ferruginea			
Apis mellifera	-	2	6	9	11	9
Tetragona clavipes	-	-	18	12	46	12
Paratrigona lineata	-	-	14	12	2	4
Tetragonisca angustula	-	-	3	3	-	-
Scaptotrigona depilis	-	3	36	51	15	-
Trigona spinipes	-	4	6	3	-	2
Trigona hyalinata	-	33	53	13	1	-
			Vernonia rubriramea			
Apis mellifera	-	3	6	10	9	8
Tetragona clavipes	-	-	8	3	8	2
Paratrigona lineata	-	-	8	5	4	1
Tetragonisca angustula	-	-	1	3	1	-
			Diplusodon virgatus			
Apis mellifera	48	7	2	-	-	-
Trigona spinipes	14	8	2	-	-	-
			Paspalum notalum			
Apis mellifera	26	7	-	-	-	-
Tetragona clavipes	5	22	3	1	1	-
Trigona spinipes	258	139	43	1	-	-

ACKNOWLEDGMENTS

We thank the technicians of the Depto de Biologia, USP - Ribeirão Preto, for the field and laboratory work; M Mazucato for the bee survey and JA Tavares Filho for the plant and climatic data. The plant species were identified by MCH Mamed (Malpighiaceae), T Sendulski (Gramineae) and CFL Muniz (Cyperacerae), K Yamamoto and H Leitão Filho, V Mantovani, and Cesar de (other plant families). We also thank D De Jong for revising the language and style, and giving some suggestions for improving the manuscript. Climatic data of the region were provided by Usina Amália and photoperiod by the Instituto Agronômica de Campinas. We are especially grateful to J de Sampaio Moreira Netto and S de Sampaio Moreira Júnior, owners of the Santa Carlota Farm, Cajurú, SP, for providing installations and logistic support; and especially for preserving the natural areas, a family tradition which has been maintained for the past 100 years. This project received financial support from the Financiadora de Estudos e Projetos FINEP, conv 4388023300. SRM Pedro received a grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) JMFC, research associate, CNPQ, Ref 300014/84-8/ Z0/FV.

Résumé — Interactions entre l'abeille africanisée (*Apis mellifera* L) et les abeilles sauvages (Hymenoptera. Apoidea) au niveau des ressources florales dans un écosystème naturel de «cerrado», dans le Sud-Est du Brésil. On a étudié, du point de vue de l'abondance relative, de la phénologie et des visites de fleurs, les interactions entre l'abeille africanisée *(Apis mellifera)* et la communauté d'abeilles sauvages sur une végétation typique de brousse ouverte («cerrado»), à Cajuru dans l'état de São Paulo (climat tropical). Sur une parcelle d'un hectare, les abeilles présentes sur les fleurs ont été capturées au filet toutes les 2 semaines durant une année. Ces 624 heures d'échantillonnage ont fourni 4 086 individus représentant 192 espèces et 6 familles d'Apoïdes ayant visité 140 espèces de plantes sur les 184 échantillonnées dans la région. *A mellifera*, qui vient en 2e position pour l'abondance, est présente sur 33% des fleurs visitées par l'ensemble des abeilles, certaines d'entre elles n'étant pas principalement mellifères. Ses sources principales de pollen sont *Diplusodon virgatus* et *Myrcia albatomentosa*, celles de nectar sont *Hyptis marruboides* et *Gochnatia barrosii* (tableau II, fig 2). La plupart des Anthophoridae, des Halictidae et des Megachilidae exploitent des plantes qui ne sont pas visitées par *A mellifera* (tableaux II et III). Les spectres des plantes visitées par *A mellifera* et les Meliponinae, qui ont pourtant les caractères morphologiques et éthologiques les plus proches d'*A mellifera*, ne se chevauchent que sur quelques espèces: *Trigona spinipes*, sur *D virgatus* et *Paspalum notatum*; *Scaptotrigona depilis*, *Trigona hyalinata*, *Tetragona clavipes* et *Paratrigona lineata*, sur *Vernonia ferruginea*; *S depilis* et *Tetragonisca angustula*, sur *G barrosii*; *P lineata* et *T angustula*, sur *H marruboides* (fig 2). Une partie de la niche alimentaire occupée par *A mellifera* dans cet écosystème est «périphérique» pour les autres espèces, et les interférences avec la communauté des abeilles non Apidae sont probablement minimes.

abeille africanisée / Apoidea / Meliponinae / compétition alimentaire / plante mellifère / plante pollinifère

Zusammenfassung — Wechselwirkungen beim Blütenangebot zwischen afrikanisierten Honigbienen (A*pis mellifera* L) und der heimischen Bienengemeinschaft (Hymenopteren: Apoiden) in einem natürlichen "cerrado" Ökosystem in Südostbrasilien. Die Wechselwirkungen zwischen *Apis mellifera* und den heimischen Wildbienen in einem "cerrado" Sekundärbewuchs mit einer typischen offenen Buschvegetation und tropischem

Klima wurden in Cajuru, Staat São Paulo, Brasilien, in Hinblick auf relative Häufigkeit, Phänologie und Blütenbesuch analysiert. Ein ganzes Jahr hindurch wurden die blütenbesuchenden Bienen auf einer Fläche von 1 ha mit einem Netz abgefangen. Das bedeutete insgesamt 624 Stunden Probenfang. Auf 140 der insgesamt 184 einbezogenen Pflanzenarten wurden 4086 Einzeltiere aus 192 Arten und 6 Familien der Apoidea gefangen. *A mellifera*, die zweithäufigste Bienenart, war nur auf einem kleinen Teil (33%) der von Bienen besuchten Blüten zu finden, zum Teil auf solchen, die nicht primär zu Bienenpflanzen zählen. Ihre Hauptpollenquellen waren *Diplusodon virgatus* und *Myrcia albatomentosa*, wichtigste Nektarquellen *Hyptis marruboides* und *Gochnatia barrosil* (Tabelle II, Abb 2). Die meisten Anthophoridae, Halictidae und Megachilidae sammelten auf Pflanzen, die von *A mellifera* nicht besucht wurden (Tabelle II, III). Sogar die meliponinen, in Gestalt und Verhalten am ähnlichsten, überlappten mit *Apis* nur an wenigen Pflanzenarten: *Trigona spinipes* auf *D virgatus* und *Paspalum notatum*; *Scaptotrigona depilis*, *Trigona hyalinata*, *Tetragona clavipes* und *Paratrigona lineata* auf *Vernonia ferruginea*; *S depilis*, *Tetragonisca angustula* auf *G barrosil*; *P lineata* und *T angustula* auf *H marruboides* (Abb 2). Der von *A mellifera* besetzte Teil der Futternische ist in diesem Ökosystem offensichtlich für andere Arten nur von peripherer Bedeutung und die Auswirkung auf die Nicht-Apiden Gemeinschaft wahrscheinlich minimal.

Afrikanisierte Biene / Apoidae / Meliponinae / Nahrungskonkurrenz / Bienenpflanze

REFERENCES

Absy ML, Camargo JMF, Kerr WE, Miranda IPA (1984) Espécies de plantas visitadas por Meliponinae (Hymenoptera; Apoidea), para coleta de pólen na região do médio Amazonas. *Rev Bras Biol* 44 (2), 227-237

Boreham MM, Roubik DW (1987) Population change and control of Africanized honey bees (Hymenoptera: Apidae) in the Panama Canal area. *Bull Entomol Soc Am* 33, 34-39

Buchmann SL (1983) Buzz pollination in angiosperms. *In: Handbook of Experimental Pollination Biology* (Jones CE, ed) RJ Little, Von Nostrand Reinhold NY, 73-113

Cortopassi-Laurino M, Ramalho M (1987) On the pollen harvest by Africanized *Apis mellifera* and *Trigona (Trigona) spinipes* in São Paulo. *In: Proc 10th Int IUSSI Congr: Chemistry and Biology of the Social Insects* (Eder J, Rembold H, eds) VJ Peperny, Munich, 653-654

Engel MS, Dingemans-Bakels F (1980) Nectar and pollen resources for stingless bees (Meliponinae, Hymenoptera) in Surinam (South America). *Apidologie* 11 (4), 341-350

Giorgini JF, Gusman AB (1972) A importancia das abelhas na polinizacão. *In: Manual de Apicultura* (de Camargo JMF, ed) Editora Agronômica "Ceres" Ltda, São Paulo 155-214

Gottsberger G, Camargo JMF, Silberbauer-Gottsberger I (1988) A bee-pollinated tropical community: the beach dune vegetation of Ilha de São Luís, Maranhão, Brazil. *Bot Jahrb Syst* 109 (4), 469-500

Imperatriz-Fonseca VL, Kleinert-Giovannini A, Ramalho M (1987) Stingless bees and Africanized honey bees – resource sharing. *In: Proc 10th Int IUSSI Congr: Chemistry and Biology of the Social Insects* (Eder J, Rembold H, eds) VJ Peperny, Munich, 700-701

Kerr WE (1959) Bionomy of Meliponids.VI. Aspects of food gathering and processing in some stingless bees. *In: Symp Food Gathering Behav of Hymenoptera.* Cornell University, Ithaca, NY, 24-31

Knoll FRN, Bego LR, Imperatriz-Fonseca VL (1987) Relative abundance and phenology of bees (Hymenoptera, Apoidea) in São Paulo. Brazil. *In: Proc 10th Int IUSSI Congr: Chemistry and Biology of the Social Insects* (Eder J, Rembold H, eds) VJ Peperny, Munich, 702-703

Laroca S, Lauer S (1973) Adaptacão comportamental de *Scaura latitarsis* para coleta de

pólen (Hymenoptera, Apoidea). *Acta Biol Par Curitiba* 2 (1, 2, 3, 4) 147-152

Nogueira-Neto P (1972) Notas sobre a história da apicultura brasileira. *In: Manual de Apicultura* (Camargo JMF, ed) Editora Agronômica Ceres Ltda, São Paulo, 17-32

Posey DA, Camargo JMF (1985) Additional notes on the classification and knowledge of stingless bees by the Kayapó indians of Gorotire, Pará, Brazil. *Ann Carnegie Mus* 54, 247-274

Roubik DW (1978) Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201, 1030-1032

Roubik DW (1979) Africanized honey bees, stingless bees, and the structure of tropical plant-pollinator communities. *In: Proc IVth Int Symp on Pollination. Md Agric Exp Sta* 1, 403-417

Roubik DW (1980) Foraging behavior of competing africanized honeybees and stingless bees. *Ecology* 61 (4), 836-845

Roubik DW (1981) Comparative foraging behavior of *Apis mellifera* and *Trigona corvina* (Hymenoptera: Apidae) on *Baltimora recta* (compositae). *Rev Biol Trop* 29 (2), 177-183

Roubik DW (1982) The ecological impact of nectar robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63 (2), 354-360

Roubik DW (1983) Experimental community studies: time-series tests of competition between African and Neotropical bees. *Ecology* 64 (5), 971-978

Roubik DW (1988) An overview of Africanized honey-bee populations: reproduction, diet, and competition. *In: Proc Int Conf on Africanized Honey Bees and Bee Mites* (Needham G, Delfinado-Baker M, Page R, Bowman C, eds) Ellis Horwood Ltd, Chichester, UK, 45-54

Roubik DW, Moreno JE (1990) Social bees and palm trees: what do pollen diets tell us? *In: Proc 11th Int Congr IUSSI: Social Insects and the Environment* (Veeresh GK, Mallik B, Viraktamath CA, eds) Bangalore, India, 427-428

Roubik DW, Moreno JE, Vergara C, Wittmann D (1986) Sporadic food competition with the African honey bee: projected impact on neotropical social bees. *J Trop Ecol* 2, 97-111

Sakagami SF, Laroca S (1971) Relative abundance, phenology and flower visits of apid bees in Eastern Parana, southern Brazil (Hymenoptera, Apidae). *Kontyû* 39 (3), 217-230

Sakagami SF, Laroca S, Moure JSM (1967) Wild bee biocenotics in São José dos Pinhais (PR), South Brazil. Preliminary report. *J Fac Sci Hokkaido Univ Ser VI, Zool* 16, 253-291

Sommeijer MJ, De Rooy GA, Punt W, De Bruijn LLM (1983) A comparative study of foraging behavior and pollen resources of various stingless bees (Hymenoptera, Meliponinae) and honeybees (Hymenoptera, Apinae) in Trinidad, West Indies. *Apidologie* 14 (3), 205-224

Wille A (1963) Behavioral adaptations of bees for pollen collecting from *Cassia* flowers. *Rev Biol Trop* 11 (2), 205-210