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Utilization of floral resources by species of *Melipona* (Apidae, Meliponinae) : floral preferences

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Summary — The diversity of pollen collected by *Melipona* spp. in two communities in southern Brazil was evaluated. The data were compared with those obtained by other researchers in the neotropics. The main pollen and nectar sources for *Melipona* spp. appear to be plants from the families Melastomataceae, Myrtaceae, Solanaceae and Leguminosae (subfamily Mimosoideae). By analyzing the feeding habits of other stingless bees, it was hypothesized that floral preferences could play a role in this kind of choice.

***Melipona* — foraging — pollen plant — nectar plant — pollen analysis**

Résumé — Exploitation de la flore par le genre *Melipona* (Apidae, Meliponinae) : préférences alimentaires. *Les habitudes alimentaires généralistes sont essentielles pour les colonies de mélipones et de trigones, bien qu'en raison de différences dans leurs stratégies de butinage et leurs préférences florales, elles puissent utiliser des sources variées de pollen et de nectar au sein de la même communauté. On discute les préférences florales de* Melipona *en fonction des habitudes alimentaires des mélipones et des trigones. On a estimé l'exploitation des sources de pollen par l'analyse pollinique de la nourriture stockée par des colonies de* Melipona quadrifasciata quadrifasciata *Lepeletier,* M. marginata obscurior *Moure et* M. bicolor *Lepeletier dans deux régions : la forêt tropicale atlantique et la forêt subtropicale à Araucaria, situées toutes les deux dans le sud du Brésil.*

Parmi les 30 espèces de plantes, 18 et 11 sont présentes dans les échantillons de pollen à plus de 1% et 10% respectivement. Lorsqu'on regroupe ces sources polliniques en familles (Fig. 1), il apparaît que, pour l'ensemble de ces espèces de Melipona, *le pollen provient principalement des Myrtacées, Mélastomatacées, Solanacées et Mimosoidées (Légumineuses), du point de vue qualitatif aussi bien que quantitatif. D'autres études sur* Melipona *et les trigones de la région néotropicale donnent des résultats semblables (Tableau III). Par contre, pour les taxons des Palmées et des Faboidées (Légumineuses), il y a des différences manifestes entre les différentes espèces de* Melipona. *Bien que chaque espèce de* Melipona *exploite une large gamme de ressources florales, elles montrent des préférences beaucoup plus similaires que celles observées au sein des genres de trigones.*

Néanmoins on ne peut pas généraliser de telles «tendances» et on ne connaît pas le rôle joué par les facteurs historiques et écologiques dans le choix alimentaire de Melipona. *Nous proposons à titre d'essai une interprétation historique basée sur la forte abondance relative des Myrtacées, Mélastomatacées, Solanacées et Mimosoidées dans la région néotropicale. Les espèces de*

Melipona, *exclusivement présentes dans la région néotropicale, sont spécialistes de ces taxons. Leur forte taille, en comparaison des trigones, leur permet de récolter du pollen par vibration des anthères poricides des Mélastomatacées et des Solanacées, alors que les espèces de trigones doivent les couper. Cela suggère une évolution commune de* Melipona *et de ces taxons de plantes dans la région néotropicale.*

Melipona — *plante pollinifère — plante nectarifère — analyse pollinique*

Zusammenfassung — Die Ausnutzung floraler Ressourcen durch *Melipona*-Arten : Florale Präferenzen. *Generalistische Nahrungsgewohnheiten sind für Völker der stachellosen Bienen* Melipona *und* Trigona *essentiell, obwohl sie aufgrund unterschiedlicher Sammelstrategien und floraler Präferenzen in der Lage sind, in derselben Lebensgemeinschaft verschiedene florale Ressourcen für Pollen und Nektar auszunutzen.*

Florale Präferenzen bei Melipona *wurden durch Vergleich von Informationen über die Nahrungsgewohnheiten von Meliponini und Trigonini diskutiert. Die Ausnutzung von floralen Pollenressourcen wurde aufgrund einer Pollenanalyse des durch Völker von* Melipona quadrifasciata *Lepeletier,* M. marginata obscurior *Moure und* M. bicolor *Lepeletier gelagerten Pollens bestimmt. Die Untersuchungen fanden in zwei Regionen im Süden Braziliens statt : im atlantischen Regenwald und im subtropischen Araucarien-Wald.*

Von insgesamt 30 Pflanzenarten waren 18 in mehr als 1% der Pollenproben vorhanden und 11 in mehr als 10% der Proben. Wenn die Pollenspender in Familien gruppiert werden (Fig. 1), zeigen sich zwischen den Bienenarten große qualitative und quantitative Übereinstimmungen in den Pollen von Myrtaceen, Melastomataceen, Solanaceen und Mimosoideae (Leguminosen), Ledoch auffällige Differenzen in den Pollen von Palmen und Faboideae (Leguminosen). Solche Ähnlichkeiten wurden auch in anderen Untersuchungen über die Meliponini und Trigonini aus der neotropischen Region gefunden (Tabelle III). Obwohl die Melipona *Arten eine große Zahl an floralen Ressourcen nutzen, sind sie sich in der Präferenz sehr ähnlich, bei weitem mehr als im Genus Trigonini beobachtet wurde.*

Verallgemeinerungen dieser «Tendenz» sind allerdings noch nicht möglich, denn es ist nicht klar, welche Rolle historische und ökologischen Faktoren in der Nahrungswahl von Melipona *spielen. Wir neigen zu einer historischen Interpretation, die auf der hohen relativen Häufigkeit von Myrtaceen, Melastomataceen, Solanaceen und Mimosoiden in der neotropischen Region basieren.* Melipona *Arten, die nur in der neotropischen Region vorkommen, sind auf diese Pflanzentaxa spezialisiert. Ihre im Vergleich zu den Trigonini außergewöhnliche Körpergröße befähigt sie durch Erschütterung der porösen Antheren einiger Melastomataceen und Solanaceen Pollen zu sammeln, während die Trigonini gezwungen sind, diese aufzubeißen. Dies weist auf eine gemeinsame Evolution von* Melipona *und diesen Pflanzentaxa in der neotropischen Region hin.*

Melipona — *Pollenpflanze — Nektarpflanze — Pollenanalyse*

Introduction

A number of studies have appeared in the last two decades on foraging behavior and sharing of floral resources among species of stingless bees (Johnson and Hubbell, 1974; 1975; Hubbell and Johnson, 1978; Roubik, 1978; 1979; 1980; 1981; 1982; 1983; Roubik *et al.*, 1986). Generalist feeding habits are essential for these social bees, which remain active for periods longer than any plant species remains in flower (Michener, 1979; Eickwort and Ginsberg, 1980). However, different bee species may use different floral resources within the same community, probably as a result of foraging strategies and floral preferences.

Previous studies conducted in southern Brazil estimated use of floral resources by 10 species of stingless bees

for several months (Cortopassi-Laurino, 1982; Imperatriz-Fonseca *et al.*, 1984; Mouga, 1984; Ramalho *et al.*, 1985; Kleinert-Giovannini and Imperatriz-Fonseca, 1987; Imperatriz-Fonseca *et al.*, 1987; 1988). The feeding habits of *Melipona* were shown to be different from those of other species in the same community. This observation led to a study of other communities, discussed in the present paper.

Food collection was estimated for 3 *Melipona* species in the Jureia Ecological Station, São Paulo state, and in Prudentopólis, Paraná state. The data obtained were compared with those of other authors who have worked in tropical America, to verify the hypothesis of floral preferences.

Material and Methods

The species of bees studied in this survey were *Melipona quadrifasciata quadrifasciata* Lepeletier (Mq), *Melipona marginata obscurior* Moure (Mm) and *Melipona bicolor* Lepeletier (Mb). Colonies of Mq and Mm were installed at the Jureia Ecological Station (24° 30' S, 47° 15' W), in rational hives : parallel frames in horizontal position, with a cavity between them of the size of the storage pots, and a corner space for brood cell development from the bottom of the first frame to the top of the last one (Nogueira-Neto, 1970). The vegetation in the area consists basically of Atlantic rain forest and salt marsh or coastal lowland vegetation, with some small river mangrove swamps. Monthly pollen samples (3—4 g) were collected from newly constructed pots between September 1985 and January 1986. In September and November, pollen samples were also collected from colonies of Mq and Mb in Prudentópolis (25° 13' S, 50° 59' W), Paraná. Local vegetation consists of subtropical Araucaria forest.

Samples were preserved in glacial acetic acid and later treated by acetolysis, using Erdtman's method (1960). Pollen grains were identified with the help of a reference pollen collection covering the plant species in Jureia and the Bioscience Institute of the University of São Paulo, as well as the specialized literature. Identification was hindered by the lack of reference materials for the areas studied and by the fact that some taxa have stenopalynological characteristics (similar pollen grains among species or genera in a plant family).

The percentage representation of pollen types in each sample was estimated by counting 1000 pollen grains (Vergeron, 1964) on 3 slides (Ramalho and Kleinert-Giovannini, 1986).

Results

Table I contains the results of analysis of the pollen stores in colonies of *M. quadrifasciata* and *M. marginata* at the Jureia Ecological Station between September 1985 and January 1986. The number of pollen types in the montly samples varied from 3 to 14 for *M. quadrifasciata* and from 6 to 10 for *M. marginata.* Taxa with the highest representation in monthly pollen samples from *M. quadrifasciata* were : *Eugenia* spp. (Myrtaceae), Myrtaceae sp. 1, Melastomataceae sp. 1 and *Solanum* sp. (Solanaceae). The oustanding taxa in samples from *M. marginata* were : *Eugenia* spp. (Myrtaceae), *Euterpe* sp. (Palmae), *Andira* s.1 (Leguminosae) and *Schizolobium* sp. (Leguminosae).

Table II gives results of analysis of pollen taken from colonies at Prudentopólis, Paraná. Pollen grains from 10 plant species appeared in the sample from *M. bicolor,* while 5—10 pollen types were found in samples from *M. quadrifasciata. Mimosa scabrella* (Leguminosae, Mimosoideae), Melastomataceae sp. 2, *Eugenia* sp. (Myrtaceae), *Piptadenia gonoacantha* (Leguminosae, Mimosoideae), and *Solanum* spp. (Solanaceae) had the highest representation in

Table I. Plant species visited by *Melipona quadrifasciata* and *M. marginata* at the Juréia Ecological Station (São Paulo).

	Melipona quadrifasciata										Melipona marginata			
	September/85		*November/85*			*December/85*			*January/86*			*Sep/85*	*Nov/85*	*Dec/85*	*Jan/86*
	col 1	*col 3*	*col 1*	*col 2*	*col 3*	*col 1*	*col 2*	*col 3*	*col 1*	*col 2*	*col 3*				
Anacardiaceae															
Lythraea s. l						0.08			*		*				
Aquifoliaceae															
Ilex sp.			*	0.19	0.46										
Araliaceae															
Tetrapanax sp.													6.29		
Compositae															
Vernonia sp.	*														
Euphorbiaceae															
Alchornea sp.												6.97			
Leguminosae															
Acacia sp.						*						0.09			
Andira s. l	*												64.28		
Inga sp.			0.08	0.56	1.57	0.08									
Mimosa scabrella	0.09		0.08										0.09		
Piptadenia sp.						0.08					*				
Schizolobium sp.	0.09					0.08						0.09	*	15.64	
Malpighiaceae															
Byrsonima sp.		0.27			3.33	0.08									
Heteropterys sp.												0.66			
Melastomataceae															
sp. 1	*	1.55				9.09	*	92.70	0.30	0.50	4.62	5.18	0.96		*

Meliaceae															
Cabralea s. 1							*	*	*						
Myrtaceae															
Eugenia (3 spp.)	95.22	98.00	59.84	22.68	22.51	85.84	100.00	7.30	99.70	99.50	95.38	1.41	4.63	63.84	92.66
sp. 1	2.53		39.92	75.08	52.97	4.67							1.40		
Palmae															
Euterpe sp.		*		0.28		*						82.21		11.32	0.64
Rutaceae															
Citrus sp.				*											
Sapindaceae															
Matayba sp.			0.08		0.09	*						1.79	0.17		
Paullinia sp.						*						1.22			
Solanaceae															
Solanum sp.	*			*	19.07										
Umbelliferae															
Foeniculum								*				0.47		9.20	3.58
n.i. 1															
n.i. 2											*				2.94
n.i. 3											*				0.18
n.i. 4										*					
n.i. 5	1.89	*	*	0.19									22.18		
No. of pollen types	9	5	7	7	7	14	3	4	3	3	6	10	9	6	6
No. of pollen grains counted	1,108	1,100	1,185	1,076	1,080	1,177	1,000	1,069	1,013	1,000	1,061	1,061	1,145	1,228	1,090

* Pollen grains were present but were not found among 1000 grains during counts.
n.i. = not identified.

Table II. Plant species visited by *Melipona quadrifasciata* and *M. bicolor* at Prudentópolis (Paraná).

	Melipona quadrifasciata				M. bicolor
	September		*November*		
	col 1	*col 2*	*col 3*	*col 4*	
Aquifoliaceae					
Ilex sp.			*		*
Boraginaceae					
Cordia sp.			*		
Compositae					
Vernonia sp.	*	*			
Euphorbiaceae					
Sebastiania sp.					*
Leguminosae					
Acacia sp.				8.87	
Leucaena leucocephala				0.18	
Mimosa scabrella	3.00	99.30			
Piptadenia gonoacantha				39.61	
Lythraceae					
Lagerstroemia indica			*		
Melastomataceae					
sp. 2	6.90	0.20	84.42		41.94
Meliaceae					
Cabralea s. l.	0.09				
Myrtaceae					
Campomanesia guazumaefolia					55.08
Eucalyptus spp.	1.54				
Eugenia sp.	83.75	*	0.84	47.67	
Palmae					
sp. 1					*
Rutaceae					
Citrus sp.	0.09				
Metrodoria sp.					*
Sapindaceae					
Matayba sp.					*
Paullinia sp.	0.09				*
Serjania type	0.09				
sp. 1					*
Solanaceae					
Solanum sp. (3 spp)	4.45	0.50	14.74	3.67	2.98
No. of pollen types	10	5	6	5	10
No. of pollen grains counted	1101	1010	1187	1116	1142

* Pollen grains were present but were not found among 1 000 grains during counts.

samples from *M. quadrifasciata*. *M. bicolor* foraged large amounts of pollen from the flowers of *Campomanesia guazumaefolia* (Myrtaceae) and Melastomataceae sp. 2.

Figure 1A and B show the families most visited by the 3 species of *Melipona* in frequency. The most shared plant species are from the families Myrtaceae, Melastomataceae and Solanaceae. Except for Leguminosae and Palmae, there is no other family with a high representation in the diet of any *Melipona* species.

Discussion

Similar results concerning the distribution of plant taxa used by *Melipona* spp. have been reported by other researchers, as summarized in Table III. In general, plants from the families Myrtaceae, Melastomataceae, Solanaceae and Leguminosae (Mimosoideae) are very important pollen and nectar sources for all *Melipona* species. Among other plant families, Anacardiaceae, Burseraceae, Euphorbiaceae, Guttiferae, Leguminosae (Faboideae) and Moraceae are also well represented in *Melipona*'s diet.

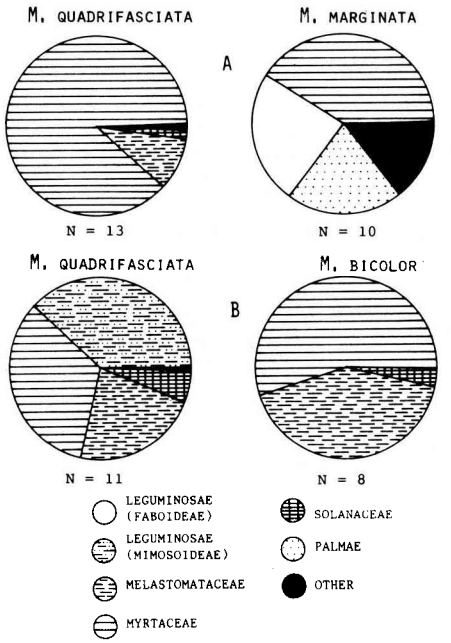

Fig. 1. The most represented family plants in *Melipona* spp. pollen samples at Juréia Ecological Station **(A)** and at Prudentópolis **(B)**. *N* = total number of plant families in samples. 360° = 100% pollen representation.

In a short period of sampling (13 days), Roubik *et al.* (1986) found what they called a heavy utilization of pollen from Guttiferae, Lecythidaceae, Moraceae, Palmae, Papilionoideae, Rubiaceae, Sapotaceae and Violaceae, by *Melipona* species. Palmae family was also highly exploited by *M. marginata* in Jureia Ecological Station (Fig. 1A).

Imperatriz-Fonseca and colleagues recorded the diversity of pollen and nectar harvest by 10 species of stingless bees during 2 months (Imperatriz-Fonseca *et al.*, 1988) and 6 months (Imperatriz-Fonseca *et al.*, 1987). They pointed out the following differences about the choice of main floral sources : *Friesella schrottkyi* visiting Bombacaceae and Euphorbiaceae; *Plebeia* spp. (4 species) visiting Balsaminaceae, Palmae and Moraceae; *Tetragonisca angustula* visiting Euphorbiaceae and Umbelliferae; *Trigona spinipes* visiting Liliaceae and Palmae; *Melipona marginata* and *M. quadrifasciata* visiting Myrtaceae, Melastomataceae and Solanaceae. Evaluation of the ecological importance of such differences among Meliponinae groups depends upon standardized quantitative analysis of food gathering. Preliminarily, it seems that *Melipona* species form a homogeneous group among Meliponinae, concerning the choice of floral sources.

If the plant taxa "preferred" by *Melipona* are considered in isolation, the

Table III. Summarized data from quantitative studies on flower visiting by *Melipona* spp. : *M. seminigra merrilae* (MS); *M. rufiventris flavolineata* (Mr); *M. favosa* (Mf); *M. compressipes* (Mc); *M. scutellaris trinitatis* (Mt); *M. marginata marginata* (Mm); *M. quadrifasciata quadrifasciata* (Mq).

Authors	*Bee Species*	*Place/Vegetation*	*No. of plant families in samples*	*No. and type of samples*				*Period (months)*
				Stored pollen	*Stored honey*	*Pollen loads*	*Nectar loads*	
Absy & Kerr (1977)	Ms	Manaus/Amazon forest	21	—	—	267	—	12
Absy *et al.* (1980)	Ms	Manaus/Amazon forest	23	—	—	—	302	12
	Mr	Manaus/Amazon forest	24	—	—	—	302	12
Engel & Dingemans-Bakels (1980)	Mf	Surinam	21	21	01	01	—	na [a]
	Mc	Surinam	10	02	02	—	—	na
Sommeijer *et al.* (1983)	Mf	Trinidad/SGV [b]	11	—	—	na	—	06
	Mt	Trinidade/SGV	15	—	—	na	—	06
Kleinert-Giovannini & Imperatriz-Fonseca (1987)	Mm	São Paulo/SGV	15	24	24	—	—	12
Imperatriz-Fonseca *et al.* (1988)	Mm	São Paulo/SGV		06	06	—	—	06
Guibu *et al.* (1988)	Mq	São Paulo/SGV	27	10	18	—	—	12
Imperatriz-Fonseca *et al.* (1989)	Mm	São Paulo/SGV	04	02	—	—	—	02
	Mq	São Paulo/SGV	04	02	—	—	—	02

[a] na = not available.

[b] SGV = secondary growth vegetation with gardens.

following characteristics can be observed : they are mainly trees and bushes (except for the family Solanaceae), with bisexual, regular flowers (radial symmetry). Myrtaceae and Mimosoideae have flowers with predominantly white coloring, while the flowers of Solanaceae and Melastomataceae tend towards purple. It is worth noting the rarity of flowers with a yellow coloring, which is one of the most attractive to bees (Baker and Hurd, 1968; Harbone, 1977) and of zygomorphous flowers among these plant taxa.

Moreover, flowers of species of Melastomataceae and the genus *Solanum* (Solanaceae) have poricidal anthers which restrict the access of visitors to pollen. Pollen grains from poricidal anthers can be extracted by vibration — a behavioral specialization observed in *Melipona* species (Wille, 1963; Laroca, 1970), or through cutting — a behavior widespread among smaller stingless bees (Trigonini) (Wille, 1963; Laroca, 1970). Buchmann (1985) states that among Apidae only large bees (such as *Bombus* spp., *Euglossa* spp. and *Melipona* spp.) have an indirect flying muscle which is sufficiently developed for pollen extraction through vibration. Those flowers also probably held small amounts of nectar (Guibu *et al.,* 1988). If vibration strategies are more efficient than cutting, *Melipona* species would have an advantage in exploiting flowers with poricidal anthers.

The biogeographical facts are interesting. The genus *Melipona* is exclusively neotropical (Sakagami, 1982). The plant taxa mentioned above occur mostly in tropical and subtropical regions around the world (Heywood, 1978) and are concentrated in neotropical America, except for the subfamily Mimosoideae which is evenly distributed. The family Myrtaceae comprises some 100 genera and 3 000 species, distributed mainly throughout America and Australia. The family Melastomataceae, with 240 genera and 3000 species, is one of the biggest plant families centered in South America and constitutes a peculiar feature of Brazilian forests. The family Solanaceae, with about 90 genera and 2000—3000 species, has centers in Australia and in central and South America, where 40 genera are endemic, but the biggest concentration is in South America. Thus, in terms of food supply, there would be sufficient conditions for these plant taxa to be intensely used by stingless bees and by other bee species in the neotropical region.

Information available on 8 species of *Melipona* (out of a total of approximately 20 species; Sakagami, 1982) subject to different environments (tropical forest and savannah, subtropical forest, *Araucaria* forest and modified communities with gardens, ornamental species, fruit trees, etc.) shows interesting convergences regarding the qualitative and quantitative utilization of floral resources. It is not our belief that food preferences are limited to the plant taxa listed above, but their flowers undoubtedly present an important source of pollen (and nectar) for these bees. In any case, generalistic food habits and opportunistic food exploitation may lead to a widespread utilization of floral resources in habitats or patches (or flowering periods) where these floral preferences would not hold.

There are differences in the range of floral resources used by *A. mellifera, Trigona* spp. and *Melipona* spp. Roubik (1979) found that Trigonini formed the most generalistic group of flower visitors, followed by *A. mellifera.* Sommeijer *et al.* (1983) observed less diversity in collecting by species of *Melipona* and related this fact to its small colony populations. The data obtained in USP gardens and in the Jureia Ecological

Station match these assumptions. In these cases, *M. marginata* and *M. quadrifasciata* showed low levels of diversity in pollen collecting compared with *A. mellifera, Trigona spinipes* and *Tetragonisca angustula* (Cortopassi-Laurino, 1982; Imperatriz-Fonseca *et al.*, 1984; Kleinert-Giovannini and Imperatriz-Fonseca, 1987; Guibu *et al.*, 1988; Ramalho, 1987).

Some *Melipona* species, such as *M. quadrifasciata* and *M. seminigra,* transmit information regarding the source location through sounds, following flying scouts and releasing pheromones (Lindauer and Kerr, 1960; Esch *et al.*, 1965; Kerr and Esch, 1965), thereby possibly further reducing the dispersal of foragers over colony home range area and hence diversification of foraging sources. The importance of the communication system among stingless bee species may be linked to productivity of floral sources (Johnson, 1982). On the other hand, the efficiency of the communication system among *Melipona* could be related to these bees greater flying range, since their small colonies (fewer than 1000 individuals) do not require highly productive food sources or sites to sustain themselves.

Melipona's small colony populations probably reduce intraspecific competition for food sources (hence the absence of aggressiveness among foragers), and a smaller number of resources can be exhaustively utilized by species of this genus, thereby also reducing interaction with other stingless bees. If these resources are differentiated or neglected by other coexisting species of Apidae (species of Trigonini and *A. mellifera*), they may play a fundamental role in maintaining the populational stability of *Melipona.*

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