

## Floral resource partitioning between native *Melipona* bees and the introduced Africanized honey bee in the Brazilian Atlantic rain forest

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**Summary** — Pollen and nectar harvested by colonies of two stingless bee species (*Melipona bicolor* and *M. quadrifasciata*) and the Africanized honey bee (*Apis mellifera*) were monitored over a year in the Brazilian Atlantic rain forest. The spectrum of plants used for pollen by the *Melipona* species was rather restricted. Only five pollen types contributed more than 1% to the total harvest over the year. The most important plant families were Myrtaceae and Melastomataceae, which also provided most of the nectar. The Africanized honey bee mainly used plants of Myrtaceae, Asteraceae, Euphorbiaceae and Arecaceae for pollen and Cunoniaceae, Rubiaceae and Myrtaceae for nectar. Measures of trophic niche overlap indicate the importance of common resource utilization for all three species of eusocial bees. Niche overlap between *Melipona* bees and *A. mellifera* was more evident for nectar than for pollen. However, the peak in pollen harvest by the colonies of stingless bees as revealed by the number of newly filled storage pots coincided with a low level of presumed competitive pressure of Africanized honey bees, which was calculated as a product of niche overlap and amount of resources harvested. This can be interpreted as indirect evidence of actual competition for food.

**stingless bees / Africanized honey bee / Brazilian Atlantic rain forest / pollen analysis / resource exploitation / trophic niche overlap**

### INTRODUCTION

In the Atlantic rain forest of tropical Brazil, stingless bees are nowadays the most abundant native flower visitors to forage with

the similarly abundant Africanized honey bee (Wilms, 1996). Records of flower visits indicate a considerable trophic niche overlap between the various highly eusocial bee species in this location (Wilms et al, 1996).

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However, the actual resource use of these bees can only be monitored by direct analysis of the pollen and nectar carried by foragers returning to their colony or stored inside the nest. As yet such studies have rarely been carried out in Brazil, and then mainly in the Amazon lowland forest (Absy et al, 1980, 1984) and in semi-natural environments such as the campus of the University of São Paulo (Kleinert-Giovannini and Imperatriz-Fonseca, 1987; Guibu et al, 1988; Imperatriz-Fonseca et al, 1989; Ramalho, 1990). The Atlantic rain forest, or *Mata Atlântica*, has been the subject of only a short survey (Ramalho et al, 1989).

Regarding the possible impact of the Africanized honey bee on this unique and endangered ecosystem, it is of special interest to know the nutritional basis of this introduced species in the *Mata Atlântica* and to compare it with that of native highly eusocial bees. In the present study, experimental colonies of two indigenous *Melipona* species and of the Africanized honey bee were used. All species are of similar worker body size. Colonies of each species were placed side by side in a primary forest. Pollen and nectar flow were recorded over a year. The bees' use of resources was reconstructed from the data on pollen and nectar collected and allowed us to determine species- and colony-specific trophic niches and to discuss possible competition among species.

## MATERIALS AND METHODS

### Study site

The study was conducted at Boracéia Biological Station, a nature reserve of the Zoological Museum of the University of São Paulo, situated 90 km east of the city of São Paulo in the Serra do Mar at about 850 m above sea level at 23°38' S and 45°52' W. The study area is covered with primary Atlantic rain forest except for a few patches of secondary growth and small man-made clearings. It is surrounded by a protected forest of more than 16000 ha.

### Bee colonies

Two colonies per species of the stingless bees *Melipona bicolor* Lepeletier and *Melipona quadrifasciata anthidioides* Lepeletier and of the introduced Africanized honey bee (*Apis mellifera* L), all originating from natural nest sites (*Melipona*) or swarms (*Apis*) from the region, were hived in *Melipona* boxes (Nogueira-Neto, 1970) and Langstroth boxes (*Apis*). In the Boracéia rain forest these species represent abundant members of the bee community (Wilms et al, 1996). The colonies were placed at least 6 weeks prior to the start of the observations in primary forest in a circle of 50 m in diameter, the entrances all pointing east. The Africanized colonies casted a few swarms. Filial nest foundation by the *Melipona* colonies was not observed.

### Pollen and honey sampling

Pollen and honey were sampled from March 1993 through March 1994. Foragers returning to the stingless bee colonies were captured and one pollen load per bee was collected. To raise the efficiency of bee capture the entrance of a colony was closed for 5 min. The foragers then accumulated in front of the hive or moved on the box and pollen carrying bees could easily be captured. This procedure was repeated every half an hour throughout the day. Different colonies were handled in turn. Pollen from Africanized honey bees was sampled in parallel using pollen traps with round-holed screens. Pollen sampling started just after daybreak (around 0600 hours in summer and 0700 hours in winter) and lasted until dusk or beginning of bad weather. Depending on pollen flow, this sampling was continued for up to 3 days and performed at least twice per month. In addition, pollen and honey were collected monthly from newly built storage pots inside *Melipona* nests. Honey from the Africanized colonies was sampled in parallel by removing two newly built combs per hive containing honey every month, and which were replaced by empty frames.

### Pollen analysis

Individual pollen loads collected from *Melipona* foragers and from pollen trap samples (*Apis*)

were colour-sorted, and the resulting fractions of the daily harvest were weighed. Mixed samples were obtained from the pollen contents of the storage pots. Slides for microscopic analysis were prepared according to Vorwohl (1977), but ethanol instead of propanol was used to wash the pollen. The pollen content of honey samples was assayed according to Louveaux et al (1970). For all preparations, unstained and fuchsin-coloured glycerine gelatin was used in parallel. For determination, a reference collection of local pollen types collected from flowers of 244 angiosperm species, mainly trees, was established. Quantitative evaluation of mixed preparations was made by counting 300 pollen grains per slide.

### Pollen weight and volume proportions

The relative importance of particular pollen types in the pollen samples was estimated by calculating weight (WP) or volume (VP) proportions. Separation of pollen loads according to pollen load colour and separate treatment of these fractions results, in theory, in relative weight proportions of the particular pollen types (Vorwohl, 1977). However, frequently more than one pollen type can be found in one pollen load colour fraction. In these cases, the relative volume proportion of a pollen type was estimated (Biesmeijer et al, 1992). The results, however, are given in relative weight proportions assuming equal specific weights of the different pollen types. Due to the combination of weighing colour fractions and estimating relative volume proportions the possible error in this assumption is restricted to particular colour fractions comprising more than one pollen type. This procedure takes into account that biomass rather than volume of the pollen is of importance for bee nutrition. However, a method that allows a direct estimate of the biomass of pollen grains is not available. Pollen from storage pots characteristically forms a yellow mass. In this case, solely the volume proportions of the pollen types were calculated as described above.

### Trophic niche overlap

The overlap of trophic niches was calculated according to Colwell and Futuyama (1971) as:

$$NO_{ih} = 1 - \frac{1}{2} \sum_k |p_{ik} - p_{hk}|$$

where  $p_{ik}$  is the relative amount of pollen type  $k$  in the harvest of species  $i$  and  $p_{hk}$  is the relative amount of pollen type  $k$  in the harvest of species  $h$ . Calculations are based on the total harvest of the colonies of one species. If harvest of one species to be compared was scarce, NO was not calculated (indicated by an asterisk (\*) in the respective figures).

This index is a widely used measure in ecological work. As it considers quantitative similarities in the use of particular food sources, it has an advantage over more simple niche overlap measures.  $NO^p$  and  $NO^v$  are used to indicate niche overlap regarding pollen or nectar harvest, respectively.

### Forage competition

Regarding the possible impact of the Africanized honey bee on native stingless bees, an index of the potential competition by Africanized honey bees ( $PC_{Am}$ ) was calculated as:

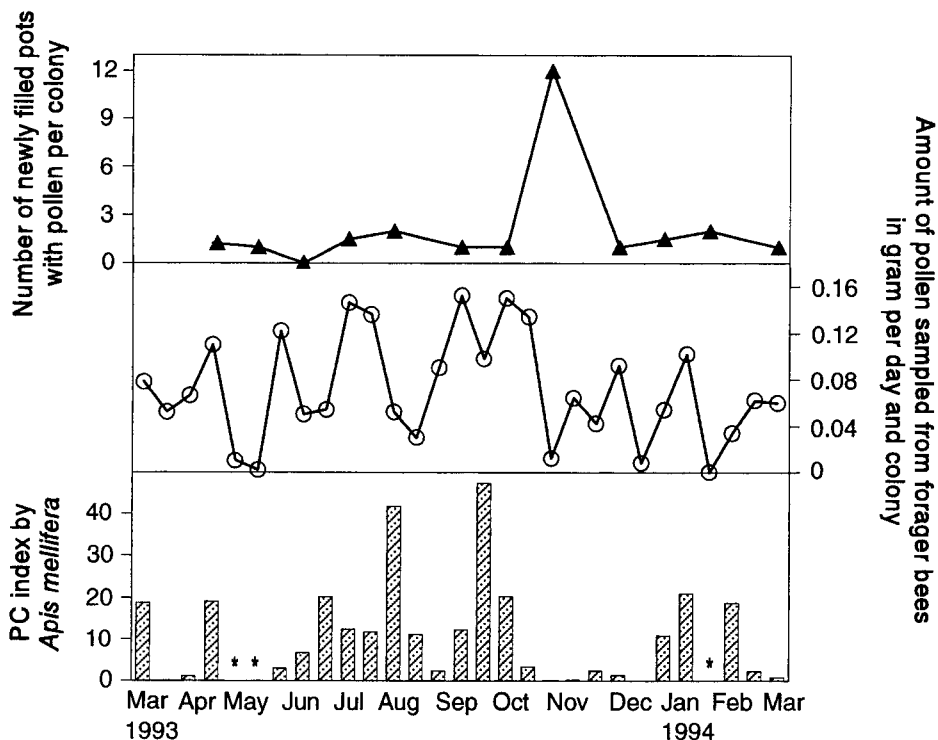
$$PC_{Am} = NO_{Am-i} \times R_{Am}$$

where  $NO_{Am-i}$  is the niche overlap between the Africanized honey bee and the *Melipona* species  $i$ , and  $R_{Am}$  is the amount of resources harvested by the Africanized honey bee.  $R_{Am}$  was calculated in grams (per day and colony) for the pollen harvested and as a percentage for the honey stored in the new frames. Thus,  $PC_{Am}$  is a relative index expressing the potential competitive load of the Africanized honey bee in terms of shared food sources.

## RESULTS

### Temporal pattern of pollen and nectar harvest

In the rain forest of Boracéia pollen and nectar were harvested throughout the year. In all four *Melipona* colonies, storage pots were built in seasonal synchrony. The number of newly filled storage pots with pollen was



**Fig 1.** Pollen influx into colonies of *M. bicolor* as seen in the number of newly filled storage pots and the amount of pollen sampled from forager bees, respectively, during the year and in relation to potential competition by Africanized honey bees. \* = PC<sub>Am</sub> not calculated.

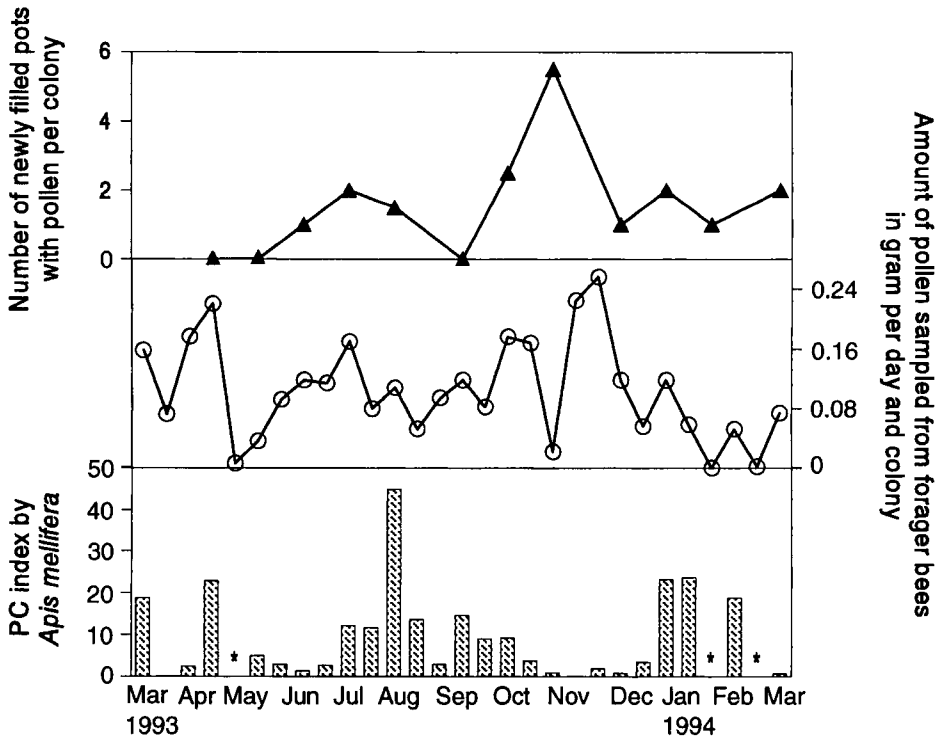
highest in November (figs 1 and 2), whereas new nectar pots were most numerous in July and December (fig 3). The honey bee colonies showed a peak in pollen harvest in August and in nectar harvest in December (fig 4).

### Use of pollen and nectar sources

In the pollen samples of the *Melipona* colonies, 20–25 pollen types were found, of which only five contributed more than 1% to the total harvest over the year (table I). Myrtaceae and Melastomataceae (fig 5) rep-

resented the main pollen sources, resulting in over 90% of the pollen pot contents by volume. Although many of the pollen loads collected from returning foragers contained *Solanum* pollen, these were detected only in minor proportions in the pollen pots.

In pollen trap samples of the Africanized colonies, 53 pollen types were found, of which 16 contributed more than 1% to the total pollen harvest over the year (table I). The main pollen sources by family with 10% or more representation were Myrtaceae, Asteraceae, Euphorbiaceae and Arecaceae (fig 5), which together comprised over 65% of the total pollen forage.



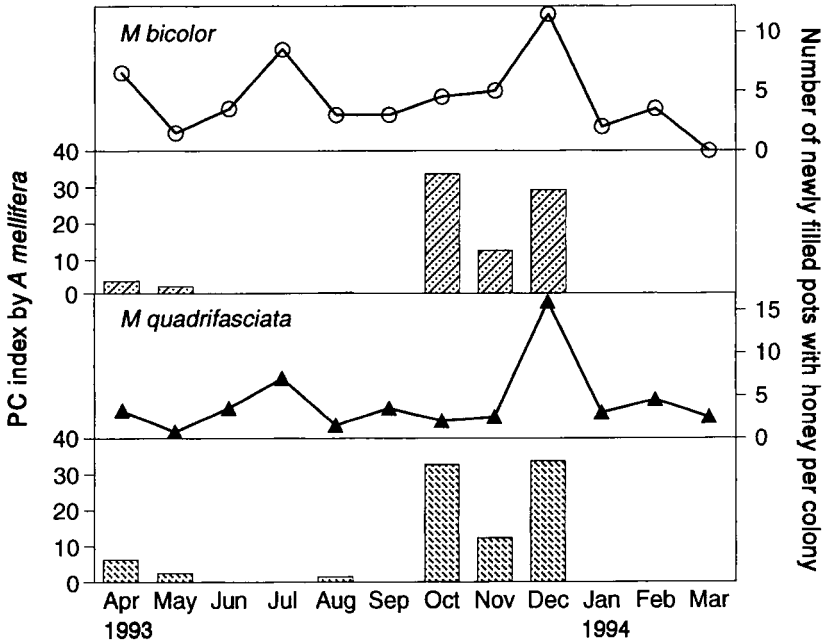
**Fig 2.** Pollen influx into colonies of *M quadrifasciata* as seen in the number of newly filled storage pots and the amount of pollen sampled from forager bees, respectively, during the year and in relation to potential competition by Africanized honey bees. \* =  $PC_{Am}$  not calculated.

The spectrum of important nectar sources was more diverse than that of pollen in all three bee species (table I). However, in the stingless bees the most important pollen sources, Myrtaceae and Melastomataceae, also supplied most of the nectar (fig 5). In addition, about one third of the nectar was collected from flowers of other taxa, especially Asteraceae, Cunoniaceae and Rubiaceae. The latter two families, in addition to Myrtaceae, were also the main nectar sources for the Africanized honey bees, which also used some of their main pollen plants for the collection of nectar.

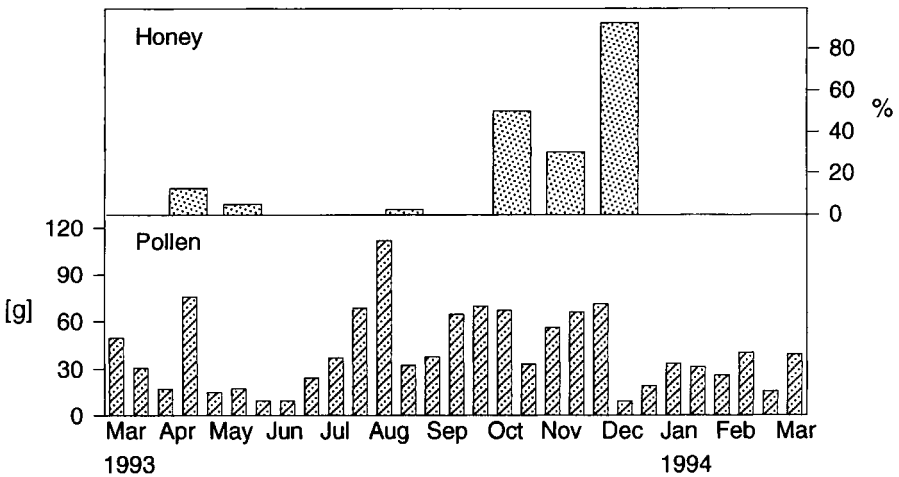
Most of the pollen was derived from mass-flowering trees, indicating the great attractiveness of these dominating sources of forage.

#### Annual schedule of major pollen and nectar sources

The annual pattern of sources of pollen and nectar was quite different for the *Melipona* species and the Africanized honey bees (tables II and III). The stingless bee colonies preferentially collected Myrtaceae and



**Fig 3.** Nectar influx into colonies of *M. bicolor* and *M. quadrifasciata* as seen in the number of newly filled storage pots during the year and in relation to potential competition by Africanized honey bees. \* =  $PC_{Am}$  not calculated.



**Fig 4.** Pollen and nectar influx into colonies of Africanized *A. mellifera* as seen in the amount of pollen sampled with pollen traps and as a percentage of the proportion of cells filled with nectar or honey on two frames placed into the colonies 1 month before.

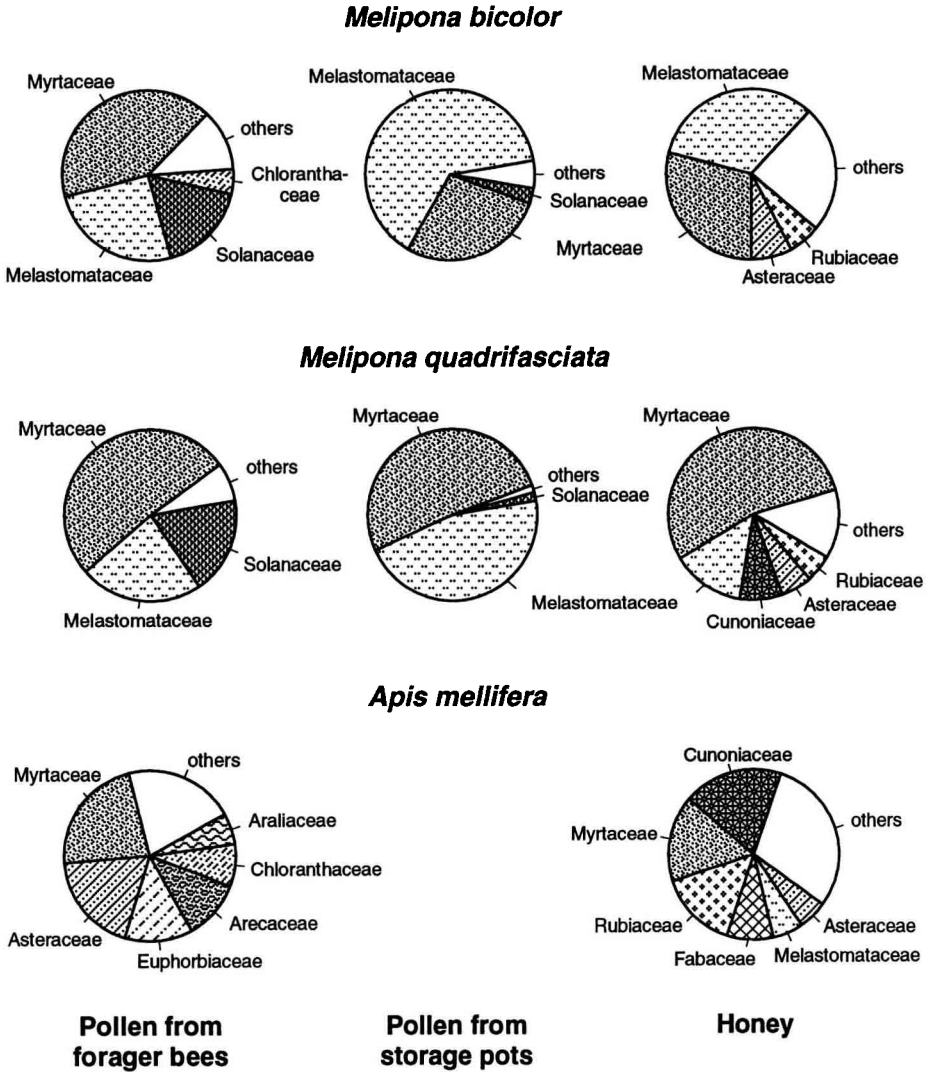
**Table I.** Important pollen types found in pollen and honey samples.

Plant family	Pollen type	Plant life-form	M bicolor			M quadrifasciata			A mellifera	
			PW	PS	H	PW	PS	H	PW	H
Aquifoliaceae	<i>Ilex</i>	t								+
Araliaceae	<i>Didymopanax angustissimus</i>	t								●
Arecaceae	<i>Euterpe edulis</i>	t								● +
	not identified	t								+
Asteraceae	<i>Mikania</i> *	c			●			●	●●	+
	<i>Vernonia / Piptocarpha</i>	t, (c)								● +
Begoniaceae	<i>Begonia</i>	e, h	+			+		+		
Caesalpinaceae	<i>Sclerolobium denudatum</i>	t				+				●
Cecropiaceae	<i>Coussapoa microcarpa</i>	t								●
Chloranthaceae	<i>Hedyosmum brasiliense</i>	t, s	+							●
Cunoniaceae	<i>Weinmannia</i>	t				+			●	●●
Elaeocarpaceae	<i>Sloanea</i>	t		+	+			+	+	+
Euphorbiaceae	<i>Alchornea</i>	t								+
	<i>Croton</i>	t							●●	+
Fabaceae	<i>Machaerium oblongifolium</i>	c				+		+		+
	<i>Pterocarpus rohrii</i> *	t							+	+
Melastomataceae	<i>Miconia / Tibouchina</i> *	t, (s)	●●	●●●	●●●	●●	●●●	●●	+	●
Myrtaceae	<i>Myrcia / Eugenia</i> *	t, (s)	●●●	●●	●●	●●●	●●●	●●●	●●	●●
	<i>Eucalyptus</i>	t					+	+	+	● +
Rubiaceae	<i>Bathysa</i>	t				●		●	+	●●
Sapindaceae	<i>Matayba</i>	t								+
	<i>Paullinia / Allophylus</i>	c		+						
Sapotaceae	<i>Chrysophyllum</i> *	t				+				
Solanaceae	<i>Solanum</i> *	t, (s, c, h)	●●	+	+	●●	+			
Theaceae	<i>Laplacea semiserrata</i>	t								+
Thymelaeaceae	<i>Daphnopsis</i>	t							+	
Not identified	A		●			+				
	B									+
	D								+	+
	D							+		+

PW = pollen from worker bees, PS = pollen from storage pots, H = honey. Frequency classes are given for the relative importance of pollen types on the total resources harvested in one annual cycle: + = 1–5%, ● = 5–10%, ●● = 10–30%, ●●● = > 30%. Percentages refer to weight proportions in PW, volume proportions in PS and frequency in honey. Plant life-forms are: t = trees, c = climbers, climbing shrubs and lianas, s = shrubs (more than 1 m in height), e = epiphytes, h = herbs, semi-shrubs and shrubs less than 1 m in height. \* = including minor taxa.

Melastomataceae pollen of many different species flowering in sequence over the year. In contrast, the Africanized honey bees changed their main pollen sources practically every month. This indicates a continuous search by workers of this species for

the most profitable resources. Nectar harvest by the stingless bees was more diverse than that of pollen, but plants of families other than Myrtaceae and Melastomataceae were important as nectar sources only for short periods.



**Fig 5.** Distribution of pollen types in the pollen harvest and honey stores of one annual cycle. Given are weight proportions for pollen from worker bees, volume proportions for pollen from storage pots and frequencies for pollen found in honey.



**Table II.** Annual cycle of major pollen types in pollen samples.

		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
		1993												1994
<i>Melipona bicolor</i>														
Begoniaceae	<i>Begonia</i>							●						
Chloranthaceae	<i>Hedyosmum</i>							●						
Elaeocarpaceae	<i>Sloanea</i>						○							
Melastomataceae	<i>Miconia/Tibouchina</i> *	●●	●●		●●				●●●					●●●
			○○○	○○○					○○	○○○	○○○	○○	○○	
Myrtaceae	<i>Myrcia/Eugenia</i> *	●●			●●	●●●	●●	●	●	●	●●●	●●●	●●●	●●●
						○○○	○○○	○			○○	○○	○○○	○○○
Ochnaceae	<i>Ouratea</i>		●●	●●●										
Sapindaceae	<i>Paullinia/Allophylus</i>			●										
Solanaceae	<i>Solanum</i> *					●	●●	●●		●●●				
						○		○○						
<i>Melipona quadrifasciata</i>														
Begoniaceae	<i>Begonia</i>							●●						
Elaeocarpaceae	<i>Sloanea</i>						●							
Melastomataceae	<i>Miconia/Tibouchina</i> *	●	●●	●●	●●			●	●●●					
					○○○				○○○	○○○	○			
Myrtaceae	<i>Eucalyptus</i>			●●									●	
													○	
	<i>Myrcia/Eugenia</i> *	●●●	●●●	●	●●	●●●	●●●	●	●	●	●●●	●●●	●●●	●●●
					○	○○○	○○○				○○○	○○○	○○○	○○○
Solanaceae	<i>Solanum</i> *							●		●●●				
<i>Apis mellifera</i>														
Aquifoliaceae	<i>Ilex</i>								●					
Araliaceae	<i>Didymopanax</i>				●	●	●	●						
Arecaceae	<i>Euterpe</i>	●●●											●	●●●
	not identified				●									
Asteraceae	<i>Mikania</i> *		●●			●●	●							
	<i>Vernonia/Piptocarpha</i>			●	●		●			●				
Bombacaceae	<i>Eriotheca</i>			●										
Chloranthaceae	<i>Hedyosmum</i>							●●	●					
Elaeocarpaceae	<i>Sloanea</i>					●								
Euphorbiaceae	<i>Croton</i>								●	●●	●			
Melastomataceae	<i>Miconia/Tibouchina</i> *		●											
Myrtaceae	<i>Eucalyptus</i>			●●							●●	●●		
	<i>Myrcia/Eugenia</i> *	●				●	●●		●			●●	●●	
Rubiaceae	<i>Bathysa</i>							●						

\* = including minor taxa. Frequency classes are given for relative importance (weight proportions for PW and volume proportions for PS): ● = 10–30%, ●● = 30–60%, ●●● = > 60%. Filled circles (●) refer to pollen removed from worker bees (PW) and open circles (○) to pollen from storage pots (PS). \* = including minor taxa.

**Table III.** Annual cycle of major pollen types in honey samples.

		Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
		1993											
													1994
<i>Melipona bicolor</i>													
Asteraceae	<i>Mikania</i>	•			•								
Begoniaceae	<i>Begonia</i>							•					
Caesalpiniaceae	<i>Sclerolobium</i>												••
Cunoniaceae	<i>Weinmannia</i>										•		
Elaeocarpaceae	<i>Sloanea</i>					••							
Fabaceae	<i>Machaerium</i>								••				
Melastomataceae	<i>Miconia/Tibouchina*</i>	••	••	•••				•	•	••	•	••	••
Myrtaceae	<i>Eucalyptus</i>		•										
	<i>Myrcia/Eugenia*</i>	•	•	•	•••	••	•				••	••	•
Ochnaceae	<i>Ouratea</i>	•											
Rubiaceae	<i>Bathysa</i>							•	•••				
Solanaceae	<i>Solanum*</i>							•					
<i>Melipona quadrifasciata</i>													
Asteraceae	<i>Mikania</i>	••											
Begoniaceae	<i>Begonia</i>							•					
Caesalpiniaceae	<i>Sclerolobium</i>												••
Cunoniaceae	<i>Weinmannia</i>										•	•	
Elaeocarpaceae	<i>Sloanea</i>					••							
Fabaceae	<i>Machaerium</i>								••				
Melastomataceae	<i>Miconia/Tibouchina*</i>	•	•	••				•	••	••		•	
	<i>Tibouchina</i>	•											
Myrtaceae	<i>Eucalyptus</i>		••									•	
	<i>Myrcia</i>	••	••	••	•••	••	•				•••	••	••
Rubiaceae	<i>Bathysa</i>							••	••				
<i>Apis mellifera</i>													
Arecaceae	<i>Euterpe</i>	•											
Asteraceae	<i>Mikania</i>	•	•										
Cecropiaceae	<i>Coussapoa</i>											•	
Cunoniaceae	<i>Weinmannia</i>	•									••		
Fabaceae	<i>Machaerium</i>								••				
Melastomataceae	<i>Miconia</i>		•						•				
Myrtaceae	<i>Eucalyptus</i>	•	•										
	<i>Myrcia</i>	•	•			•••			•	•			
Rubiaceae	<i>Bathysa</i>								••				

\* = including minor taxa. Frequency classes: • = 10–30% , •• = 30–60% , ••• = > 60% . \* = including minor taxa.

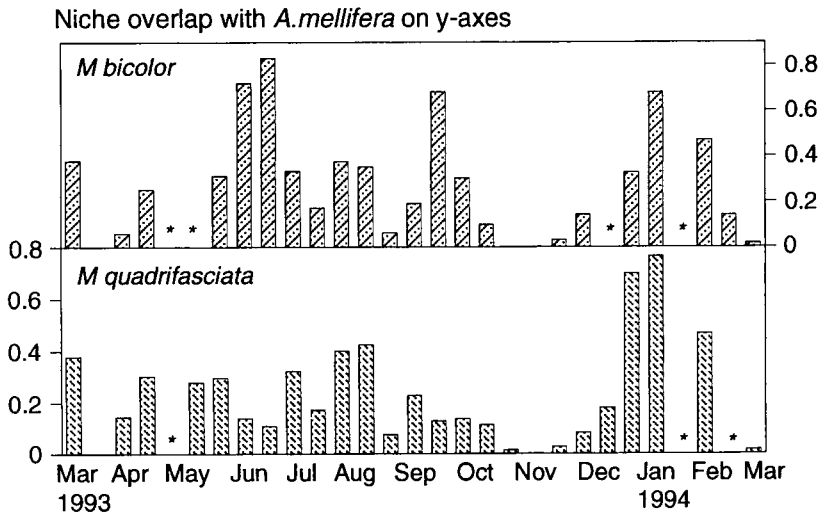
### Trophic niche overlap

Average  $NO^P$  across the 1-year period between the *Melipona* species calculated from the daily (pollen from worker bees) or monthly (pollen from storage pots) resource harvest was 0.66 for pollen loads of returning foragers and 0.82 for pollen from storage pots. Between *A. mellifera* and *Melipona* bees average  $NO^P$  was 0.27 and 0.23 regarding *M. bicolor* and *M. quadrifasciata*, respectively. However, over the year,  $NO^P$  between the honey bee and *Melipona* species varied from 0 to 0.76 (fig 6) indicating temporal specialization of resource collection and fluctuations across the year in the potential competition. Nectar harvest niche overlap was generally larger. Average  $NO^N$  between *M. bicolor* and *M. quadrifasciata* was 0.68 and between these species and *A. mellifera* 0.44 and 0.5. However, as the honey bees stored nectar or honey only during certain periods of the year on newly built combs (fig 4) the respective  $NO^N$  could only be calculated for these particular months.

The annual patterns in  $NO^P$  and  $NO^N$  depended mainly on the flowering periods of Myrtaceae which provided much pollen and nectar. This Angiosperm family represented 60 and 30% of the annual niche overlap between the *Melipona* species and the Africanized honey bee for pollen and nectar harvest, respectively. Other important sources shared by Africanized honey bees and *Melipona* bees were species of the genera *Miconia* (about 10% of  $NO^P$  and 15% of  $NO^N$ ), *Machaerium*, *Bathysa* and *Weinmannia* (each contributing about 10% of  $NO^N$ ).

### Potential competition by Africanized honey bees

It is remarkable that in the colonies of both *Melipona* species the peak in the number of newly filled pots with pollen coincides with a low index of the potential competition by Africanized honey bees (figs 1 and 2). Such concurrence was not observed in honey pots.



**Fig 6.** Variation in trophic niche overlap between *Melipona* bees and the Africanized honey bee across the year. \* =  $NO^P$  not calculated.

## DISCUSSION

### Different foraging strategies in native and introduced social bees?

Honey bees are opportunistic foragers that almost always try to exploit the most profitable food resources (Visscher and Seeley, 1982). Evidently this strategy was also followed by our Africanized honey bee colonies in the Boracéia tropical rain forest, as can be seen from their continuously changing spectrum of pollen sources. In sharp contrast to this diverse flower use by *A mellifera*, colonies of *M bicolor* and *M quadrifasciata* concentrated their foraging activities on flowering plants of only two families, Myrtaceae and Melastomataceae. Similar preferences of *Melipona* bees were reported by Engel and Dingemans-Bakels (1980), Sommeijer et al (1983), Kleinert-Giovannini and Imperatriz-Fonseca (1987), Guibu et al (1988) and Ramalho et al (1989). Most of these data, however, were not obtained in undisturbed ecosystems, and are not the result of long-term field studies. Our Boracéia data show that in a neotropical primary rain forest, members of the Angiosperm families Myrtaceae and Melastomataceae flower across almost the entire year. By coevolution the abundant *Melipona* bees may have acquired the corresponding flower preferences.

Foraging workers of honey bees and the *Melipona* bees could frequently be observed visiting the same flowering patches of Myrtaceae trees and also *Bathysa* and *Mikania*. Resource selection by the stingless bees was therefore probably not grossly altered owing to competitive pressure caused by the introduced Africanized honey bee.

In general, our analyses of the pollen and nectar harvests confirm the records of a 3-year survey of flower-visiting bees in the Boracéia forest (Wilms et al, 1996). However, in the latter study, in which the bees

were collected with insect nets while visiting flowers, plants of the families Myrtaceae and Melastomataceae were less important and plants of the families Asteraceae, Solanaceae and Rubiaceae were more important as food sources for *Melipona* bees relative to the present results. Both Myrtaceae and Melastomataceae comprise many species with a conspicuous mass-flowering syndrome. Single plants in blossom are characteristically visited by many bees, which results in a rapid depletion of the resources. As a consequence, flower visiting bees were often observed there for only a few hours, mainly in the early morning; for example, 75 and 51% of all bees visiting flowers of Myrtaceae and Melastomataceae, respectively, were collected before 1000 hours and 95 and 92% before noon. In contrast, the number of bees collected on flowers of Solanaceae and especially of Asteraceae and Rubiaceae is more equally distributed over the day. Members of these families provided resources over a longer daytime, which enhanced the chances of collecting flower-visiting bees upon them. From our observations, this, in general, concerns the plant specimen as well as the family level with different species having slightly different flowering peaks over the day.

Palynological analysis of honey only has limited value for determining the origin of the nectar, since the amount of particular pollen types which ends up in honey is influenced by flower type, harvesting behavior of the bee, etc. For Brazil, a comparative data base of pollen types known to be normally over- or underrepresented regarding the actual origin of the nectar has not been established. In this regard Myrtaceae, whose flowers provide very abundant and small pollen grains are probably less important as nectar sources than is suggested by the pure pollen spectra. However, as this affects the honey of *Melipona* and of *Apis*, the calculations of trophic niche overlap between the various species probably are not biased significantly.

### **Are pollen loads or pollen stores better indicators of forage use?**

Our technique of removing pollen from foragers returning to their colony gives a good record of the actual pollen influx and allows us to calculate trophic niche overlap. However, during periods of very intense foraging activity it was not possible to collect pollen loads quantitatively from all pollen carrying bees. We did not extend sampling time (closure of hive entrance) as it hampers the information flux between the bees inside and outside the colony. Therefore, and because pollen income on particular days was very much influenced by weather conditions, we think that permanently accumulating pollen in storage pots yields better quantitative results over the year.

The general preference of the *Melipona* bees for Myrtaceae and Melastomataceae was indicated by both methods of pollen sampling. The percentage of Myrtaceae pollen was essentially the same for both methods. However, there was more pollen of Melastomataceae and less pollen of Solanaceae in samples from storage pots than in samples taken from returning foragers. These discrepancies could result from the mentioned difficulties in collecting all returning pollen-carrying bees in periods of very intense foraging activity. As a consequence, pollen of short lasting but mass-flowering resources could have been under-sampled by the method of taking pollen from returning foragers, whereas pollen of longer lasting resources could have been oversampled. In addition to this methodical reason, Sommeijer and De Bruijn (1994) state that *Melipona* house bees have a very strong tendency to close storage pots. After a continuing strong pollen flow, they may subsequently eat the pollen of other types, that comes in after the earlier strong flow has finished. As a consequence pollen that is available for short periods and in smaller quantities will hardly be stored, although over time large amounts of these types may

be consumed directly after being brought in. The true proportion of a particular pollen type in the pollen harvest probably lies somewhere between that obtained by analyses of storage pot contents and that of pollen loads removed from forager bees.

Differences in the pollen spectra between samples from storage pots and samples from forager bees mainly concerned the plant families Melastomataceae and Solanaceae in a reciprocal way. Neither family provided important pollen resources for honey bees. For the calculations of trophic niche overlap between *Melipona* bees and the Africanized honey bee differences due to sampling method of the pollen are therefore negligible.

### **Is the Africanized honey bee competing with native social bees?**

It is surely true that harvest of *Melipona* as well as *Apis* colonies depends strongly on flower abundance and therefore may be triggered by seasonal influences. However, flowers can be found throughout the year and harvesting of eusocial bee colonies does not stop during winter. When suitable food sources explored by *Melipona* as well as *Apis* foragers are available one can assume that colonies of both species benefit, showing a positive correlation in resource harvest. However, intra- and interspecific competition between colonies of both species would prevent maximal exploitation of that resource by any colony. As bees of many highly eusocial species rely on mass-flowering trees (Wilms et al, 1996), which can be explored efficiently by recruitment of nest mates, the occurrence of short harvest peaks in colony dynamics is a common feature (Roubik et al, 1986). A maximal resource harvest is, however, probably only possible if competition is limited. Therefore, one could expect that a competition impact of Africanized honey bees, rather than leading to a general negative correlation, will be most evident in reducing or preventing

harvest peaks in colonies of stingless bees. This is what Roubik et al (1986) found in a 2-week experiment studying the influence of honey bees on various colonies of stingless bees in Panama.

In our study a small index of potential competition by Africanized honey bees does not automatically mean abundant food availability for the *Melipona* bees. In fact, in periods of low resource supply, a small index may result from low foraging activity of the honey bees. On the other hand, a high  $PC_{Am}$  suggests the flowering of many suitable food plants, and therefore, an optimal condition for resource collection for the *Melipona* bees. However, the peak in the number of newly filled storage pots containing pollen in all *Melipona* colonies coincided with a low index of  $PC_{Am}$ . The main pollen influx during such times came from Melastomataceae trees, which were not used very intensely by the honey bees. Despite a potentially good food supply, a comparable peak in the number of pollen pots in periods with high indices of  $PC_{Am}$  was not observed. On the other hand, we found that the *Melipona* colonies were able to collect large quantities of nectar in spite of high indices of  $PC_{Am}$ . Therefore, competition by this intruder may be more important in exploitation of pollen rather than nectar resources.

Our findings, although they do not prove a causal correlation, can nevertheless be interpreted as a result of competition. However, the generality and strength of the assumed negative correlation between the occurrence of harvest peaks for pollen in colonies of stingless bees and the  $PC_{Am}$  index have to be proved by future investigations.

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**Résumé — Partage des ressources florales entre les abeilles mélipones indigènes et l'abeille africanisée introduite, dans la forêt ombrophile cotière du Brésil.** Dans une zone protégée de la forêt ombrophile cotière près de São Paulo, on a prélevé sur une année des échantillons de pollen et de miel dans deux colonies de *Melipona bicolor* et deux de *M. quadrifasciata* (abeilles sans aiguillon) et dans deux colonies d'abeilles africanisées, *Apis mellifera*, et on a fait des analyses polliniques de ces échantillons. Des pelotes de pollen ont été récoltées au moins deux fois par mois i) sur des ouvrières capturées devant le trou de vol (*Melipona*), ii) dans des trappes à pollen (*Apis*). En outre des échantillons de pollen et de miel ont été prélevés chaque mois dans les pots de réserve nouvellement remplis des colonies de *Melipona* et dans les nouveaux rayons des colonies d'*Apis* (dans deux cadres suspendus le mois précédent).

Les échantillons ont été traités et les préparations polliniques réalisées selon Vorwohl (1977) et Louveaux et al (1970). Pour les échantillons de pollen, on a estimé les pourcentages relatifs en poids et en volume des types polliniques (Vorwohl, 1977; Biesmeijer et al, 1992). Le recouvrement des niches alimentaires (NO) a été calculé d'après Colwell et Futuyama (1971). Pour mesurer l'impact potentiel de l'abeille africanisée on a défini un indice de compétition ( $PC_{Am}$ ), qui est le produit du recouvrement des niches et de la récolte globale des abeilles africanisées.

Dans la forêt ombrophile de Boracéia les colonies de mélipones ont récolté du pollen et du nectar tout au long de l'année. La récolte de pollen (nombre de pots à pollen nouvellement remplis) a été maximale en

novembre (figs 1 et 2), tandis que la récolte de miel (nouveaux pots à miel) a présenté deux maximums, l'un en juillet et l'autre en décembre (fig 3). Août et décembre ont été les mois où les colonies d'abeilles africanisées ont engrangé le plus de pollen et de miel, respectivement (fig 4). Dans les échantillons de pollen et de miel des colonies de *Melipona*, les Myrtacées et les Mélastomatacées ont dominé presque toute l'année (tableau II et III; fig 5); cela confirme les études d'autres auteurs réalisées dans des habitats principalement influencés par l'homme. L'abeille africanisée a utilisé un large spectre de plantes nourricières (tableau I), caractérisé par un renouvellement presque mensuel des principales ressources (tableaux II et III). Les différences entre les échantillons provenant des ouvrières et ceux issus des pots à pollen s'expliquent par les faits suivants : i) par butinage intense, toutes les ouvrières rentrant à la colonie avec des pelotes ne peuvent pas être capturées devant le trou de vol, c'est pourquoi, dans ces échantillons, les plantes qui fleurissent en masse et peu longtemps sont sous-représentées; ii) selon Sommeijer et De Bruijn (1994), les abeilles *Melipona* ont une forte tendance à fermer les pots à pollen; après une forte rentrée de pollen il est possible que le pollen rapporté soit traité sans passer par les pots à pollen, si bien que les pollens qui ne sont disponibles que peu de temps et en petites quantités sont à peine présents dans les pots à pollen. La quantité absolue du pollen prélevé sur les butineuses ne dépend pas seulement de l'offre pollinique mais aussi des conditions météorologiques les jours où les prélèvements sont faits. Le nombre de pots à pollen nouvellement remplis nous semble plus approprié pour évaluer la quantité de pollen rapporté à la colonie.

Le recouvrement des niches est plus important pour les deux espèces de mélipones entre elles (moyenne annuelle 0,66 et 0,82 pour les échantillons de pollen provenant respectivement des butineuses et des

pots à pollen et 0,68 pour les échantillons de miel) qu'entre les mélipones et l'abeille mellifère (0,27 et 0,44 pour *M bicolor*, 0,23 et 0,5 pour *M quadrifasciata*, respectivement pour les échantillons de pollen et de miel). Le recouvrement, en fonction de la saison, des niches alimentaires des mélipones et de l'abeille africanisée dépend en premier lieu des différentes périodes de floraison des Myrtacées. Les plantes de cette famille fournissent 60 et 30 % respectivement de la récolte annuelle en pollen et en nectar.

En ce qui concerne la concurrence possible d'*A mellifera*, il est frappant de voir que, dans les colonies des deux espèces de mélipones, on trouve la plupart des nouveaux pots à pollen à des périodes où l'indice  $PC_{Am}$  est le plus bas (figs 1 et 2). Cela peut être d'autant plus interprété comme un signe d'une concurrence réelle de l'abeille mellifère qu'un indice  $PC_{Am}$  élevé indique un bon potentiel de ressources pour les mélipones. Contrairement au pollen, le nectar des colonies de mélipones est engrangé en grandes quantités même lorsque l'indice  $PC_{Am}$  est élevé (fig 3). La concurrence alimentaire entre les abeilles africanisées et les mélipones de la forêt ombrophile cotière du Brésil existe plus pour l'approvisionnement en pollen que pour celui en nectar.

***Melipona* / abeille africanisée / butinage / compétition alimentaire / niche trophique / recouvrement / forêt ombrophile / Brésil**

**Zusammenfassung — Aufteilung floraler Ressourcen zwischen *Melipona*-Bienen und der Afrikanisierten Honigbiene im Brasilianischen Küstenregenwald.** In einem Waldschutzgebiet des brasilianischen Küstenregenwaldes bei São Paulo wurden über ein Jahr hinweg Pollen- und Honigproben von jeweils zwei Völkern der Stachellosen Bienen *Melipona bicolor* und *M*

*quadrifasciata* sowie der Afrikanisierten Honigbiene (*Apis mellifera*) genommen und pollenanalytisch untersucht. Pollenhöschchen wurden mindestens zweimal pro Monat von vor dem Flugloch abgefangenen Arbeiterinnen (*Melipona*) bzw in Pollenfallen (*Apis*) gesammelt. Zusätzlich wurden monatlich von den *Melipona*-Völkern Pollen- und Honigproben aus neu gefüllten Vorratstöpfen und von den *Apis*-Völkern Honig aus neuen Waben (in zwei im Vormonat neu eingehängten Rähmchen) gewonnen. Die Aufbereitung der Proben und die Herstellung von Pollenpräparaten erfolgte nach Vorwohl (1977) und Louveaux et al (1970). Für Pollenproben wurden die relativen Gewichts- bzw Volumenanteile der einzelnen Pollentypen bestimmt (Vorwohl, 1977; Biesmeijer et al, 1992). Die Überschneidung der Nahrungsnischen (NO) wurde nach Colwell und Futuyama (1971) berechnet. Als Maß für den potentiellen Konkurrenzdruck, der von der Afrikanisierten Honigbiene ausgeht, wurde ein Index ( $PC_{Am}$ ) als Produkt von Nischenüberschneidung und dem Gesamteintrag der Honigbienenvölker definiert.

Im Regenwald von Boracéia wurden Pollen und Nektar das ganze Jahr hindurch von den Völkern der eusozialen Bienen gesammelt. Die Anzahl neugefüllter Vorratstöpfen mit Pollen war im November am höchsten (Abb 1 und 2), wogegen neue Honigtöpfe im Juli und Dezember am zahlreichsten waren (Abb 3). Die Völker der Afrikanisierten Honigbiene brachten den meisten Pollen im August und den meisten Nektar im Dezember ein (Abb 4). In den Pollen- und Honigproben der *Melipona*-Völker dominierten praktisch das ganze Jahr über Myrtaceen und Melastomataceen (Tab II, III; Abb 5), wodurch Untersuchungen anderer Autoren in zumeist anthropogen beeinflussten Habitaten bestätigt werden. Die Afrikanisierte Honigbiene nutzte ein breiteres Spektrum an Nahrungspflanzen (Tab I), wobei die Hauptressourcen nahezu jeden Monat wechselten (Tab II, III).

Unterschiede zwischen den von Arbeiterinnen und aus Pollentöpfen gewonnenen Proben sind dadurch zu erklären, daß bei starkem Sammelflug nicht alle pollentragenden Arbeiterinnen vor dem Flugloch abgefangen werden konnten; daher sind in diesen Proben nur kurzzeitig blühende, massenblütige Ressourcen offensichtlich unterrepräsentiert. Auch haben nach Sommerjäger und De Bruijn (1994) *Melipona* Bienen eine starke Tendenz, Pollentöpfe zu schließen. Nach einem starken Polleninflux ist es möglich, daß anschließend eingebrachter Pollen ohne den Umweg über Pollentöpfe verarbeitet wird, so daß nur kurzzeitig und in geringer Menge angebotener Pollen kaum in Pollentöpfen gefunden werden kann. Die absolute Menge des von den Sammelbienen abgenommenen Pollens war nicht nur vom Pollenangebot, sondern auch von Witterungseinflüssen an den einzelnen Untersuchungstagen abhängig. Zur Abschätzung des quantitativen Polleneintrags erscheint uns daher die Anzahl neu gefüllter Pollentöpfe geeigneter.

Die beiden Arten Stachelloser Bienen zeigten untereinander eine größere Nischenüberschneidung (im Jahresdurchschnitt 0,66 bzw. 0,82 für Pollenproben von Sammelbienen und aus Vorratstöpfen und 0,68 für Honigproben) als mit der Honigbiene (für Pollenproben 0,27 und 0,23 bezüglich *M bicolor* und *M quadrifasciata* und für Honigproben 0,44 und 0,5). Für das zeitliche Muster der Nischenüberschneidung von *Melipona*- und Honigbienen (Abb 6) waren in erster Linie die verschiedenen Blühperioden von Myrtaceen verantwortlich. Pflanzen dieser Familie machten 60% bzw 30% der jährlichen NO für Pollen und Nektar aus.

Unter dem Aspekt einer möglichen Konkurrenz von *Apis mellifera* fiel auf, daß in den Völkern beider *Melipona*-Arten die meisten neuen Pollentöpfe in solchen Zeiten gefunden wurden, für die ein niedriger  $PC_{Am}$ -Index berechnet wurde (Abb 1 und



2). Dies kann umso mehr als Hinweis auf eine tatsächlich bestehende Konkurrenz der Honigbiene interpretiert werden, als ein hoher  $PC_{Am}$ -Index auch eine gute potentielle Ressourcensituation für die Stachellosen Bienen bedeutet. Im Gegensatz zu Pollen wurde Nektar von den Stachellosen-Völkern auch bei hohem  $PC_{Am}$ -Index in größerer Menge eingebracht (Abb 3). Nahrungskonkurrenz zwischen der Afrikanisierten Honigbiene und den Stachellosen Bienen besteht im brasilianischen Küstenregenwald somit eher bei der Pollen- als der Nektarversorgung.

**Stachellose Bienen / Afrikanisierte Honigbiene / Brasilianischer Küstenregenwald / Pollenanalyse / Ressourcennutzung / Überschneidung von Nahrungsniischen**

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