Stud Neotrop Fauna & Environm (1996) Vol. 31: 137-151

0165-0521/96/3103-0137$12.00

Resource Partitioning between Highly Eusocial Bees and Possible Impact of the Introduced Africanized Honey Bee on Native Stingless Bees in the Brazilian Atlantic Rainforest

Wolfgang Wilms[1,2], Vera L. Imperatriz-Fonseca[2] and Wolf Engels[1]

[1]Zoological Institute, University of Tübingen, Germany
[2]Department of Ecology, University of São Paulo, Brazil

Received: 29 May 1996

Accepted: 22 October 1996

ABSTRACT

The highly eusocial bee community of the neotropical Atlantic Rainforest was studied at Boracéia Biological Station in the state of São Paulo, Brazil. In this reserve, 17 species of stingless bees and the introduced Africanized honey bee were found, the latter being the most abundant flower visitor. Of all flowering plants, Asteraceae and Myrtaceae were particularly important as resources for bees. Trophic niche overlap between the various species of stingless bees is evident, and it was generally larger within the tribes Meliponini and Trigonini than between members of different tribes. Nevertheless, in the stingless bee community the competitive pressure is rather uniformly spread. The trophic niche of the Africanized honey bee can be positioned between those of Meliponini and Trigonini. Today this introduced species represents the main competitor in this bee community. However, its impact on native stingless bee populations is apparently buffered by mass-flowering trees which are the most important food plants of the indigenous highly eusocial bees.

KEYWORDS: Atlantic Rainforest of Brazil, bee community, stingless bees, Africanized honey bee, nutritional resource partitioning, mass-flowering.

INTRODUCTION

Highly eusocial bees have permanent colonies often comprising large numbers of individuals which represent the main flower visitors and pollinators in tropical ecosystems (Roubik 1989; Pedro & Camargo 1991; Wilms 1996). Stingless bees (Meliponinae) are highly eusocial bees of pantropical distribution, though they are most species-rich in the Neotropics (Roubik 1989). Honey bees (*Apis mellifera* L.) were introduced to the Americas in historical times (Crane 1990). The accidental release of the African honey bee subspecies *A. m. scutellata* in Brazil 40 years ago gave rise to the Africanized honey bee. Possible impacts of this introduced eusocial species on the native bee community were not investigated during its initial spread. In the context of ecosystem functioning, competition with the similarly highly eusocial stingless bees is particularly important but still poorly understood. Only after the arrival of the Africanized honey bee in the northern parts of South

Correspondence to: Wolfgang Wilms, Zoologisches Institut, Universität Tübingen, Auf der Morgenstelle 28, D-72076 Tübingen, Germany. Fax: +49-7071-296950. E-mail: wolfgang.wilms@uni-tuebingen.de

and Central America was competition between it and native bees studied and claimed to exist (Roubik 1978, 1980, 1983), and a decline of stingless bee colonies was predicted (Roubik *et al* 1986). However, Roubik (1988) concluded that the real long-term effect of the Africanized honey bee, especially in wild habitats, had yet to be documented. Since all eusocial bees have evolved generalized patterns of foraging but also exhibit some flower preferences (Ramalho *et al* 1990), Africanized honey bees potentially compete for nutritional resources with either all, many, or only a few of the indigenous social bees and, consequently, they will affect the abundance of sympatric species in quite different ways. These alternative hypotheses could hopefully be evaluated by trophic niche overlap calculations.

The aim of this study was to analyse such trophic relationships in the highly eusocial bee community of an undisturbed area in the Brazilian Atlantic Rainforest. In this unique neotropical ecosystem, the apifauna and the exploitation of floral resources have never been investigated. The data were also used to estimate the possible impact of the Africanized honey bee on populations of native stingless bees.

MATERIAL AND METHODS

Study site

The study was conducted at Boracéia Biological Station which is located between 800 and 900 m NN in the Serra do Mar of São Paulo State (23°38' S, 45°52' W), circa 90 km east of the city of São Paulo and 10 km from the Atlantic Ocean coast. Boracéia lies in the Atlantic Forest Morphoclimatic Domain (Ab'Sáber 1977), in the middle of a forest-covered water reserve of over 16,000 ha. Sampling of bees was carried out mostly in an area of approximately 5 km in diameter around the station. The vegetation consists mainly of primary Atlantic Rainforest with some patches of secondary growth. The upper canopy is approximately 15 m high with few emergents. A total of over 650 plant species was recorded, including the survey of Custodio-Filho (1989). Of these, 240 are trees, mainly of the families Myrtaceae, Melastomataceae and Lauraceae. The similarly species-rich Asteraceae include many climbers. The overall picture of the plant distribution is that of a mosaic structure without dominance by a single species. Only the palm *Euterpe edulis* is exceptionally abundant.

Bee sampling

From September 1991 through March 1994, over 7,000 bees were collected when visiting flowers. Nets attached to long poles were used to reach the upper canopy. In our random sampling approach, bees were captured wherever plants were encountered in bloom, taking in mind, as far as possible, the overall abundance and flowering periods of plant species in the study area. In a sampling effort, all bees visiting flowers were collected. However, for standardization, not more than 50 bee individuals were taken on a single plant specimen. Of the total sample, 4,465 bees were of highly eusocial species. For identification of bee species the collections of the Zoological Museum of the University of São Paulo, the Camargo collection at the University of São Paulo at Ribeirão Preto and the Moure collection at the Federal University at Curitiba were used. Voucher specimens of our survey will be deposited in the Zoological Museum of the University of São Paulo. Branches of the flowering plants visited by bees were sampled and dried. Identification was carried out in the Botanical Institute of the State of São Paulo and samples will be deposited there.

Ecological indices

For calculation of the trophic niche breadth of a bee species, the number of different resources used as well as their frequency of use were considered. This is because analysis of purely the number of used plant species is only of limited value. In fact, use by a bee species of many resources of low importance can suggest a broad trophic niche when, in reality, most food is supplied by only one resource.

Trophic niche breadth (NB) was calculated as the *Shannon index* (Pielou 1969):

$$NB_i = -\sum_k p_{ik} \times \mathrm{eln} p_{ik}$$

where i = a particular bee species, $p_{ik} = N_{ik}/Y_i$, N_{ik} = number of individuals of bee species i collected on flowers of species k, and Y_i = total of all individual bees of species i that were collected on flowers.

Trophic niche overlap (NO) was calculated from the formula of Colwell and Futuyama (1971) as:

$$NO_{ih} = 1 - ½ \sum_k |p_{ik} - p_{hk}|$$

where i and h represent the two species under comparison.

The values for the relative use of a particular flower, p_{ik} and p_{hk}, may be somewhat dependent on the absolute number of foragers collected. Transformation to equal sample size, i.e. to the smaller number of collected bees of the two species, that is $\min(Y_i, Y_h)$, and recalculating the NO index revealed a deviation of less than 1% from the uncorrected NO values. Differences in sample size are therefore negligible.

The trophic niche overlap indices were used to create a matrix of dissimilarities or "niche distances" calculated as 1 – NO. This distance matrix was used to visually represent the trophic niche relationships between the species by ordination (Orloci 1973) using the multidimensional scaling procedure (Kruskal 1964) in the SPSS statistics program (SPSS for Windows, release 6.0, SPSS Inc. Chicago).

Niche overlap alone does not indicate the extent of interspecific competition very well because abundance and body size are also important factors in modulating competition. Considering these factors, we calculated the competitive load (CL) imposed by one species (i) upon another (h) as:

$$CL_{ih} = NO_{ih} \times \text{relative abundance}_i \times \text{body weight}_i \text{ [g]}$$

Notice that, in contrast to niche overlap, the competitive load is uni-directional. The corollarly of the competitive load (CL) of species i on species h is the competitive pressure (CP) that species h suffers from species i.

Within the bee community, if one species would, in part or even completely, replace another by occupying a trophic niche common to both, then interspecific competition can be expressed simply in terms of biomass: species x would become rare, and instead species y more abundant. Accordingly, the present population of the Africanized honey bee can be transformed into a biomass of hypothetically replaced native stingless bees in relation to particular plant resources. If, for example, 1g of Africanized honey bees was reared on a certain amount of collected pollen, this biomass may be regarded as equivalent to 1g of stingless bees. The hypothetical relative population decline (PD) of a bee species can then be calculated as:

$$PD_i = 1 - \frac{B_i}{EB_i}$$

where B_i = the actual biomass of bees of species i, given as: number of bees captured × body weight, and EB_i = the potentially expected biomass of species i before the arrival of the Africanized honey bee, where:

$$EB_i = \sum_k \frac{B_{ik} \times TB_k}{(TB_k - B_{ak})}$$

where B_{ik} = the actual biomass of stingless bee species i on flowers of plant species k, TB_k = total biomass of highly eusocial bees (stingless bees and Africanized honey bees) foraging on flowers of plant species k, and B_{Ak} = biomass of Africanized honey bees foraging on flowers of plant species k.

All calculations were carried out only for the 11 most abundant stingless bee species and the Africanized honey bee. Data of flower visitations for the remaining highly eusocial species were not sufficient to warrant inclusion in the analyses.

RESULTS

The highly eusocial bee community as part of the apifauna at Boracéia

Altogether 255 bee species (Apoidea) were recorded at Boracéia. Of these, 18 belong to the highly eusocial group (Fig. 1), 17 species of native stingless bees and the introduced Africanized honey bee. Despite the relatively small species number, highly eusocial bees make up approximately 2/3 of all flower visiting bees. The Africanized honey bee turned out to be the most abundant species, representing about 20% of all individuals, or 30% of all highly eusocial bees (Fig. 2). Thus, today, the Africanized honey

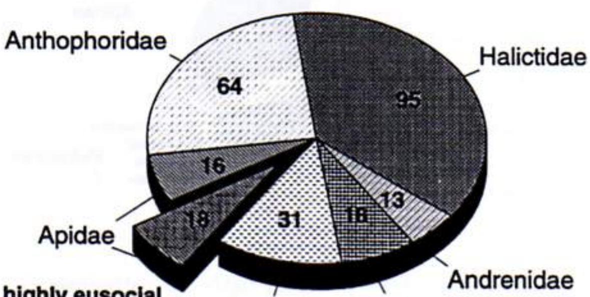

Fig. 1. Composition of the apifauna of Boracéia: families and number of species per family.

bee is predominant in this tropical rainforest ecosystem.

Of the indigenous stingless bees, 11 species can be ranked as abundant flower visitors representing 1% or more of the sample, and 5 species are rare (Fig. 2). The workers of an additional stingless bee species present at Boracéia, the kleptoparasitic *Lestrimelitta limao*, do not visit flowers but instead rob pollen and honey stores from the nests of other eusocial bees.

Resource exploitation by the highly eusocial bees

In order to elucidate the nutritional basis of this highly eusocial bee community, resource use was monitored for the 16 species of flower-visiting meliponines and the Africanized honey bee. Pollen or nectar foraging bees were observed on the flowers of 207 species of angiosperm plants belonging to 56 plant families (Table 1). According to forager abundance, Asteraceae and Myrtaceae contributed most to the nutritional input of highly eusocial bee colonies (Fig. 3). Plant genera that can be considered as important food resources are: *Mikania* and *Vernonia* (Asteraceae), *Myrcia* and *Eugenia* (Myrtaceae), *Bathysa* and *Psychotria* (Rubiaceae) and several others such as *Ocotea*, *Euterpe*, *Solanum*, *Didymopanax* and *Guapira* belonging to different plant families (Table 1).

Solitary bees visited more flowering herbs and climbers in comparison to workers of the highly eusocial species that collected resources more on flowering trees (Fig. 4). These trees usually exhibit a mass-flowering syndrome, in which a burst of numerous blossoms lasting for rather a short period was observed in the majority of trees of a particular species. For instance almost all the flowers of a *Myrcia tomentosa* tree opened on the same day and, for some hours, were heavily frequented by foraging bees. For the rest of the year, hardly any flowers could be observed on that tree. In other mass-flowering trees, flowering lasted up to a few weeks, but the peak of abundant flowering was always rather restricted. Of all the melittophilous tree species which were visited by stingless bee foragers when in blossom, over 30% exhibited a pronounced, and more than 50% a moderate mass-flowering syndrome (Table 1). However, quantifying the degree of mass-flowering was subjective and was carried out more in a comparative manner.

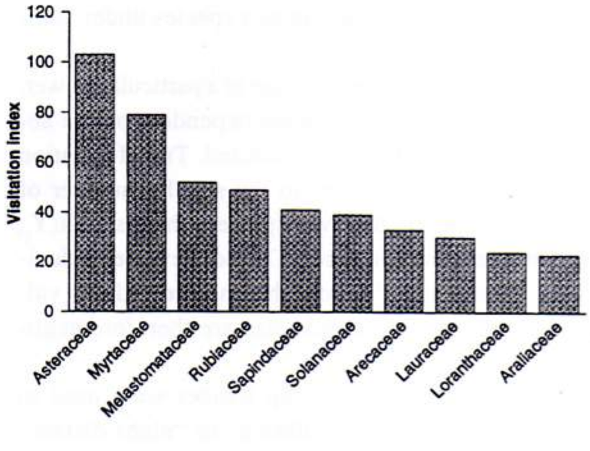

Fig. 3. Ranking of food plant families according to their importance for highly eusocial bees. The ten most-visited plant families for each bee species, indicated by the number of captured individuals, were given rank points, i. e. 10 points for the most important family, 9 points for the second most important, and so on. Addition of rank points gives the visitation index.

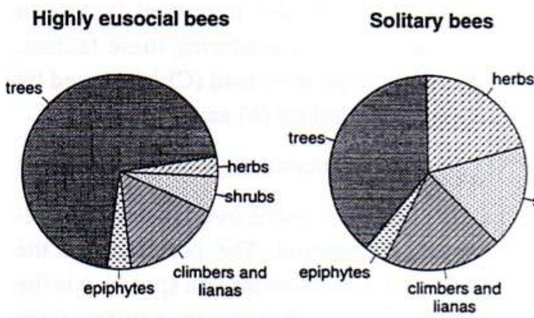

Fig. 4: Distribution of bee captures per life-form of food plants. "Solitary bees" include all non-highly eusocial bees, regardless of their different levels of social organization. Grouping of plant life-forms as described in the legend of Table 1.

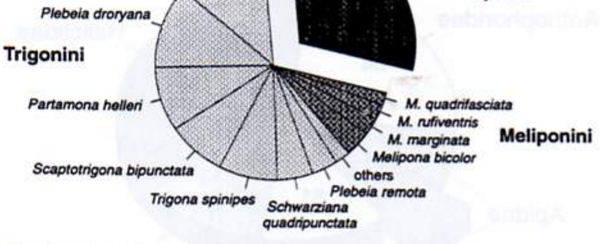

Fig. 2. Abundance of flower-visiting highly eusocial bee species, calculated over the whole study period and across all flowers. "Others" are *Cephalotrigona capitata* (Smith), *Leurotrigona muelleri* (Friese), *Plebeia nigriceps s. l.* (Friese), *Tetragonisca angustula* (Latreille) and *Trigona fulfiventris* Guerin.

Table 1. Food plant spectra of highly eusocial bee species at Boracéia. Data given are frequency classes of relative flower use: + = < 1%, • = 1 – <2%, •• = 2 – <5%, ••• = ≥5%. Plant species with non-bee flowers are marked with an asterix (*). Plant life-forms are: t = trees, c = climbers, climbing shrubs, and lianas, s = shrubs (more than 1m in high), e = epiphytes (including parasitic and hemi-parasitic life-forms), h = herbs, semi-shrubs and shrubs less than 1m in height. Observed degree of mass-flowering (subjective classification): ◇ = moderate mass flowering, ◇◇ = pronounced mass-flowering. Abbreviations for bee species' names: Am = Africanized *Apis mellifera* L., Mb = *Melipona bicolor* Lepeletier, Mm = *Melipona marginata* Lepeletier, Mq = *Melipona quadrifasciata anthidioides* Lepeletier, Mr = *Melipona rufiventris* Lepeletier, Pd = *Plebeia droryana* (Friese), Ph = *Partamona helleri* (Friese), Pr = *Plebeia remota* (Holmberg), Ps = *Paratrigona subnuda* Moure, Sb = *Scaptotrigona bipunctata* (Lepeletier), Sq = *Schwarziana quadripunctata* (Lepeletier), Ts = *Trigona spinipes* (Fabricius).

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Amaranthaceae														
Pfaffia pulverulenta	c	◇	+								••	•	•	+
Apocynaceae														
Mandevilla funiformis *	c													+
Aquifoliaceae														
Ilex paraguariensis	t	◇	+	+					•					+
Ilex theezans	t	◇◇	+		••									+
Araliaceae														
Didymopanax angustissimus	t	◇	••					•	•••	••		••		••
Oreopanax capitatum	t	◇	+		•			+		•	••	••		•
Arecaceae														
Acrocomia spec.	t													
Arecastrum romanzoffianum	t	◇	+					••		•	•			•
Euterpe edulis	t	◇	••						•••	•••	••			•••
Geonoma gamiova	t								+	+	•			
Asclepiadaceae														
Asclepias curassavica *	h													+
Orthosia urceolata	c			••	+	•			•				+	+
Asteraceae														
Baccharis anomala	s	◇	+					••		••		+	+	+
Baccharis grandimucronata	s	◇	+		•			+	+	•		•		
Baccharis cf. microdonta	s	◇						•		+				
Baccharis spec.	t	◇	+		•			•	+	+		+	+	•
Bidens segetum	h, (c)		+			•		+						
Erigeron bonariensis	h				+					•				
Erigeron maximus	h									+			+	
Erigeron spec.	h		+											
Eupatorium itatiayense	h, s		+					+					•	
Eupatorium vauthierianum	h, s		+							+				+
Jaegeria hirta	h									+				
Mikania biformis	c	◇◇	+							+		•	+	•
Mikania catharinensis	c	◇	+		•			••	+	•		•	••	
Mikania conferta	c	◇◇	+	•				+	••	•	•			+
Mikania cynanchifolia	c	◇	+					•				••		
Mikania eriostrepta	c	◇◇	••		••		••	••	••	•		••	••	+
Mikania cf. hoffmanniana	c	◇	+						+	+		+	•	+
Mikania laevigata	c	◇	+			•			+					
Mikania lanuginosa	c	◇◇	+						+					
Mikania lindbergii	c	◇◇			•									
Mikania pachylepsis	c	◇	+					+						
Mikania cf. smaragdina	c	◇◇	•		+			•		+	•		•	+
Mikania trinervis	c	◇◇	+		+				+	+	•	+	+	
Mikania aff. trinervis	c	◇◇	+						+		+			
Mikania ulei	c	◇			•			+	+	•	•	••	+	+
Piptocarpha axillaris	t	◇	+		••				•					
Piptocarpha macropoda	t	◇◇								+				+
Piptocarpha oblonga	c	◇◇	+	•				•	•	•	+		••	••
Piptocarpha obovata	t	◇	+											
Senecio brasiliensis	h		•						+				••	+
Senecio desiderabilis	c	◇◇						+		••	••	•	•	•

Table continues

Table 1. (continued)

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Trixis pinnatifida	h		+											
Vernonia diffusa	t	◇◇	••	•	••	••	•••	••	•	+				
Vernonia discolor	t	◇◇	+					+		+			+	
Vernonia petiolaris	s	◇	+			•••	••	+	•					+
Vernonia puberula	t	◇	•			•		•	•	+				
Vernonia aff. puberula	t	◇◇	••	••			•••	•	+	+				+
Vernonia quinqueflora	t	◇	•						•					
Vernonia westiniana	s	◇	+			•••			+					
not identified	h		+					+					+	
Balsaminaceae														
not identified *	h		+							+				+
Begoniaceae														
Begonia boraceiensis	h		+	•										
Begonia fruticosa	c			+	+		•						•	
Begonia integerrima	e, c						•							
Begonia luxurians	h			+							•			•
Begonia solananthera	e						•							
Begonia spec.	h													+
Bignoniaceae														
Arrabidaea rego	c							+						
Clytostoma cf. callistegioides	c									+				
Jacaranda puberula	t	◇						••		+				+
Lundia nitidula	c													+
Boraginaceae														
Cordia sellowiana	t	◇◇				•		••	+	•			•	
Cordia trichoclada	t	◇	•	+			••		•	•			••	
Bromeliaceae														
Vriesea friburgensis *	e								+					+
Vriesea cf. platynema *	e													+
Caesalpiniaceae														
Bauhinia microstachya	c		+									+		
Sclerolobium denudatum	t	◇◇	+	••	••	••	•••			••	•	••		•
Celastraceae														
Maytenus cf. subalata	t	◇								+				
Chloranthaceae														
Hedyosmum brasiliense *	s, t	◇	•							••	••		+	••
Clethraceae														
Clethra scabra	t	◇	••	+	••			••	•	•	•	•••	+	
Commelinaceae														
Dichorisandra thyrsiflora	h									+				+
Tripogandra diuretica	h									+				
Concolvulaceae														
Ipomoea spec.	c													+
Cucurbitacae														
Cayaponia spec.	c		+	•		••			+					+
Cunoniaceae														
Lammanonia ternata	t	◇	+					+	+					
Weinmannia discolor	t	◇◇						+		+		•	+	+
Weinmannia pauliniifolia	t	◇◇	+							+	+			+
Weinmannia pinnata	t	◇◇	•		••			•	+	+	•••	+	••	

Table continues

Table 1. (continued)

Plant families and species	Life-form	Mass-flowering	Highly eusocial bee species											
			Am	Mb	Mm	Mq	Mr	Ps	Ph	Pd	Pr	Sb	Sq	Ts
Ericaceae														
Gaylussacia spec.	s													+
Euphorbiaceae														
Actinostemon spec.	t	◇	+					+		+			•	
Alchornea triplinervia	t	◇	+					+						+
Croton floribundus	t	◇	•	+			•		•			•	•	+
Croton macrobothrys	t	◇	+								•			
Croton cf. paulinianus	t	◇	•	•	+			+				•		
Croton priscus	t	◇	+	+				+	+	•				•
Sapium glandulatum	t	◇	+							+			+	
Fabaceae														
Andira anthelmia	t	◇						+		+				
Dahlstedtia pinnata *	t							+						+
Dalbergia frutescens	c	◇	•	•	•	•								
Dioclea rufescens	c								+					
Erythrina speciosa *	s									+				+
Machaerium oblongifolium	c	◇	••	••		•								
Flacourticaceae														
Casearia decandra	t	◇◇						+			•	••		
Casearia sylvestris	t	◇◇	••	+	••		•	••	••	+		•••	•••	+
Lauraceae														
Aiouea cf. trinervis	t	◇	+					+			•	+		+
Ocotea dispersa	t	◇	+	+	•			••	••	•			•	••
Ocotea glaziovii	t	◇	•	•				••	+	+	••	+	••	••
Ocotea cf. paranapiacabensis	t	◇	+					•	+		•		+	
Persea alba	t	◇									••			
Liliaceae														
not identified *	h									+				+
Loranthaceae														
Struthanthus concinnus	e	◇	••	••	•••		•	•	+			•	••	
Struthanthus confertus	e	◇	+	+										
Struthanthus salicifolius	e							+		+			+	
Struthanthus staphylinus	e				+			••		••	+		+	••
Struthanthus uraguensis	e	◇	•					•		+			+	+
Malpigihiaceae														
Byrsonima ligustrifolia	t													•
Malvaceae														
Sida rhombifolia	h		+							+				+
Marcgraviaceae														
Marcgravia polyantha *	c								+					+
Norantea brasiliensis *	c									+				•
Melastomataceae														
Miconia cabucu	t	◇		••	••	•	••	•	+				••	
Miconia fasciculata	t	◇◇		•	•	••							+	
Miconia inaegidans	t	◇◇		••	•	•••	•	+	+				+	
Miconia rigiduscula	t	◇◇							••			•		
Miconia theaezans	s, t	◇◇	•	•	••		••		+	••	+	••		••
Tibouchina cerastifolia	h							••						
Tibouchina kuhlmannii	s, t	◇						+						
Tibouchina pulchra	t	◇						+						••
Tibouchina scaberrima	t	◇						••						+
not identified	s			+				•						••

Table continues