Bee Visitors of Quaresmeira Flowers (*Tibouchina granulosa* Cogn.) in the Region of Dourados (MS-Brasil)

by

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ABSTRACT

This research was developed in the center-urban area at the city of Dourados (MS), in *Tibouchina granulosa* trees, a plant popularly known as "quaresmeira" in Brazil. The floral visitors of this species were recorded in three daily periods: 7 - 8 a.m., 1 – 2 p.m. and 4 – 5 p. m. Bee visitors of those plants were collected with an entomological net when they landed on the flowers. The bees were anesthetized in a closed camera containing etila acetate, conserved in Dietrich´s fixative and, soon afterwards, transferred to 70% ethyl alcohol for subsequent identification. Almost 300 specimens of Africanized *Apis mellifera, Trigona spinipes* and *Tetragonisca angustula* were collected. The presence of these three species of bees in the flowers of *T. granulosa* suggests that they can be considered the main floral visitors of that vegetal species. *T. angustula* workers did not visit the flowers of *T. granulosa* between 7 and 8 a.m., but they were the main floral visitors from 4 to 5 p.m. The workers of *T. spinipes* presented a very aggressive behavior against the Africanized *A. mellifera* workers on the quaresmeira flowers, defending the food sources with strength and efficiency and provoking a drastic reduction in the number of honeybee visits between 1 and 2 p.m. Nevertheless, they did not interfere in the opportunistic activity of foraging by *T. angustula* workers, mainly between 4 and 5 p.m. The most important result of this research was the detection of the Competitive Exclusion Principle between *A. mellifera* and

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T. spinipes species in relation to the foraging behavior, when they exploit the floral resources of *T. granulosa.*

Keywords: Quaresmeira, *Tibouchina granulosa,* Foraging behavior, Bees, Competitive Exclusion Principle.

INTRODUCTION

The species *Tibouchina granulosa* (Cogn.) belongs to the Melastomataceae family, being popularly known as quaresmeira. It is a characteristic plant of Atlantic Pluvial Forest and blooms twice a year (from July to August and from December to March). Their flowers present coloration that varies from rose to purple. The tree grows to between 8 and 12 meters in height, with a trunk of 30-40 cm diameter and pubescent tough leaves in both faces (Lorenzi 1992). In the city of Dourados (MS) it is used in forestation and ornamentation of the main streets.

One of the most important subjects in research on conservation of biodiversity is the study of the interactions between floral visitants and vegetal species in natural ecosystems. According to Kearns and Inouye (1997), the loss of pollination is as severe and harmful in any ecosystem as the physical alterations of the habitat, but, frequently, it is generally considered of minor importance in relation to the loss of species. In tropical regions such as Brazil, the main pollen vectors are bees (Silberbauer-Gottsberger & Gottsberger 1988, Bawa 1990, Renner & Feil 1993, Rincón *et al.* 1999, Barbola *et al.* 2000, Aguiar & Santos 2007), simply because these organisms are strictly dependent on floral resources for their survival (Roubik 1989, Michener 2007).

Brazil is a very rich environment in species of social stingless bees of the subfamily Meliponinae. The life cycle and the social regulation of these bee species are intrinsically dependent on a very good brood feeding during all the developmental phases, and also during adult life.

One of the main advantages of the socialization is the development of efficient mechanisms of communication among the members of the colony, which provide conditions to explore the habitat and to collect information on alternative sources of foraging. This ability improves their capacity to use the floral resources at a given moment, as well as to recruit additional foragers to seek the source of food that is being explored (Beekman *et al.* 2007, Díaz *et al.* 2007). This strategy makes possible the selective exploration of more profitable sources in a frequently unstable natural environment (von Frisch 1967, Seeley 1995), because the food sources are frequently ephemeral and dispersed, although they can be diversified in some habitats. The communication systems, still little studied for most species, are also quite diversified. Each of many behavioral characteristics can be potentially changed in order to improve the strategy for exploitation of the floral resources and also the individual and collective alimentary economy (Ramalho *et al.* 1991). Therefore, the foraging efficiency of social bees depends on the influence of many abiotic factors, as well as of conditions of the habitat, as the space and temporary distribution of food sources (Sherman & Visscher 2002, Dornhaus & Chittka 2004, Pasquet *et al.* 2008). The profitability of the alimentary sources and the amount of food stocked in the nest are also essential factors in the regulation of the foraging activity of the colony (Seeley 1989, Pírez & Farina 2004, Grüter & Farina 2007). For this reason, the stingless bees present foraging strategies that vary from individual and opportunists to collective and monopolists.

Apis mellifera is an exotic species, of relatively recent introduction in the American Continent. After the importation of African honeybees, *A. m. scutellata* (Lepeletier 1836), from South Africa and Tanzania to Brazil in 1956 (Kerr 1967), a new organism which resulted from crossings among these bees and four European subspecies of honeybees was produced (Ruttner 1986, Stort & Gonçalves 1994, Pereira & Chaud-Netto 2005). These poly-hybrid bees presented *scutellata*-like characteristics, such as reproductive, foraging and defensive behaviors. For this reason they received the name of Africanized honeybees (Diniz *et al.* 2003). The relationships between these bees and the neotropical environment surprised researchers all over the world, as they have high adaptability to variable ecological conditions, produce a great number of swarms, and their workers are very efficient foragers, competing for floral resources with many species of native bees (Pereira & Chaud-Netto 2005, Traveset & Richardson 2006, Carbonari *et al.* 2009, Brizola- Bonacina 2009).

The scientific community considers scarce the knowledge on the influence of the honey bee on the Brazilian flora. Furthermore, minimal information is available on the interference of the natural sources of floral resources and environmental factors in the foraging activity of this eusocial bee. The efficient system of communication and the fast population growth of *A. mellifera* make this bee a dominant floral visitor in natural environments and also in agriculture areas, especially in the tropics. Nevertheless, its presence can produce a potentially negative effect on the reproduction of many native plants, which are not adapted to pollination by this bee. The workers of *A. mellifera* consume all the floral resources of these vegetable species and, consequently, this harmful behavior reduces the activity of the native pollinators (Traveset & Richardson 2006, Carbonari *et al.* 2009). On the other hand, many native plants already have their reproductive effectiveness maximized as a result of the intense activity of pollination of the honey bee in their flowers.

The relationships between floral visitors and angiosperms are based on exchange of rewards. Most of the time, a floral visit is motivated by the food offer or, in other words, the vegetal species offer attractives, as nectar and pollen, and receive the benefits of pollination (Pesson 1984). Complex interactions between floral visitors and the vegetable species which are visited can be observed in different environments. The visitants developed varied strategies to explore the floral resources produced, including the exploitation of different plant species (Pleasants 1980), the search for nectar and/or pollen at different times of the day or even in different periods of a determined season (Ginsberg 1983, Koptur *et al.* 1988, Morato & Campos 2000), and foraging in different patches of resources (Carpenter 1979) and at different densities in the patches (Johnson & Hubbell 1974, Ginsberg 1983).

The objective of this research was to get information on the species of bees that visit the flowers of *T. granulosa*, as well as the interactions among these organisms in relation to the use of the alimentary resources produced by this species.

MATERIAL AND METHODS

The bees were collected with an entomological net in trees of *T. granulosa* (quaresmeira) in the center-urban area of the city of Dourados (MS). Three intervals of one hour each were established for the collections: the first from 7 to 8 a.m., the second from 1 to 2 p.m. and the third from 4 to 5 p.m. During the time elapsed in each interval the bees foraging the flowers of *T. granulosa* were collected, anesthetized in a camera containing ethyl acetate, and grouped considering the collection interval. Soon afterwards the specimens were fixed in Dietrich (Beçak & Paulete 1976), for 12 hours. After the fixation they were conserved in ethyl alcohol to 70% for subsequent selection and identification in species level, with base in morphologic characters.

The number of bees collected in the flowers of *T. granulosa* was recorded, and the relative frequencies obtained for each species were calculated, using formula (ni / N) X 100 where, ni = number of collected bees of a certain species and N = total number of collected bees. The number of visitors of each bee species to the flowers of *T. granulosa* was used to perform a faunistic analysis of abundance, setting a 5% confidence interval (CI) and 1% probability (p) (Kaps & Lamberson, 2004). For this finality the floral visitors were classified in one of the following classes of abundance (Silveira Neto *et al.* 1976): 1. **Very abundant** - in this case, the number of visitors of a certain species was higher than the upper limit of the CI at 1% p level; 2. **Abundant** – the number of individuals observed was between the upper limits of the CI at 5% and 1% p level; 3. **Common** –the number of visitors recorded on the flowers was within the CI at 5% p level; 4. **Dispersed** – the number of visitors was within the lower limits of the CI at 5% and 1% p level; **Rare** – in this case, the number of visitors was smaller than the lower limit of the CI at 1% p level. The results of this analysis permit to determine the characteristics of the floral visitors and their importance to the flowers of *T. granulosa*. To verify whether the environmental factors were related to the foraging activity of the floral visitors the Pearson´s correlation test was applied to the data. The main objective of this analysis is to determine the functional dependency between the foraging activity and each abiotic variable. The SPSS Program for Windows was used to determine the confidence intervals and to perform the Pearson's correlation tests.

The frequencies of visitors of the species observed on the flowers of *T. granulosa* were calculated and the G Test of Independence was used to compare the data. For this purpose the software BioEstat 5.0 (Ayres *et al.* 2007) was used.

RESULTS AND DISCUSSION

Workers of three bee species [*Apis mellifera* (L. 1758), *Trigona spinipes* (Fabr. 1793) and *Tetragonisca angustula* (L. 1911)] foraged the flowers and

Table 1. Bees collected on the flowers of *T. granulosa* in three daily intervals of observation.

Daily Intervals	BEES		
	Apis mellifera	*Trigona spinipes*	*Tetragonisca angustula*
7 to 8 a.m.	51	37	0
1 to 2 p.m.	7	82	27
4 to 5 p.m.	23	16	51
Total	81	135	78

were considered the predominant visitors of *Tibouchina granulosa*. In total, 294 bees were collected throughout the experiment (Table 1).

The relationship among the species of bees collected in the flowers of *T. granulosa* during the daily intervals of observation can be observed in Fig. 1. An analysis of that figure revealed that the frequency of bees on the flowers of *T. granulosa* varied according to the period of the day and the behavior of each visitor species. The workers of *T. spinipes* were the most aggressive visitors in the food source.

In the first daily interval of observations, *A. mellifera* was more abundant in number of individuals. In Brazil, this species is represented mainly by the

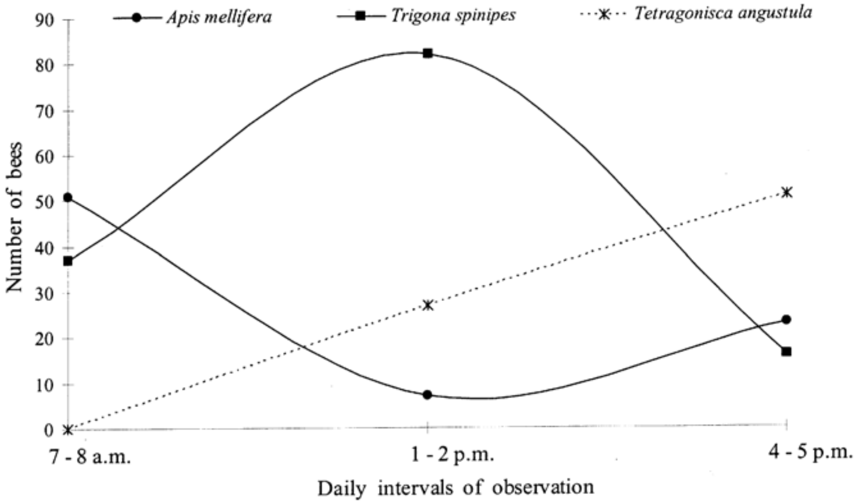

Fig. 1. Relationships among the species of bees collected on the flowers of *T. granulosa* during the daily intervals of observation.

Africanized honeybees, a polyhybrid bee resulting of crossings among four subspecies of European origin (*A.m.ligustica*, *A.m.caucasica*, *A.m.mellifera* and *A. m. iberica*) and the African subspecies, *A. m. scutellata* (Ruttner 1986, Stort & Gonçalves 1994, Pereira & Chaud-Netto 2005). According to Free (1980), Africanized honeybees are extremely efficient in the recruitment of foragers, and rapidly attract a great number of collectors for the exploitation of food sources.

In the second daily interval of collections the most representative bee species observed in the flowers of *T. granulosa* was *T. spinipes* ("irapuá"). The workers of this species presented a very aggressive behavior against the Africanized *A. mellifera* workers on the quaresmeira flowers, defending the food sources with strength and efficiency, and provoking a drastic reduction in the number of honeybee visits between 1 and 2 p.m. The workers of Africanized honeybees practically were expelled from the food sources in this period. Nevertheless, the workers of *T. spinipes* did not interfere in the opportunistic activity of foraging by *T. angustula* workers, mainly between 4 and 5 p.m. According to Johnson & Hubbell (1974), the recruitment system of *Trigona* workers is not as efficient as the observed in *A. mellifera*, but they compensate for this apparent disadvantage with an extremely aggressive behavior in the sources of food. This peculiar behavior, to the detriment of the great number of "rivals", can vary from an alarm posture to direct corporal confrontations. Engels & Engels (1980) noted many aggressive exhibitions of meliponids in relation to foragers of *A. mellifera,* in the exploitation of floral resources. In all the cases they observed that the stingless bees were victorious, as some honeybee workers had their wings damaged and most of them could not fly after the confrontations.

In the third daily interval of observation and collection, the workers of *T. angustula* ("jataí") were more abundant. These small-sized meliponids do not enter in direct competition with the larger bees by the floral resource that is being explored. They act only as collectors of the remaining pollen found in the floral structures, resulting from the foraging activity of other organisms which visited the same source of food before them (Laroca 1970).

There was a significant negative correlation between the number of visits (N.V.) performed by workers of *T. spinipes* and relative air humidity (R.H.) values (r = - 0.9532; t = - 31.54; df = 1), but not with the temperature (T) (r = 0.4003; t = 0.4369; df = 1). For *T. angustula* there was a non-significant correlation between N.V. and R.H. (r = - 0.0243; t = - 0.0243; df = 1), and also between N.V. and T (r = 0.7683; t = 12.00; df = 1), although this last value obtained for **t** is very close to the critical value of significance (12.70) at 2.5% of probability indicated in the table for t values, in the bicaudal test (Kaps & Lamberson 2004). In the case of *Apis mellifera* there was a significant negative correlation between N.V. and T (r = - 0.9868; t = - 60.99; df = 1), but a non-significant positive correlation between N.V. and R.H. (r = 0.7716; t = 12.13; df = 1). The effect of both climatic variables on the foraging activity of *T. spinipes*, *T. angustula* and *A. mellifera* workers was clearly different.

The bees usually forage more intensely when the relative humidity of the air is low and the environmental temperature is high. The results obtained for *T. spinipes* in this research are similar to those registered by Hilário *et al.* (2000) and Kasper *et al.* (2008), in what concerns to the relationship between food collection and relative humidity of the air. On the other hand, although the correlation between the number of flower visits of *T. spinipes* and the temperature has not been significant, there was a tendency of increase in the N.V. in higher temperatures. In the case of *A. mellifera* there was a decrease in the N.V. under higher temperatures and lower values of R.H. and an increase in the N.V. in opposite conditions. These results are different from those obtained in other research (e.g. Coelho 1991, Polatto *et al.* 2012). The results of the correlation tests performed in this research represent an argument in favor of the occurrence of competitive exclusion between *T. spinipes* and *A. mellifera* regarding food exploitation: the foraging activity of the Africanized honeybees was moved to less favorable schedules, particularly the beginning and the end of the day, to avoid the trophic overlapping with *T. spinipes* in the middle of the day, considered the period in which the environmental conditions are more favorable.

The frequency of visits of *T. spinipes* workers to the flowers of *T. granulosa* (45.92%) was greater in relation to the frequencies recorded for workers of *A. mellifera* (27.55%) and *T. angustula* (26.53%) (G = 155.34; p< 0.0001; df= 4). Renner (1983) observed 34 species of plants of the family Melastomataceae, common in Neotropical communities (Atlantic Forest and Amazonian Forest), and verified that all of them were visited by species of *Trigona* (5 species and 4 subspecies, respectively).

In the present research, considering the classes of abundance proposed by Silveira Neto *et al.* (1976), *T. spinipes* was classified as a very abundant species in relation to *A. mellifera* and *T. angustula,* considered two common species. In relation to the foraging behavior, the three species were classified as constant organisms. *T. spinipes* was the dominant species on the flowers of *T. granulosa*. The predominance of *T. spinipes*, followed by *A. mellifera* and *T. angustula*, three bee species with eusocial lifestyle, may be a consequence of the large number of members in their colonies and their generalist habits. Vieira & Marchini (2009) studied the diversity of bees in a Brazilian Cerrado area in the city of Cassilândia, Mato Grosso do Sul, and observed that the two most abundant species were also *A. mellifera* and *T. spinipes.* In a particular environment, the most abundant alimentary sources are efficiently exploited by these bees, and they generally forage in groups (Kerr *et al.* 1981, Wilms *et al.* 1996, Johnson & Steiner 2000).

The workers of *Apis* and *Trigona* established, amongst themselves, a competition relationship for exclusion in relation to the foraging behavior, when they explore the floral resources of *T. granulosa.* In other words, the presence of one of them on the flowers drastically reduced the presence of the other (Fig. 1).

The way bees explore floral sources of pollen and nectar depends on relative selection pressures regarding the bee, the flower and also the environment. The environmental characteristics and the time that the food sources stay available to the visitor are fundamental variables in the consumers' economy. In an environment with previsible resources in time and space, specialization can present advantages in relation to the search and use of food (MacArthur & Pianka 1966). Specialization eventually brings a competitive advantage in the use of specific resources. On the other hand, the generalist alimentary habit makes possible the adaptation of the species to the variations in the food offered, besides those due to the competitors' presence (Morse 1980). The social apids maintain a great colonial biomass for a long period and, for this reason, they cannot specialize (Michener 1979). Additionally, they present morphologic and functional characteristics (for instance, the corbicle and a long proboscis) that favor the generalist alimentary habit (Michener *et al.* 1978, Loken 1981). For this reason they are predisposed to interspecific interactions in the use of the floral sources of food.

There is some indirect evidence that competition alters the method of use of the floral sources among Apidae (Inouye 1978, Heinrich 1978, 1979, Pyke 1982). The foragers of some species of meliponids exhibit aggressive and monopolist behaviors during the bloomed periods of the year (Johnson & Hubbell 1974, 1975, Hubbell & Johnson 1978), and some species which form great colonies make demarcations with pheromones in the area where the colony is acting, with the apparent purpose of avoiding the installation of new nests (Hubbell & Johnson 1977). Koeniger & Vorwohl (1979) observed that, among four species of Apidae (*Apis dorsata*, *A. florea*, *A. cerana* and *Trigona iridipennis*), the smallest of them (*T. iridipennis*) exhibited aggressive behavior in relation to the other three species. Those authors admitted that this behavior may be related to the smaller area of food exploration by the colony of *T. iridipennis,* and would have the function of preserving the foraging space of this species. They also observed a larger diversification of *T. iridipennis* in relation to food collection. This peculiarity apparently attests to the efficiency of that bee to defend its feeding territory.

The hypothesis postulated by Koeniger and Vorwohl establishes a certain difficulty for the analysis of the coexistence among meliponid species. For instance, Trigonini, the larger species which form great colonies and, therefore, have a larger action area, exhibit aggressive and monopolist behaviors (Johnson & Hubbell 1975, Hubbell & Johnson 1978, Roubik & Johnson 1982), while the smaller species avoid direct contact with the larger ones and are passive and opportunist in relation to the gathering of floral resources. Engel & Dingemans-Bakels (1980) noticed that small species of stingless bees, as *Plebeia minima*, *Tetragonisca* spp. and *Trigona jaty* foraged some types of flowers which were not visited by larger bees, and suggested the existence of some alimentary specialization related with the size of the species.

CONCLUSIONS

The data obtained in this research allowed the following conclusions: (1) The capture of bees in foraging activity on the flowers of *T. granulosa* indicates the possibility of effective pollination; (2) The floral resources are collected by the bees *A. mellifera*, *T. spinipes* and *T. angustula;* (3) The constant presence of *Apis* and *Trigona* on the flowers of *T. granulosa* indicates that this vegetable species is an important food source for them; (4) Of the bees that visited the flowers of *T. granulosa*, *T. spinipes* appeared dominant to the others, probably due to their aggressive behavior in the exploitation of that food source; (5) There is a competition relationship for exclusion between *Apis* and *Trigona* in relation to the foraging behavior, when they explore the floral resources of *T. granulosa* : the presence of one of them on the flowers drastically reduced the presence of the other.

REFERENCES

Aguiar, C. M. L. & G. M. M. Santos 2007. Compartilhamento de recursos florais por vespas sociais (Hymenoptera: Vespidae) e abelhas (Hymenoptera: Apoidea) em uma área de Caatinga. Neotropical Entomology 36: 836–842.

Ayres, M., M. Ayres JR, D. Lima Ayres & A. A. Santos Dos Santos 2007. BioEstat 5.0. Belém– PA, Brasil: Sociedade Civil Mamirauá, 2007, 364 p.

Barbola, I. F., S. Laroca & M. C. Almeida 2000. Utilização de recursos florais por abelhas silvestres (Hymenoptera, Apoidea) da Floresta Estadual Passa Dois (Lapa, Paraná, Brasil). Revista Brasileira de Entomologia 44: 09–19.

Bawa, K. S. 1990. Plant-pollinator interactions in tropical rain forests. Annual Review of Ecology and Systematics 21: 399-422.

Beçak, W. & H. Paulete 1976. Técnicas de Citologia e Histologia. Livros Técnicos Ltda., Rio de Janeiro.

Beekman, M., A. L. Gilchrist, M. Duncan & D. J. T. Sumpter 2007. What makes a honeybee scout? Behavioral Ecology and Sociobiology 61: 985-995.

Brizola-Bonacina, A. K. 2009. Presença de *Apis mellifera* L. em uma região de cerrado em Dourados (MS) e sua relação com a fauna de abelhas nativas. Tese (Doutorado)— Universidade Estadual Paulista, Instituto de Biociências de Rio Claro, SP.

Carbonari, V., L. P. Polatto & V. V. Alves-Junior 2009. Evaluation of the impact on *Pyrostegia venusta* (Bignoniaceae) flowers due to nectar robbery by *Apis mellifera* (Hymenoptera, Apidae). Sociobiology 54: 373-382.

Carpenter, F. L. 1979. Competition between hummingbirds and insects for nectar. American Zoologist 19: 1105–1114.

Coelho, J. R. 1991. The effect of thorax temperature on force production during tethered flight in honeybee (*Apis mellifera*) drones, workers, and queens. Physiological Zoology 64: 823-835.

Díaz, P. C., C. Grüter & W. M. Farina 2007. Floral scents affect the distribution of hive bees around dancers. Behavioral Ecology and Sociobiology 61: 1589-1597.

Dornhaus, A. & L. Chittka 2004. Why do honey bees dance? Behavioral Ecology and Sociobiology 55: 395-401.

Diniz, N. M., A. E. E. Soares, W. S. Sheppard & M. A. Del Lama 2003. Genetic structure of honeybee populations from Brazil and Uruguay. Genetics and Molecular Biology 26: 47-52.

Engel, M.S. & F. Dingemans-Bakels 1980. Nectar and pollen resources for stingless bees (Meliponinae, Hymenoptera) in Surinam (South America). Apidologie 11: 341-350.

Engels, W. & E. Engels 1980. Experiments with caged and free-flying *Scaptotrigona postica* in South America and Europe, with special reference to the question of food resource competition between stingless bees and honeybees. Insectes Sociaux 27: 280-281.

Free, J. B. 1980. A organização social das abelhas (*Apis*). Coleção Temas de Biologia. E.P.U. - EDUSP, São Paulo, 79p.

Frisch, K. von 1967. The dance language and orientation of bees. Harvard University Press, Cambridge, Massachusetts, 566 p.

Ginsberg, H. S. 1983. Foraging ecology of bees in an old field. Ecology 1: 165–175.

Grüter, G. & W. M. Farina 2007. Nectar distribution and its relation to food quality in honeybee (*Apis mellifera*) colonies. Insectes Sociaux 54: 87-94.

Heinrich, B. 1978. The economics of insects' sociality, pp. 97-128. *In*: Krebs, J. R. & N. B. Davies (Eds.), Behavioral Ecology – an Evolutionary Approach. Oxford, Blackwell Scientific Publications.

Heinrich, B. 1979. Bumblebee Economics. Cambridge, Harvard University Press.

Hilário, S. D., V. L. Imperatriz-Fonseca & A. M. P. Kleinert 2000. Flight activity and colony strength in the stingless bee *Melipona bicolor bicolor* (Apidae, Meliponinae). Revista Brasileira de Biologia, 60: 299-306.

Hubbell, S. P. & L. K. Johnson 1977. Competition and nest spacing in a tropical stingless bee community. Ecology 58: 949-965.

Hubbell, S. P. & L. K. Johnson 1978. Comparative foraging behavior of six stingless bees species exploiting a standardized resource. Ecology 59: 1123-1136.

Inouye, D.W. 1978, Resource partitioning in bumblebees: Experimental studies of foraging behavior. Ecology 52: 672-678.

Johnson, L. K. & S. P. Hubbell 1974. Aggression and competition among stingless bees: field studies. Ecology 55: 120-127.

Johnson, L. K. & S. P. Hubbell 1975. Contrasting foraging strategies and coexistence of two bee species on a single resource. Ecology 56: 1398-1406.

Johnson, S. D. & K. E. Steiner 2000. Generalization versus specialization in plant pollination systems. Trends in Ecology and Evolution 15: 140–143.

Kasper, M. L., A. F. Reeson, D. A. Mackay & A. D. Austin 2008. Environmental factors influencing daily foraging activity of *Vespula germanica* (Hymenoptera, Vespidae) in Mediterranean Australia. Insectes Sociaux 55: 288-295.

Kearns, C. A. & D. W. Inouye 1997. Pollinators, flowering plants, and conservation biology. Bioscience 47: 297–306.

Kerr, W. E. 1967. The history of the introduction of African bees to Brazil. South African Bee Journal 39: 3–5.

Kerr, W.E., M. Blum & H. M. Fales 1981. Communication of food source between workers of *Trigona* (*Trigona*) *spinipes*. Revista Brasileira de Biologia 41: 619–623.

Koeniger, N. & G. Vorwohl 1979. Competition for food among four sympatric species of Apini in Sri Lanka (*Apis dorsata, A. florea, A. cerana* and *Trigona iridipennis*). Journal of Apicultural Research 8: 9-109.

Koptur, S., W. A. Haber, G. W. Frankie & H. G. Baker 1988. Phenological studies of shrub and tree let species in tropical cloud forests of Costa Rica. Journal of Tropical Ecology 4: 323–346.

Laroca, S. 1970. Contribuição para o conhecimento das relações entre abelhas e flores: coleta de pólen das anteras tubulares de certas Melastomataceae. Revista Floresta 2: 69-74.

Loken, A. 1981. Flower-visiting insects and their importance as pollinators. Bee World 62: 130-140.

Lorenzi, H. 1992. Árvores brasileiras: manual de identificação e cultura de plantas arbóreas nativas do Brasil. Editora Plantarum, São Paulo, 358p.

MacArthur, R. H. & E. R. Pianka 1966. On optimal use of patchy environment. American Naturalist 100: 603-609.

Michener, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277-347.

Michener , C. D. 2007. The bees of the world. 2nd ed. The Johns Hopkins University Press, Baltimore, 913p.

Michener, C. D., M. L. Winston & R. Jander 1978. Pollen manipulation and related activities and structures in bees of the family Apidae. University of Kansas Science Bulletin 51: 575-601.

Morato, E. F. & L. A. O. Campos 2000. Partição de recursos florais de espécies de *Sida Linnaeus* e *Mauvastrum coromandelianum* (Linnaeus) Garcke (Malvaceae) entre *Cephalurgus anomalus* Moure & Oliveira (Hymenoptera, Andrenidae, Panurginae) e *Melissoptila cnecomala* (Moure) (Hymenoptera, Apidae, Eucerini). Revista Brasileira de Zoologia 17: 705–727.

Morse, D. H. 1980. Behavioral Mechanisms in Ecology. Cambridge, Harvard University Press.

Pasquet, R. S., A. Peltier, M. B. Hufford, E. Oudin, J. Saulnier, L. Paul, J. T. Knudsen, H. R. Herren & P. Gepts 2008. Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. Proceedings of the National Academy of Sciences of the United States of America 105: 13456-13461.

Pereira, A. M. & J. Chaud-Netto 2005. Africanized Honeybees: Biological Characteristics, Urban Nesting Behavior and Accidents Caused in Brazilian Cities (Hymenoptera: Apidae). Sociobiology 46: 535- 550.

Pesson, P. 1984. Transport du pollen par les animaux: zoogamie, pp. 97-139. *In:* Pesson, P. & J. Louveaux (Eds.), Pollinisation et Productions vègètales. Paris, Institut National de la Recherche Agronomique.

Pírez, N. & W. M. Farina 2004. Nectar-receiver behavior in relation to the reward rate experienced by foraging honeybees. Behavioral Ecology and Sociobiology 55: 574-582.

Pleasants, J. M. 1980. Competition for bumblebee pollinators in rocky mountain plant communities. Ecology 6: 1446–1459.

Polatto, L. P., J. Chaud-Netto, J., J. C. S. Dutra & V. V. Alves –Junior 2012. Exploitation of floral resources on *Sparattosperma leucanthum* (Bignoniaceae): foraging activity of the pollinators and the nectar and pollen thieves. Acta Ethologica 15: 119-126.

Pyke, G. H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: Competition and community structure. Ecology 63: 555-573.

Ramalho, M., V. L. Imperatriz-Fonseca & A. Kleinert-Giovannini 1991. Ecologia nutricional de abelhas sociais, pp. 101-122. *In*: Panizzi, A. R. & J. R. P. Parra (Eds.), Ecologia nutricional de insetos e suas implicações no manejo de pragas, vol. IV. Manole, Brasil.

Renner, S. S. 1983. The widespread occurrence of anther destruction by *Trigona* bees in Melastomataceae. Biotropica 15: 251-256.

Renner , S. S. & J. P. Feil 1993. Pollinators of tropical dioecious angiosperms. American Journal of Botany 80: 1100–1107.

Rincón, M., D. W. Roubik , B. Finegan , D. Delgado & N. Zamora 1999. Understory bees and floral resources in logged and silviculturally treated Costa Rican rainforest plots. Journal of the Kansas Entomological Society 72: 379–393.

Roubik, D. W. 1989. Ecology and natural history of tropical bees. Cambridge University Press, New York.

Roubik, D. W. & L. K. Johnson 1982. The aggressive foraging syndrome in highly social bees: Ecological correlaters and evolutionary origin, p. 38. *In*: Breed, M. D., C. D. Michener & H. E. Evans (Eds.). The Biology of Social Insects. Boulder, Colorado. Westview Press.

Ruttner, F. 1986. Geographical variability and classification, p. 23-56. *In*: Rinderer, T. E. (Ed.). Bee genetics and breeding. Orlando: Academic Press.

Seeley, T. D. 1989. Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. Behavioral Ecology and Sociobiology 24: 181-199.

Seeley, T. D. 1995. The wisdom of the hive: the social physiology of honey bee colonies. Harvard University Press, Cambridge, MA.

Sherman, G. & P. K. Vischer 2002. Honeybee colonies achieve fitness through dancing. Nature 419: 920-922.

Silberbauer-Gottsberger, I. & G. Gottsberger 1988. A polinização de plantas do Cerrado. Revista Brasileira de Biologia 48: 651–663.

Silveira Neto, S., O. Nakano, D. Barbin & N. A. Villa Nova 1976. Manual de ecologia dos insetos. Editora Agronômica Ceres, São Paulo.

Stort, A. C. & L. S. Gonçalves 1994. A africanização das abelhas *Apis mellifera* nas Américas, pp. 33-47. *In*: Barraviera, B. (Ed.). Venenos Animais: Uma visão integrada. Rio de Janeiro: EPUC, Editora de Publicações Científicas Ltda.

Traveset, A. & D. M. Richardson 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution 21: 208-216.

Vieira, G. H. C. & L. C. Marchini 2009. Diversity of bees (Hymenoptera: Apoidea) in a Cerrado Area in the city of Cassilândia, Mato Grosso do Sul, Brazil. Sociobiology 53: 597–607.

Wilms, W., V. L. Imperatriz-Fonseca & W. Engels 1996. Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honey bee on native stingless bees in the Brazilian rainforest. Studies on Neotropical Fauna and Environment 31: 137–151.