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Pollen and nectar foraging by *Melipona quadrifasciata anthidioides* Lepeletier (Hymenoptera: Apidae: Meliponini) in natural habitat

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Abstract

This study shows the influence of meteorological factors on the collection of nectar and pollen by *Melipona quadrifasciata anthidioides* Lepeletier foragers in their natural habitat. Five *M. quadrifasciata anthidioides* colonies were studied in Parque das Neblinas, Mogi das Cruzes district (23°44′52″S/46°09′46″W), from October 2009 to September 2010. The foraging activity of the worker bees was observed monthly and the temperature and relative humidity were registered and the pollen grains types from the pollen loads were identified. The peaks of pollen collection occurred between 08:30-09:50 am, while nectar was gathered along the day. The relation between resources sampling and environmental temperature is best described with a polynomial function, while in relation to relative humidity the curves of foraging activity is slightly asymmetric to left. A total of 24 pollen types were identified and the most frequents were Myrtaceae (*Eucalyptus, Myrcia*), Melastomataceae and Solanaceae. The tolerance to the environmental conditions is discussed, as well as the plants explored for pollen sources.

Introduction

Flight activity in stingless bees have been studied for many species in Brazil, such as: *Melipona quadrifasciata quadrifasciata* Lepeletier, *Melipona marginata marginata* Lepeletier, *Melipona obscurior* Moure, *Melipona bicolor bicolor* Lepeletier (review in Hilário et al., 2000), Trigona *hyalinata* Lepeletier (Contrera et al., 2004), Tetragona clavipes Fabricius (Rodrigues et al., 2007), *Melipona bicolor schencki* Gribodo (Ferreira-Junior et al., 2010), *Melipona rufiventris* Lepeletier (Fidalgo & Kleinert, 2010), *Melipona eburnea* Friese (Nates-Parra & Rodríguez, 2011), *Plebeia remota* Holmberg (Hilário & Imperatriz-Fonseca, 2012), *Scaptotrigona depilis* Moure (Figueiredo-Mecca et al., 2013) and *Geotrigona mombuca* Smith (Gobatto & Knoll 2013). In the majority of these studies the flight activity of the workers was associated with environmental conditions like temperature, barometric pressure, relative humidity, wind speed and even time of the day. However, any of these conditions can interact with biotic factors such as bees' physiology or biological clocks (Hilário et al., 2003; Gouw & Gimenes, 2013), influencing the performance of the individuals. In fact, the amplitude of tolerance to many ecological factors (with the minimum and maximum limits of tolerance) may have synergistic effects.

Besides the environmental conditions, the availability of food resources also play an important role on the limits where the species can live, grow and reproduce. In stingless bees, the essential food resources are pollen and nectar, which are stored in pots inside the nest (Michener, 1974; Roubik, 1989). The health and size of the colonies may reflect



the availability of the floral resources in the field. Thus, the number of individuals in the nest and the colony survival along the years are dependent, among other factors, on the amount of food collected and stored. On the other hand, the population size of each nest characterizes the colony as small (or weak), medium or large (or strong) and has a direct relationship with the foraging activities among other factors (Kleinert-Giovannini & Imperatriz-Fonseca, 1986; Hilário et al., 2000; Hilário et al., 2003; Hilário & Imperatriz-Fonseca, 2009).

Melipona quadrifasciata Lepeletier, has a relative broad geographic distribution along eastern Brazil, reaching the Misiones region in Argentina and Paraguay (Camargo & Pedro, 2008; Batalha-Filho et al., 2009). This species is commonly associated with the Atlantic Rainforest habitats in Southern and Southeastern Brazil. The colony of this species is less numerous than other stingless bees, approximately 300-400 individuals (Tóth et al., 2004). In nature the nest is constructed inside trees hollows, but it is easily kept and maintained into artificial hives. Concerning the plants visited by *M. quadrifasciata* this species is considered generalist, but several species of Myrtaceae, Asteraceae, Melastomataceae and Solanaceae are among the preferred floral resources (Ramalho et al., 1989; Wilms & Wiechers, 1997; Antonini et al., 2006a; Antonini et al., 2006b).

The aim of this study was to evaluate the pattern of pollen and nectar collection by *M. quadrifasciata* and their relationship with environmental factors like the temperature and relative humidity under natural conditions. This species has an economic importance for the beekeeper and can be used as pollinator in greenhouse, in tomato production for example (Del Sarto et al., 2005; Bispo dos Santos et al., 2009; Bartelli et al., 2014; Bartelli & Nogueira-Ferreira, 2014).

Material and Methods

Study area

This study was conducted in the Parque das Neblinas, located in the Mogi das Cruzes district in Sao Paulo state, Brazil (23°44'52'S/46°09'46''W; 700 to 1100m a.s.l.). The park has 2,788.15 hectares and the main vegetation is the Atlantic Rainforest. The climate of the region according to Köppen is *Af*, considered as tropical and always humid with the average temperature above 18°C during the summer. Annual precipitation varies between 1600 and 2000 mm. There is no winter dry season and only a decrease of precipitation is registered.

External Activities of the Bees

Five colonies of *M. quadrifasciata* were maintained in free-foraging wooden nest boxes at the Park. During the first month the colonies were fed every 2 weeks with a sugar syrup (1:1 sugar and water).

The flight activity of the bees was observed monthly

between October 2009 and September 2010. For each month, the number of bees returning from the field to the nest was registered along two consecutive days, during five minutes per hour, between 05:30 am to 04:30 pm, which corresponded to 1430 observations. Pollen was easily observed on the corbiculae of foragers, due to the color and texture of the load. On the other hand, foragers returning to the colonies, without load on the legs, were considered as nectar foragers considering that nectar is stored and transported inside the honey stomach (Roubik, 1989; Pierrot & Schlindwein, 2003; Souza et al., 2006). Other materials, like resin and mud were not considered in the analysis.

During the observations the temperature and relative humidity were registered every 30 minutes, using dataloggers *(HOBO Pro RH/Temp)*, which were installed in the area and later the data were transferred to the computer.

Pollen analysis

One day after the field observations, samples of the honey collected from the pots and the pollen collected from the corbiculae of the foragers were taken from the five nests from December 2009 to September 2010. For that, the entrance of the colony was closed for five minutes and five arriving foragers were caught with entomological net. The pollen loads were extracted from their corbiculae and kept on separated plastic tubes (eppendorff) and the bees were released. For each colony samples of 10mL of honey from three new storage pots were sampled with syringes and kept separated into sterilized vials. In February honey and pollen were not sampled due to excessive rainfall.

The honey samples and pollen pellets were prepared fresh according to the standard European protocol (Maurizio & Louveaux, 1965) for palynological studies. Three microscopic slides with glycerine jelly were prepared for each sample and were sealed with paraffin.

Pollen grains identification was carried out using literature data (e.g., Barth, 1989; Roubik & Moreno, 1991) and the reference of pollen grains previously identified and maintained in slides in the collection from the Research Center of Palynology, Botanical Institute, Department of Environment of São Paulo State. The pollen grains were identified using the term "pollen type" that means pollen from a single plant species as well as a group of species or higher taxa presenting similar pollen morphology.

Data analyses

Since our data had a non-normal distribution, we performed nonparametric correlation Spearman's rho (Zar, 1999) to verify if there was relationship between the meteorological factors and the pattern of nectar and pollen collection. For statistical analysis the SPSS for Windows release 8.0 was used.

Results

The temperature range during the experiment was between 5.8° and 37.0°C, and the relative humidity range was between 15% and 100%. Foraging flights were registered within a temperature range of 13.7°-36.8°C, while relative humidity (RH) oscillated between 15.7% and 100%.

The number of pollen and nectar foragers was positively correlated to the air temperature, and negatively with the relative humidity (Table 1). These correlations were weak, since that there was a peak in intermediates temperature and relative humidity ranges (Figs 1 and 2).

Table 1. Spearman's correlation coefficients (rho) for pollen and nectar collection by *Melipona quadrifasciata anthidioides* foragers and meteorological factors.

		rho	р
Pollen	Temperature	0.174	0.001 (S)
	Relative Humidity	-0.057	0.030 (S)
Nectar	Temperature	0.208	0.001 (S)
	Relative Humidity	-0.063	0.017 (S)

N=1430; S= Significat, NS=Non-Significat; p=probability.

The relation of resources sampling and environmental temperature was best described with a polynomial function, showing an optimal interval between ca. 17.0°C -29.0°C, which corresponded to an intense foraging activity for nectar and pollen (Fig 1). It is also possible to observe that there is a limit of tolerance in temperature below 13.7°C, and above 35.0°C. Peaks of pollen and nectar collection occurred at the temperature intervals of 20.1°-23.0°C and 17.1°-20.0°C, respectively (Fig 1).

In relation to relative humidity the tendency to polynomial function is not clear and the curves of resources sampling are slightly asymmetric to left (Fig 2). Foraging activity increased with 40% relative humidity. Both peaks of

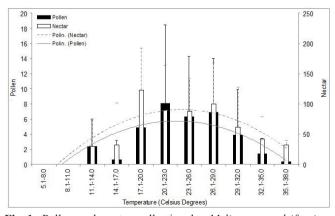


Fig 1. Pollen and nectar collection by *Melipona quadrifasciata anthidiodes* related to the environmental temperature intervals. Solid and dashed bars represent standard deviation of pollen and nectar collection, respectively.

pollen and nectar collection occurred at the relative humidity intervals of 60.1-70.0% (Fig 2).

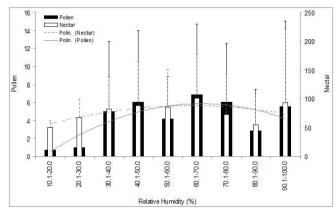


Fig 2. Pollen and nectar collection by *Melipona quadrifasciata anthidiodes* related to the relative humidity intervals. Solid and dashed bars represent standard deviation of pollen and nectar collection, respectively.

The number of bees collecting resource increased until 09:50 am, with a peak of nectar sample between 08:30-08:50 am and pollen gather between 09:30-09:50 am. After this period the income of pollen decreased gradually, while the bees remain collecting nectar for the rest of the day (Fig 3).

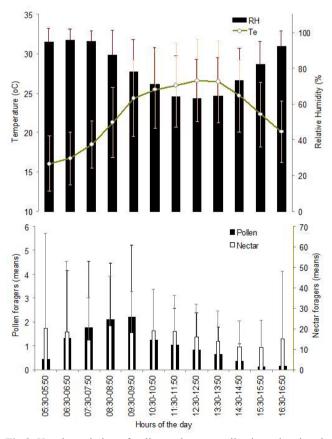


Fig 3. Hourly variation of pollen and nectar collection related to the meteorological factors (temperature and relative humidity). Solid and dashed bars represent standard deviation of pollen and nectar collection, respectively.

The number of pollen types from honey pots and corbiculae was moderately correlated to the number of bees entering inside the nest with pollen and nectar (rho = 0.410; p = 0.009; Fig 4).

In samples of the honey pots and pollen of the corbiculae a total of 24 pollen types were recorded, recognizing 18 genera, 16 families. The most frequent pollen types in samples of honey and pollen of were Myrtaceae (*Eucalyptus, Myrcia*), Melastomataceae and Solanaceae, which were also presented along all the year (Table 2; Fig 5).

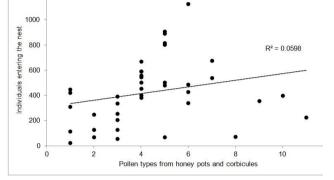


Fig 4. Relationship between the number of pollen grain types (from corbiculae loads and honey from pots) with the total numbers of pollen and nectar foragers returning to the nest.

Discussion

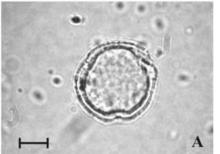
The concept of niche proposed by Hutchison (Hutchinson, 1957) refers to the way that the tolerance and needs of the many conditions interact with the resources used by a species. The variables analyzed in this work are part of the ecological niche of *M. quadrifasciata anthidioides* in their natural environment, since we recorded the ideal temperatures and humidity for the foraging activity. In other words, environmental conditions influences the adaptative value in this species. In addition another important component of the niche, which are the plants explored for pollen sources, was also recorded.

According to Cobert et al., (1993) the temperature is the environmental factor that most affects the flight activity on bees. The extreme values of temperature affect the individual thermoregulation prerequisite to flight behavior (Heinrich & Esch, 1994).

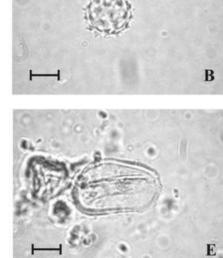
Our results demonstrate that *M. quadrifasciata* anthidioides reduces the collection of resources with temperatures below 13.7° C and over 29.0° C when the foraging activity decreases considerably, in the studied area. The lowest value is very similar to temperatures found to this species in an urban

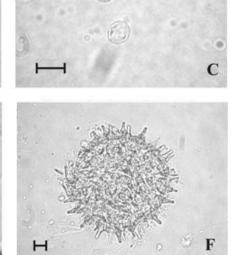
Table 2. Pollen types present on the corbiculae of the workers (*) and honey pots (+) in 5 *Melipona quadrifasciata* nests, sampled during 9 months (December 2009 to September 2010) in the Parque das Neblinas.

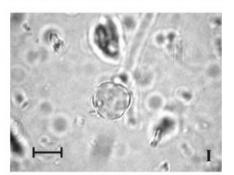
Pollen types/ Months	Dec	Jan	Mar	Apr	Mai	Jun	Jul	Ago	Sep
Aegiphila (+)		X							
Alchornea (+)			Х						
Baccharis (*) (+)	Х	Х	Х		Х		Х	Х	
Begonia (*)							Х		
Eucalyptus (*) (+)	Х	Х	Х	Х	Х	Х	Х	Х	Х
Euterpe/Syagrus (+)		Х			Х				
Hibiscus (+)		Х	Х						
Inga (+)		Х							
Machaerium (+)	Х	Х	Х						
Maranthaceae (+)		Х							
Melastomataceae (*) (+)	Х	Х	Х	Х	Х	Х	Х	Х	Х
Mimosa caesalpiniaefolia (+)			Х	Х		Х			
Mimosa scabrella (*)							Х		
Monocot (+)		Х		Х					
<i>Myrcia</i> (*) (+)	Х	Х	Х	Х	Х	Х	Х	Х	Х
Schefflera (+)				Х					
Serjania (+)		Х	Х		Х	Х			
Solanaceae (*) (+)	Х	Х	Х		Х	Х	Х	Х	Х
Sorocea (+)				Х					
Struthanthus (+)		Х							
<i>Stylosanthes</i> (+)							Х		
Triumfetta (+)			Х						
Vernonia (*) (+)		Х						Х	Х
Not identified (+)		Х							

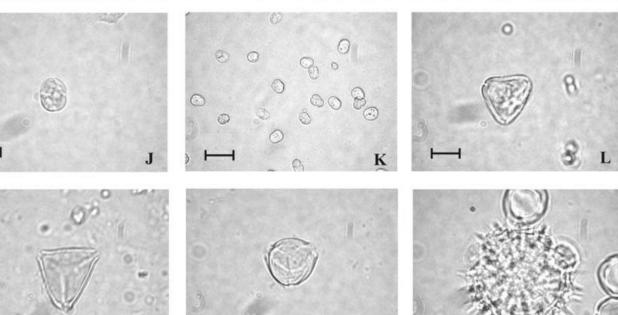












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Fig 5. Light microscopic (LM) pollen grain types micrographs observed in both honey and pollen pellets samples of *Melipona quadrifasciata* in Parque das Neblinas, Mogi das Cruzes district, São Paulo, Brazil. Figure A. *Aegiphila*. B. *Baccharis*. C. *Begonia*. D. *Eucalyptus*. E. *Euterpe/Syagrus*. F. *Hibiscus*. G. *Inga*. H. *Machaerium*. I. Melastomataceae. J. *Mimosa caesalpiniaefolia*. K. *Mimosa scabrella*. L. *Myrcia*. M. *Serjania*. N. Solanaceae. O. *Vernonia*. Scales = 10µ.

M

area (Guibu & Imperatriz-Fonseca, 1984), but the highest temperature limits seems to be higher in our studied area, comparing also to other *Melipona*. This may occurs because of the local shaded environment.

The relation between gathering food and temperature fits better in a quadratic curve, demonstrating an optimum range and limits of tolerance. This seems to be truth for many other stingless bees, but the limits vary a lot among the species. Sometimes the limits are tested, for instance when a sudden mass flowering provoke a copious collection of pollen outside the foraging pattern (Pierrot & Schlindwein, 2003). In the subtribe Trigonina (tribe Meliponini) the optimal range seems to be shorter, starting with temperature higher. For example Mouga (1984) observed that for Paratrigona subnuda Moure the greatest flight activity occurs between temperatures of 24.0°C and 25.0°C; in Plebeia saiqui Friese in southern Brazil, the collection of pollen had a higher intensity in the range of 18.0° to 19.0°C (Pick & Blochtein, 2002). Some Melipona species shows the optimal range wider and the lowest limit lower, like M. marginata (19.0°-30.0°C), M. bicolor bicolor (16.0°-26.0°C) and M. rufiventris (16.0°-30.0°C) for the activity of related pollen and nectar collection (Kleinert-Giovannini & Imperatriz-Fonseca, 1986; Hilário et al., 2000; Fidalgo & Kleinert, 2007). In Cruz das Almas, Bahia, northeastern Brazil, Nascimento et al., (2012) recorded a significant negative correlation of temperature to the flight activity of M. quadrifasciata, and the peaks of bee flow occurred in temperature between 21.2° and 23.3°C. All these mentioned bee species are of different size, and probably the body dimension plays an important role on the tolerance of most suitable climatic factors for foraging.

Another important dimension of the niche for *Melipona* bees is the environmental relative humidity. In this case we recorded that humidity higher than 30-40% is ideal for pollen gathering, while nectar collection occurred in a wide range of RH. But, it is important to consider that pollen is more available earlier in the day, when humidity is higher, while nectar in general is available the whole day. Furthermore, the habitat of the coastal Atlantic Rainforest is moist almost all over the year, due to the dynamic of the trade winds producing precipitation or fog daily. More than $1/_3$ of our data were recorded with RH above 90%, in the studied area. Silva et al., (2011) suggested that foragers from large species of *Melipona* use RH as indicator of pollen availability in the environment.

As it was expected for *Melipona* bees the foraging activities are concentrated early in the morning and tend to decrease after midday. But in the studied area the peaks of pollen and nectar collection are slightly delay, probably due to the fogs formed at dawn and early in the morning. For many *Melipona* species the peaks of pollen harvest occurs before 08:00 am (Bruijn & Sommeijer, 1997; Fidalgo & Kleinert, 2007) for example.

The moderate correlation among the number of pollen types and bees entering the nest suggest that an increasing in flowering plants elicited an increasing in foraging intensity. But we need to consider that pollen type diversity not necessary correspond to floral abundance. It is know that Meliponini species use massive flowering plants (Roubik, 1989; Wilms & Wiechers, 1997).

According to Antonini et al., (2006a) M. quadrifasciata anthidioides is considered a generalist species, since it visited more than ten plant species. But, there is no doubt that Myrtaceae (Eucalyptus) pollen play an important role in the diet of M. quadrifasciata anthidioides. This was also verified in other areas (Ramalho et al., 1989; Wilms & Wiechers, 1997; Antonini et al., 2006b). Similarly, more than 75% of Myrtaceae pollen grains was found in the honey and in the larval food from five species of Melipona in the Amazon forest (Cortopassi-Laurino et al., 2007). Luz et al., (2011) and Serra et al., (2012) also found preference for Myrtaceae pollen in Melipona capixaba Moure and Camargo. According to Roubik (1989) the foraging behavior of a bee is determined by the resources it has access, being influenced by the quality, dispersion, quantity and competition for these resources plus the environmental conditions. In the study area, Eucalyptus is abundant, since it was used in the park reforestation program for a period, and so represents no competition with other foragers.

Hilgert-Moreira et al., (2014) demonstrated that regardless of the landscape characteristics, *M. obscurior* foragers were able to collect pollen from *Eucalyptus* throughout the year. According to these authors, this persistence is due to the capability of *Eucalyptus* in supporting more than one foraging species, which results in low or inexistent competition for the resources.

In samples of the honey pots many species were represented just once during the year. We believe that some of these species (like the first of the list: *Aegiphila*, Verbenaceae) are just nectar sources for *M. quadrifasciata anthidioides*, and probably the foragers were contaminated with the pollen on the body during nectar collection. An alternate explanation would be that their bloom just for short period.

The environmental conditions and availability of particular resources define where the species can live, grow and reproduce. Furthermore, we have to remember that the niche dimensions (temperature and relative humidity for example) act together. Under natural conditions the ecological niche of *M. quadrifasciata anthidioides* is composed of multiple dimensions, i.e. tolerance to many other conditions and requirements that were not measured in this study, but it seems that in the studied area, *M. quadrifasciata anthidioides* are finding the good requirements since the five colonies kept the reproduction the whole year.

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References

Antonini, Y., Costa, R.G. & Martins, R.P. (2006a). Floral preferences of a Neotropical stingless bee, *Melipona quadrifasciata* Lepeletier (Apidae: Meliponina) in an urban Forest fragment. Braz. J. Biol., 66: 463-471. doi: 10.1590/S1519-69842006000300012.

Antonini, Y., Soares, S.M. & Martins, R.P. (2006b). Pollen and nectar harvesting by the stingless bee *Melipona quadrifasciata anthidioides* (Apidae: Meliponini) in an urban forest fragment in Southeastern Brazil. Stud. Neotrop. Fauna Environ. 41: 209-215. doi: 10.1080/01650520600683088#. VHPJI9LF-No.

Bartelli, B.F., Santos, A.O.R & Nogueira-Ferreira, F.H. (2014). Colony performance of *Melipona quadrifasciata* (Hymenoptera, Meliponina) in a Greenhouse of *Lycopersicon esculentum* (Solanaceae). Sociobiology 61: 60-67. doi: 10.13102/sociobiology.v61i1.60-67

Bartelli, B.F. & Nogueira-Ferreira, F.H. (2014). Pollination services provided by *Melipona quadrifasciata* Lepeletier (Hymenoptera, Meliponina) in greenhouses with *Solanum lycopersicum* L. (Solanaceae). Sociobiology 61: 510-516. doi: 10.13102/sociobiology.v61i4.510-516

Barth, O.M. (1989). O pólen no mel brasileiro. Editora Luxor: Rio de Janeiro, 151p.

Batalha-Filho, H., Melo, G.A.R, Waldschmidt, A.M., Campos, L.A.O. & Fernandes-Salomão, T.M. (2009). Geographic distribution and spatial differentiation in the color pattern of abdominal stripes of the Neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera, Apidae). Zoology, 26: 213-219. doi: 10.1590/S1984-46702009000200003.

Bispo dos Santos, S. A., Roselino, A. C., Hrncir, M. & Bego, L. R. (2009). Pollination of tomatoes by the stingless bee *Melipona quadrifasciata* and the honey bee *Apis mellifera* (Hymenoptera, Apidae). Genet. Mol. Res., 8: 751-757.

Bruijn, L.L.M. & Sommeijer, M.J. (1997). Colony foraging in different species of stingless bees (Apidae, Meliponinae) and the regulation of individual nectar foraging. Insectes Soc., 44: 35-47. doi: 10.1007/s000400050028.

Camargo, J.M.F. & Pedro, S.R.M. (2008). Meliponini Lepeletier, 1836. *In* J.S. Moure, D. Urban & G.A.R. Melo (Orgs). Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region - online version, 2008. Available at http:// www.moure.cria.org.br/catalogue. Accessed Set/28/2014. Contrera, F.A.L., Imperatriz-Fonseca, V.L. & Nieh, J.C. (2004). Temporal and climatological influences on flight activity in the stingless bee *Trigona hyalinata* (Apidae, Meliponini). Rev. Tecn. Amb., 10: 35-43.

Corbet S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A. & Smith, K. (1993). Temperature and the pollination activity of social bees. Ecol. Entomol., 18: 17-30. doi: 10.1111/j.1365-2311.1993.tb01075.x

Cortopassi-Laurino, M., Velthuis, H.H.W. & Nogueira-Neto, P. (2007). Diversity of stingless bees from the Amazon forest in Xapuri (Acre), Brazil. Proc. Neth. Entomol. Soc. Meet., 18: 105-114.

Del Sarto, M.C.L., Peruquetti, R.C. & Campos, L.A.O. (2005). Evaluation of the neotropical stingless bee *Melipona quadrifasciata* (Hymenoptera: Apidae) as pollinator of greenhouse tomatoes. J. Econ. Entomol., 98: 260-266. doi: 10.1603/0022-0493-98.2.260.

Ferreira-Junior, N.T., Blochtein, B. & Moraes, J.F. (2010). Seasonal flight and resource collection patterns of colonies of the stingless bee *Melipona bicolor schencki* in an Araucaria forest area in southern Brazil. Rev. Bras. Entomol., 54: 630-636. doi: 10.1590/S0085-56262010000400015.

Fidalgo, A.O. & Kleinert, A.M.P. (2007). Foraging behavior of *Melipona rufiventris* Lepeletier (Apinae; Meliponini) in Ubatuba, SP, Brazil. Braz. J. Biol., 67: 137-144. doi: 10.1590/S1519-69842007000100018.

Fidalgo, A.O. & Kleinert, A.M.P. (2010). Floral preferences and climate influence in nectar and pollen foraging by *Melipona rufiventris* Lepeletier (Hymenoptera: Meliponini) in Ubatuba, São Paulo State, Brazil. Neotrop. Entomol., 39: 879-884. doi:10.1590/S1519-566X2010000600005.

Figueiredo-Mecca. G., Bego, L.R. & Nascimento, F.S. (2013). Foraging behavior of *Scaptotrigona depilis* (Hymenoptera, Apidae, Meliponini) and its relationship with temporal and abiotic factors. Sociobiology, 60: 277-282. doi: 10.13102/sociobiology.v60i3.277-282.

Gobatto, A.R. & Knoll, F.R.N. (2013). Influence of seasonal changes in daily activity and annual life cycle of *Geotrigona mombuca* (Hymenoptera, Apidae) in a Cerrado habitat, São Paulo, Brazil. Iheringia, Sér. Zool., 103: 367-373. doi: 10.1590/S0073-47212013000400006.

Gouw, M.S. & Gimenes, M. (2013). Differences of the daily flight activity rhythm in two Neotropical stingless bees (Hymenoptera, Apidae). Sociobiology, 60: 183-189. doi: 10.13102/sociobiology.v60i2.183-189.

Guibu, L. & Imperatriz Fonseca, V.L. (1984). Atividade externa de *Melipona quadrifasciata* Lepeletier (Hymenoptera, Apidae, Meliponinae). Ciên. e Cult., 36(7): 623.

Heinrich, B. & Esch, H. (1994). Thermoregulation in Bees.

Amer. Sci., 82: 164-170.

Hilário, S.D., Imperatriz Fonseca, V.L. and Kleinert & A.M.P. (2000). Flight activity and colony strength in the stingless bee *Melipona bicolor bicolor* (Apidae, Meliponinae). Rev. Bras. Biol., 60: 299-306. doi: 10.1590/S0034-71082000000200014.

Hilário, S.D., Gimenes, M. & Imperatriz Fonseca, V.L. (2003). The influence of colony size in diel rhythms on flight activity of *Melipona bicolor* Lepeletier, 1836 (Hymenoptera, Apidae, Meliponini). In G.A.R. Melo & I. Alves dos Santos (Eds.), Apoidea Neotropica: Homenagem aos 90 anos de Jesus Santiago Moure (pp. 191-197). Criciúma: UNESC.

Hilário, S.D. & Imperatriz Fonseca, V.L. (2009). Pollen foraging in colonies of *Melipona bicolor* (Apidae, Meliponini): effects of season, colony size and queen number. Genet. Mol. Res., 8: 664-671.

Hilário, S.D. & Imperatriz Fonseca, V.L. (2012). Can climate shape flight activity patterns of *Plebeia remota* (Hymenoptera, Apidae)? Iheringia, Sér. Zool., 102: 269-276. doi: 10.1590/S0073-47212012000300004.

Hilgert-Moreira, S.B., Fernandes, M.Z., Marchett, C.A. & Blochtein, B. (2014). Do different landscapes influence the response of native and non-native bee species in the *Eucalyptus* pollen foraging, in southern Brazil? Forest Ecol. Manag., 313: 153-160. doi: 10.1016/j.foreco.2013.10.049.

Hutchinson, G.E. (1957). Concluding remarks. Cold Spr. Harb. Symp. Quant. Biol., 22: 415-427.

Kleinert-Giovannini, A. & Imperatriz Fonseca, V.L. (1986). Flight activity and responses to climatic conditions of two subspecies of *Melipona marginata* Lepeletier (Apidae, Meliponinae). J. Apic. Res, 25: 3-8.

Luz, C.F.P., Fernandes-Salomão, T.M., Lage, L.G.A., Resende, H.C., Tavares, M.G. & Campos. L.A.O. (2011). Pollen sources for *Melipona capixaba* Moure & Camargo: an endangered Brazilian stingless bee. Psyche, 2011, Article ID 107303. doi: 10.1155/2011/107303.

Maurizio, A. & Louveaux, J. (1965). Pollens de plantes mellifères d'Europe. Un. Des. Group. Apic. Franç., Paris.

Michener, C.D. (1974). The Social Behavior of the Bees: A Comparative Study, Cambridge, Massachussets: The Belknap Press of Harvard University Press, 404p.

Mouga, D.M.D.S. (1984). Coleta de pólen e néctar em *Paratrigona subnuda* e Atividade externa de *Paratrigona subnuda*. Cienc. Cult., 36: 696-697.

Nascimento, A.S., Pereira, L.L., Carvalho, C.A.L., Machado, C.S., Oda-Souza, M. & Souza, B.A. (2012). Flight activity of the eusocial bee *Melipona quadrifasciata anthidioides* (Hymenoptera: Apidae, Meliponini). Magistra, 24: 112-118.

Nates-Parra, G. & Rodríguez, A. (2011). Forrajeo en colonias de *Melipona eburnea* (Hymenoptera: Apidae) en el piedemonte llanero (Meta, Colombia). Rev. Colomb. Entomol., 37: 121-127.

Pick, R.A. & Blochtein, B. (2002). Atividades de coleta e origem floral do pólen armazenado em colônias de *Plebeia saiqui* (Holmberg) (Hymenoptera, Apidae, Meliponinae) no sul do Brasil. Rev. Bras. Zool., 19: 289-300. doi: 10.1590/S0101-81752002000100025.

Pierrot, L.M & Schlindwein, C. (2003). Variation in daily flighty and foraging patterns in colonies of uruçu-*Melipona scutellaris* Latreille (Apide, Meliponini). Rev. Bras. Zool., 20: 565-571. doi: 10.1590/S0101-81752003000400001.

Ramalho, M., Kleinert-Giovannini, A. & Imperatriz-Fonseca, V.L. (1989). Utilization of floral resources by species of *Melipona* (Apidae, Meliponinae): floral preferences. Apidologie, 20: 185-195. doi: 10.1051/apido:19890301.

Rodrigues, M., Santana, W.C., Freitas, G.S. & Soares, A.E.E. (2007). Flight activity of *Tetragona clavipes* (Fabricius, 1804) (Hymenoptera: Apidae) at the São Paulo University Campus in Ribeirão Preto. Biosc. J., 23: 118-124.

Roubik, D.W. (1989). Ecology and natural history of tropical bees. New York: Cambridge Univ. Press, 514p.

Roubik, D.W. & Moreno, J.E.P. (1991). Pollen and spores of Barro Colorado Island. St Louis: Miss. Botan. Gard. Press, Monogr. Syst. Bot., 36: 268.

Serra, B.D.V, Luz, C.F.P. & Campos, L.A.O. (2012). The use of polliniferous resources by *Melipona capixaba*, an endangered stingless bee species. J. Insect Sci., 12(148): 1-14. doi: 10.1673/031.012.14801.

Silva, M.D., Ramalho, M. & Rosa, J. (2011). Por que *Melipona scutellaris* (Hymenoptera, Apidae) forrageia sob alta umidade relativa do ar? Iheringia, Sér. Zool., 101: 131-137. doi: 10.1590/S0073-47212011000100019.

Souza, B.A., Carvalho, C.A.L. & Alves, R.M.O. (2006). Flight activity of *Melipona asilvai* Moure (Hymenoptera: Apidae). Braz. J. Biol., 66: 731-737. doi: 10.1590/S1519-69842006000400017.

Tóth, E., Queller, D.C., Dollin, A. & Strassman, J.E. (2004). Conflict over male parentage in stingless bees. Insectes Soc., 51: 1-11. doi: 10.1007/s00040-003-0707-z.

Wilms, W. & Wiechers, B. (1997). Floral resource partitioning between native *Melipona* bees and the introduced Africanized honeybee in the Brazilian Atlantic rain Forest. Apidologie, 28: 339-355.

Zar, J.H. (1999). Biostatistical Analysis. Fourth ed. Upper Saddle River, New Jersey: Prentice-Hall, 664p.

